The breeding biology and survival of the Razorbill *Alca torda* L.

by

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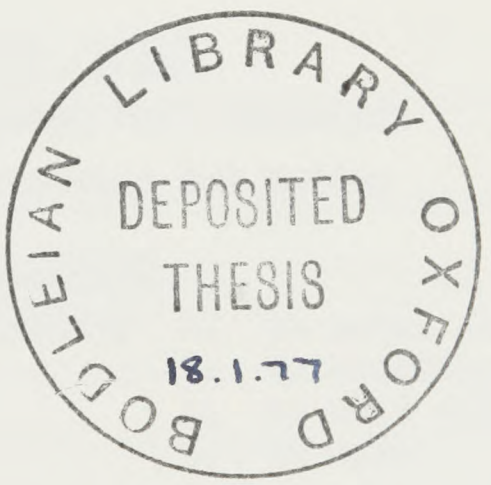

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DECLARATION

I declare that all the work described here was conducted by myself assisted by those mentioned in the Acknowledgements and Introduction below. Material contained in the thesis which has been published elsewhere, as listed in the Introduction, is included as reprints at the back of this volume.

ABSTRACT

The purpose of this study was to collect information on the breeding biology and life history of the Razorbill for comparison with similar studies in other species. An estimated 205,000 pairs of Razorbills breed in colonies either side of the northern Atlantic; about 70% of the birds are found in British and Irish colonies (Chapter 1).

The study was conducted on the island of Skokholm, Pembrokeshire (Dyfed), South Wales between 1971 and 1973, with additional observations in 1970 and 1974. Adult Razorbills and varying numbers of chicks have been ringed on the island nearly annually since 1934 and since 1968 the chicks have been given colour rings to denote age classes. Adults trapped in the present study were colour ringed so that they could be identified without repeated retrapping. The sexes proved impossible to distinguish on body measurements but head size provided an alternative method of sexing adults (Chapter 2).

Colony attendance was recorded (Chapter 3), both during the pre-laying period and the breeding season. Breeding and non-breeding birds were separated whenever possible and diurnal and seasonal attendance at two types of colony compared. The effect of prevailing weather on attendance was evaluated.

Courtship behaviour and mating frequency were recorded (Chapter 4A). Most birds returned to their natal colony to breed and remained there, usually retaining the same nest site. Birds appeared to keep the same mate so far as the annual mortality allowed (Chapter 4Bi). Laying (in May) occurred on average 10-13 days later in 1972 than in 1971 or 1973 (Chapter 4Bii). Birds advanced their laying date with age so that those breeding late in the season were mainly young birds. The little information available on the seasonal abundance of the Razorbills' chief food species *Ammodytes* spp., suggested that the onset of breeding

coincided with an increase in available food which appeared to be the main factor determining the timing of the breeding season. The development of synchronised colony attendance during the pre-laying period was also thought to play an important part in timing breeding.

Length, breadth, weight, shell thickness and pigmentation pattern were measured on samples of eggs in the 3 years. Shell thickness in 'fresh' eggs from Skokholm appeared similar to that of museum eggs collected before 1940. Shell pigmentation patterns were consistent from one year to the next in eggs laid by the same female. A seasonal decline in egg volume was recorded, apparently related to the age structure of the population. Young birds laid small eggs but egg volume increased with age. On average 30% of all eggs laid failed to hatch and more than 70% of this loss was attributable to gulls and particularly Jackdaws Corvus monedula; the latter first bred on the island in 1965 and are increasing annually. About a quarter of the eggs lost, mainly those laid and lost early in the season, were replaced. At least some of the two egg clutches found were produced when a replacement egg was laid for a first egg which had become chilled during incubation.

Incubation was on average 35 days and the nestling period averaged 17 days. About 7% of all chicks hatched failed to fledge (Chapter 4Biii). Most losses occurred in the first five days of life whilst chick weight was still related to the size of the egg from which it hatched. Behaviour at fledging (the female of the pair usually took the chick to the sea) is discussed in relation to the brevity of the nestling period and similar behaviour in other species.

The frequency and composition of feeds to the chicks were examined and growth recorded by regular measurements of weight, feather length and tarsus length. Growth rates were fastest in 1973. Growth was independent of hatching date although chicks from early eggs were the heaviest at fledging. As this was not associated with the seasonal trend in egg size,

it appeared that the older parents were more efficient at feeding their chicks. Presumed date (and hence possibly weight) of fledging of birds in previous years was not related to subsequent survival.

Chicks in ledge sites, where one adult was always present, grew as fast as those in boulder sites where both adults fed the chick at once. Weather appeared to have little effect on growth in the present study.

In 1973 a second chick was introduced into 14 sites; 16 of the twinned chicks fledged though their growth was slower and weight at fledging lower than controls. Competition between the chicks led to the death (or disappearance) of one twin in three sites although in five other sites both chicks reached fledging age and weight together. Failure of the second chick to fledge in these cases may have been due to the inability of the remaining adult to take the chick to the sea.

Breeding success was generally high in the present study with 0.69 young produced per pair per annum (Chapter 4Biv). Success was low in young birds but increased with age, possibly to a peak between 6 and 10 years.

Chapter 4C summarises the information available of the birds' behaviour outside the breeding season. Almost all chicks born on Skokholm returned to breed there (Chapter 5). Up to 4% were seen on Skomer in their pre-breeding years but few remained to breed. No birds returned to the breeding colony in their first summer; a few (c.3%) returned at two years old and more (11%) when they were three. Just over a third of the birds breeding for the first time were four years old and most of the rest were five.

Adult survival averaged 89% in one study colony on Skokholm and 92% on Skomer, compared with the estimated 91% survival from British ringing recoveries. Only 13 young per 100 pairs of Razorbills on Skokholm

survive to breeding age which seems inadequate in view of the 10% annual adult mortality.

Population regulation in the Razorbill is discussed (Chapter 6). Food availability appears to affect Razorbill numbers mainly through the limitations it imposes on the potential reproductive output. The Razorbill's population dynamics make it especially vulnerable to 'artificial' causes of mortality in adult or pre-breeding birds. Population monitoring and the detection of threats to birds is considered of special importance.

Chapter 1: INTRODUCTION

The main factor limiting the study of many seabird species is that the birds only come to land for a relatively short time each year. Compared with a passerine species, for example, which can be watched not only on its breeding ground but also often on migration and during winter, little is known about a seabird such as the Razorbill Alca torda which spends two thirds of each year at sea. Furthermore, due to the relative inaccessability of most Razorbill breeding colonies, few detailed studies of the species' breeding biology have been undertaken.

The purpose of the present study was to obtain information on the breeding biology and life history of the Razorbill for comparison with similar studies of other species. This was considered especially worthwhile since the species has declined in numbers over most of its range during about the last 20 years and data on population dynamics could be important for its conservation.

The study was limited to the population of Razorbills breeding on one small island and was also restricted to three breeding seasons and part of a fourth. Thus no geographical and few annual variations could be studied. In common with most other species of seabird, the main gap in our knowledge now lies in what happens to the birds when they are away from the breeding colonies.

The earliest published study of the Razorbill (Paludan 1947) consists mainly of a detailed descriptive account of the species on the isle of Graesholm in the south Baltic Sea, based on a single summer of observations in 1944. More recently, Bédard (1969) has produced the results of two years of intensive study at a Razorbill colony on Îles Sainte Marie in the Gulf of St Lawrence, Québec, made in the summers of 1962 and 1963. This deals with several aspects of the breeding biology covered in the present study and has provided a useful basis for the

comparison of east and west Atlantic populations. Bédard also gives detailed observations of Razorbill behaviour, although he was unable to make any estimates of survival.

Other authors who have discussed the breeding biology of the species include Keighley (1950), Nordberg (1950) and Plumb (1965). Some have confined their observations to part of the season: Keighley and Lockley 1947, Brun 1959, Greenwood 1964, Ingold and Tschanz 1970, Ingold 1974, Lawman 1975. Data on adult measurements and censuses at breeding colonies are given in several more general publications (eg Salomonsen 1944) and details of egg measurements on Skokholm in Moyse (1963) and Diamond (1964). Ticehurst (1936) discussed measurements collected from adult Razorbills, with reference to their subspecies and Verwey (1923) gives details of moult. Reprints of my own publications relevant to this study (Lloyd 1972; 1973; 1974; 1975a; 1975b; 1975c; 1976a; 1976b; in press; Lloyd et al 1974; Lloyd and Bourne 1975) are bound into the back of this thesis.

Data collected in the present study included details of breeding behaviour, egg size, difference in timing and success of breeding in successive seasons and the birds' fidelity to mate and nest site. Razorbills on Skokholm had been ringed almost annually since 1934 and since 1968 many of the chicks had been colour-ringed. Without this investment of ringing effort before the start of the present study in 1970, little of the data on survival discussed below could have been collected. I am therefore indebted to all those who have caught Razorbills on Skokholm from a time before I was born!

Through colour ringing, the age of first return to the colony by young birds and the age at first breeding were established. Records of individually colour ringed individuals provided further information on the survival of breeding birds. Detailed counts were conducted at certain

colonies in an attempt to determine the best method of censusing Razorbill breeding populations. Comparison of data collected in the three main years of the study showed considerable differences in the timing and other aspects of breeding in 1972; this and other annual variations are discussed. A list of Latin names of birds and mammal species mentioned in the text is given in Appendix 1.

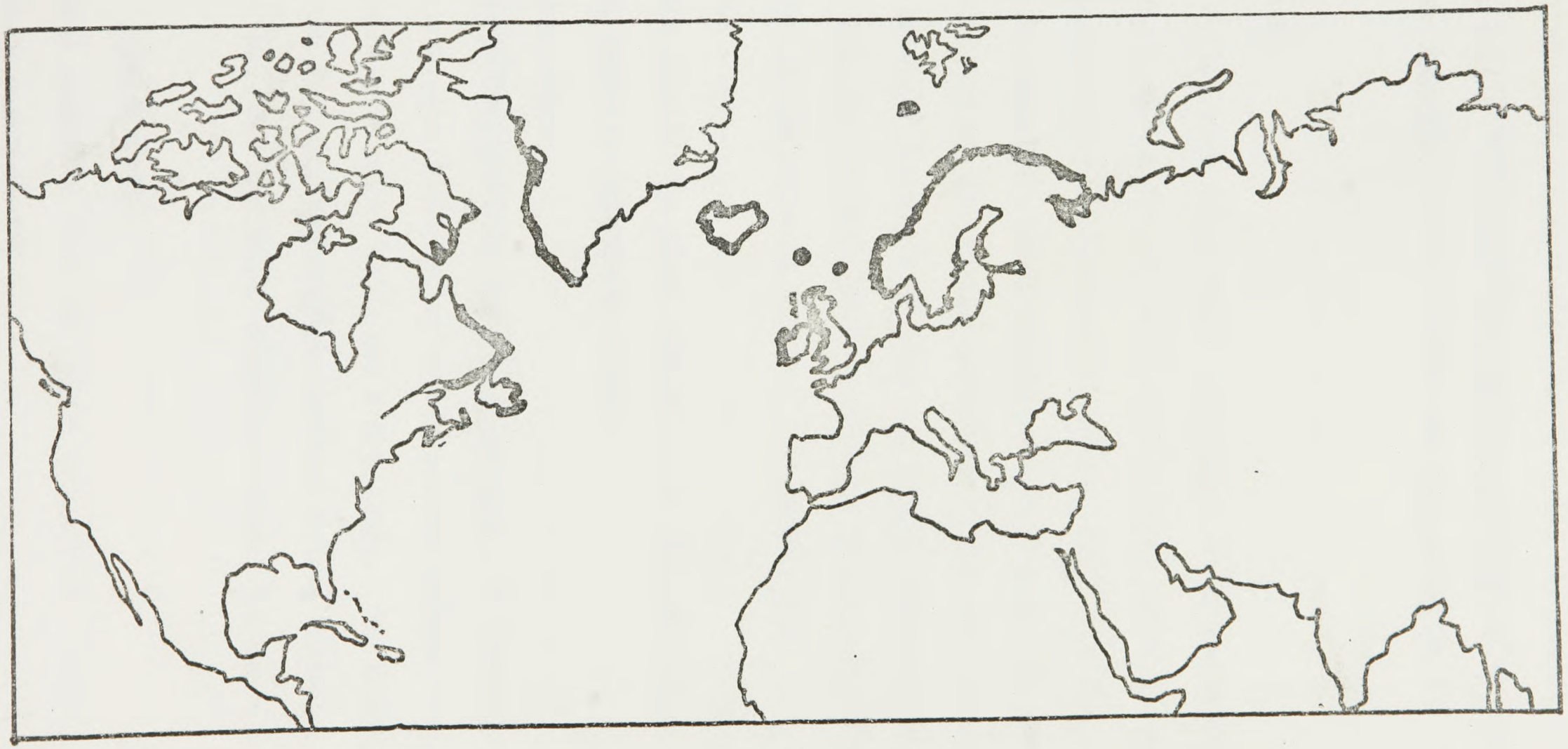
ii. History, present breeding distribution and status of the Razorbill

History

The Razorbill is the only remaining species of the genus Alca. Its nearest known relative, the Great Auk (Pinguinus impennis), became extinct in 1844 or 1845 (Grieve 1885) although Dr B Campbell has drawn my attention to 2 apparently authentic records as late as 1852 and 1953 (Newton 1861). The family Alcidae is also known from Pliocene fossil deposits of the north Atlantic (eg Proturia, Protocepphus [illegible] and Udvardy 1963). The different genera probably arose from a common ancestral form either in the Atlantic (Storer 1952) or the Pacific (Udvardy 1963). Invasion of the Atlantic by the north Pacific stock would have been possible whilst the Bering Straits were open in the mid Eocene. The distribution of the Razorbill today (Figure 1.1) is entirely confined to the boreal and low-arctic zones of the north Atlantic (Voous 1960) and it seems unlikely that the species could have spread from the Pacific if in doing so they had to tolerate arctic conditions (Koslova 1961).

The present day distribution on several auk genera, including Alca, have been compared with those of certain species of seals whose evolution and colonisation were affected by the glaciations (Ekman 1922; Davies 1958). The Puffin Fratercula arctica has both high arctic and boreal subspecies and so does Phoca fasciata in the Pacific and P.groenlandica

Figure 1.1 The breeding distribution of Alca torda, indicated by shading.
(after Voous 1960)



in the Atlantic. The Ringed Seal Phoca hispida once had a circumpolar distribution but is now confined to several isolated relict populations whose distribution has been compared with the isolated subspecies of the Guillemot Uria aalge, Pigeon Guillemot Cepphus columba and Cassin's Auklet Ptychoramphus aleutica in the Pacific and Alca torda in the Baltic.

Breeding distribution

In the western Atlantic, Razorbills breed from Maine (43°N) northwards to south Baffin Island with a few colonies still further north in west Greenland (to approximately 73°N Joensen and Preuss 1972). In the eastern Atlantic, the Razorbill breeds further north than in the west of its range possibly due to the warming influence of the Gulf Stream. A few pairs still nest off the coast of Brittany (49°N) (Brien 1970) and colonies occur from the Channel Isles northwards to west Spitsbergen (78°N) and eastwards to the Murmansk coast of the Barents Sea (Gerasimova 1961).

The differences between the three subspecies in the genus Alca are outlined below, based on Salomonsen (1944).

Alca torda islandica Brehm

This subspecies has also been described as A.t.britannica by Ticehurst (1936) from a type specimen collected on Skomer island, Dyfed.

These birds have relatively small bills and short wings. The breeding distribution includes Iceland, Faroe Isles, British Isles, Channel Isles, the coast of Brittany and once, though no longer, Helgoland Island.

Alca torda torda Linnaeus (1758)

The subspecies, first described from the Baltic islands of Stora Karlsø, has longer wings and a consistently deeper and on average longer bill than A.t.islandica; the bill has on average fewer grooves than the latter

race. The nominate subspecies is confined to the Baltic where it breeds in both fresh and brackish water from the skerry of Graesholm in the Christiansø archipelago northwards to the head of the Gulf of Bothnia and eastwards to the shores of the Gulf of Finland and possibly to Lake Ladoga (east of Leningrad) although it seems unlikely that the latter colonies still exist. The breeding distribution of A.t.torda is thus entirely separated from that of the Norwegian subspecies (whose nearest colony is at Stavanger in south west Norway).and the subspecies may represent a relict population from the Pleistocene.

Alca torda pica Linnaeus (1766)

This was first described from Norway and differs from A.t.torda only in the more grooved structure of its bill (See Salomonsen 1944, p.22). A.t.pica breeds from Stavanger in Norway northwards to Spitsbergen and the Murmansk coast of Russia. The Razorbills breeding on the west coast of Greenland and eastern Canadian coast as far south as the Gulf of St.Lawrence, New Brunswick and Maine, U.S.A. also belong to this race.

Table 1.1 gives a summary of wing and bill measurements obtained from the three subspecies of Razorbills by Salomonsen (1944) and others. Additional measurements of A.t.islandica were obtained as part of the present study from the specimens in the British Museum (Natural History) in Tring and Liverpool Museum (see Appendix II).

Status

The Razorbill is a relatively rare auk; in no part of its breeding range is it as numerous as the closely related guillemots. Brunnich's Guillemot (Uria lomvia) colonies on Novaya Zemlya, USSR for example have been alleged to hold two million pairs of breeding birds (Uspenski 1956). By comparison the available estimates of the world population of the Razorbill (Table 1.2) amount to only about 208,000 pairs of which at least 70% breed in Britain and Ireland (Lloyd 1975a; in press); these

Table 1.1 Published ranges of measurements (mm) in different subspecies of the Razorbill

Source		n	Sex	Wing Length	Bill Length	Bill Depth
Alca torda islandica						
Ticehurst	1936	31	♂♀	186-198	-	19-21
Witherby et al.	1941	14	♀♀	185-200	29-34	20-22
		14	♂♂	185-203	30-35	21-23
Salomonsen	1944	3	♀♀	192-195	31-34	20-23
		4	♂♂	187-192	32-34	21-21.5
Løvenskiold	1947	?	♀♀	185-200	29-34	20-23
		?	♂♂	185-203	30-31	
Vaurie	1965	22	♂♀	181-202	-	19-22.5
Haftorn	1971	?	♀♀	185-200	29-34	20-22
		?	♂♂	181-203	30-35	19-23
Present study	1971-73	15	♀♀	-	29-35	19-21
		21	♂♂	-	30-37	18-23
Alca torda torda						
Salomonsen	1944	19	♀♀	201-213	33-36	22-25
		14	♂♂	205-218	32-38	22-26
Haftorn	1971	18	♀♀	-	32-38	21-25
		20	♂♂	196-216	32-37	22-27
Alca torda pica						
Salomonsen	1944	18	♀♀	206-218	31-37	
		24	♂♂	202-220	33-38	
Belopol'skii	1957	51	♀♀	Mean:208.5	Mean:33.6	
		73	♂♂	Mean:207.5	Mean:34.6	
Bédard	1969	4	♀♂	187-204	33	

Note: Wing Length. Several different methods probably involved in wing length measurement.

Bill Length. In all cases where details are given, measured from the tip of the upper mandible to the base of the bill at its junction with the feathers.

Bill Depth. Width of the bill at its widest part.

Table 1.2 An estimate of the world breeding population of the Razorbill Alca torda. Nomenclature after Salomonsen (1944).

Country	Subspecies	Approx number of breeding pairs	Reference	Year of Census*[1]
Greenland	A t pica	567(417)*[2]	(Joensen & Preuss 1972	1965
			(Salomonsen 1950)	1936,1949
Canada	A t pica	20,636 (4,688)*[2]	Brown et al 1975	1928-74
Maine	A t pica	28 (28)*[2]	Brown et al 1975	1971-74
N USSR	A t pica	2,200	Gerasimova 1961	
Norway	A t pica	25,440 *[3]	Brun 1969; 1971	1968-70
Sweden	A t torda	4,000	V Olsson - in litt	1975
Finland	A t torda	875	Lippens & Wille 1972	
Denmark	A t torda	200	Franzmann 1974	
Iceland	A t islandica	5,000	A Petersen - pers comm	1973
Faeroe Islands	A t islandica	5,000	B Olsen - in litt	1974
Britain & Ireland	A t islandica	144,000 *[4]	Cramp et al 1974	1969-70
France	A t islandica	100	Brien 1970	
Estimated total		208,046		

Note *[1] Year of census, when known to be different from that of publication.

*[2] Count includes estimated number of pairs (in parentheses) from counts of individual birds. Such counts were "corrected" for the presence of non-breeding birds and off-duty mates (see Lloyd in press). Observations at Twinlet in 1972 and 1973 (June) showed that on average a count of 100 birds on the cliffs represented 56 breeding pairs.

*[3] Maximum, assumes a 33% decline in only 12% of population - see text.

*[4] Minimum - see text.

counts must be regarded as very approximate since Razorbills, like other auks, are impossible to count accurately.

Bédard (1969) gave a total of 47,000 pairs of Razorbills in west Greenland, Canada and U.S.A. but some of the counts included were outdated. A more complete survey of these colonies, given by Brown et al (1975), totals 20,644 pairs. However, counts at 33 of the 59 colonies they listed, which account for 39% of the total, are pre-1967. Earlier counts are available for 14 of the colonies covered by Nettleship et al in 1967-74 and these suggest extensive changes in the last 10 to 20 years. Numbers had apparently declined at seven colonies and remained stable (3) or increased (4) at the rest; there had been an overall reduction of about 50%. The best documented change in the north American Razorbill population has occurred in the colonies on the north coast of the Gulf of St Lawrence where regular surveys at 7 sites have shown a decline from 16,216 individuals in 1960 (Moisan 1962) to 14,950 individuals (92%) in 1965 (Moisan and Fyfe 1967), to only 4,320 individuals (27%) in 1972 (Nettleship and Lock 9173). Much of this decline has been tentatively attributed to the effect of toxic chemicals in the birds' diet.

"Small numbers of Razorbills bred in southern Spitsbergen up to 1958" (Løvenskiold 1963), though there has been no recent count. At least eight pairs bred on Bear Island in 1970 (Brun 1970) where "very small numbers" had been reported in 1932 (Bertram and Lack 1933). The only available estimate for the breeding population in northern Russia is outdated and no records have been found for the White Sea where the species also breeds (Voous 1960).

No precise information is available on numbers of Razorbills breeding in Iceland although Hachisuka (1927) reports them to be more common in the south; however "although the Razorbill is a fairly common bird ...

it is less numerous than both the Common and Brunnich's Guillemots" (F Gudmunsson in litt 1973). Equally little is known of the population of the Faeroe Islands but in 1974 Guillemots outnumbered Razorbills by an estimated 100:1 on the cliffs and 100-150:1 on the sea and about 5,000 pairs bred (B Olsen in litt 1974).

Brun (1969) gives details of all colonies in Norway in about 1968, but by 1970 numbers had declined by 33% in at least one colony in southern Norway (Runde) which previously held 12% of the total population (Brun 1971). Brun suggested that this order of decline could be expected for other colonies in the area, due to pressures from oil pollution and hunting and birds becoming caught in fishing nets.

The history of the Razorbill colonies in the Baltic has been well documented. During the 1930s the colonies in Sweden were relatively large (Wahlin 1943a; Nordberg 1950) and those in Finland were increasing in size (von Haartman 1947). The extremely cold winters of 1939/40 and 1940/41 caused the whole Baltic to freeze over for several months. Paludan (1947) describes how many Razorbills were trapped by the ice or drowned in the unfrozen patches as sheets of ice capsized. The increased mortality of birds during these winters almost led to the extinction of the Baltic breeding population (Wahlin 1943b, Salomonsen 1943, Paludan 1947, von Haartman 1947, Nordberg 1950). Few colonies have gained their pre-1939 numbers and many are now extinct; Merikallio (1958) estimated that the Baltic population was only half of what it was in the 1930s.

In Sweden the largest colonies, on the Stone Karlsø islands, were estimated to have held 7,500 pairs of Razorbills in 1918 (Möhler 1919), although this may have been an exaggeration. About 1,500 pairs are thought to have bred there in 1975 (V Olsson - in litt). Human disturbance (Paludan 1947; Olsson 1974; Andersson - in prep.) and adverse weather conditions are the main causes of decline at other Swedish colonies. Levels of toxic chemicals (DDT

derivatives, PCBs and mercury) in Razorbill eggs from Swedish colonies are high, although this has not appeared to affect breeding success yet (Andersson et al 1974).

Twelve pairs of Razorbills bred on the German island of Helgoland in 1939, though by 1956 these had declined to a single pair (Vauk 1957); Lippens and Wille (1972) reported "less than five pairs". About 450 pairs of Razorbills bred at the only colony in France (Les Sept Îles, Brittany) before oil from the Torrey Canyon reduced them to only 50 pairs (Milon 1967; Milon and Bougerol 1967; Monnat 1969); this colony was thought to be declining before the oil spill. Numbers have doubled since 1967 but the colony shows no sign of returning to its previous strength.

Numbers have also declined at many Razorbill colonies in Britain and Ireland, especially in the south of England and the Channel Isles, during this century (Cramp et al 1974). The Operation Seafarer survey in 1969/70 gave a total of 144,000 pairs of Razorbills, consisting of 108,736 "pairs" and 35,147 "individual birds". Excluded were two colonies of "Order 1" (1- 9 pairs), 6 colonies of "Order 2" (10- 99 pairs), 3 colonies of "Order 3" and 3 colonies of "Upper Order 3" (100- 999 pairs), 1 colony of "Low Order 4" (1,000- 9,999 pairs) and 1 colony of "Order 5" (10,000- 99,999 pairs); together these accounted for an estimated minimum 17,310 pairs. Thus the total population was probably in the region of 145,730 pairs. Results from the RSPB-Seabird Group annual monitoring scheme at about 50 sites since, suggest that numbers are currently stable (Lloyd in prep.). The largest colonies in Britain and Ireland (Figure 1.2), as in the rest of the species' range (see Figure 1.1), are found bordering oceanic areas where offshore currents systems cause extensive mixing of water layers. The resulting upwelling of nutrients and high plankton productivity causes

Figure 1.2 Razorbill breeding colonies of more than 50 pairs (after Cramp et al. 1974).



an abundance of marine life at all subsequent stages of the food chain and hence rich food supply for breeding seabirds (Mills 1969; Summerhayes et al 1974; Cramp et al 1974).

Any adverse factors affecting Razorbills could be expected to reduce the number of birds breeding in colonies at the limits of the species' range. Long-term changes in the marine environment have undoubtedly occurred this century (H W Ahlmann in Fisher 1952; Longhurst et al 1972; Cushing 1975); the amelioration of the climate has been suggested as one of the possible causes of spread in the larid gulls (Cramp et al 1974). Climatic change involving a warming of the Atlantic could affect Razorbills through their food. For example, the Herring Clupea harengus fisheries in the English Channel and Western Approaches failed about 40 years ago due to the lack of recruitment of young fish from 1920 onwards; instead there was an increase in the abundance of warm-water species especially Pilchard Sardina pilchardus as a result of prevailing changes in sea temperature (Cushing 1961; Southward 1963).

Other species of seabirds throughout the Razorbills' range are currently increasing in numbers - eg Gannet Sula bassana (Fisher and Vevers 1944), Fulmar Fulmarus glacialis (Fisher 1952), Kittiwake Rissa tridactyla (Coulson 1963a), Herring Gull Larus argentatus (Harris 1970a) and others (see Nettleship and Lock 1973). One reason for these increases may be the protection afforded the species with the introduction of the bird protection laws from 1869 onwards; it seems unlikely, however, that these would have affected the Razorbill which does not appear to have been taken (either as birds or eggs) in as large numbers as the Puffin or Guillemot. Some seabirds have increased in numbers as they adopted new feeding habits; Gannets and Fulmars are thought to have benefited from the spread of whaling and trawling (Fisher 1952) or perhaps just from the increase in shipping in coastal waters. Gulls appear to

have increased along with the human population, providing them with food in the form of rubbish and other wastes (Davis 1974; 1975a).

The auks, with perhaps a more specialised diet, have apparently failed to exploit new food supplies and, possibly as a consequence, are not currently undergoing a population expansion. Their decrease in numbers has often been associated with their vulnerability to oil pollution at sea (Cramp et al 1974). This has long been recognised as a threat to birds in British, Irish and other north European waters (eg Bourne 1967, Hope Jones et al 1970, Greenwood et al. 1971, Bourne and Bibby 1975) although recently oil has tended to kill fewer birds than during the 1960s (Lloyd and Bourne 1975; Lloyd 1976a). Auks, especially Guillemots, are still always the most frequent victims of oil spillage incidents, possibly because they spend so much of their time sitting on the sea. Oil is not, however, always lethal (Birkhead et al 1973).

Inshore waters carry other kinds of marine pollution such as the breakdown products of various pesticides (eg DDE from DDT), heavy metals (eg mercury, cadmium, zinc) and polychlorinated biphenyls, produced by various industrial processes; these reach the sea via the river systems and are taken up by the birds through the food chain. Especially high concentrations are found in both the eggs and the tissues of the birds frequenting the more enclosed coastal waters, especially the Irish Sea (Parslow et al 1972; 1973). It appears that the presence of these pollutants, though normally non-lethal, can increase mortality when the birds come under stress. The death of some 12,000 birds, mostly Guillemots, in the Irish Sea in 1969 may have been an example of this as it occurred at a time when most of the birds were moulting (NERC 1971). Similar incidents of heavy auk mortality have occurred in the same area since, following periods of stormy weather when feeding was probably difficult (Lloyd et al 1975; Beached Bird Survey records).

Earlier records, however, show that mortality incidents of "wreck" proportions had occurred in British and Irish coastal waters before pesticide residues or other toxic chemicals were present (see NERC 1971).

Chapter 2: THE PRESENT STUDY OF THE RAZORBILL

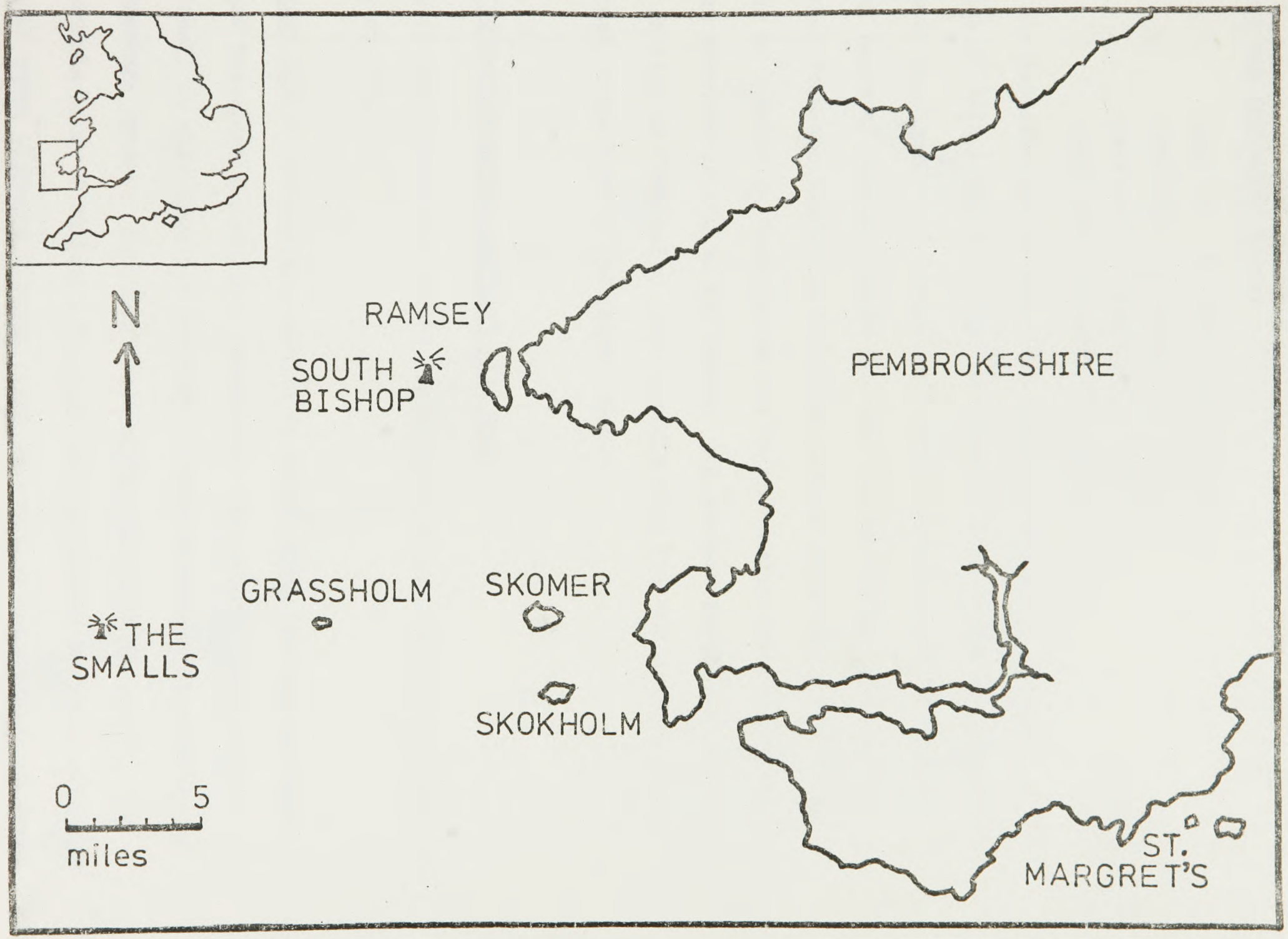
i. The study area

All field work for this study was carried out on the island of Skokholm in Pembrokeshire (Dyfed), Wales (51°.42'N 05°.16'W). The position of Skokholm and the neighbouring islands are shown in Figure 2.1. Skokholm is 106 hectares in area with cliffs from 12 to 35 m in height and a rocky shoreline. The highest point is 51m above sea level and the underlying rock composed of Old Red Sandstone. Extensive accounts of the geology and botany of the island are given by Gillham (1954 et seq).

The island was probably first inhabited by Scandinavian invaders of Pembrokeshire in the ninth centurey. Later it was used for farming, and buildings and walls were erected in the fourteenth century. From then until the late nineteenth century, the island was farmed and stock fattened on its apparently abundant grazing, indicating that the Rabbit *Oryctolagus cuniculus* population must have then been far lower than it is now. The Rabbits were apparently introduced by the Normans in the fourteenth century (Lockley 1969). From 1927 to 1940 R M Lockley occupied Skokholm, attempting to exterminate the rabbits, to reclaim the land and farm. In 1933 the first British bird observatory was opened on the island and this has functioned ever since, with the exception of the war years when only the lighthouse keepers were in occupation.

The cliffs, especially those on the west coast, provide nesting sites for Razorbills and Guillemots and about 2,000 pairs of Puffins also nest in burrows at the cliff tops around the island and beneath rocks and boulders on the cliffs (Appendix III). Other species nesting on the island include Manx Shearwaters *Puffinus puffinus* (35-37,000 pairs), Storm Petrels *Hydrobates pelagicus* (6000 pairs), Fulmars (12 pairs), Herring Gulls (1400 pairs), Lesser Black-backed Gulls *Larus fuscus* (3000 pairs) and Great Black-backed Gulls *L.marinus* (controlled

Figure 2.1 Position of Skokholm and the adjacent islands.



breeding population of about 12 pairs).

Observations were started during a preliminary visit in 1970 and continued for three whole seasons from 1971 to 1973; records were kept between the following dates:

June 20	to July 18	1970
March 27	to August 15	1971
April 3	to August 12	1972
April 28	to August 4	1973

The distribution of Razorbill nesting colonies - defined for the purpose of this study as a concentration of five or more occupied nest sites - is shown in Figure 2.2. There were eight colonies with more than twenty pairs of breeding birds and many smaller ones. Nest sites occurred from the cliff-top to within 3-4m of high tide level. The number of Razorbills breeding on the island during the study remained almost constant at 470 to 480 pairs. The pre-war population may have been as high as 1000 pairs (see Appendix III) but the maximum number recorded since 1946 is 730 pairs (1948).

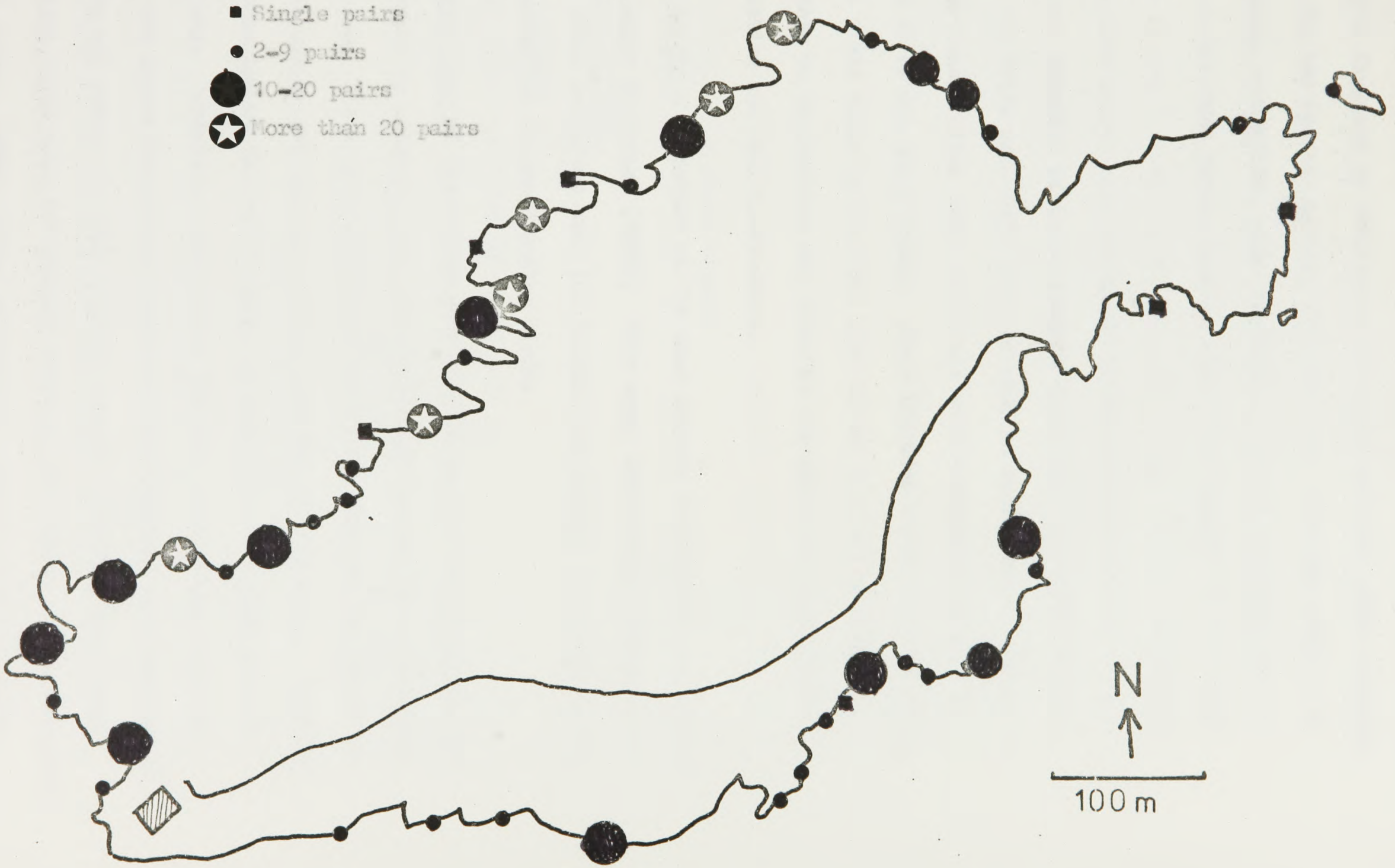
ii. Colony Structure and nest site type

Isolated nest sites were rare on Skokholm and each 'colony' had distinct parts as follows:

a. Nest site - the cavity, crevice or ledge where the egg was laid and the space immediately around it. The nesting birds moved freely in this area but defended it from intruders throughout the breeding season. In sites where nests were closely packed, for example under a boulder, the eggs were sometimes within a metre of each other although sitting birds were always out of pecking reach of other incubating birds.

Razorbills on Skokholm used two main types of nest site. 'Ledge sites' were entirely open and most common on the vertical

Figure 2.2 Skokholm Island, showing the distribution of Razorbill colonies 1970-1973.



cliffs of the northwest side of the island. This type of nest site was also favoured by Guillemots and mixed colonies often occurred with the two species nesting side by side; 'boulder sites', by contrast, were hidden under boulders. In some colonies such as that at Northern Rocks, boulder sites were located in the talus scree at the foot of a cliff; in other areas such as The Bluffs, the cliffs sloped more gradually to the sea and the slopes held boulders embedded in earth amongst which the Razorbills nested.

The birds used both types of site in approximately equal proportions. Other nest sites were rare - accounting for only about 1% of all those found. These included nests enclosed on at least three sides by rock but open to the sky, often between boulders or in crevices, and those at the mouth or inside burrows of Rabbits and Manx Shearwaters.

b. Site margin - described as "la zone commune d'activité" and called 'la marge' by Bédard (1969). This area, immediately adjacent to a nest site, was often used for landing and loafing by breeding and, occasionally, by non-breeding birds.

c. Loafing areas of the colony were similar to the 'loitering ground' described by Johnson (1941) for Guillemots in Gulf of St Lawrence colonies. These were located either on the edge of the colony or at its centre but did not overlap with the site margins. In cliff colonies ledges from which eggs had been lost were also used in this way. Especially favoured in the less precipitous colonies were the large flat-topped boulders which provided easy landing and taking off areas and good look-out points. Early in the season courting birds used the loafing areas of the colony and occasionally mated there. Later, during incubation, off-duty breeding birds

rested and preened in the loafing areas nearest their nest site. Throughout the season the areas were used for courtship, billing and mutual preening and occasionally for mating attempts by non-breeding birds. Immature birds on first arriving in the colony were frequently seen in the loafing areas.

Most~~the~~ the Razorbill colonies on the island were accessible from the cliff-top. Accessible colonies varied from those that were easily reached by climbing (eg Main study colonies - see below) to those that were visited only once a year to ring the chicks. Overall it was estimated that about two thirds of the Razorbill chicks on the island could be reached and ringed. Even if a colony was accessible, usually a few of the nest sites were out of reach. On the other hand, at least some of the sites in the least accessible cliff-face colonies could be reached and a chick ringed.

iii. General methods

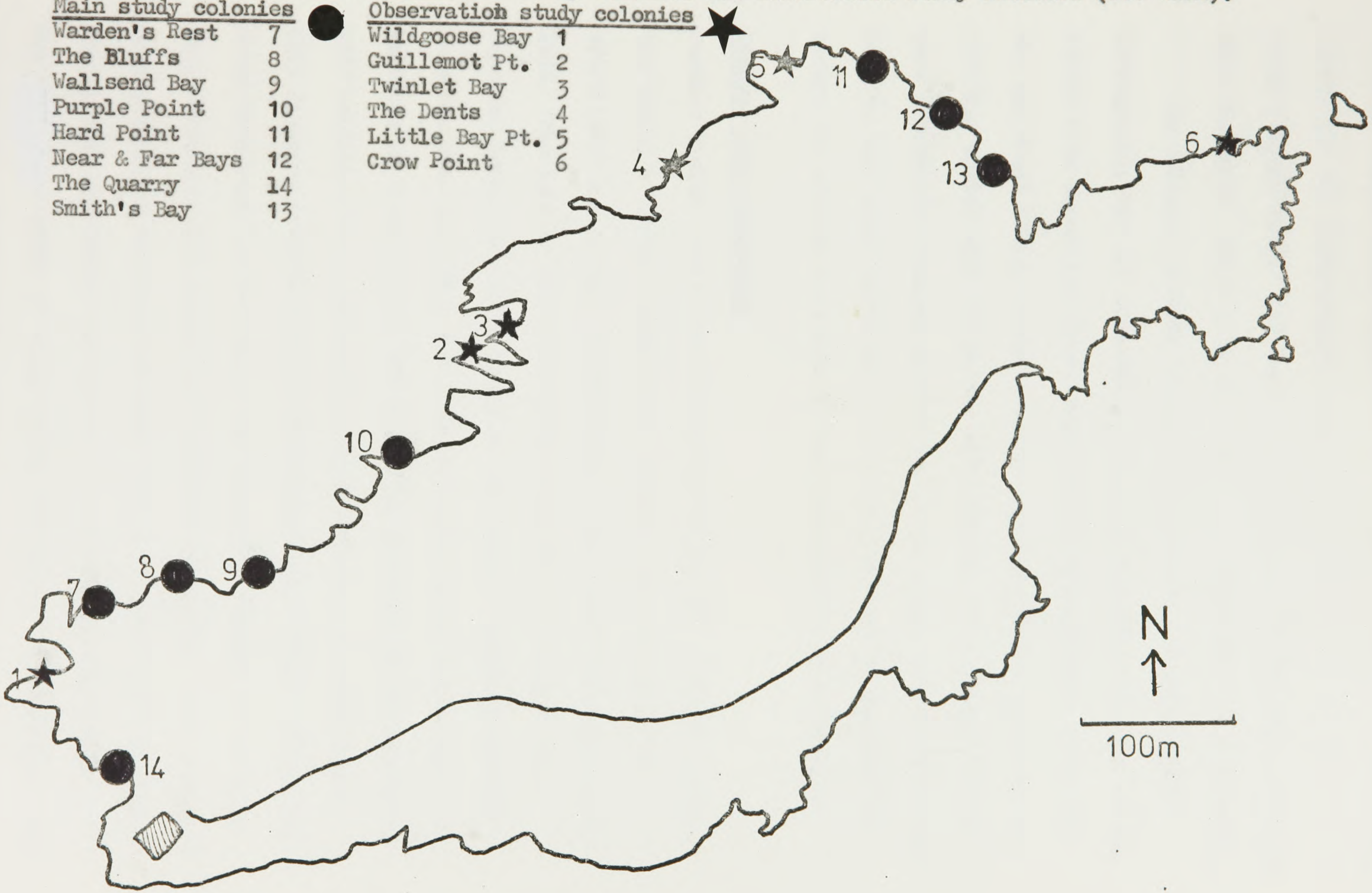
a. Study colonies

Regular visits were made to nearly all parts of the island where Razorbills bred. Many colonies could be wholly or partially observed from the cliff top although a few, especially those in the northwest of the island, were visible only from a boat.

In 1970 six 'Observation' study colonies were selected for close observation of birds on the nest without disturbance. These were all cliff colonies consisting mainly of ledge sites and, with the addition of a seventh colony (Guillemot Point), the same colonies were used for detailed observation in the three following seasons (Figure 2.3). A total of 83 pairs (18% of the total breeding population) bred in these colonies.

Figure 2.3 Distribution of the Main study colonies and Observation study colonies (see text).

Main study colonies		Observation study colonies	
Warden's Rest	7	Wildgoose Bay	1
The Bluffs	8	Guillemot Pt.	2
Wallsend Bay	9	Twinlet Bay	3
Purple Point	10	The Dents	4
Hard Point	11	Little Bay Pt.	5
Near & Far Bays	12	Crow Point	6
The Quarry	14		
Smith's Bay	13		



The 'Main' study colonies were selected in 1971 for their easy access (in all weather conditions) and were used throughout the study (Figure 2.3). 180 pairs of Razorbills (38% of total) bred in these colonies, twice as many as in the Observation study colonies.

The colonies outside these areas were visited relatively infrequently but all accessible Razorbill breeding colonies on the island were checked at least twice during each season - once for the egg count during incubation (see Appendix V) and again in the nestling period when the chicks were ringed. In a number of the more accessible colonies outside the study areas, extra visits were made to trap adult birds and to read ring numbers throughout the season but efforts were made to keep disturbance to a minimum.

b. General data collection

Regular visits to all Observation and Main study colonies enabled the timing of laying, incubation, hatching and fledging to be established and casual observations of the birds' behaviour to be made. The eggs in all sites in the Main study colonies were measured during the three years of the study. Breeding success and, whenever possible, the identity of the adult birds were also recorded in these sites. The timing of my visit to the island in 1970 coincided with the nestling period so that in that season only fledging success could be measured (Lloyd 1972). During the three main years of the study, the accessible chicks in the Main study colonies were weighed and measured regularly. More detailed observations of breeding behaviour were made from hides, mostly at the Twinlet Bay colony but also on The Bluffs, Warden's Rest and The Quarry. Records of daily colony attendance were obtained this way and the duration of incubation stints, chick feeding frequencies and behaviour at fledging were also established by watching from hides.

c. Trapping

Throughout the study adult birds were trapped either for ringing or to establish the identity of birds previously ringed or to replace worn rings. Colour rings, given to all birds caught, enabled each adult bird to be individually identified and each bird that had been colour ringed as a chick to be allocated to an age class. [A description of the rings used is given in Appendix IV] Both adults and chicks were usually trapped on the nest using a long bamboo pole with a wire hook on the end. A number of the adult birds trapped during the present study were already wearing rings; many of these had to be re-ringed because their rings had become worn.

d. Sexing adult Razorbills

Apart from the Fregatidae, males and females in all species of seabirds are not easily distinguished in the field and Razorbills are no exception. The sexes of some species can sometimes be separated by differences in overall body size or by more detailed measurements of parts of the body. The bill of certain gulls, for example, are on average longer and deeper than that of the female and the ratio of bill length: bill depth gives an indication of an individual's sex.(Harris 1964$^{a}_{\wedge}$; Harris and Hope Jones 1969; Mills 1971). An index of bill area (length x depth) has been used to sex Puffins (Corkhill 1972).

Published measurements of Razorbills, however, indicated a large overlap in the range of most body measurements (see Appendix II); my own measurements from birds of known sex in the British museums also supported this. Adult Razorbills trapped in the present study were measured in an attempt to detect any sexual dimorphism and alternative methods of sexing birds in the field were also examined.

1. Measurements. Bill length and depth were measured by the method described in Appendix II and an index of bill area was obtained, from the product of the two measurements, for 114 individuals. In 1971 wing length was also measured (to the nearest millimetre) using the flattened chord method (Spencer 1972) on 57 birds; all but one of these birds were weighed (to the nearest 5g) using a 'Salter' spring balance.

The distribution of wing, bill and body weight measurements (Figure 2.4) show no clear bimodality as would be expected if male and female birds differed markedly in size. The absence of bimodality was confirmed when the percentage cumulative frequency of each distribution was plotted on probability graph paper (Harding 1949). Thus there is a very extensive overlap in size of the two sexes in the Razorbill.

2. Other methods of sexing birds

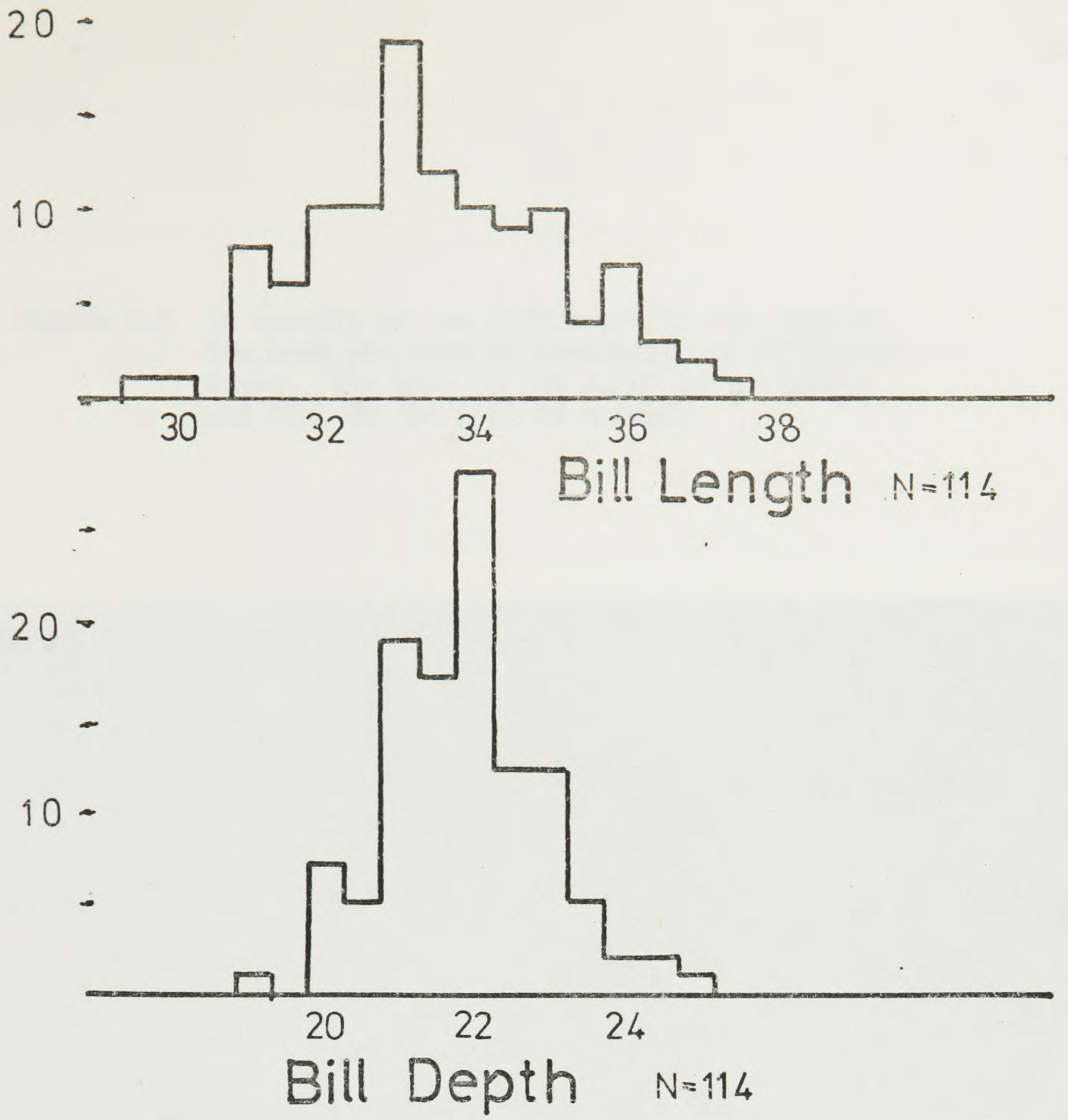
a. Birds observed during mating could be sexed readily and accurately although this was only useful if at least one bird of the pair was either ringed or distinguishable from its mate by other means (eg broken mandible or feathers).

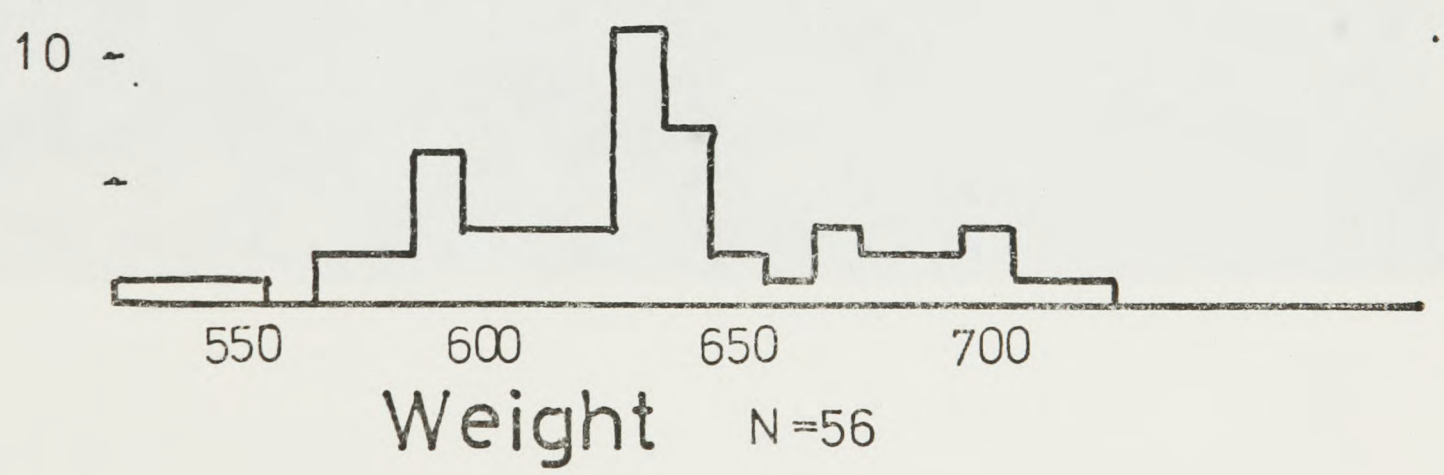
b. Differences in the thickness of the neck and head region in two birds of a pair were also used to tell the sex; the male generally had a larger head and a thicker neck (see figure 2.5). This method was only relied upon when the birds had been observed together several times and sexed consistently on head size.

c. The sex of a bird could also be deduced following a mate change, where either the sex of each bird in the previous pair had been known or those in the second pair were established.

d. Sexes were distinguished by inference from changes in the pattern

Figure 2.4 Frequency distribution of bill length (mm), bill depth (mm), wing length (mm) and body weight (g) measurements.


20
10
30
32
34
36
38
Bill Length N=114
20
10
20
22
24
Bill Depth N=114


10
550
600
650
700
Weight N=56

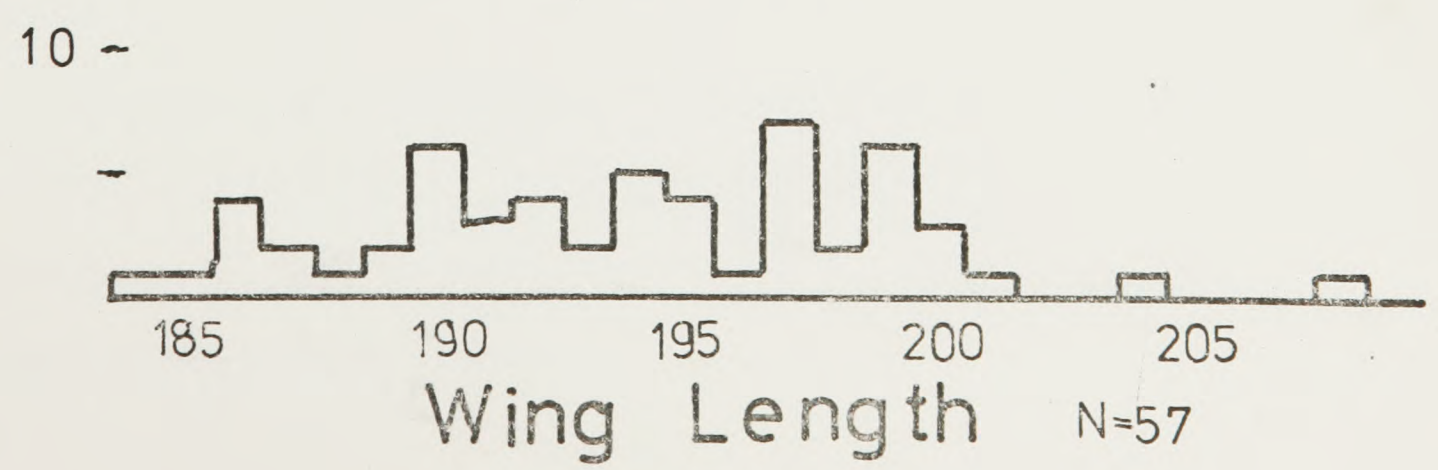

10
185
190
195
200
205
Wing Length N=57

Figure 2.5 An example of the difference in the size of the head and neck of Razorbills of different sexes. The bird on the right is a female, and that on the left is a male.



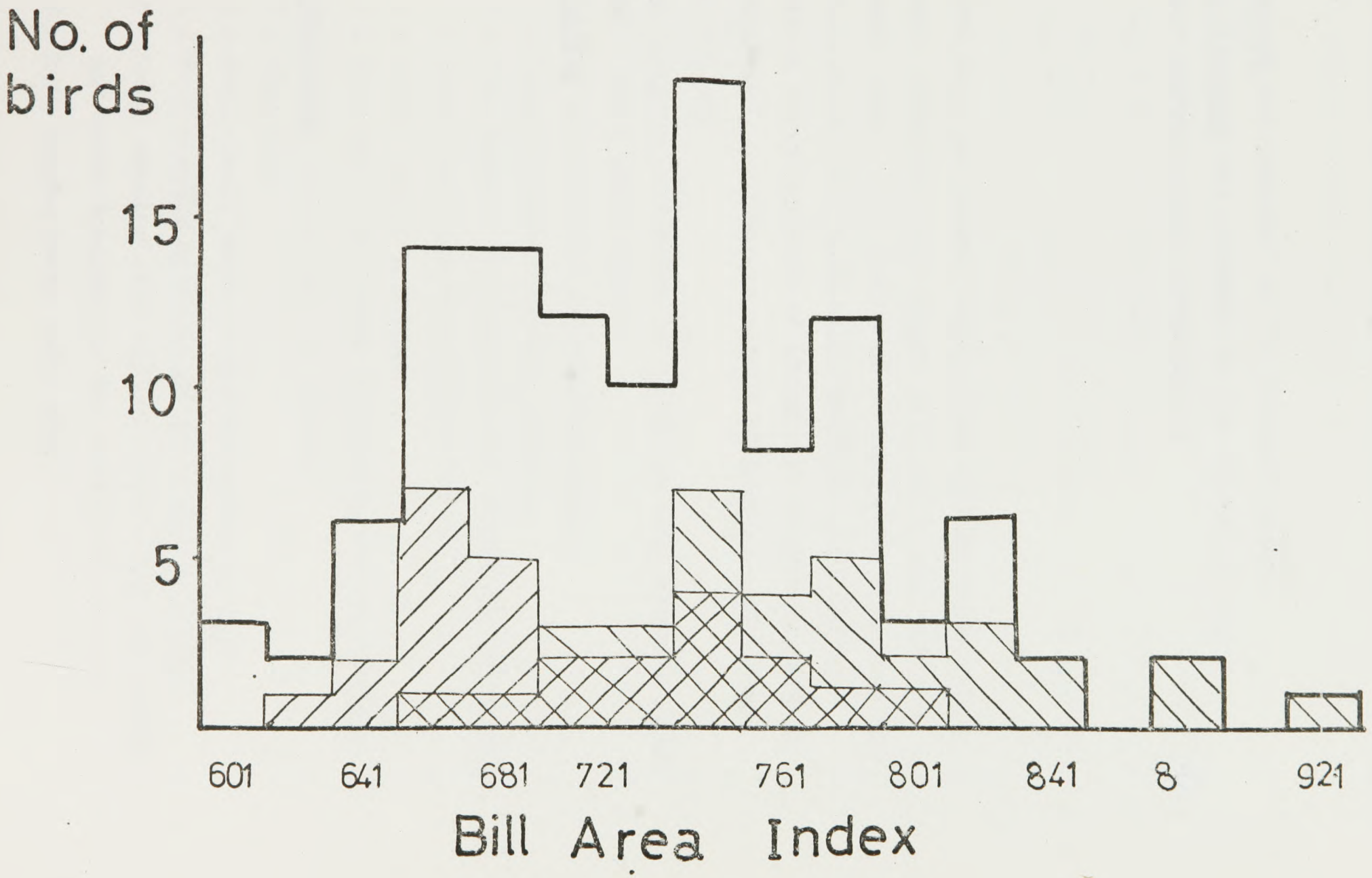
of shell pigmentation on the egg laid in a site in successive years. Each female usually produced eggs with almost identical pigmentation patterns in successive years (see Chapter 4 B ii e). In sites where one bird of the pair was known to be different from the previous year, changes in egg pigmentation pattern were taken to mean that the new bird of the pair was female whereas lack of change indicated a new male.

3. Measurements of birds of known sex. Examination of eight pairs of birds in which both birds had been measured and sexed (by one or more of the methods described above) showed that one male had a shorter bill than its mate, another had a shallower bill and a third had both measurements smaller than the female (but had been sexed on mating observed on two occasions). In the other five pairs the male bill length and depth was either equal in size or larger than that of the female. Hence bill area indices of only 4 of the 8 males were greater than that of their mates and so differences in bill size were not a reliable indication of sex.

Figure 2.6 shows the distributions of bill area indices of known sex birds compared with that for all live birds measured. This indicates that individuals with indices greater than 820 were males and those with indices of less than 661 were female; however, using this criteria alone only 19% of the birds measured could have been sexed.

In conclusion, therefore, I was not able to distinguish male and female Hazorbills on the basis of body measurements although comparison of head and neck size in paired birds was a fairly reliable alternative method.

Figure 2.6 Frequency distribution of bill area indices of 62 birds of known sex (▨ =Males, ▨ =Females), compared with that of all birds measured (n=114).



e. Measurement of weather conditions

Wind speed, wind direction and cloud cover were measured by Observatory staff each day at 1000 BST (0900 GMT) and records kept for the Meteorological Office. These records were used in the present study where details of prevailing weather were needed. Additional records of visibility and sea conditions were made as follows:

Windspeed was recorded in the Beaufort scale.

Wind direction was recorded to the nearest of eight compass points, scored numerically:

N.E. = 1	S.W. = 5
E. = 2	W. = 6
S.E. = 3	N.W. = 7
S. = 4	N. = 8

In this way, low scores represented wind in a general easterly direction (see Figure 2.1) and a high score a westerly wind. This method of scoring wind direction was unsatisfactory for statistical analysis and, had wind direction shown any sign of playing an important part in the analyses, a different method of scoring would have been adopted.

Cloud cover was estimated in eights so that overcast skies scored 8 and a clear sky 0.

Visibility was recorded numerically hence:

1 = Fog, lighthouse foghorn sounding

2 = Bad, neither the mainland nor Skomer (3 km) visible

3 = Poor, Grassholm not visible (11 km)

4 = Good, Grassholm visible

5 = Very good, the Smalls lighthouse (21 km) visible

Sea conditions were scored as follows:

1 = Flat calm

2 = Calm, small waves to gentle swell, no surf

3 = Surf visible breaking on the mainland (3 km)

4 = Swell running with surf on rocks round the island and waves breaking on the surface of the sea

5 = Very rough, heavy swell etc.

Analyses in which these subjectively scored weather parameters were used involved multiple regression in which weather and other factors were the independent variables. Independent variables used in this type of statistical analysis, however, should lie on an infinite scale. The method used here to quantify the effects of weather are therefore not well suited to statistical analysis and the interpretation of results remains tentative.

f. Miscellaneous

All field observations were made using a pair of 10 x 50 'Yashica' binoculars and a 'Nikel' (x 15-60) telescope. Analysis of data was carried out using an IME desk-top calculator, the 1906A computer at the Oxford University Computing Centre and a Nova computer belonging to Oxford University Zoology Department. All statistical methods used are described in Bailey (1959), and Siegel (1956). All times of day are British Summer Time (ie one hour ahead of GMT).

Chapter 3: ATTENDANCE

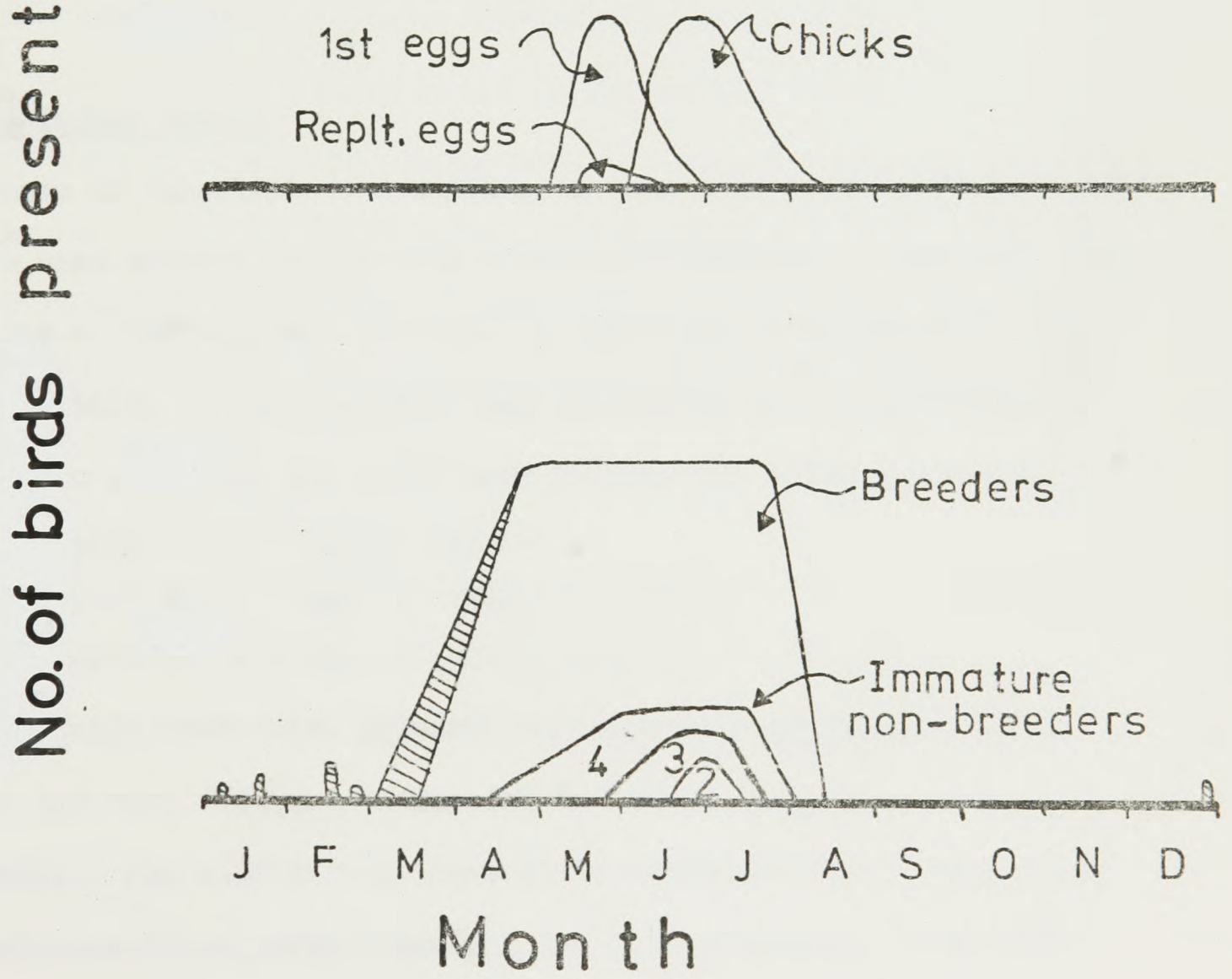
i. Attendance at the breeding colony

Introduction

Razorbills were rarely seen near Skokholm from the end of the breeding season (early August) until the following spring (March). Ringing recoveries suggest that this was because the young birds migrated southwards in autumn whilst the adult birds dispersed away from the colony into the Irish Sea and English Channel for the winter (Lloyd 1974). Unlike Razorbills, Guillemots have been recorded on land at many breeding colonies throughout the winter (Lockley 1953, Cramp et al 1970, Greenwood 1972, N Hammond in litt.) and ringing recoveries show that they tend to winter comparatively close to the colonies (Birkhead 1974a).

The Razorbills returned to the vicinity of Skokholm in early March. Although their appearances were irregular and they rarely came to land, this marked the start of the pre-laying period. By the time laying began in May, marking the start of the breeding season, patterns of attendance had become established. The numbers of breeding birds in each colony then remained fairly constant until the end of the breeding season although the proportion of failed breeders gradually increased as the season progressed. A small number of adult but non-breeding birds was also present at most colonies throughout the season. The total numbers of birds in the colony did, however, increase as the immature non-breeding birds returned to the island and came to land. Many birds left the colony when the chicks started to fledge (late July and August). The annual attendance at a Razorbill colony is summarised diagrammatically in Figure 3.1. Colony attendance is discussed with reference to population census techniques in Appendix V.

Figure 3.1 Summary of annual attendance at Razorbill colonies on Skokholm. The cross-hatching indicates the presence of birds, mainly breeders, just offshore but rarely on land. The numbers in the lower graph refer to the age class (years) of the non-breeders.



Attendance during the pre-laying period was recorded by daily counts of the number of Razorbills present on the sea around Skokholm and similar counts were made of the other species of auks for comparative purposes. Attendance during the breeding season itself was complicated by the fact that, in the boulder colonies at least, incubating birds were out of sight unless the colony was disturbed. Daily counts were made of all the birds on land in two study colonies; one of these consisted mainly of open ledge nest sites in which the sitting birds were clearly visible all the time, and in the other the nest sites were hidden under boulders. The aim of these counts was to establish the seasonal and diurnal variation in attendance and to compare the counts from the two different types of colony.

Method

a. Pre-laying period

The counts of Razorbills and Guillemots were made between 0900 and 1200; Puffins were counted in the late afternoon (1600-1800) each day. Only the birds on the sea were included in these counts although at this stage any birds on land readily took to the sea when approached. Counts were made from the cliff tops between the following dates:

April 1 - May 9 1971
April 12 - May 22 1972
March 18 - May 12 1973

The Guillemots often gathered in rafts or characteristic long strings and were thus the easiest of the three species to count accurately. The Puffins were frequently scattered over a wide area, although some dense rafts formed in the late afternoon. This made counting difficult and the Puffins seen to the north of the island doubtless included individuals from the colonies on Skomer. The daily counts were analysed further by autocorrelation aimed at detecting cyclic fluctuations.

b. Main breeding season

1. Observations at Colony A - Twinlet Bay

This colony contained both Razorbill (maximum 39) and Guillemot (maximum 23) nests; observations were made from a hide about 30m from the nearest nest between May 1 and July 15, 1972 and May 2 and July 11, 1973. The daily record involved either a single count, made at some time between 0800 and 1100, or counts made at regular intervals (usually every 2 hours) throughout the day. The latter were made once a week in 1972 and on four different days in 1973.

The single daily counts, based on preliminary observations in 1971, were timed to coincide with the maximum daily attendance. After laying, in May, it was possible to estimate the number of breeding and non-breeding birds present during any count. Off-duty birds usually sat beside their mates in the nest site or left the colony completely. Thus counts were separated into 'breeding birds', including both incubating or brooding birds and their mates when present at the site, and 'non-breeding birds' including all other birds.

2. Observations at Colony B - Bluffs

Between May 2 and July 11, 1973, the Razorbills at a second colony containing up to 55 occupied nest sites were also counted. As observations were made (with binoculars) from a distance of about 360m so that the colony was undisturbed, it was assumed that all incubating or brooding birds were out of sight in the nest. Hence the counts involved non-breeding and off-duty breeding birds only though these could not be distinguished from each other. The daily record involved either a single count some time between 0900 and 1200 or, on three days, counts at regular intervals (usually every 2 hours) throughout the day.

The counts at both Colony A and Colony B each season were started when the birds remained on land until mid-morning and did not immediately fly out to sea when approached. The diurnal counts began as soon as it was light enough to see the birds, usually just after sunrise, and stopped in the evening at sunset.

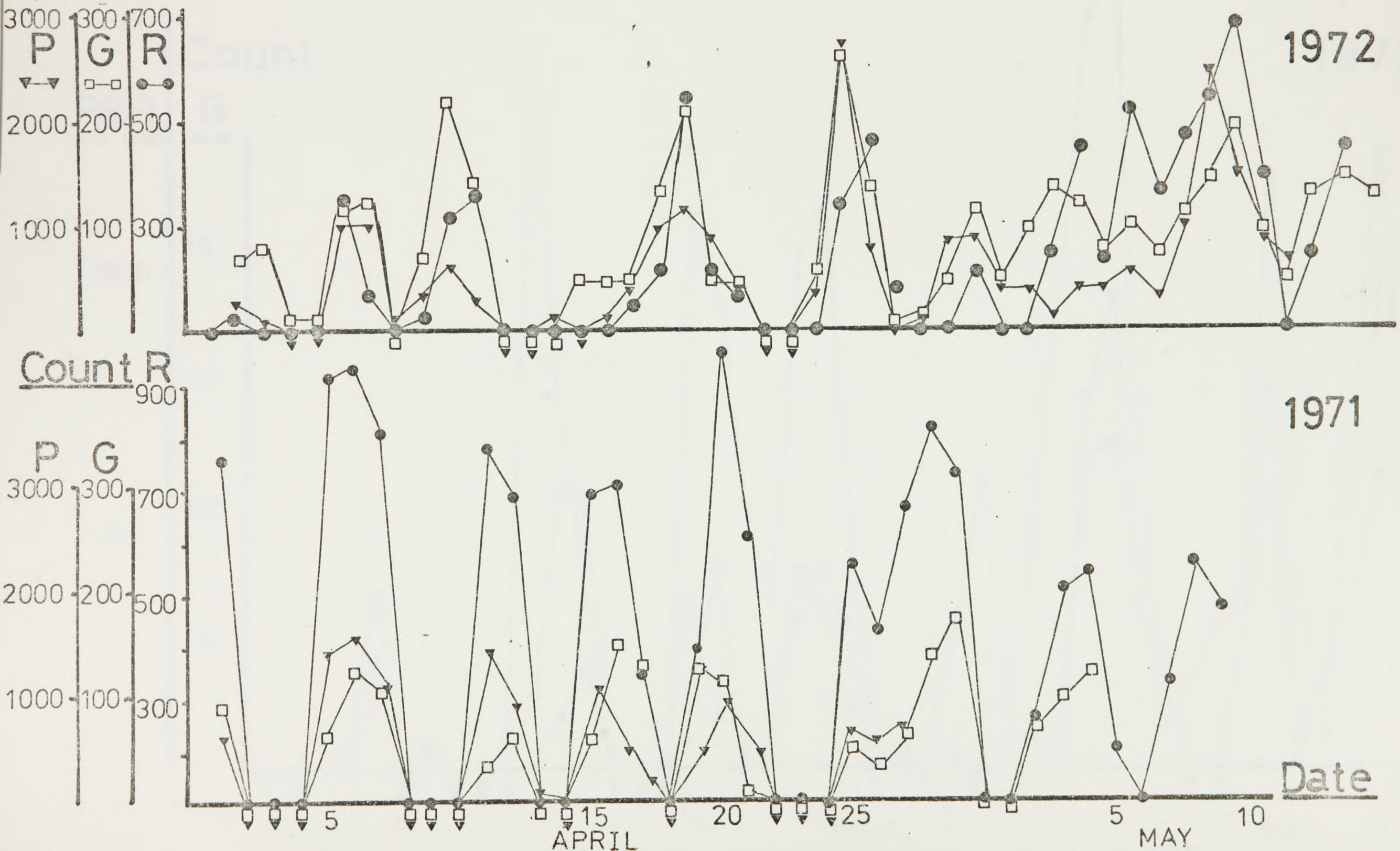
Results

a) Pre-laying period

In April the Razorbills formed rafts up to 2 km off the island and mixed freely with the Guillemots. These groups usually included a few Puffins though numbers of this species were lowest in the early morning (when Razorbill and Guillemot counts were high) but increased to a peak in the evening (cf Corkhill 1970). As the season progressed, the peak in Razorbill and Guillemot numbers occurred later in the mornings and the birds remained near the island for more of the day. Similar patterns of diurnal attendance by Razorbills at the breeding colony during the pre-laying period, with an early morning peak, have been recorded by Corkhill (1970), Bédard (1969), Perry (1940), Greenwood (1972) and N.Hammond (in litt .).

The day to day variation in numbers of Razorbills and Guillemots is shown in Figure 3.2 for the three years of the study. Although the numbers of each species fluctuated widely from one day to the next and sometimes all the birds disappeared for several consecutive days, the three species generally indicated a high degree of inter-specific synchrony (Table 3.1). On average the correlation between the counts of each species and those of the other two on the same day were highest in 1971 and lowest in 1972. Razorbill counts in both 1972 and 1973 were most closely correlated ($P \leq 0.01$) with those of Guillemots ($r=0.72$, $n=37$ and $r=0.83$, $n=36$ respectively), and least correlation was found between the counts of Guillemots and Puffins ($r=0.49$, $n=27$; $r=0.52$, $n=37$

Figure 3.2 Daily counts of Razorbills (R), Guillemots (G) and Puffins (P) during the spring in 1971 and 1972 and (PTO) 1973.


3000
300
700
P
G
R
2000
200
500
1000
100
300
1972
Count R
900
P G
3000
300
700
2000
200
500
1000
100
300
1971
5
15
20
25
APRIL
5
10
MAY
Date

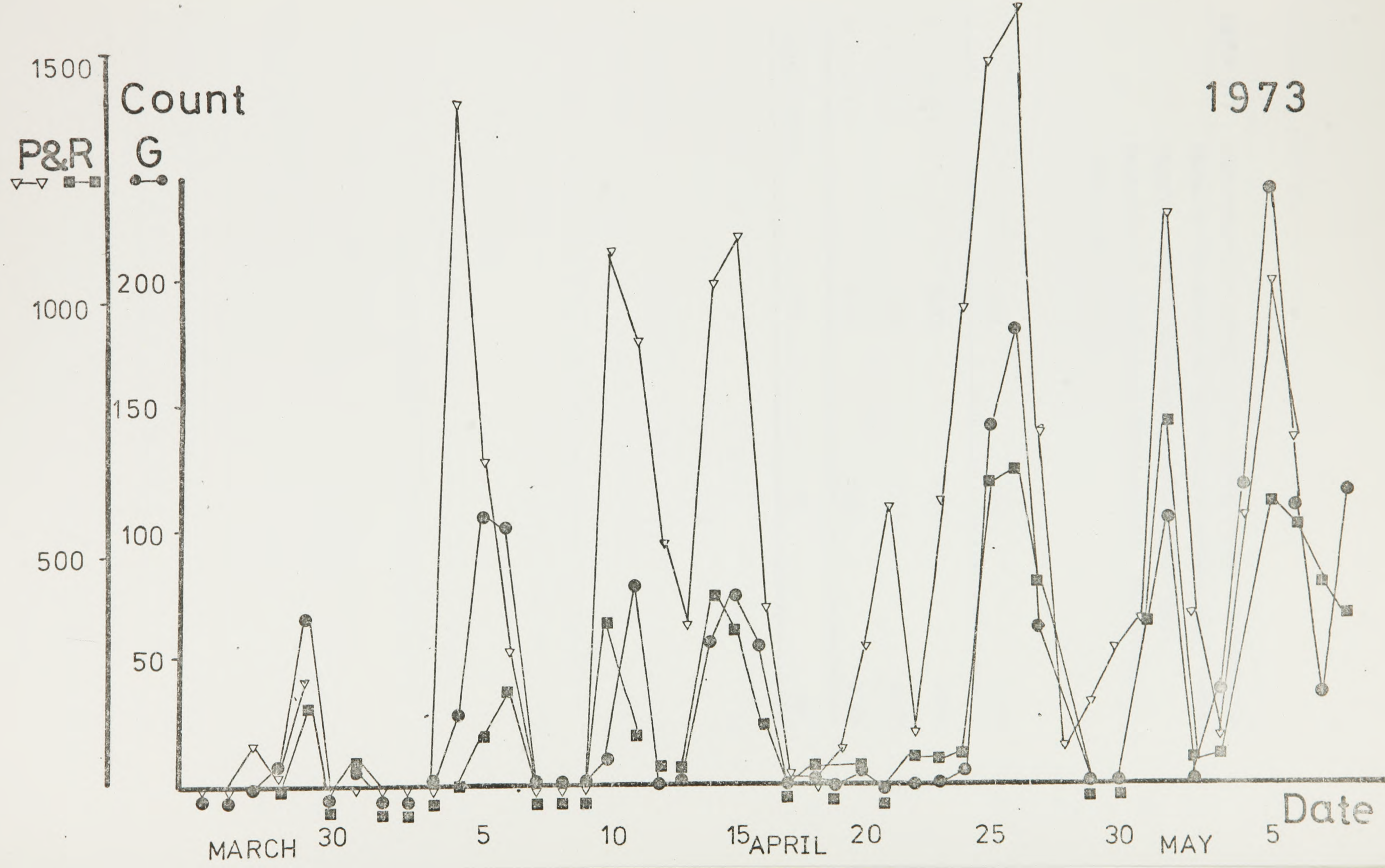

1973
1500
Count
P&R
G
1000
200
150
100
500
50
MARCH
30
5
10
15
APRIL
20
25
30
MAY
5
Date

Table 3.1 Inter-specific synchrony in spring colony attendance as shown by the amount of correlation between daily counts. Figures refer to correlation coefficients where R=Razorbill, G=Guillemot and P=Puffin. All correlations significant $P \leq 0.05$.

	1971	1972	1973
R v. G & P	0.95	0.80	0.87
G v. R & P	0.91	0.73	0.83
P v. R & G	0.93	0.67	0.72
Sample sizes	27	37	36

and r=0.63, n=36 for the three years respectively).

Autocorrelation analysis of the 1971 data showed that the counts followed a four day cycle. In 1972, however, the attendance in all three species showed no cyclic fluctuations; although the counts indicated cyclic attendance in 1973, with peaks every five days, the correlations were not significant.

b) Main breeding season

Seasonal variation in numbers

1. Colony A

The daily pattern of attendance was basically similar in 1972 and 1973 (Figure 3.3). The number of birds present fluctuated widely during the pre-laying period, but became more constant during laying. From then on, the numbers increased slowly to a peak in the season's attendance during the nestling period, after which numbers declined rapidly. The coefficient of variation (standard deviation expressed as a percentage of the mean) of counts in the different parts of the season (Figure 3.3) showed that overall attendance was least variable in the nestling period. This was also true of Razorbill attendance on Skomer in 1973 and elsewhere (Lloyd 1975b).

Counts of breeding birds remained between 40 and 50 throughout the period until numbers decreased as most of the chicks left the ledges cf Bédard 1969 and Figure 3.4.

Few non-breeding birds were present early in the season so that counts of apparently non-breeding birds probably consisted mainly of birds about to breed. Numbers of "non-breeding" birds in the late incubation and early nestling periods increased and must inevitably have included a few off duty breeding birds and failed breeders (which would have been present on the ledges but not associated with a nest site). The large number of apparently

Figure 3.3 Daily attendance of Razorbills at Twinlet in 1972 and 1973.
The counts refer to the total number of birds present and the arrows mark dates of first laying, hatching and fledging respectively.
The coefficients of variation (%) of mean counts during different parts of the breeding season (sample sizes in parentheses) are as follows:

	1972	1973
Pre-laying	78.0 (25)	80.9 (9)
Incubation	15.5 (29)	19.5 (37)
Nestling	9.0 (14)	8.1 (16)
Fledging	-	22.4 (15)
Month of June	17.0 (29)	11.8 (30)

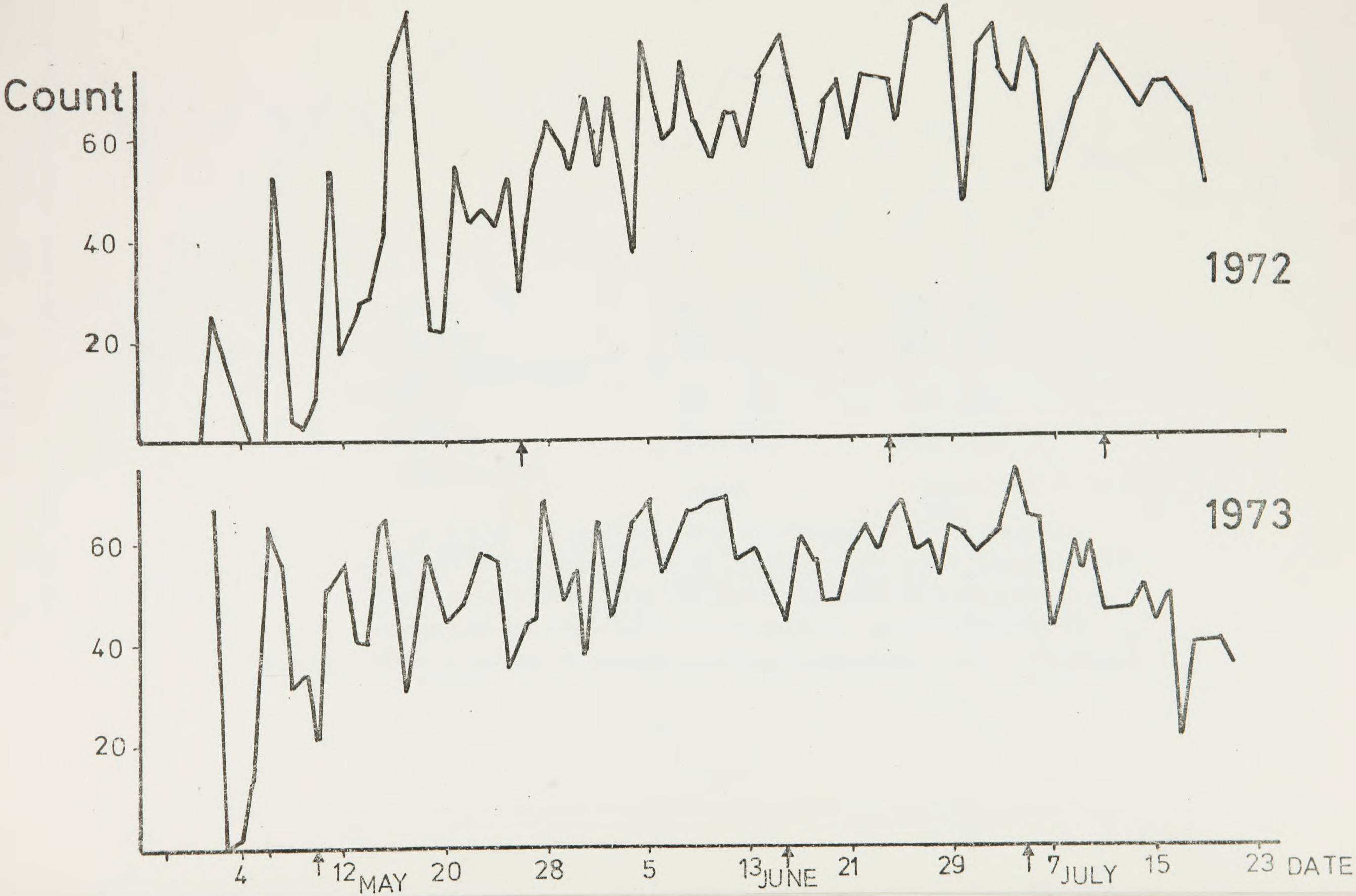
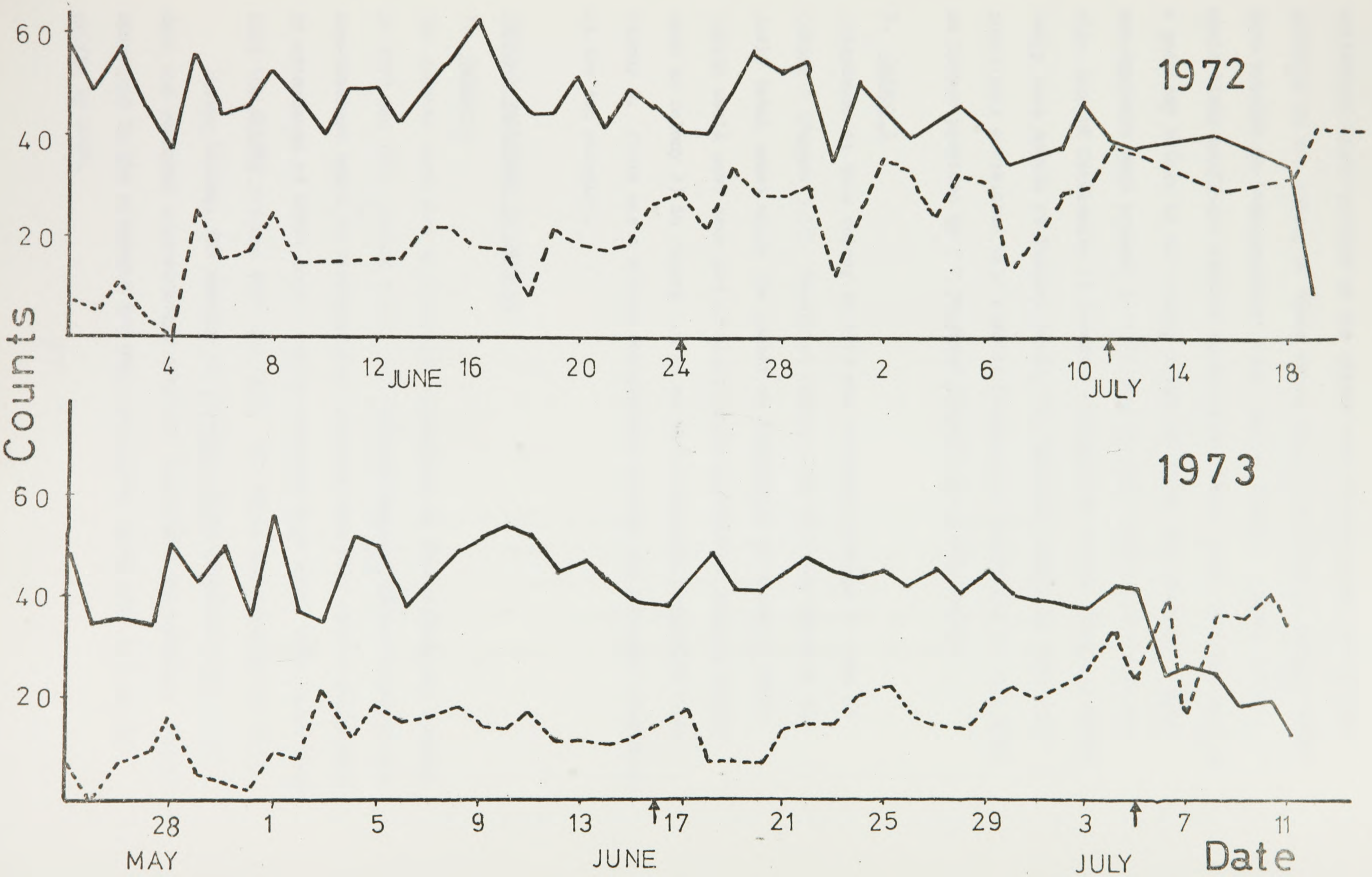

Count
60
40
20
1972
1973
4
12 MAY
20
28
5
13 JUNE
21
29
7 JULY
15
23
DATE

Figure 3.4 Daily attendance of breeding (——) and non-breeding (- - -) Razorbills at Twinlet. The counts refer to the number of birds present and the arrows mark dates of first hatching and fledging respectively. The coefficients of variation (%) of the mean counts during different parts of the season , with sample sizes in parentheses, are as follows:

	1972	1973
BREEDING BIRDS		
Incubation	13.5 (23)	16.6 (22)
Nestling	12.3 (12)	8.4 (18)
NON-BREEDING BIRDS		
Incubation	34.6 (23)	51.1 (22)
Nestling	19.1 (12)	47.1 (18)


1972
60
40
20
Counts
4
8
12 JUNE
16
20
24
28
2
6
10 JULY
14
18
1973
60
40
20
28
MAY
1
5
9
13
17
JUNE
21
25
29
3
JULY
7
11
Date

unattached birds present as the chicks were fledging was due to the presence at the colony of birds whose chicks had already fledged which were counted as 'non-breeders' (see Chapter 4Biii). Colour ringing of adult birds confirmed earlier speculation (Perry 1940) that one bird of a pair may return to the colony after the chick has fledged. More non-breeders were present in 1972 than in 1973 (Table 3.2); this was also true of Guillemots at breeding colonies on Skomer (Birkhead 1976). Daily head counts at Twinlet during the breeding season in 1973 were positively correlated with similar figures for Razorbills at Bull Hole on Skomer provided by T M Birkhead ($r=0.77$, $P<0.001$, $n=64$).

2. Colony B

Attendance at this colony in 1973 was basically similar to that at Colony A (Figure 3.5). Counts at Colony A in 1973 are shown as the daily total count minus the number of incubating or brooding birds (which would have been out of sight in an undisturbed boulder colony such as Colony B) in Figure 3.5 so as to be directly comparable with Colony B. There was a strong correlation between the seasonal attendance at the two colonies.

Diurnal variation in numbers

1. Colony A

The diurnal variation in Razorbill attendance at this colony was similar in 1972 and 1973 (Figure 3.6). Before laying, when breeders and non-breeders could not be distinguished, numbers were high with a daily peak in attendance at about 0830. Counts remained high until 1100; most birds left the cliffs between 1600 and 1800. All birds had departed by 2030.

During laying, the numbers of breeding birds increased soon after dawn and remained approximately constant throughout the morning. Counts decreased in the afternoon and only incubating birds were left on the cliffs by 2000.

Table 3.2 The average number of "non-breeding" birds present at different stages of the breeding season, expressed as a percentage of the total count. For explanation of the composition of these counts - see text.

Period	1972	1973
Laying - early incubation	20	13
Incubation	33	25
Late incubation - nestling	36	26
Fledging	70-90	70

Figure 3.5 Daily attendance of Razorbills at The Bluffs in 1973 compared with that at Twinlet, corrected for the presence of visible incubating/brooding birds (see text). Arrows mark dates of first laying, hatching and fledging respectively and all counts refer to the number of birds present. Counts at the two colonies were positively correlated ($r=0.46, P< 0.001, n=54$). The coefficients of variation (%) of the mean counts at The Bluffs in different stages of the breeding season, with sample sizes in parentheses, are as follows:

Incubation	45.7 (34)	Nestling	22.5 (12)
Fledging	34.8 (13)	Month of June	30.3 (24)

Twinlet

Corrected count

40

20

Bluffs

Count

60

40

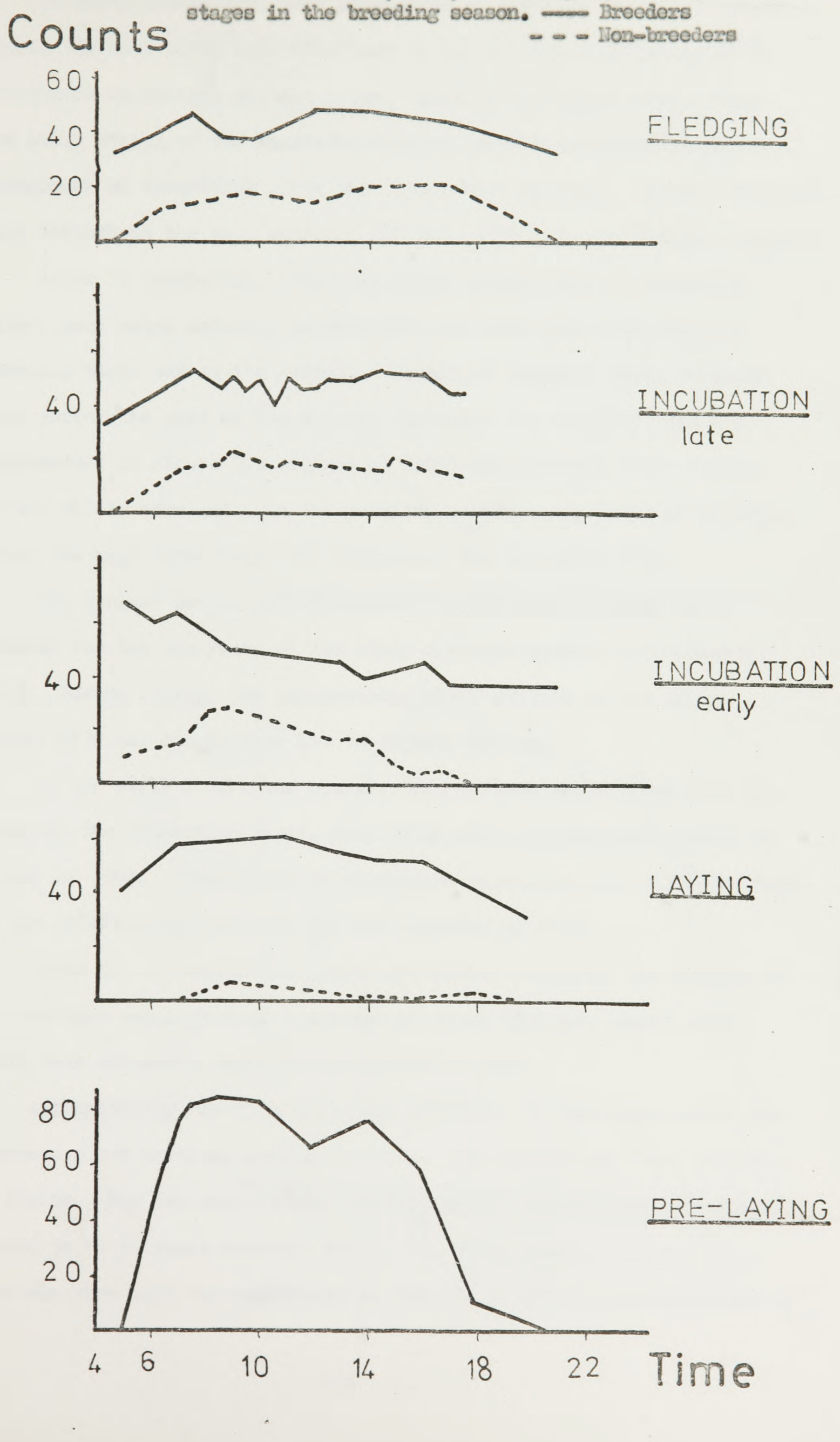
20

12 20 28 5 13 21 29 7 15 23

MAY JUNE JULY

Date

Figure 3.6 Hourly attendance at Twinlet 1972/73 shown by representative counts (birds) in both years at different stages in the breeding season. —— Breeders
- - - Non-breeders



In early incubation, peak attendance of breeding birds was recorded during the hour after dawn when many birds returned simultaneously to the cliffs to relieve sitting mates. This peak did not occur during the later stages of the incubation period, possibly because the first changeover of incubating birds took place more quickly. Numbers remained high throughout the day, although all the mates left the cliffs at night.

Later in incubation, after the first change-over of incubating birds, many mates returned between 0700 and 0800 when attendance of breeding birds was at its maximum. Counts of breeding birds remained high during the rest of the day but (although the counts on the day represented in Figure 3.6 stopped at 1800) only sitting birds stayed on the cliffs at night. In the nestling period, attendance of breeding birds was high from about 0700 throughout the day until 1700.

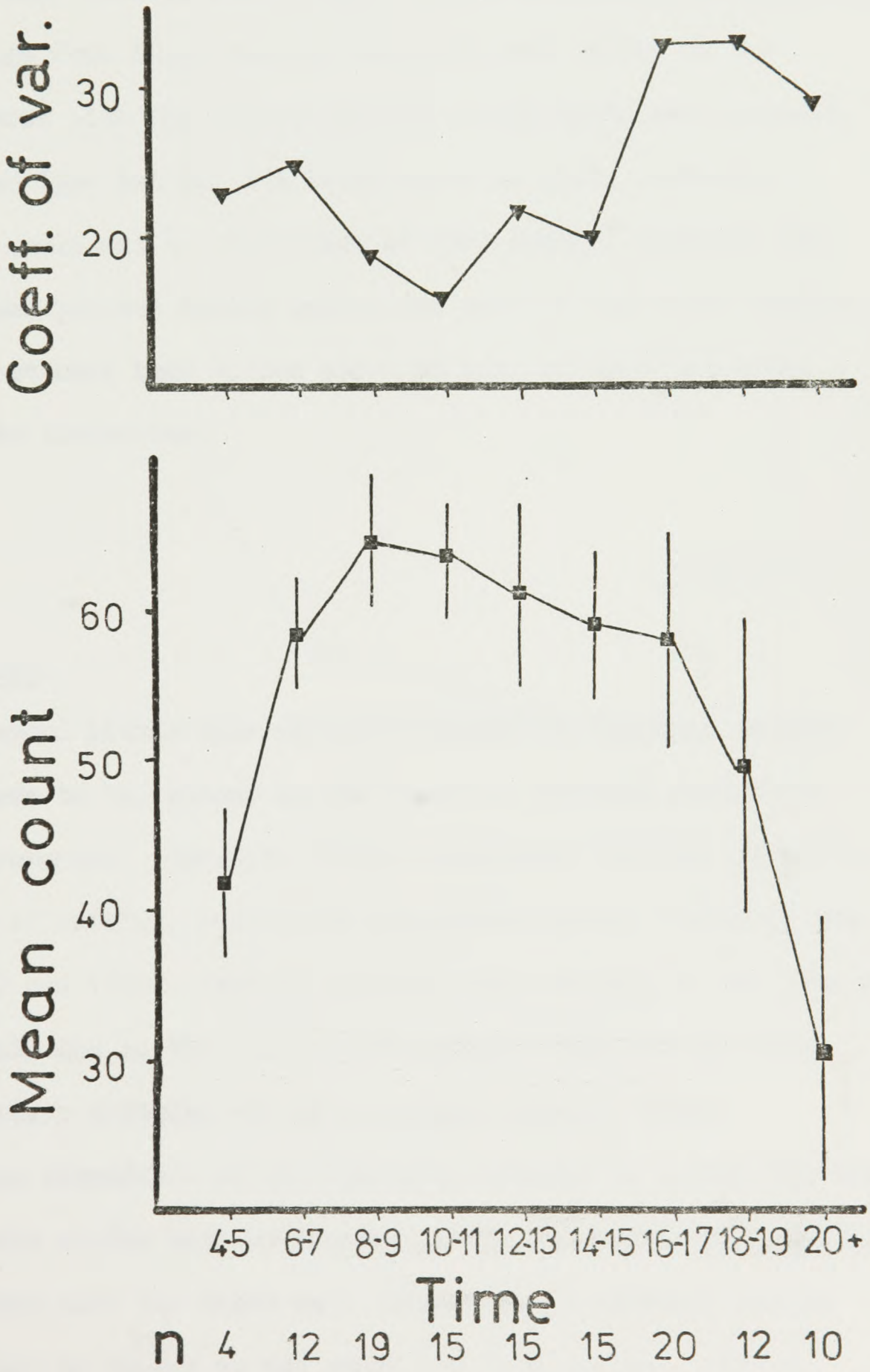
The diurnal pattern of attendance in <u>non-breeding birds</u> was similar for the two years of the study although numbers were lower in 1973. During laying, few non-breeding birds arrived at the colony before 0700 and counts were low throughout the day.

In the early incubation period, the non-breeders arrived with the mates of the incubating birds, soon after dawn and increased slowly to a peak at 0900. After this the attendance decreased; few birds remained on the cliffs after 1400 and all had departed by 1800.

Later in the incubation period and during fledging, the numbers of non-breeders again reached a maximum at about 0900 and stayed high until late afternoon when they decreased to zero.

Approximately hourly counts were available on four days during the incubation and nestling periods of 1972. The amounts by which the mean of counts in two hour intervals varied in this period showed that attendance tended to be least variable during the early morning (Figure 3.7). This was also true for Guillemots at Twinlet in 1972 and observations of

Figure 3.7 Mean counts (± 1 standard error) and coefficients of variation (%) of birds present at Twinlet at different times of the day. Counts are grouped in two hour intervals and were made during the nestling period of 1973.



these auks at breeding colonies elsewhere since have confirmed this general pattern of attendance (M P Harris, and P G H Evans - pers.comm., P Kinnear - in litt.)

2. Colony B

As at Colony A, counts during laying were high from mid-morning (0900 - 1000) onwards (Figure 3.8). Most birds left the colony after midday and few were visible after 1700. In the incubation period the numbers were high from early morning and decreased slowly in the afternoon compared with the laying period. A few birds were present between 1600 and 1900 but all had disappeared by 2000. Although breeding birds could not be identified at this colony, probably few non-breeders were present during laying and most of the birds visible at this time must have been either about to lay, or have had mates who were already incubating.

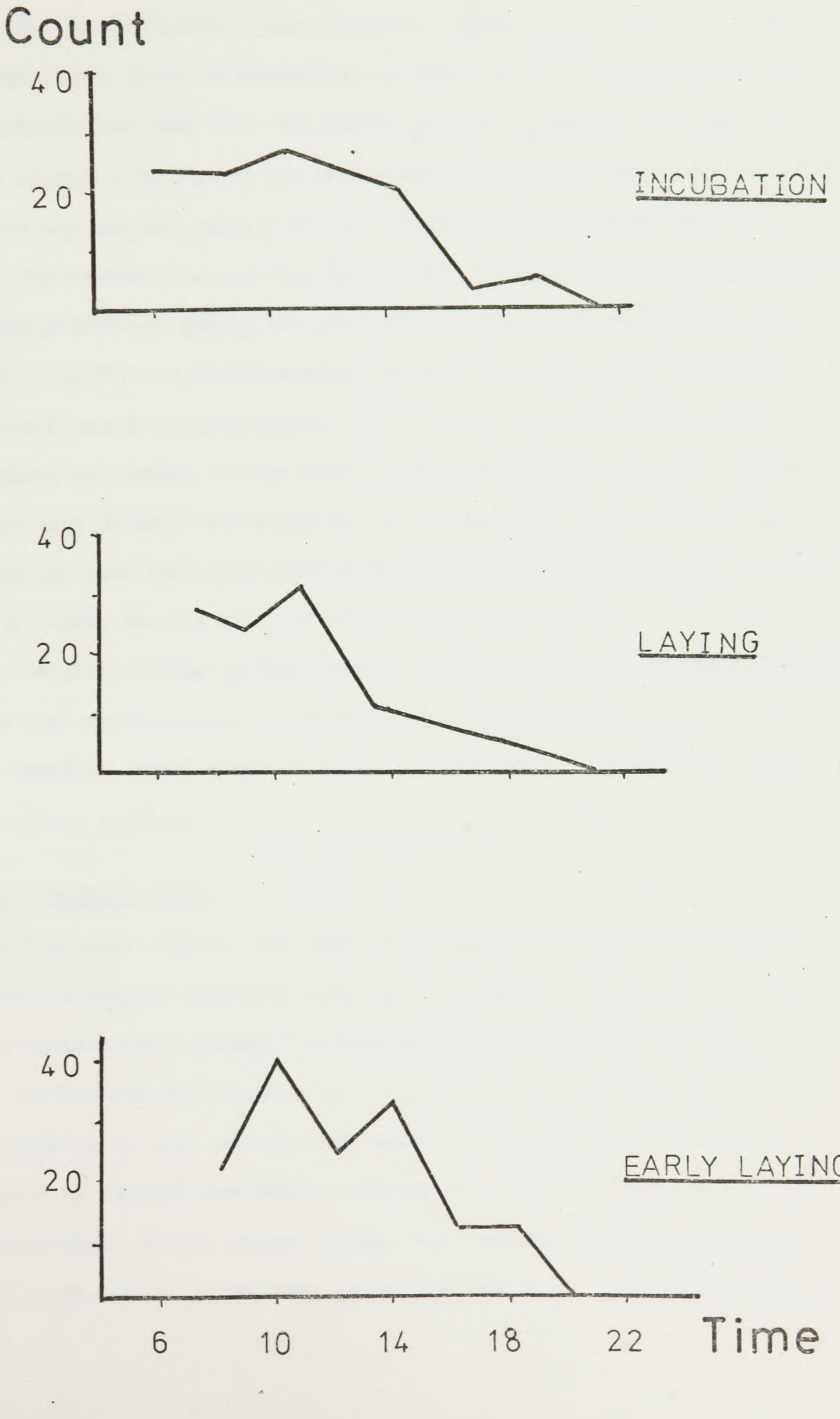
Discussion

Pre-laying period

Although auks spend little time on land outside the breeding season, the actual return to the colony at the start of breeding season has been poorly documented. Corkhill (1970) recorded a five-day cycle in the attendance of Puffins, Guillemots and Razorbills on Skomer in the springs of 1969 and 1970. Similar results were obtained in one year of the present study and in the other years numbers followed the same fluctuating pattern although not on a regular (cyclic) basis.

Fluctuating attendance at the breeding colonies in spring has been described for the Puffin both by Lockley (1953) and Nyrberget (1959). Lockley suggested that the birds were subject to an internal rhythm which caused them to depart to sea every few days to feed, whilst

Figure 3.8 Hourly attendance at The Bluffs (birds present) at different stages of the breeding season in 1973.



Corkhill (1970) thought that the inter-specific synchrony resulted from some physiological rhythm but its function was not discussed. All observations of auks feeding during the present study suggested that suitable feeding grounds were situated within easy reach of the breeding colony. This tends to contradict any idea that the birds required large amounts of time away from the colony to feed. Furthermore, even on days of peak attendance, the birds were absent from the colony for most of the day and thus must have had plenty of time in which to feed.

The reasons for the high inter- and intra-specifically synchronised colony attendance during the pre-laying period is therefore far from clear. In 1972 on Skokholm synchronised attendance was disrupted by unusually rough spring weather (see discussion below); laying also occurred on average 13 days later than in the previous year. Weather could have affected the birds in two independent ways (by producing rough sea conditions detrimental to raft formation or by making feeding difficult for female birds forming eggs) with the same result (a delay in the start of laying). However, it seems probable that the establishment and maintenance of synchronised behaviour during the breeding season plays an important part in the timing of breeding (see Chap. 4Biib).

Main breeding season

Other seabirds studied have shown that different attendance patterns exist, although a seasonal increase in numbers is a feature common to many species (eg Koskimes 1949; Cullen 1954; Myrberget 1959 ; Drent 1965).

Attendance of Razorbill at the Skokholm colonies in 1972 and 1973 was similar to that recorded by Bédard (1969), who also noted that numbers of assumed non-breeders increased slowly to a peak at the time of hatching. In the present study, the seasonal increase in total numbers in colony A was shown to be due mainly to the increase in numbers

of non-breeding birds to a peak late in incubation. Observations of colour ringed birds (Chap.5ii) provided additional evidence that this was due to a gradual return to the colony of immatures.

In some studies of other species, cyclic attendance patterns have been found to persist throughout the breeding season. Myberget (1959) recorded Puffin attendance at a colony in northern Norway and found that maximum counts occurred every 3 to 12 days throughout the breeding season, on average every 6.3 days. Nettleship (1972) also found a cyclic pattern of attendance in Puffins at a breeding colony in Newfoundland. Tuck (1960) noted high attendance in Brunnich's Guillemots at a Hudson Bay colony throughout the day in the early breeding season with peak numbers recorded during night-time hours. During the fledging period diurnal attendance at this colony was variable with five-hourly peaks. On Skomer, Common Guillemot attendance was highest in the early morning throughout the season, when the birds had returned to the cliffs after dawn (Birkhead 1976).

A diurnal rhythm in attendance of Brünnich's Guillemots was maintained in conditions of 24 hours' daylight on Jan Mayen (Cullen 1954).

ii. The effect of weather on colony attendance

One of the factors which appeared to affect the amount of time Razorbills spent both near the colony in the pre-laying period and on the ledges in the main breeding season was prevailing weather conditions. These were examined in greater detail in order to establish their importance to attendance.

Method

The daily counts of Razorbills (described above) during the pre-laying period and the main breeding season were compared with the prevailing weather variables and date by a stepwise multiple regression analysis.

a. Pre-laying period

The daily total counts of Razorbills around the island were regressed against wind speed, wind direction, cloud cover and visibility (see Chap.2iiie). Date was included as a fifth independent variable because numbers increased as the pre-laying season progressed. Separate analyses were conducted for the three years' data.

b. Main breeding season

The attendance figures obtained for Colony A in 1972 and 1973 were divided into three periods according to the stage of the breeding season and the counts of breeding birds were separated from those of non-breeding birds for the periods when these could be distinguished as shown in Table 3.3. This permitted the separate analysis of five separate groups of data from each of the two years. The five independent variables used in the regressions were date, wind speed, wind direction, sea conditions and cloud cover.

Results

a) Pre-laying period

The effect of prevailing weather conditions on the Razorbill attendance was difficult to assess accurately. Extreme weather conditions involving strong winds, heavy rainfall and rough sea had an obvious adverse effect on the counts. Such weather conditions tended to break up the rafts and scatter the birds but no such effect was observed on foggy or overcast days. The same was true for Puffin and Guillemot attendance at this time. The effect of less severe weather on the Razorbill attendance was indicated by the results of the regression analysis shown in Table 3.4. The interpretation of these results in terms of biological, rather than statistical, significance requires some caution.

In both 1972 and 1973 there was a significant increase in the counts as the pre-laying season progressed; the date alone accounted for 13% and

Table 3.3 Timing of attendance counts at Twinlet

Period	Count	1972	N	1973	N
Pre-laying	Total	May 1- May 30	30	May 2- May 23	22
Incubation	Breeding birds) Non-breeding birds)	May 31-June 30	27	May 24-June 16	24
Nestling	Breeding birds) Non-breeding birds)	July 1-July 13	12	June17-July 5	18

Table 3.4 Results of the multiple regression analysis for the effect of weather on spring attendance. The correlation coefficient (R) is given for significant correlations ($P \leq 0.05$); the combination of factors which were found to predict most efficiently the variation in the daily counts is shown with the amount of variation explained.

Year	n	Single Factors	R	Combined Factors	
1971	39	Wind speed	-0.45	Wind speed	19.9%
1972	41	Date	+0.37	Date)	43.4%
		Visibility	+0.33	Wind speed)	
				Wind direction)	
				Visibility)	
1973	55	Date	+0.41	Date)	38.6%
		Wind speed	-0.38	Wind speed)	
		Cloud cover	-0.31	Cloud cover)	
		Visibility	-0.32		

17% respectively of the total variation in the counts during the two years. The lack of a similar correlation in the 1971 data may have been due to the large fluctuations in the counts which tended to mask the seasonal increase in numbers.

During 1971 wind speed alone was responsible for 20% of the variation in the counts, high numbers being recorded on days of low wind speed regardless of other factors. In 1972 the counts decreased significantly in a period of high wind speeds and were also low in conditions of poor visibility. In 1973 maximum attendance was recorded on days with low wind speeds, especially if accompanied by clear sunny weather.

b) Main breeding season

The single factor or combination of factors which most efficiently predicted the daily count and the amount of variation explained by the multiple regression are shown in Table 3.5 for each group of data.

1. Date. In 1972 this appeared to be more important than any weather factor during the pre-laying period; it alone accounted for 41% of the variation in the daily counts at this time. The correlation was positive indicating that numbers increased significantly with date during this period in 1972. In 1973 no significant correlation was found between the date and counts of birds during the pre-laying period. This may have been due to the timing of the start of the counts. During 1972 the pre-laying period covered by the counts was longer (30 days) than in 1973 (22 days), due to the lateness of the season in the former year. Thus, in 1972 the birds increased in numbers during the pre-laying season whereas in 1973 the main increase in numbers probably occurred before the pre-laying season could be effectively observed.

During the incubation period, the effect of date was significant

Table 3.5 Results of multiple regression analysis of the effect of weather on the number of Razorbills present at the Twinlet Bay breeding colony. Correlation coefficient is given for the factors which on their own had a significant effect ($P \leq 0.05$); the combination of factors which most efficiently predicted the variation in the dependent variable is also given with the amount of variation explained by the regression.

Period	Count	1972		1973	
		Single	Combined	Single	Combined
		R		R	
Pre-egg	Total	Date+0.64	Date) W.dir.) 59.6% W.speed)	Wind sp. -0.62 Sea cond.-0.58	
Incubtn.	Breeder	-	(all 18.3%)	Wind sp. -0.47	W.speed) 51.7% W.dir.)
	Non-br.	Date+0.45	(all 19.8%)	Date +0.74 Wind sp. -0.58 Cloud -0.49	Date) Cloud) 67.5%
Nestling	Breeder	-	(all 63.5%)	Date -0.49	Date) W.speed) 50.9%
	Non-br.	Sea -0.66	43.1%	Date +0.62	38.2%

Note: Where none of the independent factors were correlated with the dependent, the amount of variation explained by the regression with all 5 variables is given in parentheses.

only for the non-breeding birds. In 1972 it accounted for almost 20% of the variation in these counts; and no other factors were significantly correlated. In 1973 a significant increase in numbers of non-breeding birds was observed during the incubation period; date accounted for 55% of the variation in the counts.

In 1973 there was a significant decrease in the numbers of breeding birds with date, which accounted for 24% of the variation during the nestling period. Non-breeders also increased significantly during the nestling period in 1973 but neither of these trends held in the nestling period of 1972.

Thus, during the early breeding season the numbers of birds preparing to breed increased as time progressed. During incubation there was no change in the numbers of breeding birds although counts of non-breeders increased significantly throughout the period. In the nestling period the numbers of breeding birds decreased whilst the counts of non-breeders increased, possibly as a result of birds returning to the cliffs after their chicks had fledged.

2. Wind speed. There was a significant negative correlation between wind speed and attendance counts during the pre-laying period of 1973 and for both breeding and non-breeding birds in the incubation period of the same year. Wind speed accounted for 38% of the variation in the counts during the pre-laying period and for 22% and 34% of the variation in the counts of breeders and non-breeders respectively in the incubation period. Hence, high wind speeds were associated with low attendance, and vice versa.
3. Wind direction. This factor on its own was not significantly correlated with any of the counts in either year.
4. Cloud cover. During the incubation period of 1973 the non-breeders' counts were negatively correlated with cloud cover to which 24% of

the variation was attributable. Few birds were present on heavily overcast days.

5. Sea conditions. These were negatively correlated with the pre-laying counts in 1973 and accounted for 34% of the variation in numbers. Sea conditions also affected the birds during the fledging period of 1972; the attendance of non-breeders was negatively correlated with this variable which explained 43% of the variation in their numbers. Thus, attendance tended to be low in rough weather.

Discussion

a) Pre-laying period

The effect of weather on colony attendance early in the breeding season has not been examined in great detail in other species. Lockley (1953) noted that on Skokholm Puffins were most abundant in spring when the weather was warm, and were driven away by cold spells. Corkhill (1970) examined patterns of pre-laying attendance in all three species of auk on Skomer in relation to prevailing wind speeds. He found that counts were negatively correlated with wind speed although the birds followed a regular cyclic attendance pattern. Myrberget (1959) working at a Puffin colony in Norway, found that attendance was related to weather conditions, especially to the calmness of the sea near the colony. Other authors have tried to evaluate the importance of weather to attendance during the main part of the breeding season.

During the present study, pre-laying attendance appeared to be determined mainly by the seasonal increase in numbers, the pattern of which was modified by changes in wind speed. The effect of the other weather factors varied from year to year but maximum attendance tended to occur on days with good visibility and sunshine and low wind speeds in the different years of the study.

It was not clear how prevailing weather actually affected the birds.

Wind speed usually determined the roughness of the sea with the notable exception of calm weather after a gale when the sea remained rough due to a residual swell. Counts were low in conditions of high wind speed; other observations showed that raft formation was readily hindered by rough seas, sometimes associated with high wind speeds.

Possibly the weather at, or before, dawn out to sea in the areas where the birds spent the night was more important in determining whether or not they returned to the colony for the day, than the weather measured on the island in the mid-morning. Unfortunately it was not feasible during the present study to record the weather out at sea, though I doubt that it actually differed significantly from that on the island and inshore waters.

On Skokholm, the different attendance patterns of the three species of auks between years can be partly accounted for by the different overall spring weather conditions. In 1971 and 1973 the weather remained mild and calm from March onwards but in 1972 the weather was extremely unsettled from late March until the beginning of June. Gale force winds and heavy rainfall were frequently recorded. This is summarised in Table 3.6 which shows the number of days in April and May each year on which wind speeds of force 4 or greater were recorded.

Comparison of the results for 1971 and 1973 with those for 1972 indicates that the effect of persistently bad weather was to disrupt both the inter- and intra-specific synchrony in attendance. The Razorbill counts were low in 1972 compared with those in 1971 and 1973, although there was no change in the size of the breeding population on the island in 1972. This suggests that there was no single day in the spring of 1972 when most of the birds gathered at the colony. Inter-specific synchrony was also on average weakest in 1972 when least correlation was found between the counts of one species and the other two. There was no regular (cyclic) pattern to the attendance in 1972.

Table 3.6 Comparison of weather conditions as indicated by wind speed in April and May during the three years of the study.

Year	Number of days on which winds of Force 4 or above were recorded.	
	APRIL	MAY
1971	5	1
1972	15	20
1973	5	6

There was no evidence in the present study that any of the weather factors measured, either on their own or combined together, caused the synchronous attendance of the three species. Only wind speed (and possibly wind direction which was not measured adequately in the present study) was related to attendance but this was responsible for only a small proportion of the total variation in the counts in any one year. The main effect of adverse weather was principally to disrupt the inter- and intra-specific patterns of attendance. Although the causation of synchrony was by no means clear as a result of this part of the study, the functions of inter- and intra-specific synchrony during the pre-laying period of the breeding season are discussed later in relation to the timing of the breeding season.

b) Main breeding season

Observations of the effect of weather on colony attendance in auks during the breeding season suggest that wind speed and associated sea surface conditions are probably the most important factors. Myrberget (1959) and Plumb (1965) found that numbers of Puffins and Razorbills respectively were highest when conditions were calm, and that many birds left the colony in rough weather. Guillemot attendance at colonies on Skomer during the breeding seasons of both 1973 and 1974 decreased as wind speed increased. This was the only one of several weather factors examined which was significantly correlated with attendance (Birkhead 1976). In similar studies of Puffin attendance at a sample of Irish colonies later in the breeding season, different patterns were recorded at different colonies on the same island. This was thought to be due to the direction in which each colony faced. Those in more sheltered positions, below which the sea was calm, had relatively few birds sitting on land and many in rafts in the sea (P G H Evans - pers.comm.).

The weather factors measured in the present study appeared to have

little effect on attendance in 1972 during the main part of the breeding season. Before laying in 1972 the numbers showed a seasonal increase but were also significantly decreased by strong winds, so that the highest counts during this period were recorded on days when the wind was light. Other observations suggested that strong winds, resulting in choppy sea below the colony, not only tended to break up the rafts on the sea but also tended to decrease the number of Razorbills on land.

The variation in the counts of breeding birds during the incubation and nestling periods was due mainly to the presence or absence of the mates of the incubating brooding birds. In the incubation period of 1973 few mates remained on the cliffs on days with high winds; this may have been associated with conditions on the ledges at the nest sites or with feeding conditions at sea or with the increased amount of time required to fly between the colony and the feeding grounds in such weather.

Although the numbers of non-breeders were also reduced by high wind speeds during the incubation period, their attendance otherwise appeared to follow the steady seasonal increase in numbers. Non-breeder attendance was negatively correlated with the amount of cloud cover although this factor had no significant effect on attendance in any of the other groups examined. Further evidence for the importance of cloud cover - and hence presumably the amount of sun and rain - to the non-breeding birds in the 1972 incubation period was given by the comparison of attendance at this time for these birds with the daily rainfall. A significant decrease in numbers was recorded on rainy days (Mann-Whitney U test $p < 0.05$); rainfall had no significant effect on any of the other counts at other times.

In the nestling period attendance appeared to be mainly determined by the seasonal decrease in numbers of breeding birds and increase in "non-breeders" (the reasons for this are discussed above:ib). Attendance

of breeding birds during this period in 1973 decreased in conditions of high wind speed; counts of non-breeders in 1972 were similarly reduced when the sea was rough. Sea conditions may have affected the non-breeders in 1973 but unfortunately no records were kept.

Although the main pattern of attendance at the colony was the result of a direct effect of date on numbers, it appears that weather factors, especially wind (speed and possibly direction), also influenced numbers.

The way in which these factors actually affect the birds remains speculative but it seems probable that, in conditions of high wind speed and rough sea, feeding conditions deteriorate, at least for surface feeding species (Howard 1968, Salt and Willard 1971, Dunn 1973). There is some evidence that in such weather conditions shoals of fish tend to move further below the surface of the sea and are thus more difficult to locate or possibly to catch. This may mean that the birds need more time to feed and can thus spend less time in the breeding colonies.

If finding suitable feeding areas, or the actual method of fishing in the Razorbill, depended to any extent on maintaining visual contact with the other individuals in a group, the breaking up of the sea surface by a heavy swell could be expected to have an adverse effect on fishing. In plunge diving species such as the terns (*Sterna* spp) however, weather conditions involving moderate winds and sea conditions have been shown to be advantageous to fishing (Dunn 1973). This may be because such conditions render the birds less conspicuous to their prey by the disturbance of the sea surface.

Chapter 4: BREEDING BIOLOGY

A. PRE-LAYING PERIOD

i. Spring raft formation

Razorbills spent as much time in rafts on the sea below the colonies during the pre-laying period as they did on land during the breeding season itself. Preliminary observations suggested that pair formation was an important component of rafting and this behaviour was examined in greater detail.

Paludan (1947) thought that the lengthy pre-laying period in the Razorbill enabled the birds to become accustomed to life inshore after their pelagic winter existence. In the Puffin this pre-breeding attendance has been interpreted as allowing the birds to form pairs on the water so reducing the amount of time spent ashore before breeding and the chance of attack by predators (Corkhill 1970). However, few adult birds are taken by predators and there is no evidence to suggest that attacks are rarer on the sea than on land, so it seems unlikely that this is the main function of spring rafts. According to Lockley (1953), the rafts are necessary for the stimulation of courtship and mating in the Puffin.

The numbers of birds in each raft varied in the present study, but the largest rafts gathered under the largest breeding colonies. As few, if any, immature Razorbills were present at this time of year (see Chap.3i), the number of birds below each colony was approximately the same as the number that later bred in the colony.

Observations of colour ringed adult birds suggested that the same individuals were present in the rafts each day. The rafts attract birds returning to the colony and presumably facilitated the pairing or re-pairing of birds preparing to breed. As the season progressed,

the number of paired birds in the flocks increased; so far as I could tell individual birds were consistent in their pairing.

Early in the season there was much aggression between individuals and there appeared to be a critical individual distance (Conder 1949). Lockley (1953) observed comparatively high levels of aggression in Puffins early in the pre-laying period. Possibly this is a reaction to the crowded conditions in the rafts compared to the pelagic conditions the birds experience during winter.

Some of the courtship activities observed on the water early in the season were the same as those described for birds on land (Perry 1940) but the behaviour of birds in the rafts on the sea during the pre-laying period has received little attention in the literature. The main features of this behaviour are as follows:

a. Line abreast formation (Conder 1950).

This was observed most often early in the pre-laying period. Groups of Razorbills and Guillemots would form a long line, with all the birds facing the same way and floating or swimming in the same direction. The line was usually maintained for several minutes before the birds joined together again into a tight-packed raft of milling birds ('swimming together' Conder 1950). This behaviour was first recorded by Paludan (1947), described by Conder (1950) and later also referred to by Cordon (1951).

b. Wing flapping.

A single bird would raise itself from the water, exposing its breast and belly, and flap its wings vigorously. This often occurred after displays of aggression or preceding billing with another bird.

c. Preening.

The birds spent long periods of time preening; this behaviour appeared to stimulate similar activity in other birds. Razorbills rarely rolled

over on their sides in the water as Guillemots did when preening.

d. Head shaking.

This occurred frequently in flocking birds and consisted of a brisk side to side shake of the head. The bill was sometimes 'clattered' (rapidly opened and closed) as in similar courtship displays on land. Head shaking was often observed in connection with billing and aggressive displays. Both tail and head shaking were performed in the closely grouped part of the swimming together behaviour (described in a. above) and the birds spun round in small circles. Turning away, resulting in the hiding of the prominent white neck markings, was often observed and this spinning movement may have been important in appeasement behaviour.

e. Yawning and sleeping were also recorded quite frequently in individuals in the flocks. Unlike Puffins, few Razorbills slept in rafts (with heads tucked under the wings) although periods of inactivity did occur when the birds bobbed about with head and neck sunk into the body.

f. Movements in relation to the mate.

Displays in the rafts included energetic swimming away from the bird assumed to be a mate. This sometimes led to a chase, both birds splashing over the water using both wings and feet for propulsion. More frequently this sort of activity consisted of one bird swimming forward with a sudden turn of speed or paddling with its wings for some distance, then turning and swimming hastily back to the mate in a characteristic flattened posture - the tail low and neck and head outstretched.

g. Billing.

During billing two birds would touch their bills together for periods of a few seconds to one minute or more. Billing apparently only involved paired birds, and often began almost aggressively, the first bird lunging at the other with its bill. It was also observed when the birds reunited after aggressive or swimming forwards displays. Wing flapping

preening and billing was observed in groups of birds throughout the breeding season, and these activities also took place on land.

h. Head-up display.

This behaviour has not previously been described although it may have been referred to by Paludan (1947) who noted that in mixed Guillemot-Razorbill flocks at long distance, the Razorbills could be distinguished as "they appeared to float higher in the water, have shorter tails lifted higher from the surface and thicker bills". [I have however observed head-up displays in both Razorbills and Guillemots.]

The posture involves the bird holding its neck vertical and the head pointing forwards; the white of the breast is thus clearly displayed and the black inverted V at the throat made particularly conspicuous. The tail was drawn up showing the white under-tail coverts and giving an impression of an overall shortening of the body. In the more exaggerated form of this display the wings were sometimes slightly opened and trailed below the tail thereby displaying the white stripe on the secondaries. Every feature of the posture appeared to show off the black and white plumage to its best advantage.

The head-up display was frequently seen in the larger, more dense rafts and may play some part in the selection of attraction of a new mate. The display was also recorded in paired birds but during several minutes of observation on single pairs, only one bird of the pair was ever seen to adopt it. Unfortunately because the sexes are not distinguishable in the field (Chap.2iiid), it was not possible to establish whether birds of both sexes behaved in this way.

j. Aggressive displays.

These either took the form of low intensity threat, by gaping, or slightly greater intensity threat shown by swimming towards the intruder and gaping. Gaping was accentuated by the yellow inside to the mouth. Such displays occasionally developed into a chase or attack.

During the spring of 1972, quantitative data were collected on these raft activities in order to estimate the frequency with which each piece of behaviour occurred and attempt to evaluate its importance. Small flocks of Razorbills were observed for periods of 2-15 minutes (average 7.0 mins) and the occurrence of six of the activities were recorded (Table 4.1). Thus, for example, the number of times that wing flapping occurred in any member of the flock under observation was counted and an index of the frequency obtained as follows:

$$\frac{X \times 100}{N \times T}$$

where X is the number of times wing flapping was recorded, N the number of Razorbills in the flock and T the number of minutes the flock was observed. This expression takes no account of how long each activity took to complete.

Billing was recorded very frequently, on average once every five minutes, though it reached frequencies of two per bird per minute. Wing flapping and preening were observed about half as frequently and the other activities even less than these.

The mean number of activities recorded per bird per minute was greater for large groups (ten or more birds) than for small ones but the difference was not significant ($t = 0.55$, $n = 39$, $P > 0.05$). In the absence of other species in the flock, the frequency of behavioural interactions in Razorbills was significantly greater than in the presence of the other two species ($t = 2.59$, $n = 39$, $P = 0.02$). The amount of activity in rafts from the different parts of the island was not significantly different nor did the level of activity scored change during the eleven days' observation at the start of May. Observations in late May and early June, at the onset of the laying period, showed that the frequencies of all activities were low except for preening and wing flapping.

Table 4.1 Quantitative observations on the spring raft activities; for explanation - see text.

Activity	Total number of observations	Average frequency per bird per 100 minutes of observation
Wing flapping	359	10.8
Preening	165	5.4
Flying/swimming forwards	94	3.0
Swimming towards mate	56	3.3
Billing	766	21.4
Aggression	113	3.9
Other activities, including "head-up" display	37	0.6

Note: Observations were made on the mornings of 11 days (May 9-21 1972) involving 70-536 bird-minutes of observations (average 336) per day. Group sizes were between 5 and 25 individuals (average 13) and the number and species of other birds present were also recorded.

Billing involved two birds yet only scored once each time it was started, hence true frequency is 42.8/bird/100 minutes.

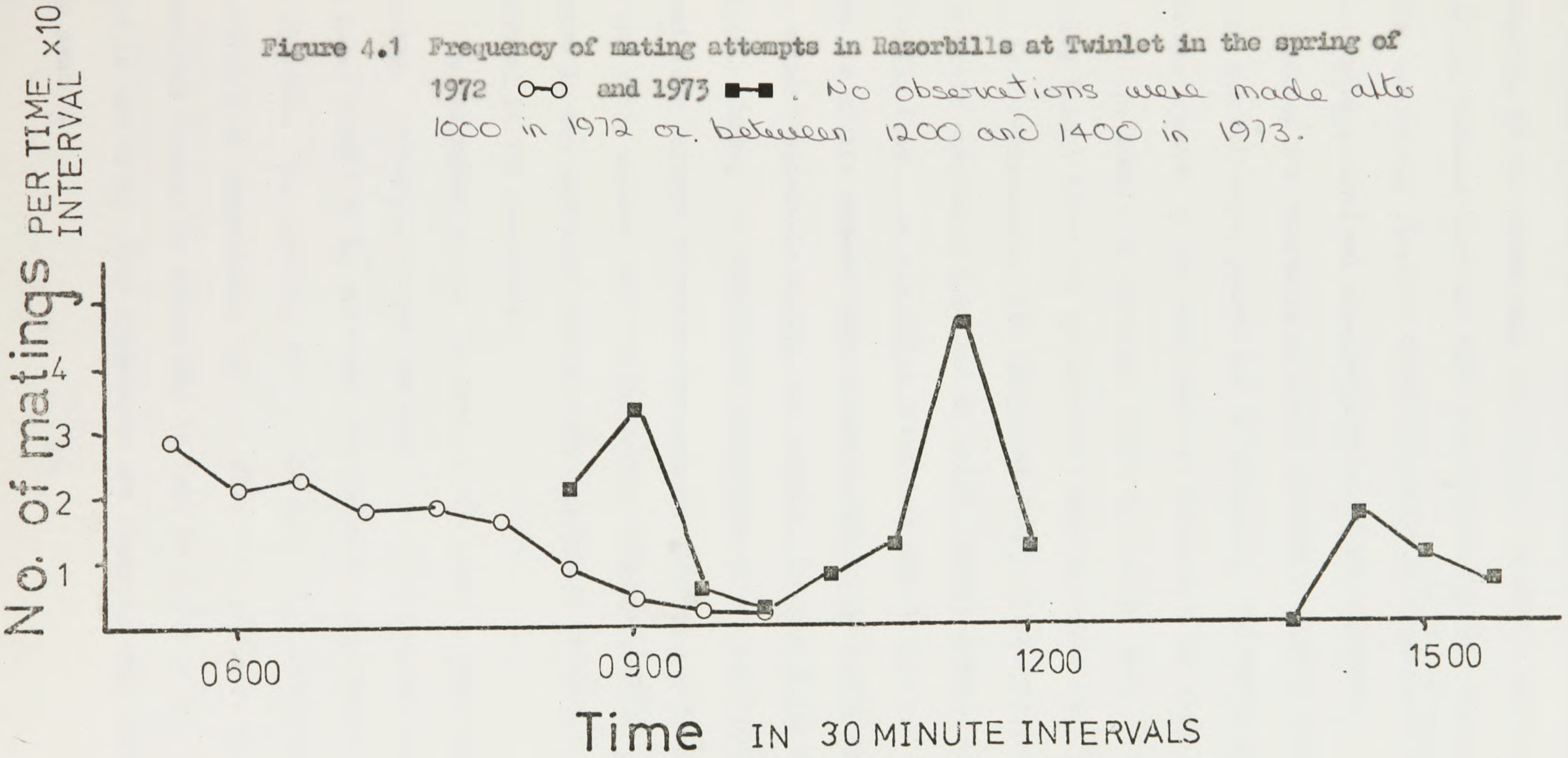
ii. Courtship and mating

From the time of their arrival at the breeding colonies in March, the Razorbills occasionally came to land. At first their visits were brief, irregular and often confined to the first hours after dawn. As the season progressed, the number of birds and the duration of their stay on land increased. Early in the season when the weather was calm birds often sat and even mated on weed-covered rocks exposed at low tide or on the less sloping rock faces. Later the birds collected in the loafing areas of the breeding colony itself. At first they were very nervous, leaving the cliffs when disturbed by a gull or a human. As a result, observations of birds ashore could not be made until most of the pairing and site selection had already taken place.

Mating usually took place in the communal areas of the colony or, most frequently, in the nest sites themselves; it rarely occurred on the sea. The frequency of mating attempts was measured from observations on a group of 24 pairs of Razorbills in Twinlet Bay nesting in open ledge sites (Figure 4.1). These observations were made, mostly before noon, on 5 days in 1972 and 3 days in 1973. Morning watches were kept between dawn (0530 - 0600) and 1230 in both years and further observations were made between 1430 and 1600 in 1973; watches lasted from 1 to 3½ hours (average 2½ hours) each.

In 1972 observations were made immediately before and during the start of laying (3 days before and 4 days after the first egg was laid) whereas those in 1973 were made well before laying began (4 to 9 days before the first egg appeared in the colony). This difference in timing of the observations may account for the apparent difference in diurnal pattern of mating during the two years. In 1972, the number of matings observed when the birds returned to the cliffs after dawn was relatively high but this decreased as the day progressed; mating was infrequent

Figure 4.1 Frequency of mating attempts in Razorbills at Twinlet in the spring of 1972 o–o and 1973 ■–■. No observations were made after 1000 in 1972 or between 1200 and 1400 in 1973.



after 0830. In 1973, however, the number of matings recorded between 0830 and 0930 was higher than at any time of day in 1972. After 0930 the frequency of mating dropped to a low level but increased again to a peak between 1130 and 1200. Although mating still occurred in the afternoon, it was relatively infrequent. Paludan (1947) recorded a peak in mating between 0800 and 1000 and another between 1600 and 1800. Mating was rarely observed after the start of incubation in the present study and then it almost always involved non-breeders or failed breeders.

Much of the courtship observed resembled Perry's (1940) description, though the following points are of interest. The birds spent most time with their mates in the nest site but also left the site to fly around the cliffs, singly or together, or to sit on the sea. The "butterfly" display flight described by Conder (1950) was often used in these flights. This is a conspicuous, slow-wing beat flight which has been observed in most other species of auks and in gulls, terns, pigeons and waders. Butterfly flight in Razorbills often occurred during the downward flight from the cliffs and was also observed briefly in birds taking off from the water (especially during the swimming forward display described above). During the pre-laying occupation of the nest sites, the birds spent long periods billing, preening, or sitting inactive, often asleep in the site, either alone or in pairs. Courtship presentation of fish occurs in the Guillemot at this time (Birkhead 1976) but was never observed in the Razorbill.

On alighting beside its mate at the nest, a bird would usually start billing. Occasionally the resident bird attacked the newcomer, although it later proved to be its mate, and drove it away before billing could be started. The incoming bird of the pair (apparently having no difficulty in recognising the nest site with its mate in situ) would sometimes persist in attempting to land in spite of the aggression of the bird in the site. Such aggression was observed most frequently early in the season.

Chapter 4

B. BREEDING SEASON

i a. Fidelity of birds to their natal colony

Razorbills have been ringed as pulli and retrapped breeding on Skokholm since 1933. In recent years the colony in which the birds were caught was also recorded and these data enabled the amount of interchange between colonies on the island to be assessed. Out of 132 birds ringed as pulli on Skokholm since 1960 and retrapped breeding on the island, 61 (46%) bred in the natal colony, 86 (65%) in the natal colony or one close by.

Although the nest sites from which these birds came were not recorded, most of the colonies on Skokholm were broadly homogeneous in the type of nest site available (either ledge or boulder). Thus an estimated two thirds of the chicks which survived returned to breed in the type of nest site in which they spent their nestling period.

In their pre-breeding years individually identified birds were seen mostly at their natal colony, although they occasionally visited other colonies, nearby. In all areas on Skokholm, apparently suitable nest sites were available throughout the season so all birds had the chance to breed in their natal colony. There were no records of pairs where both birds had been reared in another colony, so movement away from a natal colony probably only occurred when birds from different colonies paired.

b. Fidelity to breeding colony

Breeding birds very rarely changed colony; of 245 birds ringed as breeding adults since 1969, 232 (95%) were retrapped breeding in the colony where they were ringed and only 5% had moved. Some of the latter records actually may have been due to the mis-naming of colonies

in ringing records.

c. Fidelity to nest site

Razorbills exhibit a high degree of site fidelity; 129 sites in the study colonies were used by colour-ringed birds in two or more successive years. Eleven birds (8.5%) moved from the site in which they were first caught but none changed colony. In each case a change of mate was either definitely established or suspected (see iie). Eight of the 11 birds that moved site were sexed; seven were females and only one known to be a male, suggesting that the male may select the site and the female go where she can, even if when she is widowed it means changing site. (There was no reason to suppose that females were more easily identified than males.) The single male was a member of a colour-ringed pair which, having failed to hatch an egg in two consecutive years, moved to a new site.

d. Fidelity to mate

The mates of most of the colour-ringed adults were identified during the years of the study by their rings or other peculiarities. Of 58 colour-ringed birds whose mates were identified in two or more years, 18 pairs remained intact for at least three years and a further 22 birds had the same mate in two successive years. The rest changed mates once (11) or twice (7) in the three seasons. Only two pairs broke up when both birds were still alive and all together 72% of the birds retained the same mate between seasons. As only about 10% of the breeding adults die each year (see Chap.5), few birds are actually available to form new pairs.

ii. Laying and incubation periods

a. Laying

1. Population laying date

The laying dates for all birds in the study colonies between 1971 and 1973 are shown in Figure 4.2. Laying in each year was divided into three 'Laying Periods' so that the middle period covered the time during which about half of all the eggs were laid, and the first and third periods each covered about 25% of all layings. The whole laying season was also divided into five 'Laying Intervals' (Table 4.2) for further analysis.

The mean laying dates for each season were May 17 1971, May 29 1972 and May 20 1973 and differed significantly (Figure 4.2).

2. Effect of colony size on laying date

In 1971, the mean laying date in the main study colonies was inversely correlated with colony size (number of breeding pairs), birds in larger colonies laying earlier than those in small colonies (Figure 4.3). The spread of laying (measured by the coefficient of variation of the mean laying date) was not, however, related to colony size ($r = -0.41$, $P > 0.05$, $n = 8$). Laying date in the other years of the study was independent of colony size. The effect of colony size on laying date is discussed further below.

3. Laying date of individual birds

Comparison of individual birds' laying dates in successive years showed that 1972 was an exceptionally late season. There was on average a difference of only about three days in these birds' laying dates in 1971 and 1973 but they laid on average 13 days later in 1972 than in 1971 (Table 4.3).

In both 1972 and 1973, laying in the earliest birds compared to

Table 4.2 Divisions of laying; numbers of eggs laid in sites in the study colonies during each are given in parentheses.

		1971	1972	1973
LAYING PERIOD	Early	Up to May 11 (42)	Up to May 26 (46)	Up to May 15 (43)
	Middle	May 12-18 (110)	May 27-31 (85)	May 16-21 (102)
	Late	After May 18 (58)	After May 31 (51)	After May 22 (65)
LAYING INTERVAL	I	Up to May 10 (26)	Up to May 25 (25)	Up to May 15 (43)
	II	May 11-15 (75)	May 26-30 (103)	May 16-20 (92)
	III	May 16-20 (65)	May 31-June5 (41)	May 21-25 (46)
	IV	May 21-25 (27)	After June 5 (13)	After May 25 (29)
	V	After May 25 (17)		
Total number of eggs		210	182	210

Table 4.3 Difference in the laying date of the same individuals in successive years.

	1971-72	1971-73
Mean difference (days)	12.9	2.7
Standard deviation	5.9	5.0
n	85	75
	$t = 11.83$, $P < 0.001$	

Note. In both 1972 and 1973 laying occurred on average later than in 1971.

Figure 4.2 Frequency distribution of laying dates 1971-73. Dotted lines mark the middle laying period (see Table 4.2) and arrows mark mean laying dates ± 1 standard error; all differences between means are significant ($P \leq 0.05$).

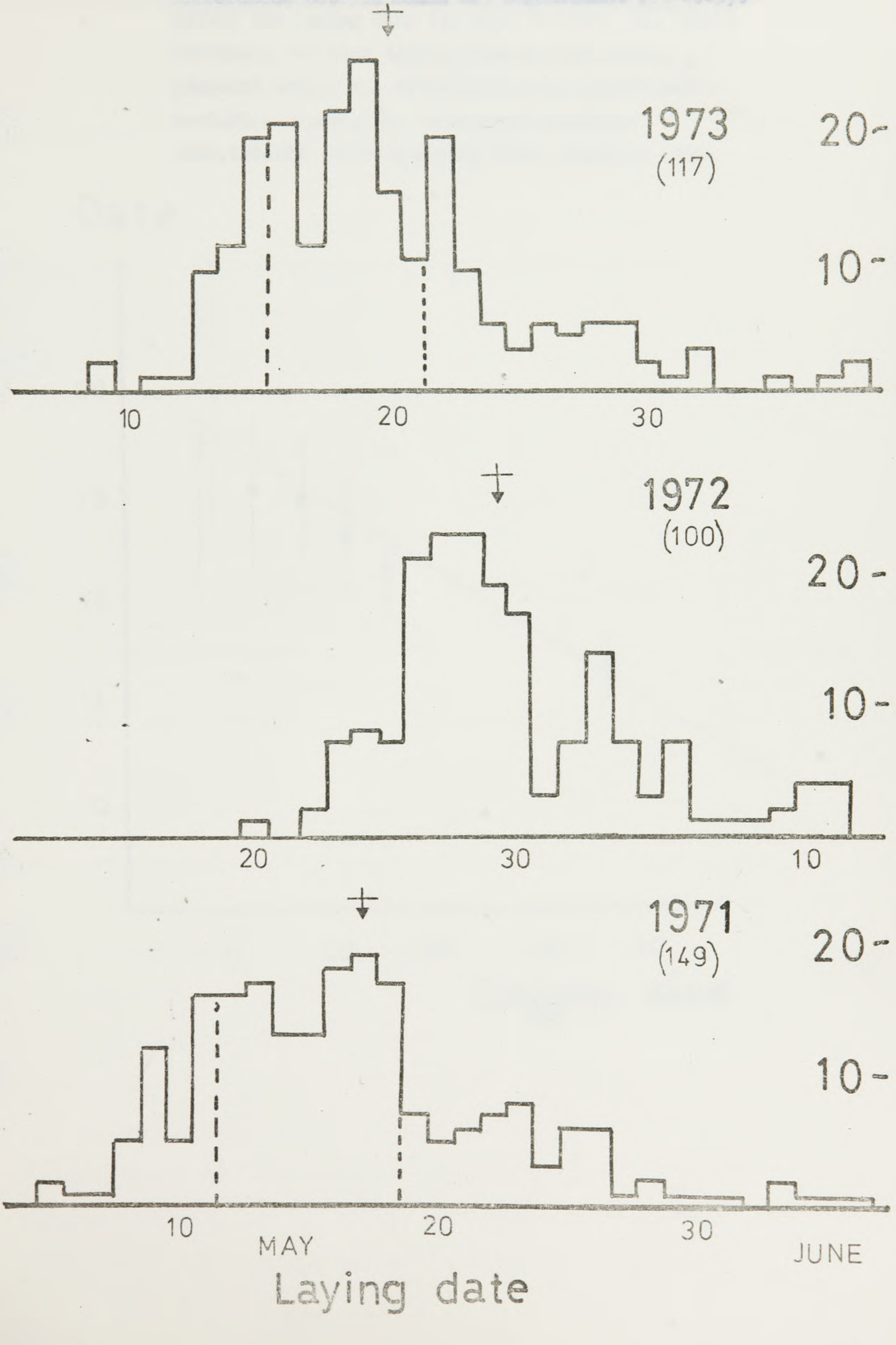
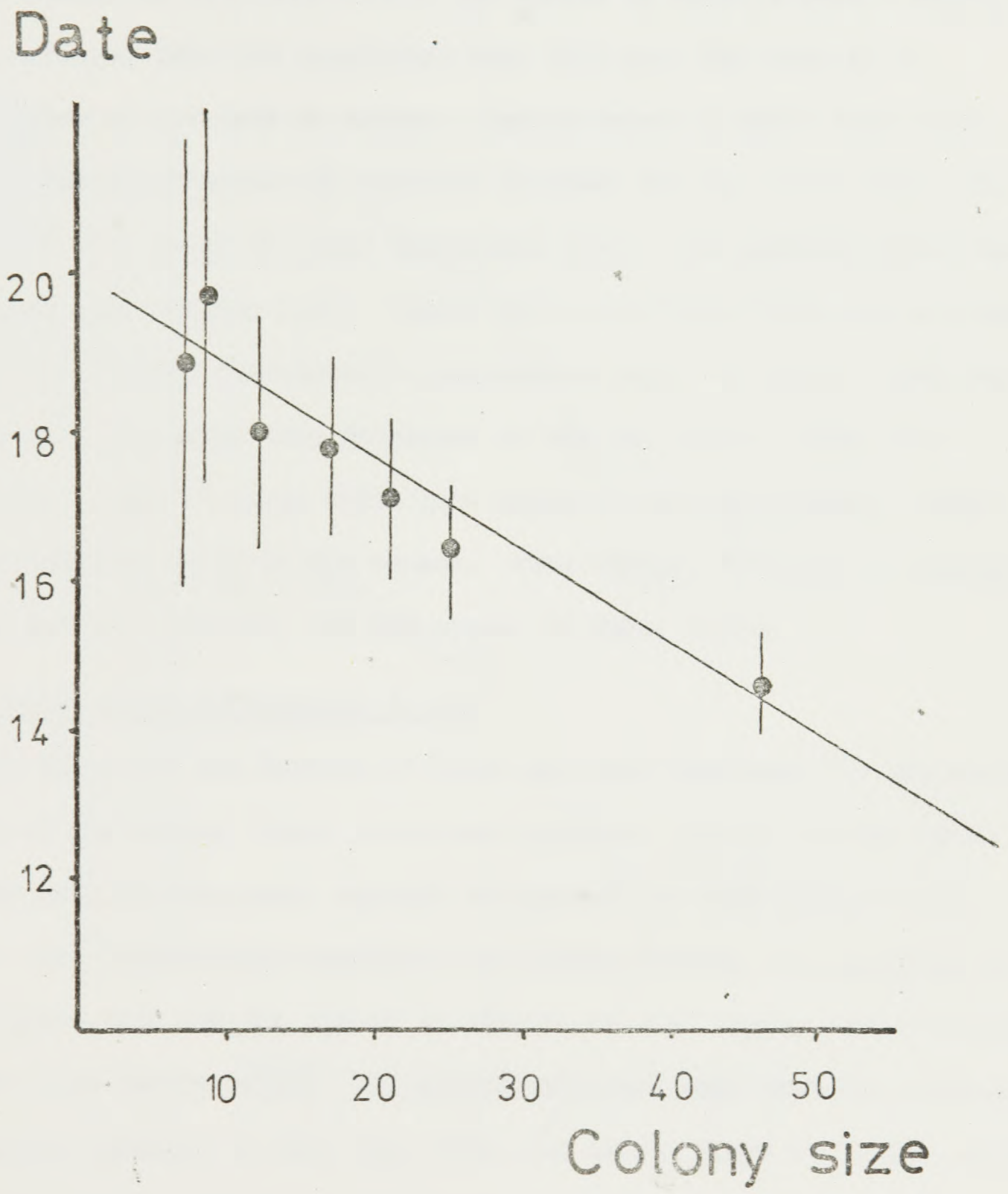


Figure 4.3 Relationship between colony size (number of breeding pairs) and laying date (in May) in 1971. The points represent the mean laying date in each colony ± 1 standard error. The correlation was significant - $r=-0.93, P < 0.001, n=7$, regression equation: $Y=20.1-0.12X$ where x=laying date, Y=colony size.



1971 was retarded by significantly more time than laying in the later birds (Figure 4.4). This suggests some intrinsic differences between the birds laying at the beginning and end of the season (see below).

The effect of previous breeding experience on laying date was also examined. In order to compare laying seasons which differed in their timing in different years, the amount by which a bird's laying date differed from the population mean that year was used as an indication of its date of laying. Laying dates in pairs where both birds were experienced but breeding together for the first time were compared with those in pairs where both birds were unchanged from the previous year (Figure 4.5). Laying dates for birds which had not changed mate were closely correlated in successive years but laying dates for birds with new mates were unrelated in the two years. Thus, for example, a pair of birds which laid early in one year alsways tended to lay relatively early in the season. Mate change, although it clearly disrupted this pattern, did not appear to delay laying.

4. Laying dates in relation to age

Laying dates for ten females of known age were available for one or more years of the study. These dates were plotted, relative to the mean laying date in each year, against the age of the bird (Figure 4.6). There was a significant negative correlation between the logarithm of the laying date and the age of the female so that laying became earlier as the bird became older. The relationship was such that the advancement of laying appeared to slow down after the birds' third or fourth breeding attempt. Hence, the birds laying late in the season consist mainly of young birds.

In order to examine the effect of 'old age' more closely, the laying dates of 16 females, ringed (1959-1971) as breeding adults therefore at least five years old, were compared with the annual mean laying date. There was no significant correlation between laying date and

Figure 4.4 Change in laying date (days) in 1972 and 1973 for birds which bred in the early (E), middle (M) and late (L) laying periods of 1971. Points represent mean laying dates ± 1 standard error.

Analysis of variance

	1971-1972	1971-1973
F	23.88	26.26
P	0.01	0.01
n	85	75
V_1, V_2	2,82	2,72

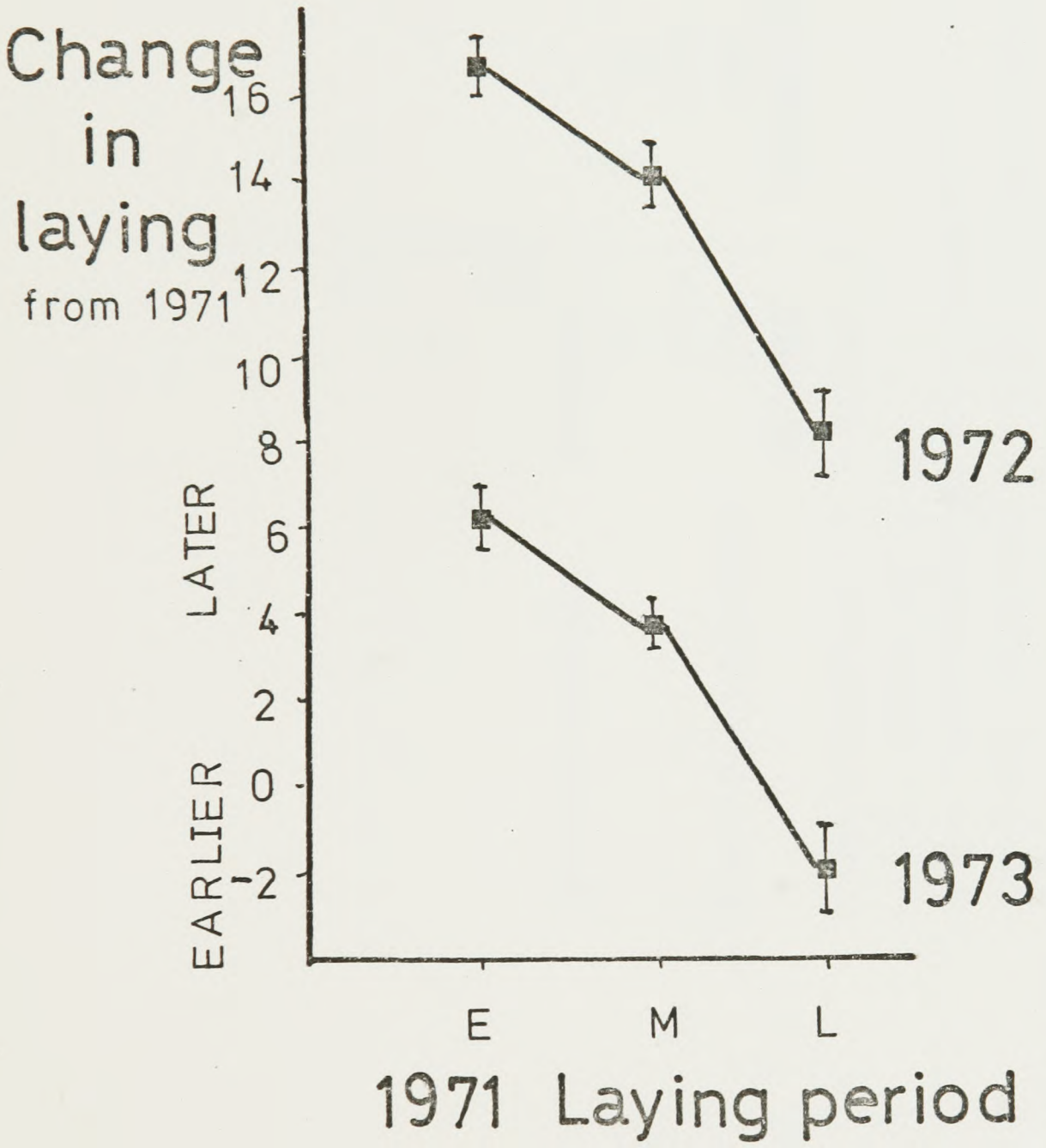
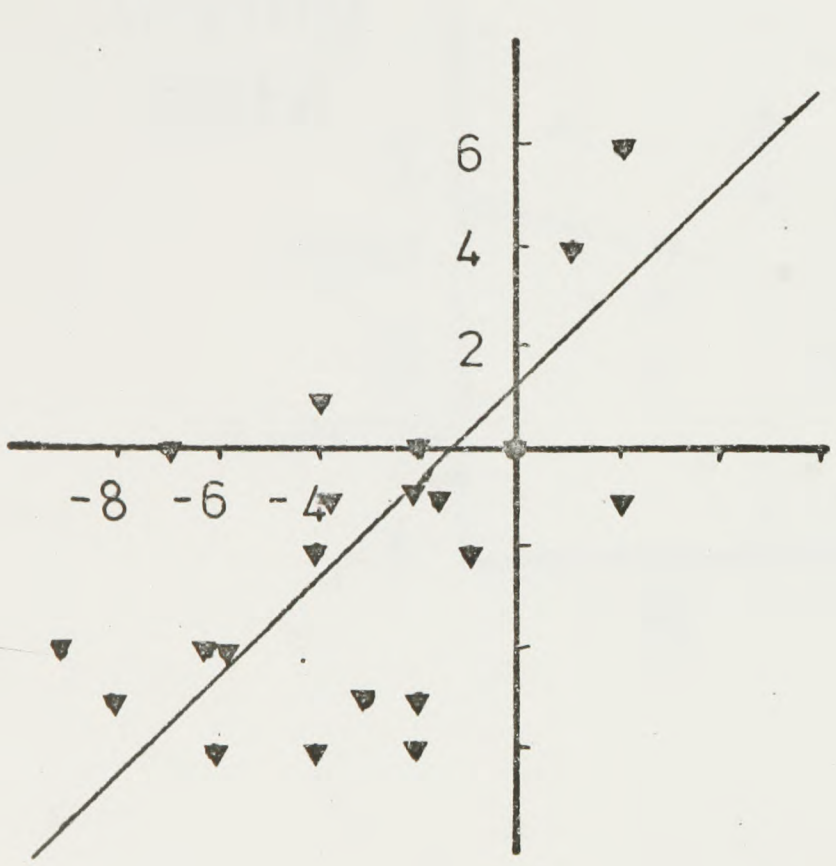
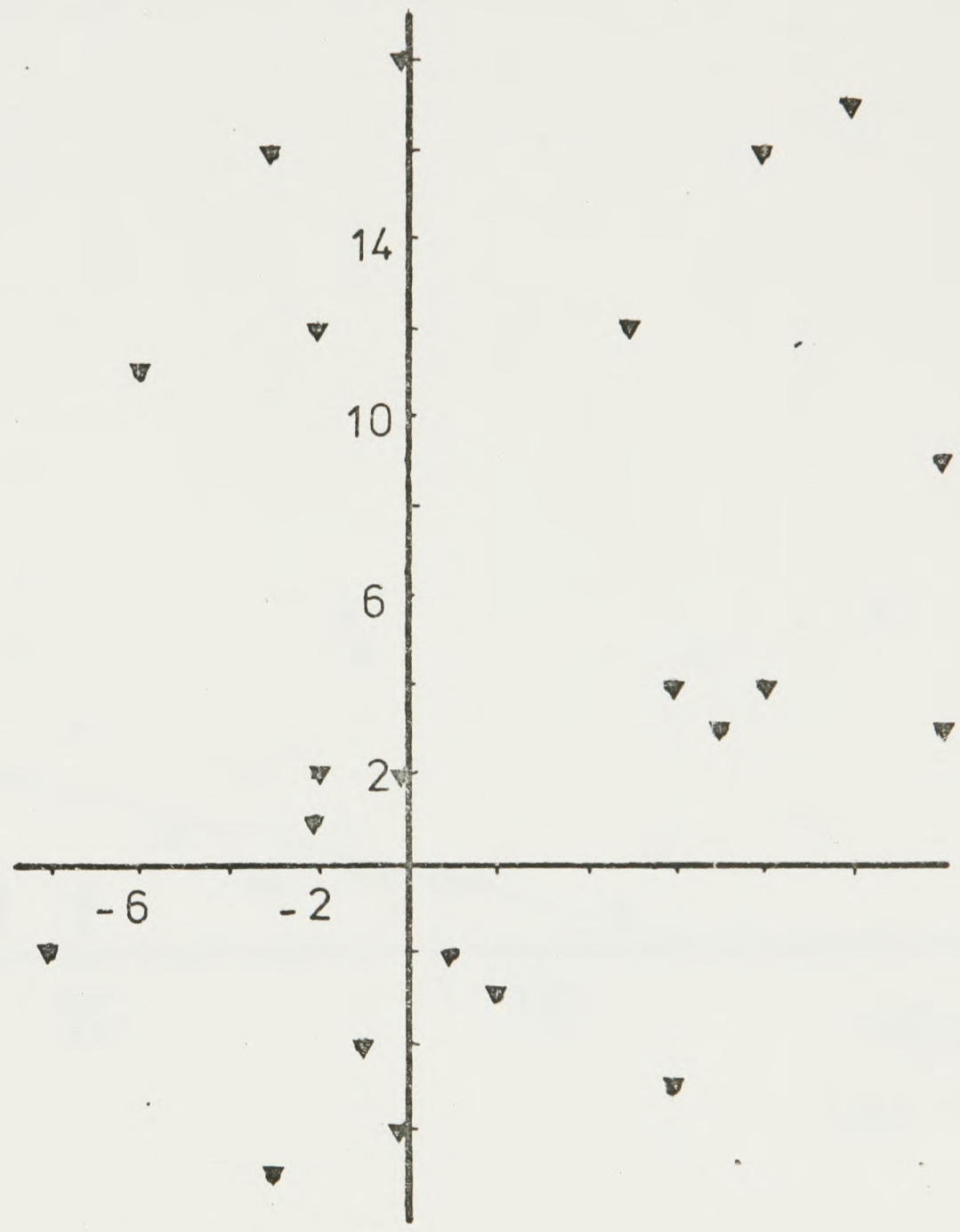


Figure 4.5 Laying dates in successive years (shown as the deviation from the annual mean laying date, in days) of birds a.with the same mate as the previous year, and b.with a new mate.
X axis = laying date in year n
Y axis = laying date in year (n+1)

	Same mate	Different mate
Correlation coefficient	0.46	0.23
P	0.02	>0.05
n	21	22
Regression equation	X=0.5Y-2.3	-

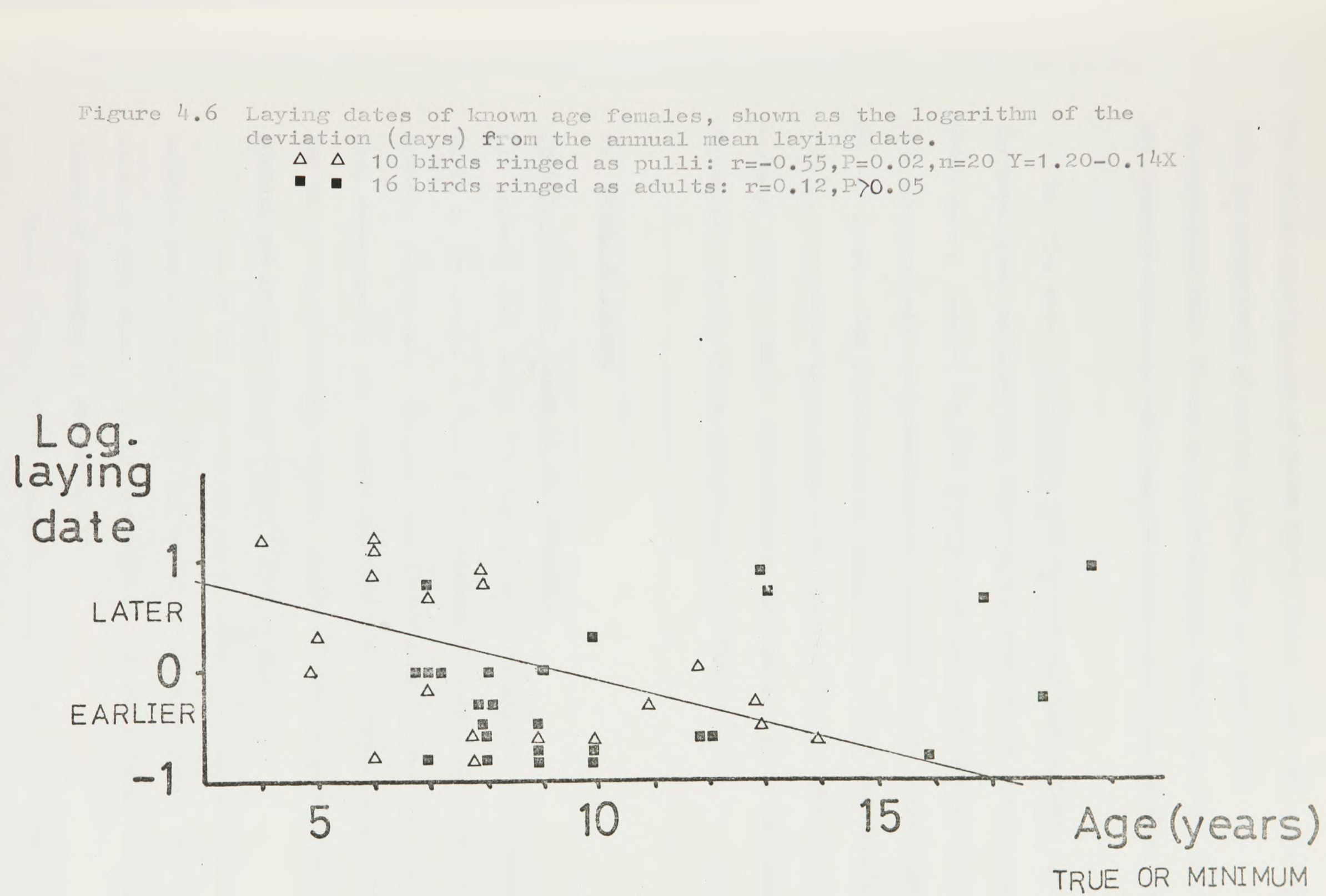


Same mate



Different mate

Figure 4.6 Laying dates of known age females, shown as the logarithm of the deviation (days) from the annual mean laying date.
△ △ 10 birds ringed as pulli: r=-0.55,P=0.02,n=20 Y=1.20-0.14X
■ ■ 16 birds ringed as adults: r=0.12,P>0.05



the minimum possible age of these birds, though there was no indication that the advancement of laying slowed down in older birds. ~~of regression lines fitted to points for both known age birds (above) and presumed known age birds did not differ significantly (d = 1.803,~~

In 1972, when exceptionally bad weather may have delayed laying, the birds least affected were those laying late in the season, mainly young birds. Some of the late breeders actually advanced their laying date (compared with the previous year) in spite of the overall lateness of the season. The advancement of laying with age was also evident in 1973 when the birds laying late in the season produced eggs on average two days earlier than in 1971 although the laying date of the whole population was on average three days later than in 1971.

b. Timing of laying

Factors affecting laying in the Razorbill

The present study showed that laying can be determined by conditions early in the season so that if the weather is unsettled, the start of breeding is delayed. This was also observed on a wider scale in 1975 when exceptionally cold weather may have been at least partly responsible for the delay in breeding and low success at certain seabird colonies in Britain and Ireland and in Norway (Lloyd in press b).

In one of the years of the present study, the mean laying dates in eight of the colonies were correlated with the number of breeding pairs, but it seems unlikely that colony size is generally an important factor determining timing of breeding in the Razorbill.

Fraser Darling (1938) suggested that, in colonial species, displays by neighbouring birds at the start of the breeding season accelerated individuals' reproductive cycles and brought about the synchronised

breeding of a majority of the birds in the colony. Later this hypothesis was extended to territorial species (Darling 1952). An implication of this idea is that in larger colonies, which by virtue of their numbers receive greater 'social stimulation', breeding occurs earlier and is more synchronised than in small colonies. Although the theory has been applied to several species including seabirds (Lockley 1942; Coulson and White 1960; Nelson 1966) and also suspected to act inter-specifically (Fisher and Lockley 1954), little proof has been found for the existence of the 'Darling effect' (Mackoberts & Mackoberts 1972). Failure to take into account the effect of age on the timing of breeding has also received criticism (Lack 1943; Armstrong 1947) and Orians (1961) suggested that, if such an effect were real, it would be most likely to occur in a nomadic colonial species where individuals in breeding condition might be attracted to areas of the colony where other birds were already on territory.

The present study also showed that a Razorbill's laying date is related to its age and that birds bred progressively earlier as they became older. Coulson and White (1960) found that there was little advancement of laying date in the Kittiwake after the fourth year of breeding. Red-billed Gulls Larus novaehollandiae actually mature earlier each year as they become older (Mills 1973), and hence are able to advance their laying date.

Factors affecting the timing of the breeding season

Razorbills, like most other seabirds, breed in one restricted season of the year. The timing of the breeding season can vary from one year to the next and certain factors are associated with its timing each year. As with other species, these are broadly separable into proximate and ultimate factors (Baker 1938). Proximate factors determine actually when a bird can start to breed, for example those governing the physiological

changes, such as development of the gonads, necessary for breeding to occur. Increasing daylength is a proximate factor which stimulates these changes in a number of species (Lofts and Murton 1968). Temperature - probably sea temperature in a species such as the Razorbill - may also be a contributing factor. On Skokholm the sea temperature rose steadily for at least one month preceding the Razorbills' laying period (pers.obs) although it seems likely that this affected the birds' breeding through their food supplies, rather than in a directly proximate manner.

Ultimate factors are those directly responsible for timing the breeding season so that the greatest production of young can be achieved. Breeding, in almost all species examined, occurs so as to coincide with the time of year when most food is available for the young; many examples of this are given by Lack (1954). Laying date in many birds may also be related to the time it takes the female to find enough food to form an egg (Perrins 1970). Generally most young are produced by birds breeding early in the season but, due to apparent individual differences in age and egg forming capacity ('fitness'), not all birds in a population breed at the optimum time. Although food availability early in the season appears to be an important factor timing breeding in many species, other factors, such as predation pressure or climatic effects on the breeding terrain, have also been shown to be important. In parts of Greenland for example, both Eider Ducks (Somateria mollissima) and Arctic Terns (Sterna paradisaea) nest on islands which are accessible to predatory Arctic Foxes (Alopex lagopus) whilst the sea is frozen. The birds do not start to lay until the sea thaws in spring, making the breeding grounds inaccessible to predators (Braestrop 1941) or until the ground dries out (Lack 1933). Similarly, waders returning to their breeding grounds in the arctic must await the spring thaw before they can take up territories and breed (Holmes 1966, Green and Lloyd - in prep.). Brunnich's Guillemots at colonies in northern Russia cannot breed until

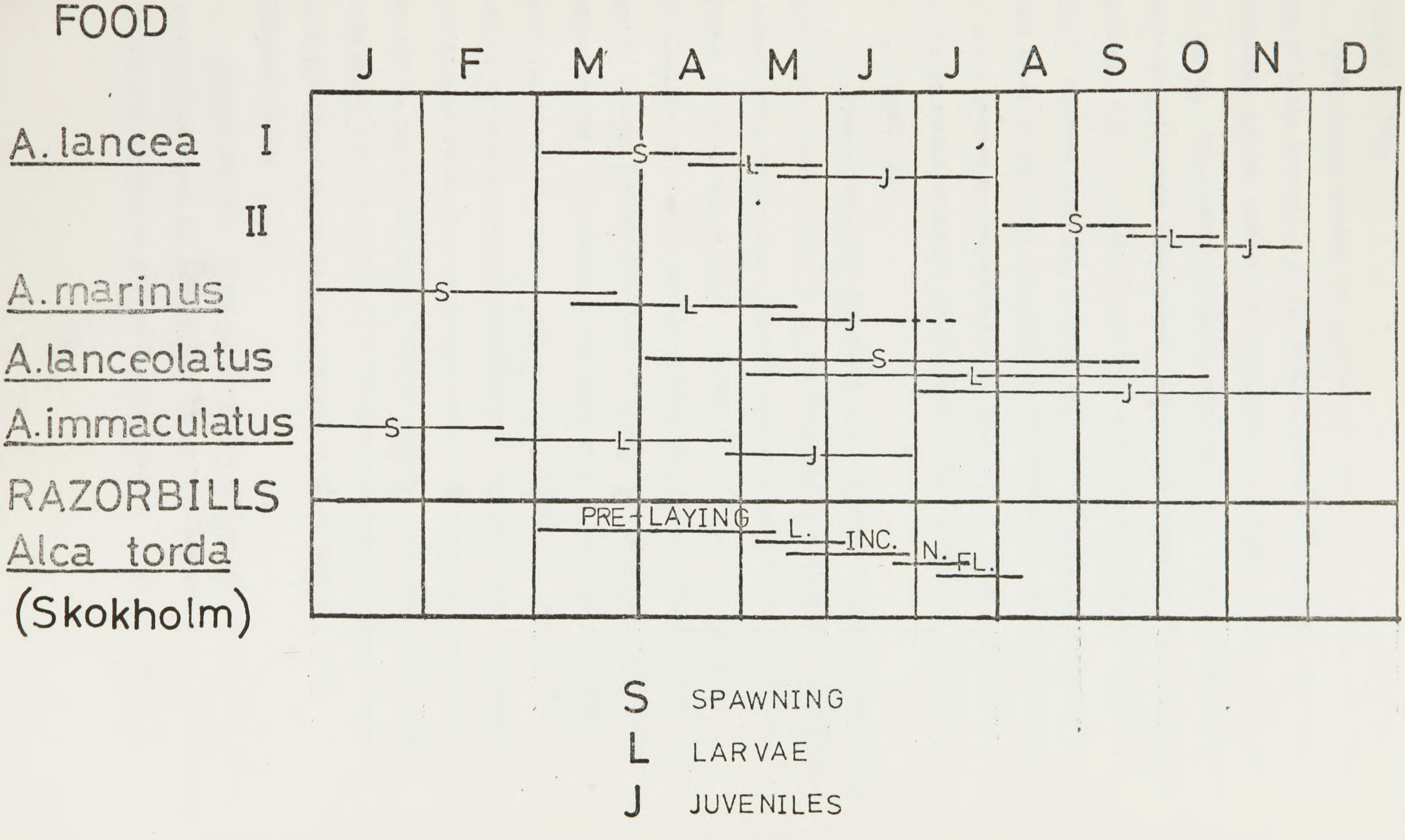
at least some of the ice has melted off their breeding ledges (Belopol'skii 1957). In Britain Great Crested Grebes Podiceps cristatus are said to await the growth of sufficient vegetation on which to support their floating nest before laying (Harrison & Hollom 1932).

Seasonal changes in the proximate factors most likely to affect Razorbills (daylength, sea temperature) follow relatively constant patterns each year although the timing of breeding varies. Thus other more variable factors must also affect the timing of breeding and the most important of these is usually food availability.

The main food species upon which Razorbills in the Irish Sea depend during the breeding season are the small sandeels and their larvae belonging to the family Ammodytidae. Sprats (Clupea spp.) and Whitebait (Gadus spp.) are taken in smaller numbers and elsewhere other fish species and even invertebrates form an important part of the diet (Belopol'skii 1957). A detailed study of Ammodytes in the Isle of Man area (Cameron 1959) has shown that this area, with the rest of the Irish Sea, is an important spawning ground. Samples taken throughout the year showed the timing of spawning and abundance of the different species; the results are summarised in Table 4.4. Similar, but less comprehensive, data are available for the English Channel and these show that spawning starts slightly earlier further south (Corbin & Vati 1949). Thus the timing of spawning in the south Irish Sea, off Pembrokeshire, probably occurs slightly earlier than that in the Isle of Man waters.

The Razorbills' laying period on Skokholm (mid May) coincides with increased availability of juvenile forms of the three main species of Ammodytes in the Irish Sea. The fish spawn mostly in the first two months of the year and many larvae and post-larval forms are present in the surface waters from March onwards; young sandeels are especially

Table 4.4 Summary of the abundance of Ammodytes spp. in Isle of Man waters (after Cameron 1959).



abundant in May.

Other marine species breeding in the Irish Sea which may form the food of adult Razorbills follow similar patterns of seasonal abundance. Planktonic species such as the large Chaetognath worms, breed mainly in the spring. These rely for their distribution on the prevailing currents (Kahn and Williamson 1970) caused by the differences in water temperature resulting from the influx of the warm Gulf stream in spring (Southward 1962). Mackerel (Scomber scombrus) and Pilchard (Sardina pichardus) also breed in the Irish Sea; early in the season the spawning grounds of these species are concentrated to the south of Ireland but they gradually spread eastwards to the south Irish Sea by April (Corbin 1947, Russell 1930).

It appears then, that the onset of laying in the Razorbill coincides with a considerable increase in the abundance of potential food species around Pembrokeshire which suggests that food availability early in the season is an important ultimate factor in the timing of breeding. Availability of food which is readily affected by climatic factors, may partly account for the variation in date of first laying, through its effect on the female. Weather to the south west of Britain, especially cold winter months or persistent westerly gales, have been shown to affect the spring plankton composition of the Irish Sea (Southward 1961). The species characteristic of cold water, which usually move northwards in spring, persist longer in southern waters. Similarly, other studies have shown that the timing of the maximum abundance of young teleostean fish can vary from one year to the next by as much as one month (Russell 1930).

Another ultimate factor in the timing of breeding in birds is that which brings about the synchronisation of breeding with other individuals in the same species or even with other species. This is especially

important in colonial nesting birds. Possible advantages of colonial nesting suggested for the various species studied include protection from predators (Cullen 1960) and stimulation by the presence of other birds (Fisher and Lockley 1954; Tinbergen 1953; Lack 1954). Many seabirds, especially offshore feeders, characteristically breed in a relatively few, large colonies whilst species which feed inshore tend to form more numerous small colonies (Lack 1967). Seabirds often feed in large interspecific groups at locally abundant food supplies, usually shoaling fish, during the breeding season (Sealy 1973b); the present study showed these occurred off the Pembrokeshire islands. Synchronisation, which enhances feeding by this method (Ward and Zahavi 1974), may be facilitated by colonial breeding.

Synchronous breeding can be brought about by food shortage at certain times of the year - these are usually regular, ie seasonal in temperate latitudes or aperiodic in tropical areas (Harris 1969b). Synchronous breeding is especially important in auks which are highly colonial. Some of the largest seabird colonies in the world consist mainly of auks eg Little Auk Plautus alle (Freudchen and Salomonsen 1959 ; Breumer 1972), Brünnich's Guillemot Uria lomvia (Uspenski 1956), Puffin Fratercula arctica (Harris in press). This synchrony develops gradually following the birds' return to the vicinity of the nesting colony at the start of the pre-breeding season. The pattern of regular colony attendance demonstrated by the present study probably plays an important part in the establishment and maintenance of inter- and intra-specific synchrony. In highly colonial species such as the auks, synchronised behaviour may actually influence the timing of breeding. When colony attendance was disrupted by adverse spring weather in 1972, breeding was also delayed.

In conclusion, therefore, though food is probably the main factor

ultimately determining the timing of breeding in the Razorbill, it is suggested that the development of synchrony amongst birds in a breeding colony through patterns of attendance during the lengthy pre-laying period is also important.

c. Egg measurements

All accessible eggs in the Main study colonies and some others in the Observation study colonies were measured in the three seasons. Length and maximum breadth were measured using vernier calipers, accurate to 0.02 mm. Replicate measurements showed the average error on these measurements was 0.3 mm (0.4%) of the length and 0.1 mm (0.25%) of the breadth.

A sample of 64 freshly laid eggs were both weighed and measured in 1971. From these data a mean value of the "egg constant" (K) was obtained (Barth 1953; 1967/68) so that estimates of volume from linear measurements (length and breadth) could be corrected for the shape of the egg, assuming a specific gravity (not measured in the present study) of 1. The volume of all eggs measured was calculated from:

$$V = \frac{L \times B^2 \times K}{1000}$$

where L = length (mm) K = 0.54
B = breadth (mm) V = Volume (cc)

Volume is used as a measure of egg size in all subsequent discussions. Measurements of a sample of museum eggs (see below) and published data were also used for comparison with the Skokholm eggs.

The distribution of lengths and breadths of the eggs measured in 1971 are shown in Figure 4.7. The parameters of these data and the calculated volumes are given in Table 4.4.

The mean measurements of eggs laid by Razorbills on Skokholm in 1953 (Moyse 1963) and 1963 (Diamond 1964) were compared with the results of the present study for 1971 (Table 4.5). The lengths of eggs laid in 1963 and 1971 and the breadths of eggs laid in 1953 and 1963 were similar but all other measurements differed significantly from one another. The eggs measured in 1963 were not only smaller in volume than those laid

Figure 4.7 Frequency distributions of length and breadth measurements (mm) of Razorbill eggs in 1971. n=206.

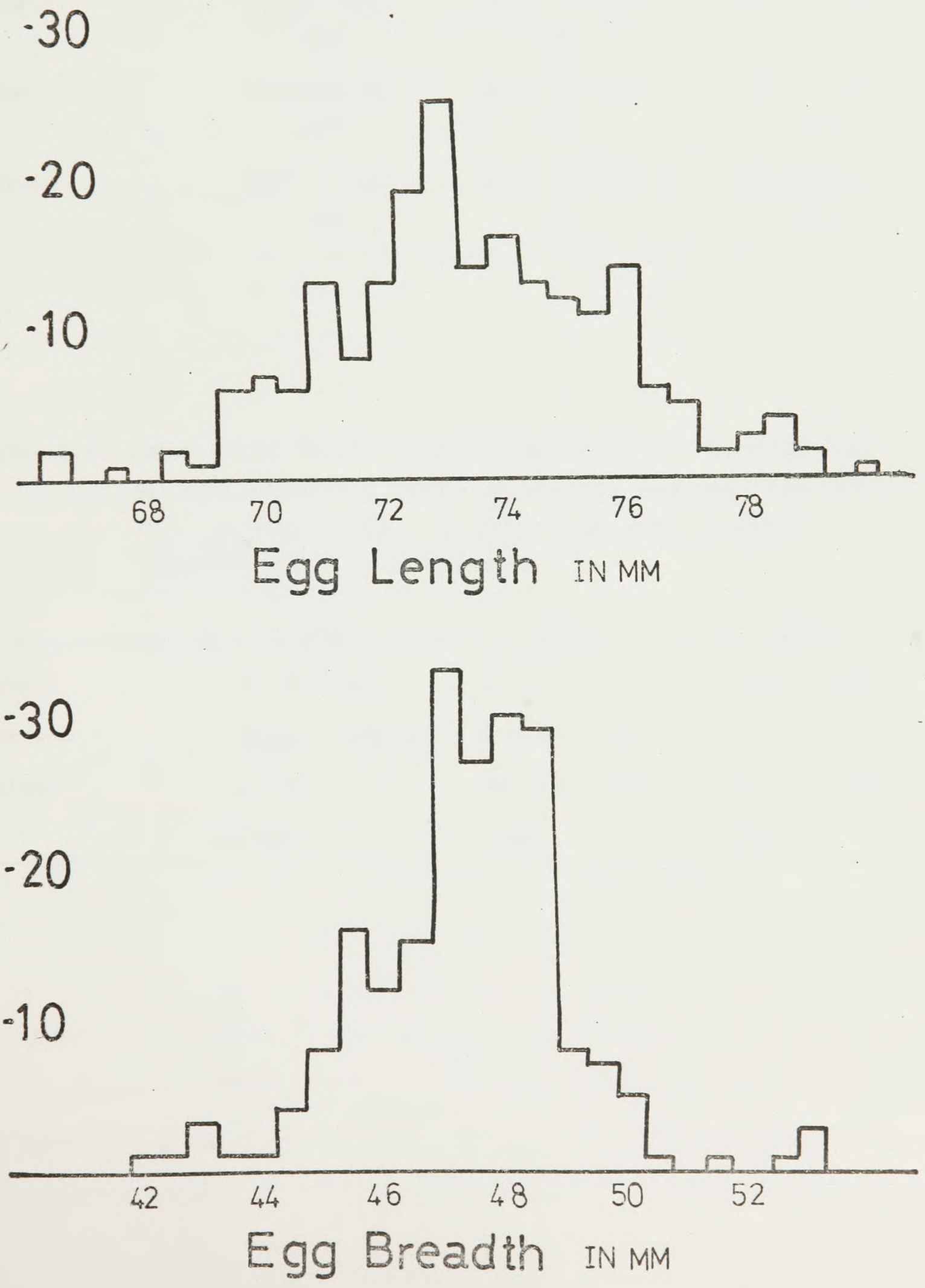


Table 4.4 Parameters of egg size in Razorbills on Skokholm. Means are given in mm ± one standard deviation. For each measurement, differences are significant ($P \leq 0.01$) for 1971-1972 and 1972-1973 but not for 1971-1973.

		1971	1972	1973
Length		73.65 ± 2.41	72.91 ± 2.67	73.56 ± 2.68
	n	206	154	182
Breadth		47.55 ± 1.65	46.79 ± 1.68	47.27 ± 1.51
	n	206	155	182
Volume		83.29 ± 6.89	81.06 ± 9.77	82.03 ± 6.24
	n	206	154	182

Table 4.5 Measurements (mm ± 1 standard deviation) of Razorbill eggs on Skokholm in 1953 (Moyse 1963), 1963 (Diamond 1964) and 1971 (present study). All differences are significant ($P \leq 0.01$) <u>except</u> those marked *.

	1953		1963		1971
Length	74.33 ± 2.48		73.6 ± 2.59	- * -	73.66 ± 2.41
Breadth	46.70 ± 1.56	- * -	46.7 ± 1.58		47.55 ± 1.65
Volume	81.08 ± ?		80.50 ± 6.51		83.29 ± 6.89
n	123		123		206

in 1953 but also than those in all three years of the present study. This may have been a result of adverse spring conditions following the exceptionally hard winter of 1962/63. Similarly the effect of apparently adverse spring conditions on egg size was also seen in 1972 (see f.).

Comparison of the size of eggs laid by Razorbills on Skokholm with those laid by individuals of the northern subspecies (Table 4.6), indicate that the populations with the largest average body size (see Table 1.2) produce the largest eggs. This relationship has also been recorded in several birds, eg the Kittiwake (Coulson 1963), Ringed Plover, Charadrius hiaticula (Väisänen 1969), Shag, Phalacrocorax aristotelis (Snow 1960) and Song Sparrow, Melospiza melodia (Nice 1937).

The weight of three eggs laid in 1971 by females of known body weight, were 14.3%, 14.7% and 16.6% respectively (average 15.2%) of the female's weight. A figure of 13.8% female weight was obtained by Johnson (1944) for North American Razorbill eggs. The findings of the present study agree well with those presented by Sealy (1975a) which demonstrated that the larger alcids lay relatively small eggs and vice versa (cf Ancient Murrelet Synthliboramphus antiquus 22% adult weight, Xantus' Murrelet Brachyramphus hypoleuca 24%, Common Guillemot 11%).

d. Measurements of shell thickness

These were made on two samples:

1. Fresh eggs

Fragments of shell from eggs broken by predators and newly hatched eggshells were collected. The inner membrane was removed and the thickness measured using a 'Mercer' dial caliper gauge accurate to 0.002 mm. Ten measurements on different pieces of shell or at different points on larger shell fragments were averaged in order to avoid the biasing effect of variations in shell thickness at different points on the egg

Table 4.6 Average measurements (mm) of eggs laid by the different subspecies of Razorbills

Origin	Subspecies	Source	n	Length	Breadth
North American coast	A.t. pica	Bent 1919	80	75.9	47.9
Gulf of Saint Lawrence	A.t. pica	Bédard 1969	100	74.5	48.5
Denmark	A.t. torda	Paludan 1947	15	75.0	48.1
Great Britain: Outer Hebrides	A.t. islandica	Diamond - pers.comm.	100	72.2	47.0
Skokholm		Present study	206	73.6	47.5

Table 4.7 Shell thickness (mm) in fully and partly incubated Razorbill eggs. Mean values are given ± one standard deviation.

	1971	1972	1973
Fully incubated	0.383 ± 0.009	0.367 ± 0.012	0.369 ± 0.005
n	38	37	31
Partly incubated	0.396 ± 0.008	0.399 ± 0.011	0.387 ± 0.032
n	6	10	4

Note Mean 1971-1973 0.360 ± 0.008 n = 106 Fully incubated) $t=3.76$ $P<0.01$
0.378 ± 0.022 n = 20 Partly incubated)

Differences between separate years are significant ($P \leq 0.01$) for fully incubated eggs 1971-1972 and 1971-1973, and for all partly incubated eggs.

(Tyler 1961). A series of shells measured twice indicated the average error of the measurements was 0.006 mm or less than 0.02% of the thickness. A sample of shells with and without the inner membrane intact was measured so that the average thickness of the membrane could be calculated.

The specific gravity of the egg-shell, with membrane, was determined in the following way. Five almost complete egg-shells (from blown unincubated eggs) were first weighed and then broken into small pieces. All the pieces of each egg were then dropped into a water filled measuring cylinder graduated to the nearest 0.1 ml. The volume of water displaced by the known weight of egg-shell and specific gravity of egg-shell were calculated.

2. Museum eggs.

Ninety-seven blown eggs from the Oxford University Museum were measured; all of these had been collected in the British Isles before 1940. Each egg was weighed (to the nearest 0.1 g) and the length and breadth measured (to the nearest 0.1 mm). From these measurements an estimate of the thickness of the egg-shell and membrane were made using the method described in the Appendix VI.

Results

1. Fresh eggs

Measurements of shell thickness from hatched eggs were analysed separately from the measurements of shells from eggs taken by predators, most of which had scarcely been incubated. The mean shell thickness for each group in the three different years of the study is given in Table 4.7. There were significant differences ($P < 0.05$) in the thickness of shell of unhatched eggs during the three years. Shells of fully incubated eggs were significantly thicker in 1971 than those in the other two years.

Within each year, samples of unincubated egg-shells were small, but

the thickness of these shells was significantly greater than the shells of hatched eggs which had been fully incubated. The difference in mean shell thickness in the two groups amounted to 4.9% of the unincubated thickness. Differences in shell thickness of incubated and unincubated eggs laid by the same female were 7% of the thickness of the newly laid shell in the Quail Coturnix coturnix (Kreitzer 1972); in the American Woodcock Philohela minor this difference can be as great as 10% (Kreitzer 1973). The thinning of the shell during incubation has been attributed to the uptake of calcium by the developing embryo though this should not affect shell thickness as it is removed from the interstices of the shell. The thinning of Razorbill eggs during incubation by at least 5% of the freshly laid thickness (biased by the partial incubation of predated eggs) compares well with Kreitzer's findings, although Anderson et al (1974) found no difference in shell thickness in Razorbill eggs collected at the beginning and end of incubation. The shells of three replacement eggs which failed to hatch were also measured during the present study and in all cases the second egg was thinner shelled than the first by an average of 13.4%.

Measurements of eight shells (6 from fully incubated eggs) with inner membrane intact indicated that the membrane increased the 'shell' thickness measurement by an average 18.5 $\pm$ 1.4% (0.43 $\pm$ 0.03 mm). This fact was then used to estimate the true shell thickness of museum eggs which had membranes intact.

2. Museum eggs

The mean shell thickness of the museum Razorbill eggs measured was 0.38 $\pm$ 0.025 mm, including the inner membrane. As these were all blown eggs, it could reasonably be assumed that they were either addled or collected early in incubation. The comparable estimated thickness of Skokholm eggs was 0.45 mm (118.5% of 0.38), considerably thicker than

pre-1940 eggs.

Toxic chemical residues are known to cause egg-shell thinning in predatory birds (Ratcliffe 1970) and a 12% decline in the average thickness of Razorbill eggs in the Baltic between 1861-1940 and 1970-1972 has also been reported (Anderson et al 1974). In the present study however, the difference in thickness of shell from "fresh" eggs and that of the museum specimens probably is mainly attributable to the inaccuracy in the estimation of thickness from the measurements available from museum specimens.

e. Egg shell pigmentation

Razorbill eggs found on Skokholm were mostly white or off-white in colour, covered with specks and patches of darker pigment. The colour of the pigmentation varied from one bird to another but was usually black or brown. The amount of pigmentation also varied greatly between individuals. Eggs from a series of sites were photographed during the three seasons of the study, to determine whether a bird laid eggs with a similar pattern of pigmentation in successive years.

Eggs with unusual background coloration were recorded in colour, using Kodachrome II film, and all other eggs in black and white, using PF4, 125 ASA film. The camera used was a 35mm, single lens reflex Zenith E with a standard lens. The eggs were removed from the nest site and balanced on a sheet of card to be photographed. Records of eggs from 27 sites were obtained in this way for two of the three years and eggs from another five sites recorded in all three years of the study. Eggs from 13 sites in which two eggs were laid during one year - either due to the replacement of an egg that had been lost or the rare occurrence of 'two-egg clutches', (see h.) were also photographed.

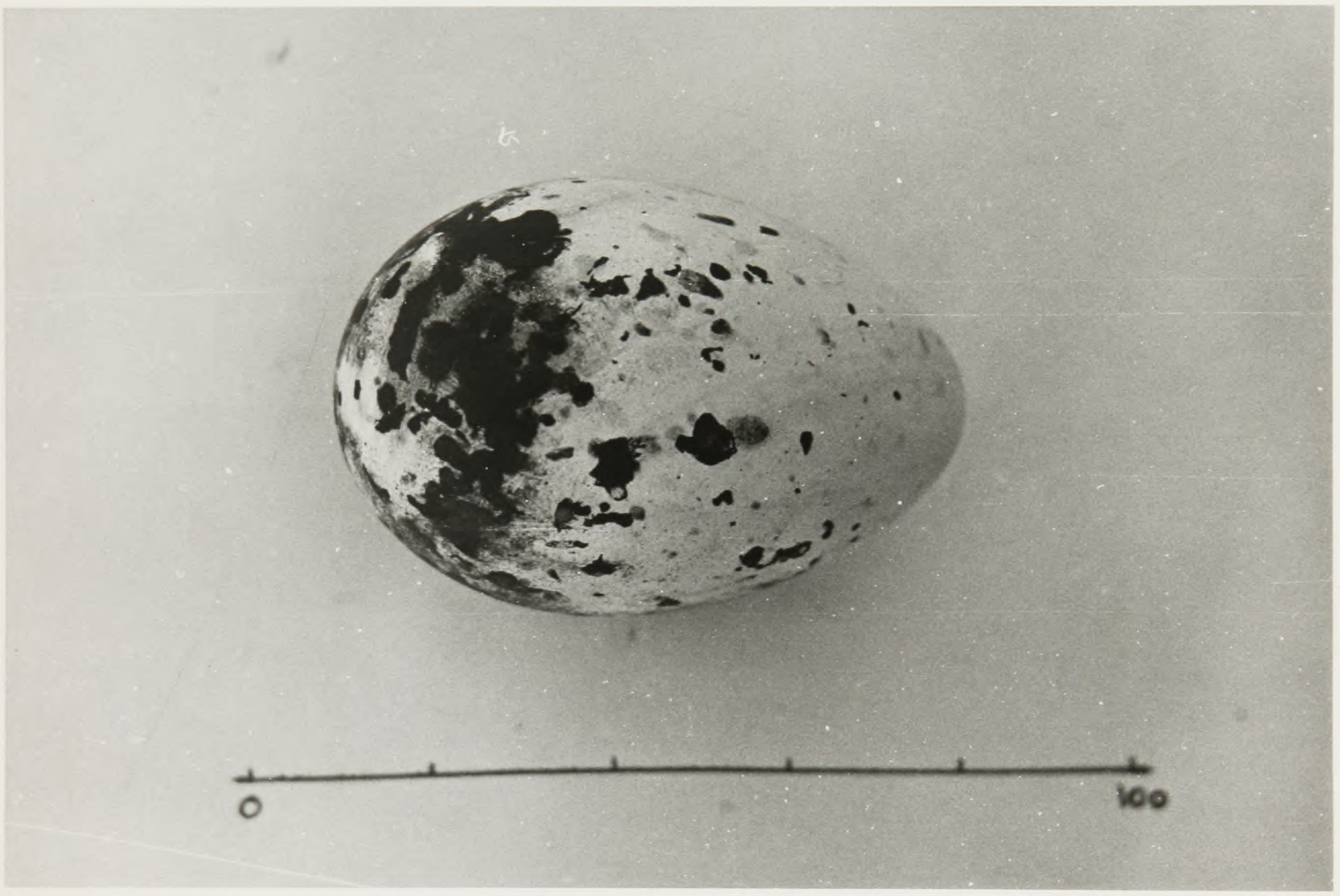
The pattern of pigmentation on the eggs laid by the same female in successive years was very similar. Figure 4.8 shows a representative

Figure 4.8 Eggs laid in one site by the same female during 1971, 1972 and (PTO) 1973. NB. The scale in these and in all subsequent photographs is in mm.





Figure 4.8 continued.



set of photographs of eggs laid in one site during the three years of the study.

A quantitative test was designed to compare the amount of difference between the eggs laid in one site by the same and different females in two successive years. A series of 15 paired photographs of eggs laid in the same site two years running were shown independently to five different people. In ten of the 15 sites concerned ('no change sites') the eggs photographed were laid by the same bird in both years; in the other five sites ('change sites') the eggs were laid by different birds in both years. Each subject was asked to rank the pairs of photographs according to whether he thought the eggs looked similar in pattern ("amount and arrangement") of pigmentation. The ranking of the eggs from the no change sites were compared with those of the eggs from change sites by a χ^2 test. This was highly significant ($\chi^2 = 46.0$, $P < 0.001$) indicating a better than random chance of ranking the no change photographs between 1 and 10 and the change photographs from 11 to 15. Thus, even to inexperienced observers, the pigmentation patterns of eggs laid by the same female in successive years looked similar.

Figure 4.9 is an example of a photograph of 2 eggs laid in the same site during 1972. The first egg was found deserted after the site had been flooded and the second was laid later as a replacement. The pigmentation pattern of the two eggs was very similar; this was also true of all other replacement eggs recorded.

The photographs in Figure 4.10 show examples of the different pigments on eggs laid in the same site in successive years when both birds are known to be new to the site in the second year. The eggs in this and all other similar cases recorded were very different. The effect on the pigmentation of the eggs laid in a site when only the female is new to the site (Figure 4.11) is also extreme. This fact allows certain assumptions to be made on the sexes of the birds using some sites.

Figure 4.9 Eggs laid in one site in 1972 by the same female. The egg on the right was laid as a replacement for the one on the left which became chilled during incubation.



Figure 4.11 Eggs laid in one site in consecutive years when only the female was new to the site in the second year.



For example, the eggs shown in Figure 4.12 were laid in the same site in two successive years. In the second year, however, one of the birds was new to the site although I did not know whether it was male or female. The similarity of the egg laid in the second year to that laid in the first indicated that the female had not changed so that the new bird was a male. The sex of several individuals was established by this method (see Chap.2iid).

Figure 4.13 shows one of the two-egg clutches found (Appendix VIII and h below). These eggs, from Site V, were not thought to have been laid by the same female.

Eggs in which the shell pigmentation and/or the background was of unusual colour were also photographed. The records of eggs laid in these sites in subsequent years indicated that the colour effect was not persistent from one year to the next. This is also clearly shown by the eggs in Figure 4.14 which were laid by the same bird in one site during 1973. The egg on the right was laid to replace that on the left which was deserted early in incubation. Although the pattern of pigmentation is very similar, the first egg to be laid had a peculiar dark pinky brown background colour but the second egg had a normal white background. The pigments producing shell colour may vary from predominantly haemoglobin-derived (porphyrins), resulting in a brownish colouration, to predominantly bile-derived (cyanins), resulting in a grey, blue or green colouration (Welty 1962). Individual variations in the shell colour of domestic hen's eggs are more usually observed early in the season due to the accumulation of pigment during the non-laying period (Romanoff and Romanoff 1949). Colour variations in the eggs of the Kittiwake have been shown to result from fluctuating feeding conditions during laying (Maunder and Threlfall 1972). Either of these factors may have caused the Razorbills to produce eggs with different background colours at different times.

Figure 4.12 Eggs laid in one site in consecutive years when one bird of unknown sex (but concluded to be male) was new to the site in the second year.

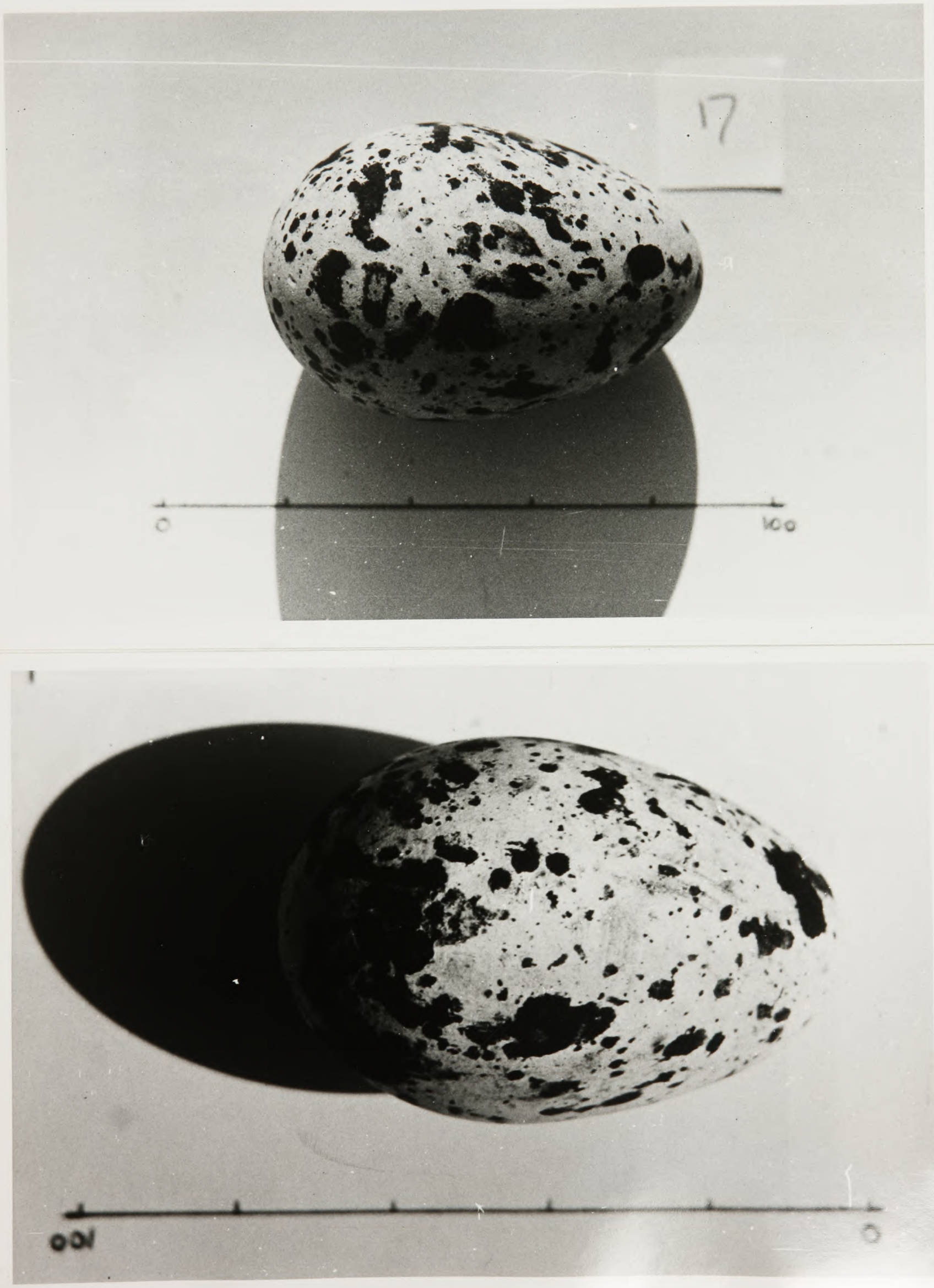


Figure 4.13 Two egg clutch: eggs laid in one site in the same year, apparently by two different females.



Figure 4.14 Eggs laid by the same female in one site; the egg on the right was produced as a replacement for the one on the left. Note the unusual background colour (actually dark pink) in the first egg produced and the similar pigmentation patterns.



f. Factors relating to egg size

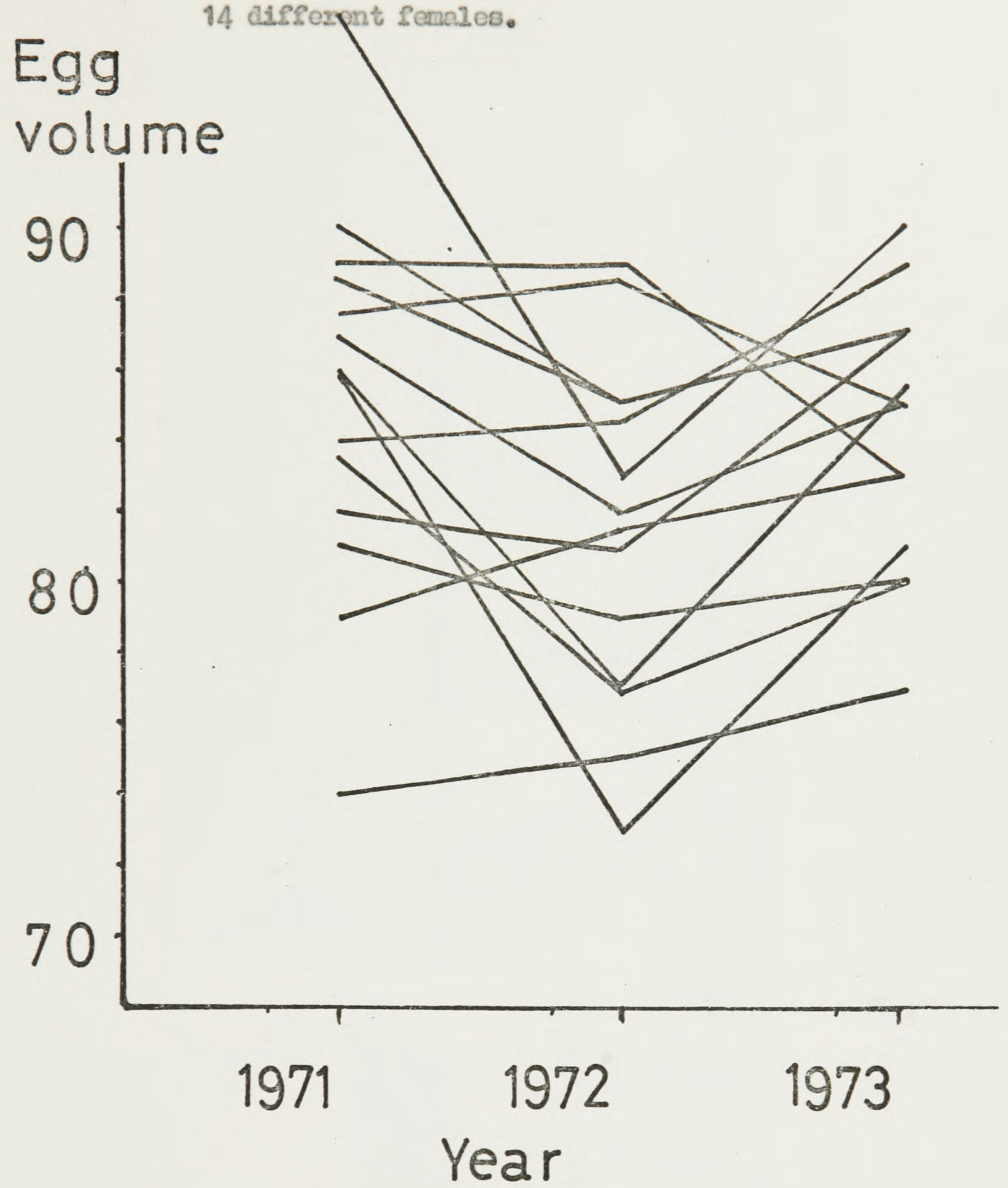
The data presented above (c) showed that Razorbill eggs produced in 1972 were smaller than those laid in 1971 or 1973. In 1972 nearly all individuals also laid eggs equal or lower in volume than those they laid in 1971 (Figure 4.15). As discussed earlier, the inclement spring weather in 1972 disrupted colony attendance and may have affected the timing of breeding, and egg size.

Examination of other differences between eggs laid in the three years (Fig. 4.16), showed that in 1971 many of the eggs produced during the first three laying intervals were relatively large. In the later part of 1971 and throughout the season in both 1972 and 1973, a marked decrease in egg volume was recorded as time progressed. In 1971 laying started earlier than in the other two years which indicates that conditions may have been especially favourable early in the season.

As young birds tended to lay later than old birds (see a4.), the seasonal decline in egg size may have been related to the age structure of the population. The volumes of eggs laid in six sites belonging to females of known age were calculated and corrected for annual overall differences in egg size using the relationships indicated in Figure 4.15. Egg volume was found to increase significantly with the age of the female (Figure 4.17) thus younger birds in the population not only bred late in the season but also produced relatively small eggs. There was, however, no sign of a decrease in volume of eggs laid by the oldest birds as has been reported in other species (Andersen 1951; Richdale 1955; Davis 1973).

The seasonal trend in egg volume recorded in the Razorbill has also been observed in many other species which lay clutches of eggs, such as the Kittiwake (Coulson and White 1961; Coulson 1963b; Maunder and Trelfall 1972), Shag (Coulson et al 1969), Lesser Black-backed Gull

Figure 4.15 Volume (cc) of eggs laid in successive years by 14 different females.



The relationships between the volume of eggs laid in the same nest site (where there was no reason to suppose that the breeding birds had changed) in successive years were as follows:

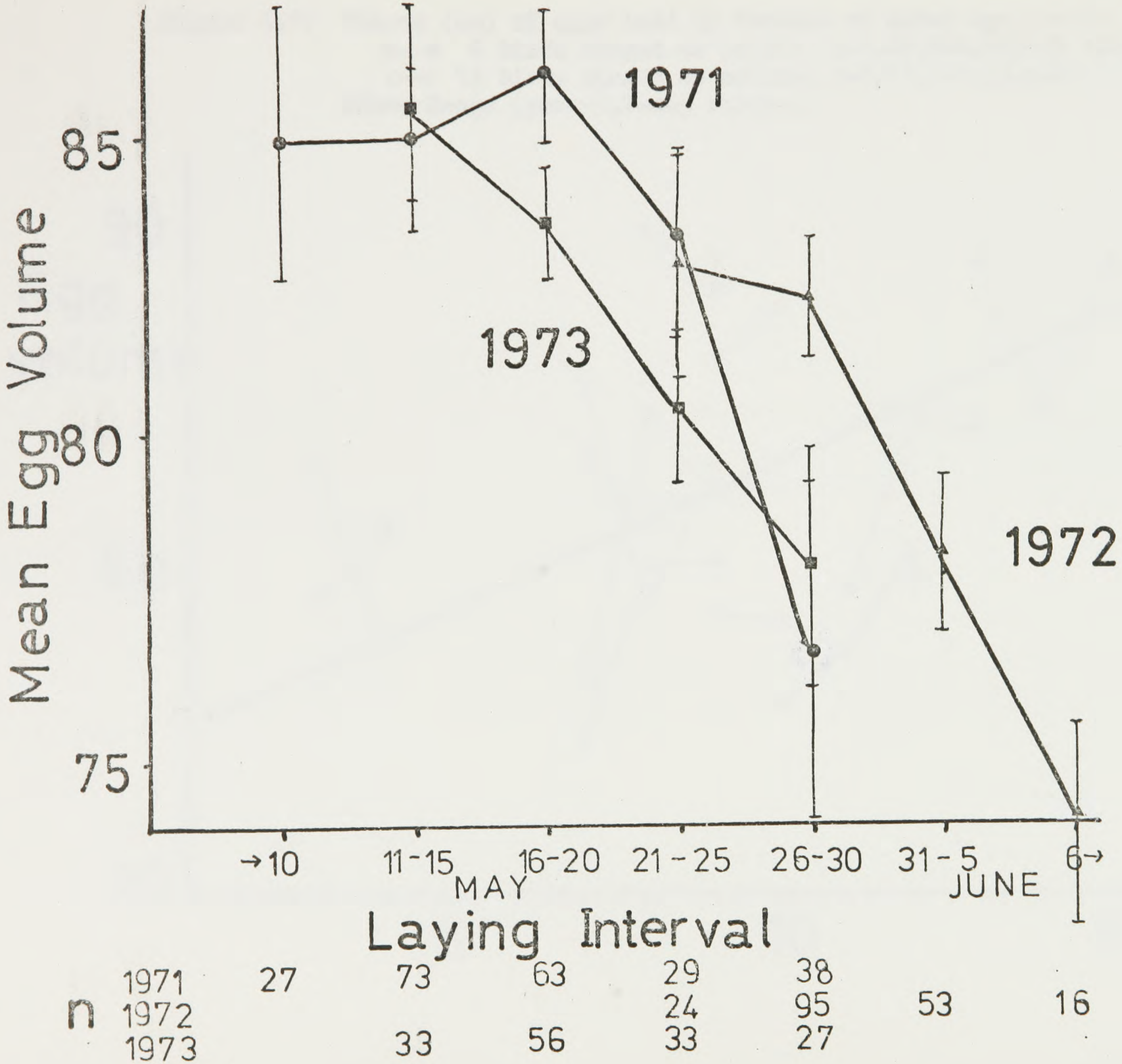
$V^{72} = 49.0 + 0.4\,V^{71}$ $r = 0.50$, $n = 89$, $P < 0.001$

$V^{73} = 54.7 + 0.3\,V^{71}$ $r = 0.48$, $n = 84$, $P < 0.001$

where V^{71}, V^{72}, V^{73} = the egg volumes (cc) in 1971 1972 and 1973 respectively.

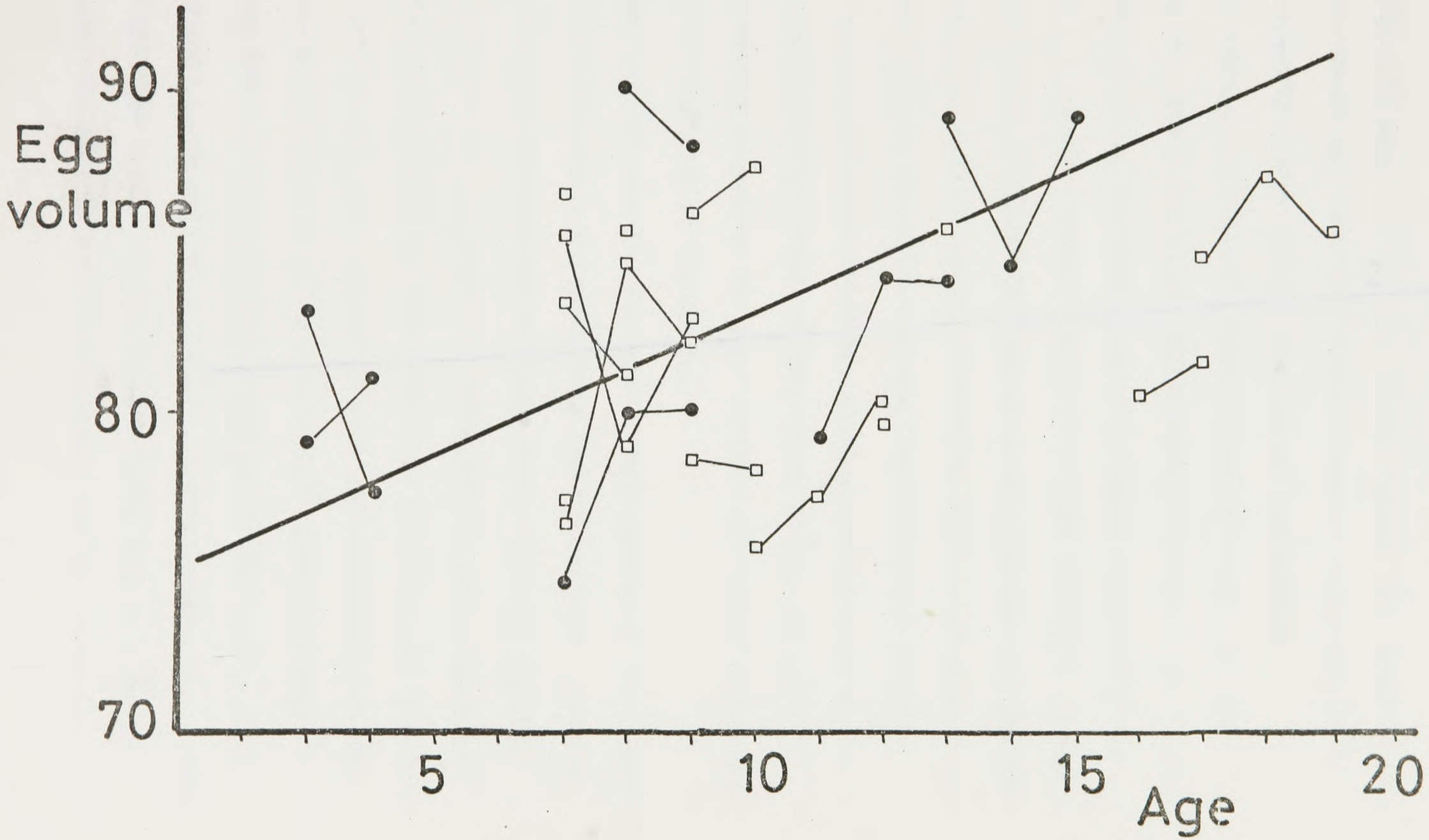
Figure 4.16 Volume (cc) of eggs laid in different laying intervals in 1971 (●—●), 1972 (▲—▲) and 1973 (■—■). Means are shown ± 1 standard error. For all data in each year correlations between egg volume and laying date were as follows:

	1971	1972	1973
Correlation coefficient	0.19	0.32	0.83
P	0.05	0.001	0.001
n	149	100	117
Regression equation where X=laying date Y=egg volume	Y=89.16-0.28X	Y=96.92-0.55X	Y=87.82-0.27X



n								
	1971	27	73	63	29	38		
	1972				24	95	53	16
	1973		33	56	33	27		

Figure 4.17 Volume (cc) of eggs laid by females of known age, corrected for difference between years - see text.
●—● 6 birds ringed as pulli: r=0.62, P=0.02 n=15 1. Y=0.89X+74.35
□—□ 14 birds ringed as adults: r=0.13, P=0.05, n=25
where X=age (years), Y=egg volume.



(Davis 1973) and Herring Gull (Davis 1975b), a wide range of passerine species (see Coulson 1963b) and the Black-headed Gull Larus ridibundus (Svärdsson 1958), Velvet Scoter Melanitta fusca (Koskimes 1957) and Redhead Aythya americana (Low 1945). The reason for this decrease in egg or clutch volume has been attributed in most of these species to the later laying by younger individuals in the population.

In many species the date of laying is influenced by the food available to the female who has to collect enough "extra" food to form the egg (Perrins 1970); this factor can also affect the size of the egg produced. A seasonal decline in egg size could therefore at least partly result from a declining food supply during the breeding season. This seems unlikely in most species however, as food is presumably most plentiful when demands are highest in the later stages of breeding (when the chicks need food). Moreover, in some species which show unusually extended laying periods eg Shag (Snow 1960), the earliest breeders are feeding chicks as the last breeders are laying indicating an abundance of food late in the season.

Variations in egg size in successive laying periods in the Razorbill may have partly reflected local prevailing food conditions. Available data on the seasonal variation of the Razorbills' main food species Ammodytes (Cameron 1959) suggests that the onset of laying coincided with an increasing abundance of both larvae and adults in the waters of the south Irish Sea (see b). These fish form the characteristic food of the Razorbills at this time (late April-May). Thus conditions appear to have favoured an early start to laying in 1971 and to have enabled relatively large eggs to be produced throughout the first three laying intervals (15+ days). Similarly, the later intervals of the 1973 laying period appear to have been suitable for the production of large eggs.

Coulson et al (1969) were able to separate the effects of age of the female and the date of laying upon egg size in both Kittiwake and Shag, thereby showing that, within any age group, the later breeding birds produced smaller eggs than the earlier layers. This indicates that basic physiological differences exist between individuals which affect both the timing of laying and the size of eggs produced, further demonstrated by the fact that the later laying Kittiwakes in any age group were also the lightest in body weight.

In the present study, relatively few young Razorbills (colour ringed four year olds or unringed five and six year olds) bred for the first time in the late season of 1972 (see Chap.5ii). In spite of this, however, the seasonal decline in egg size still persisted indicating that age alone was not responsible for the size of eggs produced. Some of the variation in egg size may be attributable to intrinsic differences in the birds' breeding condition such as those referred to in the Kittiwake.

g. Egg loss

On average about 30% of all eggs laid failed to hatch; these were either found cold or broken in the site, disappeared without a trace, or failed to hatch after 35 days and were finally deserted by the adults. The main species taking Razorbill eggs on Skokholm were Jackdaws (Corvus monedula) which displayed much skill and agility in finding and reaching the eggs. These were sometimes removed from the site by the Jackdaw or, more frequently, pierced and wholly or partially eaten in the site. Eggs apparently eaten by a Jackdaw were usually found in or near the site with a neat hole in the shell through which the contents had been removed.

Herring gulls were also observed taking Razorbill eggs usually from open nest sites where the eggs were clearly visible and relatively unprotected. Gulls taking eggs from such sites either removed them whole or broke them open and ate the contents in the nest site. In the latter case the shell was usually left in several pieces. Unhatched eggs, which were not immediately eaten, sometimes remained in the site for several weeks until the shell disintegrated. Predation by Herring Gulls was also reported to have caused heavy egg losses in the Razorbill colony on Graesholm (Paludan 1947). Nine of the 27 eggs lost in Plumb's (1969) study on Skokholm were attributed to "the parents often rolling them down a slope from their holes on to the rocks below." In view of the findings in the present study, it seems more likely that these were eggs removed from the sites by gulls or Jackdaws and found half-eaten close by. In addition, six of the other eggs lost in Plumb's study disappeared and were assumed to have been taken.

An egg which disappeared without trace from a site in the present study was generally considered to have been taken by a gull if the site was relatively accessible, or by a Jackdaw if the site was well hidden. Such eggs were porbably first deserted by both adult birds as observations of Jackdaws approaching Razorbill nest sites showed that they were readily driven off by a sitting bird. When an egg had been taken or eaten it was not always possible to determine whether the period of absence by the adult bird was sufficient for the egg first to have become chilled or whether the adults would have returned to incubate had the egg not been attacked. Birds which were slow in returning to the site after being disturbed and those which left the egg unattended during incubation were most vulnerable to predation, especially if the nest was on a ledge site. Other losses involved eggs deserted (but not taken)

during incubation, eggs found cracked soon after laying, eggs which were accidentally displaced from the site by the bird and not incubated further, eggs which were chilled as a result of flooding in the nest site and those in which the chick died during chipping or hatching. (Table 4.8) My activities in the breeding colonies undoubtedly caused a slight increase in egg loss (see iv). Nearly 45% of all loss occurred in the first ten days after laying (Table 4.9); the 11% of eggs which were lost more than 40 days after laying includes many that were infertile and finally deserted. A sample of ten deserted eggs were analysed for toxic chemical residues and heavy metals; the results of these analyses (Appendix VII) indicated that toxic chemicals were not a contributory factor in hatching failure.

Jackdaws were almost definitely responsible for 27% (64) of all eggs lost. A further 30% (71) of the losses, where eggs disappeared from open sites, and 5% (12), broken in the site, could have been the work of either a gull or a Jackdaw. Thus in 1971 and 1973 alone predation, mainly by Jackdaws, caused the loss of 73% (113) of all eggs which failed to hatch. (In 1972 the number of eggs deserted or infertile was exceptionally high (29 or 5%) so that the proportion of predated eggs appeared lower (42%). Jackdaws are increasing in numbers on Skokholm (Lawman 1975b). Records of the species in the Skokholm Bird Observatory Reports before 1962 were confined to the spring months and rarely exceeded 8 individuals; in 1965 three pairs bred but raised no young due to control measures. By 1973 the breeding population was 25-30 pairs. A similar increase has been reported on Skomer where there were about 20 pairs of Jackdaws bred in 1946 (Buxton and Lockley 1950) and about 200 pairs in 1964, with little change since (Birkhead 1974b). Thus in less than ten years a serious threat to Razorbills breeding productivity has developed on Skokholm.

Table 4.8 Causes of egg loss during incubation, expressed as a percentage of the total.

Cause		1971	1972	1973	1971-73
TOTAL number of eggs lost		78	81	77	236
Disappeared	From open site	32	18.5	39	30
	From boulder site	24	9	13	15
Broken	In site - Jackdaw	9	9	19.5	12
	In site - Jackdaw or gull	8	6	1	5
	On laying or during incubation	-	5	1	
Displaced	Cold, wet	-	6	4	
	Disappeared, broken	-	4	1	
Unhatched	Flooded out	-	5	-	
	Cold, deserted	18	23.5	16	19
	Known to be infertile	-	6	3	
Dead on chipping or hatching		3.5	5	1	
Unincubated egg of 2-egg clutch		3	2.5	2.5	
Miscellaneous		3	2	1	

Note Gulls or Jackdaws caused 73%, 42%, 73% (Average 63%) respectively of total losses in the three years.

Table 4.9 Timing of egg losses during incubation.

Time (days) after laying	1971	1972	1973	% of total
0 - 5	5	14	20	29.5
6 - 10	2	6	12	15.0
11 - 15	3	5	6	11.0
16 - 20	1	2	3	4.5
21 - 25	2	6	2	8.0
26 - 30	2	3	3	6.0
31 - 35	5	6	4	11.0
36 - 40	1	1	4	4.5
41 →	1	9	4	11.0
TOTAL	22	52	58	

h. Replacement eggs and two egg 'clutches'

Eggs lost during incubation or, more rarely, those which had been deserted during incubation were sometimes replaced (this study; Paludan 1947; Kartashev 1960; Bédard 1969). The rates of replacement laying in study colony sites during the present study were as follows:

Year	Eggs Lost	Eggs replaced	% replacement
1971	69	14	20
1972	68	16	21
1973	71	24	34
Total	208	54	25

Sleptsov in Belopol'skii (1957) observed that 35% of Razorbill eggs were replaced after loss. In Cassin's auklets, 40% of the eggs laid and not immediately incubated were replaced (Manuwal 1972).

Only those eggs laid and lost early in the season were replaced and about 14 days (14.14 ± 1.47, $n = 14$) usually elapsed between loss and replacement. Replacements were not produced for eggs lost late in the season. In 1971 and 1973, the last replacements were laid 47 and 49 days respectively after the start of laying; in 1972, no lost eggs were replaced more than 32 days after the beginning of the season. In all three years, the mean laying date of eggs that were lost and replaced was significantly earlier than that of eggs lost but not replaced ($t = 6.19$, $P < 0.001$, $n = 27$, $t = 10.71$, $P < 0.001$, $n = 43$, $t = 11.54$, $P < 0.001$, $n = 33$, 1971-73 respectively).

The second egg was always smaller than the egg it replaced, following the seasonal trend in egg volume. The average difference between the volume of 26 pairs of eggs laid by the same birds in single seasons was 7.70 ± 4.50 cc. Replacement eggs were also more successful than other first eggs laid at the same time (Table 4.10) which suggests that the adults which were able to lay early, lost their egg but replaced it

Table 4.10 Success (%) of 37 replacement eggs compared with that of first eggs laid in the same laying period.

	Number of chicks fledged/ Number of eggs laid		
	1971	1972	1973
All first eggs laid in Interval X	78	74	60
Replacement eggs (laid in Interval Y), laid for those lost from Interval X	75	69	57
First eggs laid in Interval Y	61	55	52

were still more productive - perhaps because they were better parents - than birds laying late. Overall nesting success however was not enhanced by the loss of a first egg.

Apparent two egg clutches

Seven Razorbill sites were found containing two fresh eggs (about 1% of all sites examined). Details of these are given in Appendix VIII. In three of the cases (sites I, VI, VII), the second egg was almost certainly laid as a replacement for the first egg which had become chilled. In three of the other sites with two eggs (sites III, IV, V), the second egg was apparently laid by an intruding female and was not incubated. In the last site (II), the nest appeared to have been taken over by a second bird after the first laying had occurred.

Two egg clutches were also recorded by Plumb (1965), Harris (pers. comm.) and Bédard (1969). The latter found two egg clutches in three sites during both the years of his study which suggests that the same females may have laid 2 eggs in each year.

j. Incubation behaviour

The behaviour of birds during incubation varied widely from one individual to another. Some birds were restless, frequently standing up to examine or move the egg whilst other birds sat for hour after hour without moving. In many of the sites examined, stones or fragments of vegetation were found around the egg in the form of a nest. This material tended to prevent the egg from rolling out of the site. The manipulation of potential nest material by the birds played an important part in the pre-laying behaviour in the nest. Fragments of stones were repeatedly picked up by either bird in a pair and allowed to drop to the ground immediately in front of the bird. After laying, stones were often carefully arranged and rearranged around the egg with the same lifting

and dropping motion. The same behaviour was also observed in birds returning to their nest after losing an egg and in non-breeding birds occupying potential nest sites during the breeding season. Similar use of nest material by the Razorbill has been referred to by Bent (1919), Audubon (1937), Paludan (1947, see Plate 12 p.55), Nordberg (1950), Plumb (1965) and Bédard (1969).

The length of the incubation period (usually about 35 days) was on average shorter in 1971 than the other two years (Table 4.11); comparable data from other studies are given in Table 4.12.

In most sites the egg was incubated closely and was rarely exposed for more than a few seconds except during change-overs when both birds were present. Sitting birds approached by a potential scavenger, such as a gull or a Jackdaw, would display the yellow gape in threat; this was usually enough to deter intruders. Occasionally both birds would leave the egg unattended and fly out to sea. Often these flights, although very brief, permitted a gull to alight on the ledge and break open the egg or remove it. This type of desertion was rare and, although difficult to record, appeared to be more frequent at the start of incubation. As an important part of the pre-laying behaviour involved frequent display flights by both birds of a pair from the nest site, it seems likely that the transition from pre-laying to incubation behaviour was sometimes imperfect.

During incubation the mates of the sitting birds in the colony returned to land one by one from about half an hour after dawn onwards. A change-over usually occurred at the nest on the return of the mate. The relieved bird often sat in the site with its mate for a while before flying out to sea. Most birds left the nest site within five minutes of being relieved by the mate after dawn, but the interval varied from less than one minute to several hours.

Table 4.11 Length of the incubation period (days ± 1 standard deviation).

Year	Mean length of incubation	n	t	P
1971	34.6 ± 2.8	104	2.44	0.05
1972	35.5 ± 2.0	73		
1973	35.1 ± 1.8	62	1.22	>0.05

Table 4.12 Length of incubation period (days) on Skokholm compared with other estimates.

Colony	n	Mean length of incubation	Reference
Graesholm, Denmark	7	35.5	Paludan 1947
Gulf of St.Lawrence, Quebec	9	36.9	Bédard 1969
Skokholm, Wales	18	34.3	Keighley and Lockley 1948
"	29	36.2	Plumb 1964
"	239	35.1	Present study 1973

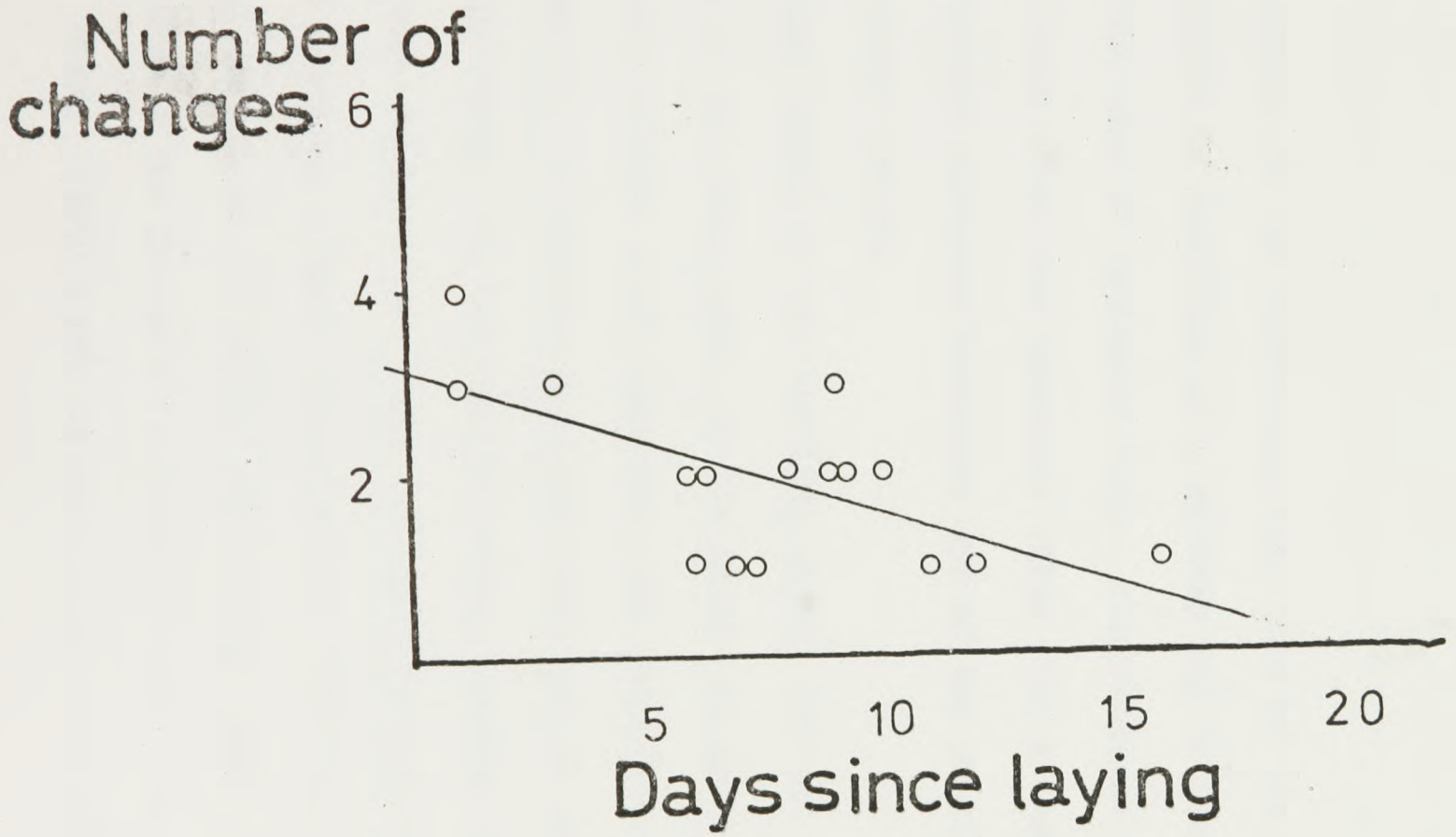
The length of absence of the off-duty bird during the day also varied widely from site to site. In some cases a bird would disappear after being relieved at dawn and would not be seen again until the late afternoon; at other sites both birds would be present throughout almost the entire day. Only incubating birds remained on land at night (see also Bédard 1969). The pattern of nest attendance by the mate of the incubating bird and the number of change-overs at the nest were established by two days of observation from dawn to dusk and a series of shorter watches during the incubation periods in 1972 and 1973. Observations (total 41½ hours) were made at the Twinlet Bay colony where about 14 sites could be watched from a hide without disturbance.

In both years an average of two change-overs occurred at each nest per day. Observations of a single pair of birds in which the female was colour-ringed suggested that, after laying, the female may incubate the egg continuously for 48 hours before assuming an incubation pattern with two change-overs per day. (Both the female and the male birds took the night shift from time to time.) This is contrary to observations by Paludan (1947) which indicated that incubation did not start at all until a few days after laying.

Observations during the early part of the incubation period in 1972 showed that the total number of change-overs at a nest site in each day decreased significantly as incubation progressed (Figure 4.18). Further records during the later part of the incubation period in 1973 indicated that at this stage the number of change-overs had stabilised at about two per nest per day.

Close observation of 14 incubating pairs on June 8 1973 showed that the off-duty bird spent on average about 46% (45.7 $\pm$ 5.6%) of the time (0430 to 1830) at the nest site with its mate. The average period of absence from the nest between the first return after dawn and midday

Figure 4.18 Number of changes in incubating birds observed at 15 Razorbill nest sites in Twinlet (June 5-6 1972). Relationship is significant r=-0.67,P=0.01,n=15 and Y=3.1-0.2X where X=days since the start of incubation (ie laying),Y=number of changes



was just over half an hour (31.6 ± 9.0 mins). Significantly more time was spent in the site during the morning (dawn to midday, 47.3 ± 1.5%) than in the afternoon (midday to dusk, 37.8 ± 1.2%); at many sites the off-duty bird disappeared to sea in the afternoon. No change-overs were recorded after 1616 and few mates remained on the cliffs after 1730, although light was still good.

iii. Nestling period

a. General

The nestling period of the Razorbill, like that of the Guillemot, has long been regarded as something of a mystery due to its shortness in duration and the lack of published data. Observations made on Skokholm during the present study are presented below with a discussion of the Razorbill's special fledging behaviour and of the possible reasons of the short nestling period.

The average length of the nestling period did not differ significantly in the three years of the study and averaged only 17 days (17.2 ± 2.2 days - Table 4.13) compared, for example, with the 35 day nestling period in the Puffin (Corkhill 1970) and 18 days in the Common Guillemot (Tuck 1960). In the present study, neither the date of hatching nor the weight of the chick at fledging were related to the length of the nestling period; Belopol'skii (1957) showed, however, that Razorbill chicks in the Arctic which hatch early in the season develop more slowly but fledge at a higher weight than those that hatch late. Bédard (1969) found no correlation between the length of

Table 4.13 Mean length of the nestling period (days) on Skokholm compared with other studies.

Colony	n	Length of nestling period	Source
Gulf of St.Lawrence	30	18.2	Bédard 1969
Vedøy, Lofoten Islands	65	19.3	Ingold 1974
Skomer, Wales	16	15.2	Keighley & Lockley 1947
Skokholm, Wales	18	15.7	Keighley & Lockley 1948
"	163	17.2	Present study
"	20	18.0	Brun 1958
"	34	18.5	Plumb 1965

the nestling period and the date of fledging.

On hatching, Razorbill chicks were covered with down which varied from almost black to pale grey in colour in different chicks. The bill was tipped with a white egg tooth which persisted for at least the first week of life. Young birds were able to stand, flap their wings and preen within 24 hours of hatching but were quite helpless if accidentally knocked onto their backs as the adult birds left the nest. All chicks were closely brooded for the first three or four days of life. After this, thermoregulation appeared to have developed and the chicks no longer relied on the adults for warmth; similar observations have been recorded by Paludan (1947) and Brun (1959).

The nestling down was gradually lost from Day 10 onwards, revealing the juvenile plumage (see Bédard 1969 p.69). The breast and belly were white and thickly feathered; the head, back and wings were black and, in some individuals, the white eye stripe was already visible. The wing feathers started to develop at this age but, although the coverts of the flight feathers grew steadily, the actual primary and secondary feathers did not emerge while the chicks were in the nest.

During this study, Razorbill chicks on ledge sites were usually accompanied by at least one adult throughout the nestling period, but in boulder sites chicks of more than a week old were often left alone. Even on ledge sites, brooding was irregular after about four days although chicks of all ages would readily shelter under the adult when disturbed or during rainstorms and would often rest under the adult's wing with the head protruding (see Perry 1940 p.145).

Chick losses during the nestling period

In the present study, an average of 93% of the 815 chicks which hatched fledged successfully (cf 95% Ingold 1974). Fledging occurred late in the evening so that if a chick old enough to fledge disappeared overnight,

it was assumed to have fledged successfully (although some, probably few, of these chicks may have died during fledging). Chicks were sometimes found dead in the nest site, but most losses were due to birds disappearing without a trace, possibly taken by gulls. Even those in sites inaccessible to gulls occasionally strayed from the nest when left alone. A few chicks drowned when the nest site was flooded after heavy rain and one was thrown from a ledge site by loafing Razorbills when briefly deserted by both adults. If one of the adults died during the nestling period, the chick had little chance of surviving. One bird was found dead in its nest with a dead chick underneath it, after catching a wing in a crack in the rock. Another adult, obviously sick, was watched on a ledge site at Twinlet, paying no attention to either its mate or its chick; the latter failed to fledge after the adult disappeared.

Of the chick losses from sites in the study colonies, 60% occurred during the first five days of life (Table 4.14). At this stage there was little chance of a chick being taken unless it was first deserted by both adults. As losses due to 'unavoidable' causes (such as flooding) were small, failure of the chick to survive appeared to be mainly associated with negligence on the part of one or both birds, possibly due to a failure to switch from incubating to brooding behaviour.

The chicks which failed to fledge were significantly lighter at hatching (Table 4.15) and grew more slowly (see c2) than those that fledged normally. Comparison of all chick weights with the volume of the eggs from which they hatched showed that chick weight was dependent on egg size during about the first week of life (Table 4.16); 75% of all chick losses occurred during this time, so egg size may have been critical to the chicks' survival. The growth rate and fledging weight of those chicks that survived the first week of life were independent of egg size. In at least two years of the study, however, the chicks

Table 4.14 The distribution of chick loss with time in days after hatching. Data from 1971-1973 combined.

Age in days	Number of chicks lost	% of total
1	7	29
2	1	4
3	6	25
4	0	0
5	1	6
6	0	0
7	3	12
8	1	6
9	0	0
10	2	8
11 onwards	3	12

Table 4.15 Mean hatching weight (g) of chicks from sites in the study colonies; comparison of chicks which fledged successfully with those that failed to reach fledging.

	n	1971 Mean	Standard deviation	n	1972 Mean	Standard deviation
Fledged	65	62.82	6.37	41	62.77	6.50
Disappeared or found dead	8	59.29	2.46	5	57.10	3.16

Note Differences are significant for both years

1971 $t = 2.89$ $P = 0.01$

1972 $t = 3.26$ $P < 0.002$

Table 4.16 Correlation between chick size (weight) and egg size (volume).

Age in days	1971			1972		
	r	P	n	r	P	n
1	0.54	0.001	45	0.81	0.001	25
2	0.31	0.02	32	0.43	0.02	23
3	0.16	>0.05	43	0.53	0.001	26
4	0.33	0.01	39	0.06	>0.05	21
5	0.28	0.05	31	0.35	0.05	19
6	0.37	0.01	30	0.15	>0.05	
7	0.34	0.05	32			
8	0.19	>0.05	34			
9 onwards		>0.05				

Note All values of r are significant except those $P > 0.05$

which failed to fledge (hatched from relatively small eggs) belonged to birds breeding late in the season - probably mostly young birds. The failure in parental behaviour, which appeared to cause the loss of some young chicks slow growth (and possibly feeding rate) in chicks which did not reach fledging may therefore have been associated with a lack of experience in younger birds.

Behaviour at fledging

All departures of Razorbill chicks observed in the present study took place late in the evening and the chick was accompanied by one parent. Some of the previous records of Razorbill chicks leaving the cliffs by day may have been due to disturbance (eg Yarrell 1845; Greenwood 1964); Razorbill chicks, of more than about 2 weeks old, like Guillemots, leap from an open ledge prematurely if unduly disturbed. Other studies have also shown that fledging occurs mainly in the evening (Kay 1947).

On Skokholm the Razorbill chicks were guarded by only one parent on the evening of fledging; the second adult departed to sea as usual well before sunset. The pre-fledging behaviour of both adult and chick at this time was similar to that recorded by Greenwood (1964). However more regular observations established that pre-flighting behaviour occurs on several evenings preceding fledging. At fledging the adult usually followed the chick from the nest, became reunited with it on the sea using a specific call (heard only during fledging) and the birds swam out to sea together.

Observations in 1973 from a hide situated at the bottom of a cliff below a Razorbill colony (The Quarry), enabled fledging from boulder sites to be recorded for the first time. (This has since been described by Lawman (1975a) incorporating some of my observations.) Pre-flighting behaviour started inside the nest site but later the chick would emerge on to a suitable boulder near the site entrance and continue its bobbing

and flapping. There was much calling at this stage - the chick squeaking characteristically and the adult giving the fledging call. When fledging finally occurred, the chick launched itself from a suitable boulder outside the nest site followed closely by the adult. After its first hop, the chick was usually overtaken by the adult which then led the way towards the sea. Whilst the chick and adult were together silence was maintained but as soon as the birds became separated, eg by the chick falling into a crevice, the characteristic calls would recommence.

Although there were usually about 20 Herring Gulls present in the Razorbill colony, no gull was ever seen to take a fledging chick. On one occasion, when a gull alighted near a Razorbill chick the adult immediately ran towards the gull with exceptional speed, gaping, uttering fierce loud growls, and with its wings slightly open. The gull was persistently attacked and soon flew away. The whole incident lasted no more than thirty seconds after which the Razorbill continued leading its chick to the sea. Similar observations were made by Williams (1975) whilst recording Guillemots fledging on Bear Island. Predation of a Razorbill chick after it had reached the sea, accompanied by a parent, was never recorded during the present study. Attacks by either Herring or Great Black-backed Gulls on the chick and adult as they swam out to sea were usually counteracted by diving and underwater swimming by the Razorbills (pers. obs. and C M Perrings - pers.comm.). Unsuccessful fledging attempts recorded during this study were mostly due to a breakdown in normal behaviour, which ended with the adult swimming off alone to sea.

Fledglings separated from their parents were not immediately taken by gulls but sometimes swam up and down below the colony calling all night. Most disappeared before dawn but occasionally chicks were seen below the cliffs the following morning. Usually these chicks persistently

approached groups of adult Razorbills and Guillemots sitting on the water only to be driven away by them. One chick was caught by a Great Black-backed Gull about six hours after dawn (cf Greenwood 1964). These observations, supported by those of Lawman (1975a), indicate that gulls do not constitute a serious hazard to fledging Razorbills on Skokholm. In the 1930s, Lockley recorded a number of rings from Razorbill pulli in Great Black-backed Gull pellets found on Skokholm, suggesting that the Great Black-backed Gulls were once serious predators of Razorbill chicks. Despite an increase in Razorbill ringing and systematic searches for rings, none have been found in gull pellets recently. The Great Black-backed Gull population has declined since Lockley's time through culling, but Herring and Lesser Black-backed Gulls have increased drastically in numbers in recent years.

Behaviour of adults after fledging

Feeds were sometimes brought in the early morning to sites from which a chick had fledged the previous evening. On these occasions the bird bringing the fish would sit in the empty site for a while before returning to sea with the fish. One, or occasionally both, adult birds of a pair would sometimes return to the colony after the chick had fledged. On Skokholm these birds spent considerable amounts of time each day for up to a week in their old nest sites or in the loafing areas of the colony. When both birds were seen together on land after the chick fledged, it was assumed that the chick had been lost during or shortly after fledging; young birds must be dependent on their parents for some time after fledging.

Nineteen birds were individually identified on land (without mates) after their chicks had apparently fledged. In 11 out of 12 of these cases where the sex was known, the bird seen on land was the female of the pair, indicating that the male had accompanied the chick. In other

cases the same individual (of undetermined sex) was seen on land in two or three consecutive years of the study after the chick had fledged.

The short nestling period in the Razorbill

Data on the nestling development and feeding regimes of several species of auk have been reviewed by Sealy (1973a). He described the development of those species whose chicks are precocial (eg Ancient Murrelet in which the 'nestling period' is perhaps only 24 hours) or semi-precocial such as a majority of species, including the Puffin and Black Guillemot Cepphus grylle in which the nestling period is relatively long. Three species have chicks which show an 'intermediate' pattern of development, with a 2½ week to 3 week nestling period; these are the Razorbill and the Common and Brünnich's Guillemots.

Cody (1971) has suggested that a shortening of the nestling period evolved to counteract high nestling mortality, compared with that which occurs after fledging. However, this is unlikely to be the only reason for the short nestling period in the Razorbill as nestling mortality is low in the absence of terrestrial predators. It is possible that the shortened nestling period evolved under selection pressures (perhaps involving heavy chick predation) that have since diminished.

The alternative possibility is that natural selection has favoured a system where chicks accompany the adults to the feeding grounds, enabling the exploitation of more distant food supplies (Sealy 1973a). As the main food species migrate from the Irish Sea in July (see iib), this would seem to offer an advantage to Razorbills from the Pembrokeshire island.

Adults and fledglings of both species are rarely seen from land after the end of the breeding season, possibly because they have moved after the shoals of Sandeels. At at least one other Irish Sea breeding

colony, however, young Guillemots are often seen feeding just offshore after fledging (N Hammond - in litt.) which suggests that suitable feeding conditions may persist near some colonies even late in the breeding season. Feeding conditions must vary widely at different colonies and even from one year to the next so that young which become mobile early in their lives are an obvious advantage. Equally important is the fact that the young can accompany their parents to sea at an early age, the adults can safely start their wing moult during which they are flightless. Seasonal patterns of weight change in several auk studies have shown that the adults are at their lowest annual weight immediately after the breeding season (Bédard 1967; Sealy 1972; Sealy 1975b), so that a readily available food supply may be especially important to them at this time. The short fledging period in the Razorbill undoubtedly has several inter-related potential advantages; it is impossible to distinguish the most important of these.

Discussion of fledging in the Razorbill

The fledging behaviour of Razorbills and Guillemots has been studied in detail at several British colonies by Greenwood (1964) and in the arctic by Williams (1975). Greenwood suggested that the birds fledged in the evening so as to avoid the threat of being taken by gulls, but that they had not evolved the habit of entirely nocturnal fledging (as in the Puffin for example) because of the need of parent and chick to remain together during and after the journey to the sea. Previous studies at colonies in the Arctic had shown that predation levels at fledging could be almost twice those observed during the other stages of the breeding season (Tuck 1960); the predators recorded at arctic colonies include Great Black-backed and Glaucous Gulls, Larus hyperboreus, Great Skuas Stercorarius skua, Gannets, hawks, owls and bears. Thus, the timing of fledging appears to be a compromise between two opposing selection pressures.

In Greenwood's colonies relatively little predation was actually recorded (less than 1% of 772 Razorbill and Guillemot fledgings observed), but he demonstrated a strong synchrony in the timing of fledgings on any one evening. The lack of any significant predation pressure in this study led to the suggestion that synchronous fledging, having evolved under conditions of serious threat from predators, has been maintained as a behaviour pattern although the threat had recently diminished.

Synchrony in the timing of fledging was also recorded by Williams working at a considerably larger breeding colony (approx. 70,000 U.aalge and U.lomvia). Here predation was the main cause of loss at fledging (17.5% of all chicks at risk) and the chance of predation was greater for chicks leaving the cliffs before or after the main fledging period each evening (2030-2230 hours). Thus, it appeared that at peak fledging the predators were 'swamped' by their prey enabling a majority of the chicks to fledge safely. Chicks landing on a beach or rocks at the foot of the colony were more vulnerable to predation than those landing on the sea. Williams attributed the difference in predation rate between his study and Greenwood's to a basic difference in terrain at the colonies studied. However, I know of no high levels of predation on fledging auk chicks being recorded from a wide range of different types of breeding colonies studied throughout Britain and Ireland (eg Skomer - Birkhead 1976; St Bee's, Cumbria - N Hammond in litt.; Bempton - S C Madge pers.comm.; Fair Isle - R Broad pers.comm.; St Kilda - M P Harris pers.comm.; Cliffs of Moher, Co Clare & Skellig Michael, Co Kerry - pers.obs.). A more plausible reason for this difference would seem to lie in the relative size, and hence the attraction to potential predators, offered by the huge multi-species breeding colonies of seabirds in the arctic.

In both the present study and that of Greenwood the main cause of fledging failure was a breakdown in behaviour between parent and chick though this was not an important factor in William's study. It remained difficult to explain therefore why, if the predation pressure is so insignificant, fledging does not regularly occur in daylight when the parent - chick contact is easier to maintain.

b. Feeds to the chick

Methods

The main observations of Razorbill chicks being fed were made from a hide at Twinlet Bay on four days in 1972 and six days in 1973. A total of 48½ hours' records were collected between 0400 and 2000 on these occasions; most watches were made between 0400 and 0900 when feeds were most abundant. The number of chicks under observation at any one time varied from four to thirteen. Although feeds were relatively infrequent, the speed with which the adult bird disposed of the fish to its chick after arriving at the nest limited the number of sites that could be kept under close observation at one time. Not all feeds were therefore recorded in full detail but whenever possible the following points were noted:

Species of fish in load
Number of fish in load
Approximate length of fish (compared with parent's bill)
Number of fish eaten by the chick
Time of a feed

As all the chicks were of known age, the feeds recorded could then be examined in relation to the age of the chick. Detailed records of the times of arrival and departure of the off-duty bird at each nest

site were also kept in order to determine how long each adult was absent from the cliff before returning with food for the chick.

1) Species composition of feeds

It was only possible to collect Razorbill food samples when an adult bird dropped fish in the nest site. This happened very occasionally, during feeding or when an incoming bird was surprised by a gull or a human. In spite of their non-random and incomplete nature, these samples were useful in identifying the species of fish involved in the other feeds recorded.

Sandeels, Ammodytes spp., from 20 to 150 mm long were the commonest food species, both in the samples collected and in the visual observations made from the hide. Some Clupea spp. were also found in the food samples. The most usual species was A.marinus (identified using Wheeler 1969 and Langham 1968), but a few A.lancea were also noted and a single A.lanceolatus. No attempt was made to identify any larval stages found in the samples.

Harris (1970b) noted a similar range of Razorbill prey on Skokholm and Skomer. On Gaesholm, Razorbill chicks were fed exclusively on small Herring Clupea harengus during the year of Paludan's (1947) study, although relatively few feeds appear to have been observed. On Lundy, Perry (1940) recorded Ammodytes spp. and Clupea spp. in Razorbill feeds, whilst in the Gulf of St Lawrence the chicks were fed on A.hexapterus but the adults switched to other species as they became abundant locally (Bédard 1969).

Comparison of diet in different species of seabirds is usually based on samples of food destined for the chicks (eg Pearson (1968). Most temperate seabirds breed when food is most abundant and easily obtained, so presumably interspecific competition for food is relatively

rare. At other times, competition may be avoided by more specific differences in food requirements and by the birds' distribution at sea. Little is known of the food of adult Razorbills but the distribution of a majority of the British and Irish wintering population is separated from that of the Guillemot or Puffin (eg Mead 1974).

2) Number and size of fish in a feed

Most Ammodytes and Clupea brought to the chicks in the present study were between 35 and 50 mm in length (Table 4.17); this was also the commonest size of Ammodytes collected from Puffins carrying fish for their young in 1972. The weight of each Razorbill feed in which the number, species and estimated length of fish were known was calculated using the following expression - $Y = 0.27X - 0.33$ where Y = fresh weight of fish in g, X = length of fish in mm ($r = 0.41$, $P < 0.001$, $n = 148$). The expression was obtained from a sample of sandeels collected from Puffins in 1972; too few clupeids were collected to make similar calculations worthwhile, though length for length they must have provided the chicks with more food than sandeels.

In the present study, up to about 20 sandeels were brought to the chick, held crossways in the adult's bill (see Nash 1975). Perry (1940) recorded five or six fish as being the usual size of feeds on Lundy, but the chicks rarely eat more than four fish. Between one and four sandeels per feed were recorded in Bédard's (1969) study.

There was no significant difference in the estimated weight of feeds brought to chicks of different ages ($r = 0.17$, $P > 0.05$, $n = 126$) nor did the number or length of fish vary with the chick's age ($r = 0.02$, $P > 0.05$, $n = 94$ and $r = 0.09$, $P > 0.05$, $n = 95$ respectively). Observations during four consecutive nestling periods (1970-73) at Twinlet Bay suggested that there were marked individual differences in feeding strategy - some birds tending to bring many relatively light feeds while others

Table 4.17 Size range (mm) of fish brought to Razorbill and Puffin chicks in different studies.

Colony	Ammodytes spp. n	x	St.dev.	Range	Clupea spp. n	x	St.dev.	Range
RAZORBILL								
Skokholm 1972-73	168	53.1*	20.1*	20-140	21	53.8	21.7	25-110
Skokholm & Skomer 1962-63	11	79.0*	25.5*	52-158	1	74.0	-	-
North Rona 1972	3	137.0	-	120-153				21
Shetland 1974	2	124.0	-	-				
PUFFIN								
Skokholm 1972	148	54.6*	25.6*	15-85				
Skomer 1969	207	53.1	-	33-65	529	37.4	-	24-43
Skomer 1970	551	57.2	-	33-67	97	46.0	-	26-65
Skokholm & Skomer 1962-63	66	64.0*	6.4*	42-76	10	52.0	7.5	42-79
Farne Is.	219	75-100	-	50-150				
North Rona 1972	46	71.5	-	62-82	-	-	-	21/45-109/117
Shetland 1974	(12	62.6	10.5	-	A. lancea			
	(36	120.0	20.8	-	A. marinus			

Note Sources of information as follows:

Skokholm 1972-73	Present study
Skomer 1969-70	Corkhill 1973
Skokholm & Skomer 1962-63	Harris 1970b
Farne Islands	Pearson 1968
North Rona 1972	Evans 1975
Shetland (Hermaness) 1974	Harris pers.comm.

* Comparison of 1962/63 and 1972 data for Razorbills $t = 3.302$, $P = 0.01$
for Puffins $t = 1.414$, $P > 0.05$

brought fewer heavy ones. However the relationship was not significant (Figure 4.19). It was not possible to collect sufficient quantitative data on this but the differences were undoubtedly consistent from one year to the next. Possibly the difference in feeding strategy obscured any possible effect of the chick's age on the size of the feeds.

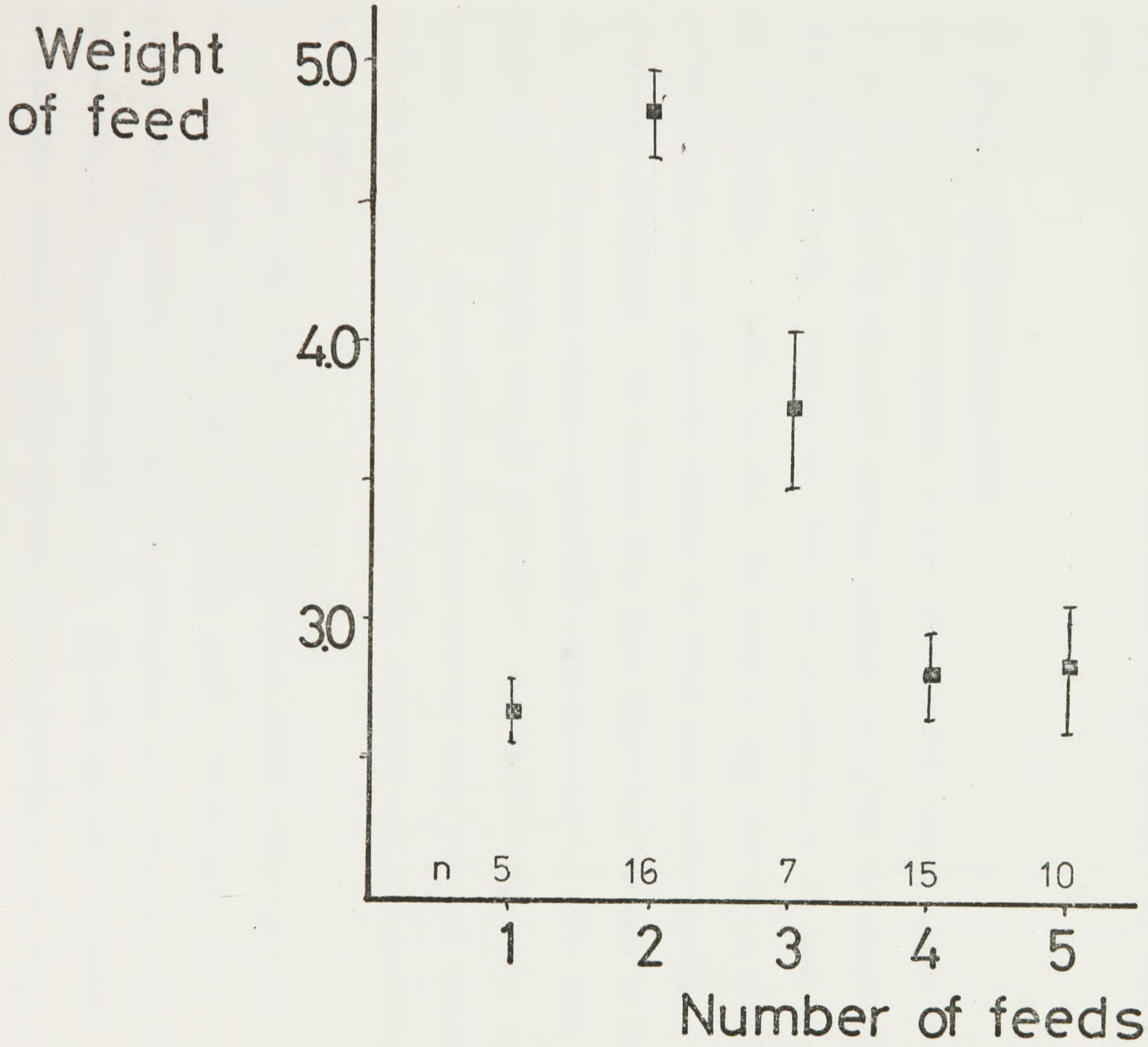
Harris (1970b) showed that the average size of fish brought to young Razorbills and Puffins differed significantly so that competition for food was reduced. Later studies (Corkhill 1973) have confirmed this difference although the overlap in the size range of fish taken by the two species, at least on the Pembrokeshire islands, is extensive (Table 4.17). Corkhill's (1973) study showed a wide variation in the range of food brought to Puffin chicks (both in species and size) during two consecuvtive years and Evans (1975) found differences within one season so care must be taken in interpreting results.

5) Feeding behaviour

Although Plumb (1965) referred to the retention of the yolk sac obviating the necessity for food until the third day of life, the chicks in the present study were fed by both adults from immediately after hatching until the day of fledging. Paludan (1947) and Bédard (1969) also recorded feeds soon after hatching.

When a bird arrived at the nest site with fish, the brooding bird stood up to expose the chick. The food was then presented to the chick by the incoming adult. The chick took one fish at a time, turned it round and swallowed it head first. If a fish was dropped it was picked up either by the chick or one of the parent birds which then presented it to the chick. The sandeels or clupeids were usually swallowed in quick succession and often after a large feed the younger chicks were unable to stand up or move. Usually all the fish brought were eaten

Figure 4.19 Mean weight of each feed ($g \pm 1$ standard error) between dawn and 1000, compared with the total number of feeds brought to the chick during that time. Relationship is not significant ($r=0.03, P > 0.05, n=46$).


Weight of feed
5.0
4.0
3.0
n 5 16 7 15 10
1 2 3 4 5
Number of feeds

but if any remained the adult bird would persistently offer them to the chick or allow the brooding adult to eat them. In some cases dropped fish was left in the nest site, ignored by both adults. This fish occasionally attracted Jackdaws but they were rarely successful in scavenging. After a feed the chick almost always defaecated, usually over the edge of the ledge or towards one corner of the nest cavity; this obviously aided nest hygiene.

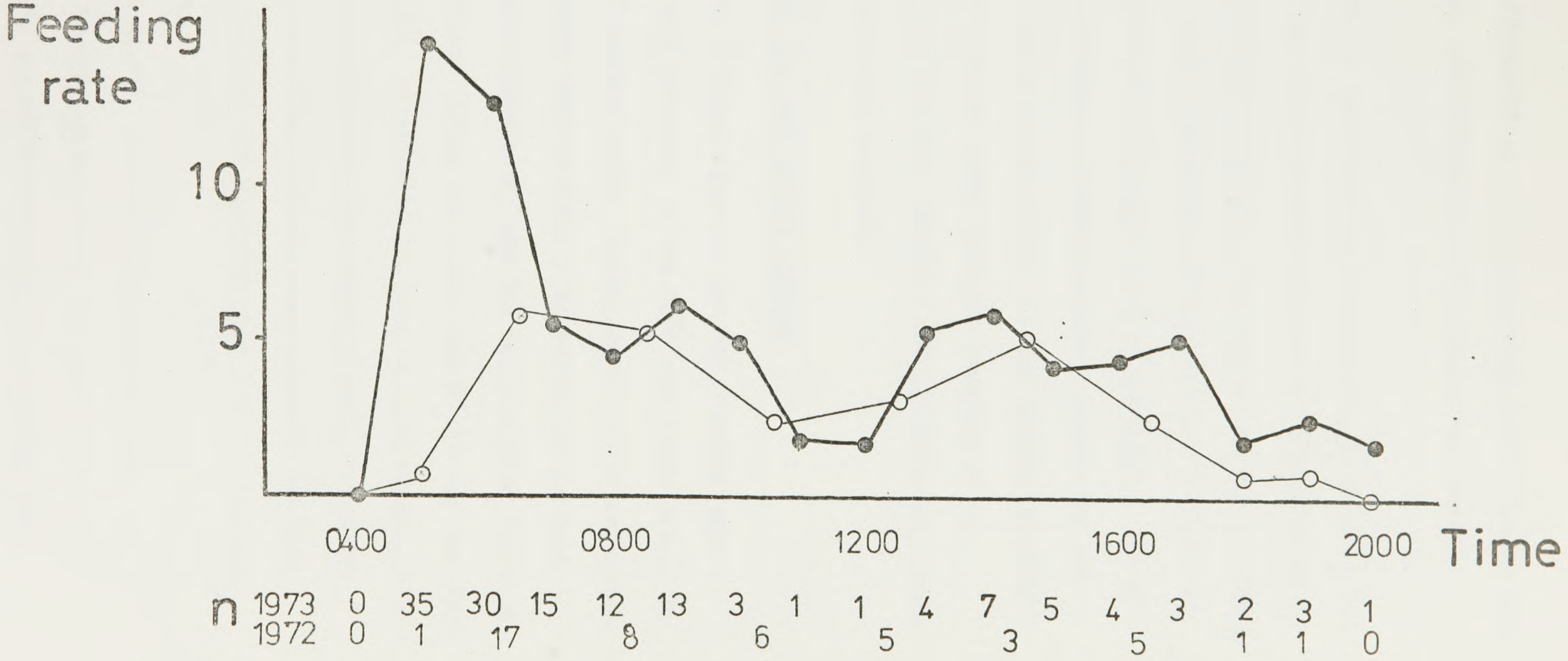
Razorbills were never seen to parasitise each other in the present study as described by Ingold and Tschanz (1970), though M P Harris has seen Razorbills chasing Puffins and successfully stealing fish (pers. comm.).

4) Timing and frequency of feeds

The diurnal pattern of feeding in both 1972 and 1973 showed a peak in the feeding rate in the early morning (Figure 4.20), but the weight of fish brought to the chick in each feed was independent of the time of day ($r = -0.03$, $P > 0.05$, $n = 81$). The state of the tide had no effect on the feeding rate, probably because the birds were mostly feeding offshore (see below). On average only three feeds were brought to each nest per day in 1972, compared with five feeds/nest/day in 1973; this difference arose mainly from an increase in the feeding rate during the morning in 1973. The difference between the two years was also reflected in the growth rates (see c2). Perry (1940) recorded only two feeds/nest/day on Lundy.

Both Perry and Birkhead (1976), on Skomer, noted early morning peaks in Razorbill feeds. In the present study, the off-duty birds spent on average more time on land in the afternoon (1200-1700) than in the morning or the evening (Table 4.18). It was, however, impossible to determine whether the birds did not need to fish for either themselves

Figure 4.20 Hourly feeding rate (number of feeds recorded per nest each hour per 100 minutes of observation) at Twinlet throughout the day on different dates in 1972 ○—○ and 1973 ●—● .The number of feeds observed are given on the bottom lines.



or their chicks in the afternoons or whether the fish were actually less available late in the day, possible because the shoals sink deeper (Russell 1930).

The chicks could only be heard calling on calm days at Twinlet but the frequency with which the chick was fed appeared to be determined by the adult birds alone: although the chicks never seemed to beg for food, they also rarely refused food. The amount of time the adults spent at sea seemed to be independent of the chicks' food requirements. Bédard (1969) suggested that the feeding rate was determined not by the age or appetite of the chick but by the abundance of food readily available locally. Observations of auks and other seabirds breeding on Les Îsles Sainte-Marie indicated that when food was locally abundant, feeds to the Razorbill chicks were most frequent.

5) Length of absence from the nest whilst fishing

More than half (22) of the 39 first feeds of the day recorded were brought by the off-duty bird returning to the nest soon after dawn. In these cases the period of absence whilst fishing could not be estimated. If the adult appeared without fish at dawn, a take-over at the nest site usually occurred almost immediately and the relieved bird departed to sea. The length of absence before the first feed of the day was then about one hour (Table 4.19). As the bird had been fasting overnight in these case, it probably collected food for itself as well as for its chick during its absence from land. For the other feeds in the day, the birds were away from the nest for anything from 4 to 177 minutes before returning with fish.

Observations of auks during five boat trips to the island of Grassholm and The Smalls lighthouse and two to the South Bishop lighthouse (see Figure 2.1) showed concentrations of feeding birds between 9 and 13 km due west of Skokholm; Razorbills were observed

Table 4.18 Attendance of non-brooding birds during the nestling period: the percentage (± one standard deviation) of time for which the off-duty bird was present, based on counts every 15 minutes during hide watches at Twinlet 1973.

	Dawn to 1200	1200 to 1700	1800 to dusk
Percentage attendance	37.4 ± 3.0	50.7 ± 3.4	17.7 ± 3.5
n	21	19	11
t	13.0	25.4	
P	<0.001	<0.001	

Table 4.19 Mean length of absence (minutes) before returning with a feed. Observations between dawn and 1000 at Twinlet in 1973.

	Length of absence	Standard deviation	Sample size
First feed	58.4	6.9	14
Second feed	67.3 *1	8.1	30
Third feed	46.5 *2	9.5	13
Later feeds	40.5	10.4	11

Note * marks significant differences ($P \leq 0.05$): $t = 2.03$ [1], $t = 2.43$ [2]

Table 4.20 Mean length of absence from nest (minutes) before returning with fish on different days in 1973. (Dawn to 1200)

Date	Length of absence	Standard deviation	Sample size
June 22	75.5	10.5	16
June 26	44.9	6.7	22
June 29	65.0	7.9	24
July 9	21.7	2.0	6

Note The difference between successive days are all significant - $t = 11.09$, $t = 9.39$, $t = 13.12$ respectively, $P < 0.001$.

flying to this area and returning in the direction of Skokholm and Skomer carrying fish. Tuck and Squire's (1955) observed Brünnich's Guillemots feeding mainly within 16 km of the breeding colony whilst Puffins from the Farne Islands are known to travel as much as 187 km (Pearson 1968); Corkhill (1973) estimated the probable maximum range of Puffins from Skomer as 37 km.

Razorbills are capable of sustained flight at at least 48 kph (McKittrick 1929) so birds from Skokholm required about 12 to 16 minutes of flying time to reach the feeding ground. This suggests that during their absence from the nest the birds had plenty of time in which to fish for themselves and to collect a feed for the chick. Razorbills off Grassholm were seen catching several fish in one dive and departing landwards with them. The fish were often still twitching when brought to land and the adult birds sometimes had water on their plumage. As the birds rarely alighted on the sea before flying to the nest, this suggests that the fish were usually freshly caught when the birds returned to the colony. It seems likely that the actual location of the shoal of fish may have occupied some of the birds' time but the constant stream of auks flying between the offshore feeding grounds and the breeding colonies on Skokholm and Skomer must have helped to guide the birds to the best fishing areas (Ward and Zahavi 1973).

The mean length of time for which the birds were absent varied significantly on different days (Table 4.20), possibly depending on the proximity of the fishing grounds. Corkhill (1973) noted that rough weather influenced the size and species composition of feeds to Puffin chicks, but no similar correlation was detected in the present study nor could the amount of time the birds spent fishing be related (albeit subjectively) to prevailing weather conditions. The idea that during the present study, fishing conditions were generally good is also

supported by the fact that in 1973 some birds could adequately feed two chicks at the same time (see iiid).

c. Growth in chicks

Introduction

Razorbill chicks were measured during the three seasons of the study in order to calculate the rate of growth and compare growth in different seasons. This was also compared with similar records published for other species. The different parameters of growth are discussed below and a further analysis made of the possible effects of prevailing weather on development.

1. Preliminary analysis

Method

Chicks in some of the easily accessible nests in the study colonies were measured regularly:

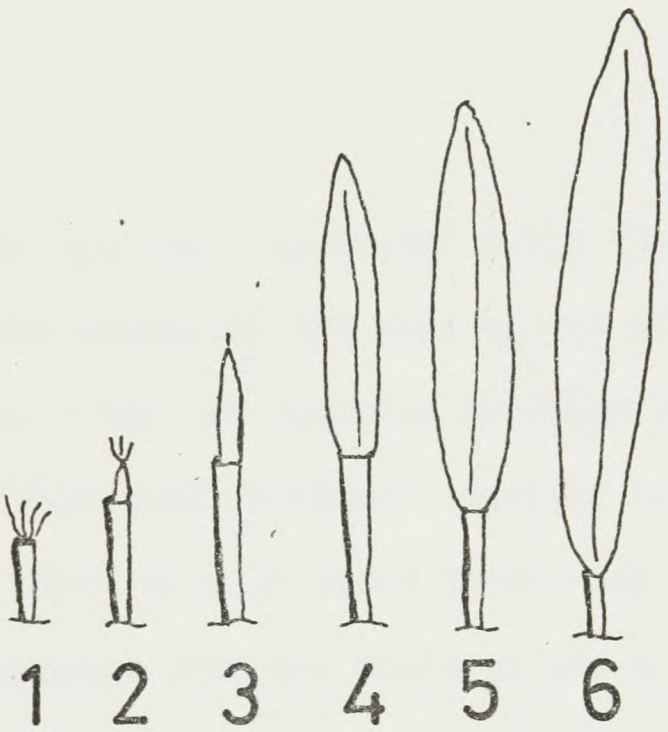
I) The chick was placed in a plastic bag and weighed (when necessary suspended inside a bucket) with a 'Pesola' spring balance to the nearest 0.5 g if it was under 100g or else to the nearest 1g. Weighings were not possible in very windy weather.

II) The total length and the total sheath length of the innermost primary covert on the right wing were measured to the nearest 0.5 mm using a pair of dividers (Figure 4.21). (The primaries themselves do not start to grow until after the chick has left the nest.)

III) The tarsus length was measured to the nearest 0.5 mm by the method shown in Spencer (1972).

During 1971 37 chicks from sites on The Bluffs were measured every day between 0700 and 1030. In addition, 60 chicks in other study colonies were weighed and measured daily from Day 1 (hatching) to Day 4,

Figure 4.21 Growth of primary covert feathers in Razorbill chicks. Stage 1:3-6 days, Stages 2 and 3:7-9 days - both the feather and the sheath lengths are measurable, Stage 4:10-11 days - length of the projecting feather twice that of the sheath, Stages 5 and 6:12 days onwards - feather continues to grow, sheath sloughs off.



at least twice between Day 5 and Day 14 and each day again from Day 15 to fledging (usually about Day 17).

The following year chicks from 29 sites on The Bluffs were weighed and measured every day and 31 chicks at other colonies usually every other day. In 1973, 26 chicks from the Bluffs were weighed each day throughout the nestling period. (Chicks from selected sites in the other study colonies were also weighed daily as part of the twinning experiment described in d. below; these are not discussed further here.) No measurements of tarsi or feathers were made in 1972 or 1973.

Results

I. Weight.

The growth curves obtained are shown in Figure 4.22; these were calculated from the mean weight of all chicks of the same age in each year. Weight increased rapidly from Day 1 and the increase levelled off about Day 14. The average daily weight increment increased steadily to a peak of 12.5 g at the end of the first week of life; after this less weight was gained each day and the average over the whole period was about 7g. Chicks weighed in 1973 were considerably heavier than those in either of the other two years.

A slight loss in weight occurred in some chicks at the end of the nestling period, although sample sizes after day 18 are small (Table 4.21). The mean weight lost in those chicks that did undergo recession amounted to about 6% of peak weight, little more than the overnight weight loss of 5%. Growth appears to check shortly before fledging and probably continued at a slower rate again afterwards.

Bédard (1969) recorded a much greater late nestling weight loss, amounting to 14% of peak weight (Day 14) at fledging (Day 17) in Alca torda pica chicks. Arrested weight increase at the end of fledging with small weight losses in some individuals are usual in auk species (Uria

Figure 4.22 Mean weights (g) of Razorbill chicks at different ages (days).
■—■ 1971 (n=716) ○—○ 1972 (n=425) ▽—▽ 1973 (n=363)
All standard errors are less than 5g.

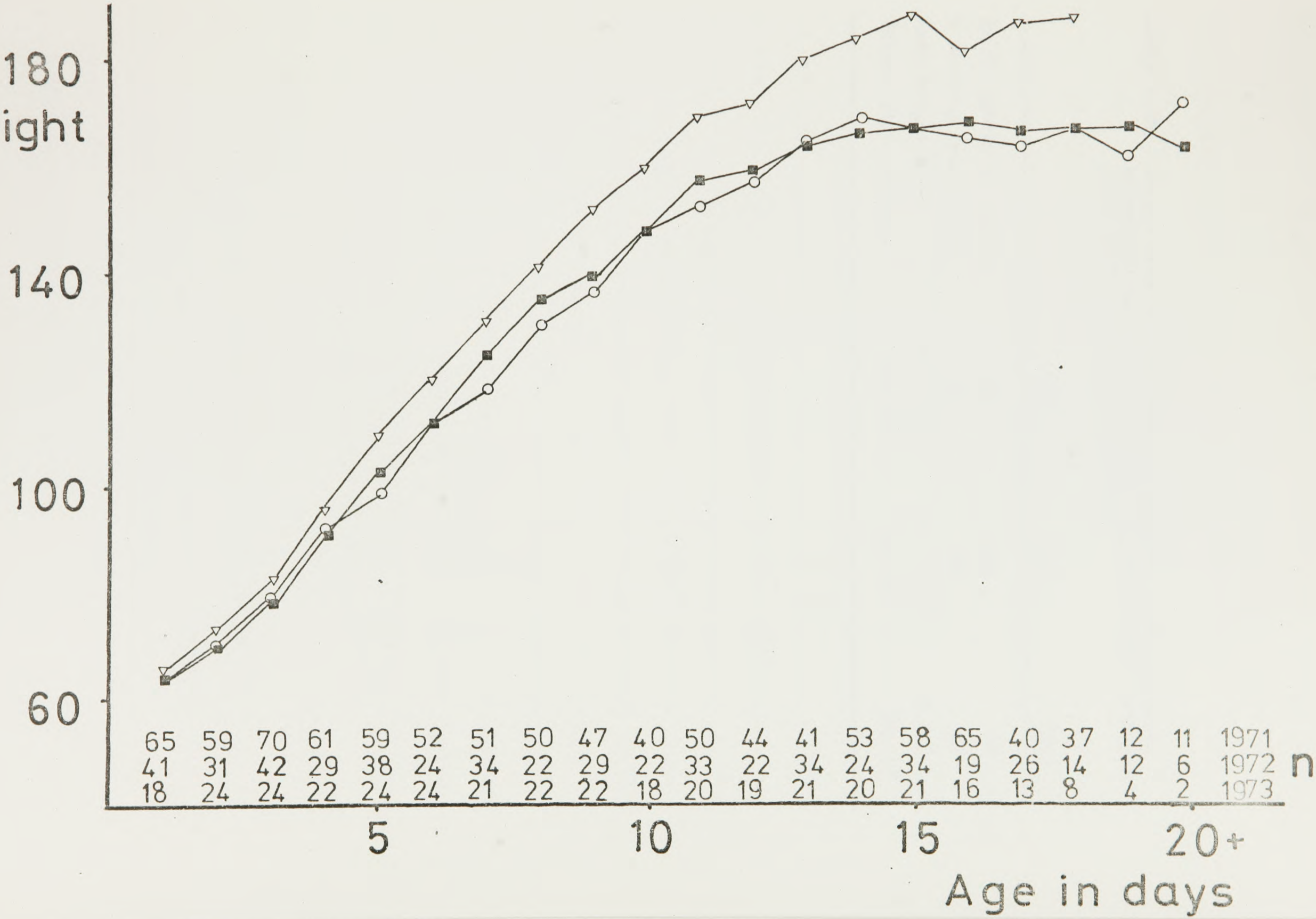

180
Weight
140
100
60
65 59 70 61 59 52 51 50 47 40 50 44 41 53 58 65 40 37 12 11 1971
41 31 42 29 38 24 34 22 29 22 33 22 34 24 34 19 26 14 12 6 1972
18 24 24 22 24 24 21 22 22 18 20 19 21 20 21 16 13 8 4 2 1973
n
5
10
15
20+
Age in days

Table 4.21 Weight loss in late nestling period; timing of loss, proportion of chicks affected and mean weight lost per chick (g ± 1 standard deviation).

	1971	1972	1973
Total number of chicks	75	40	22
% showing weight loss	44	29	41
Mean weight lost	9.9 ± 0.8	11.2 ± 2.1	10.3 ± 2.0
Weight loss started	Day 16	Day 14	Day 15

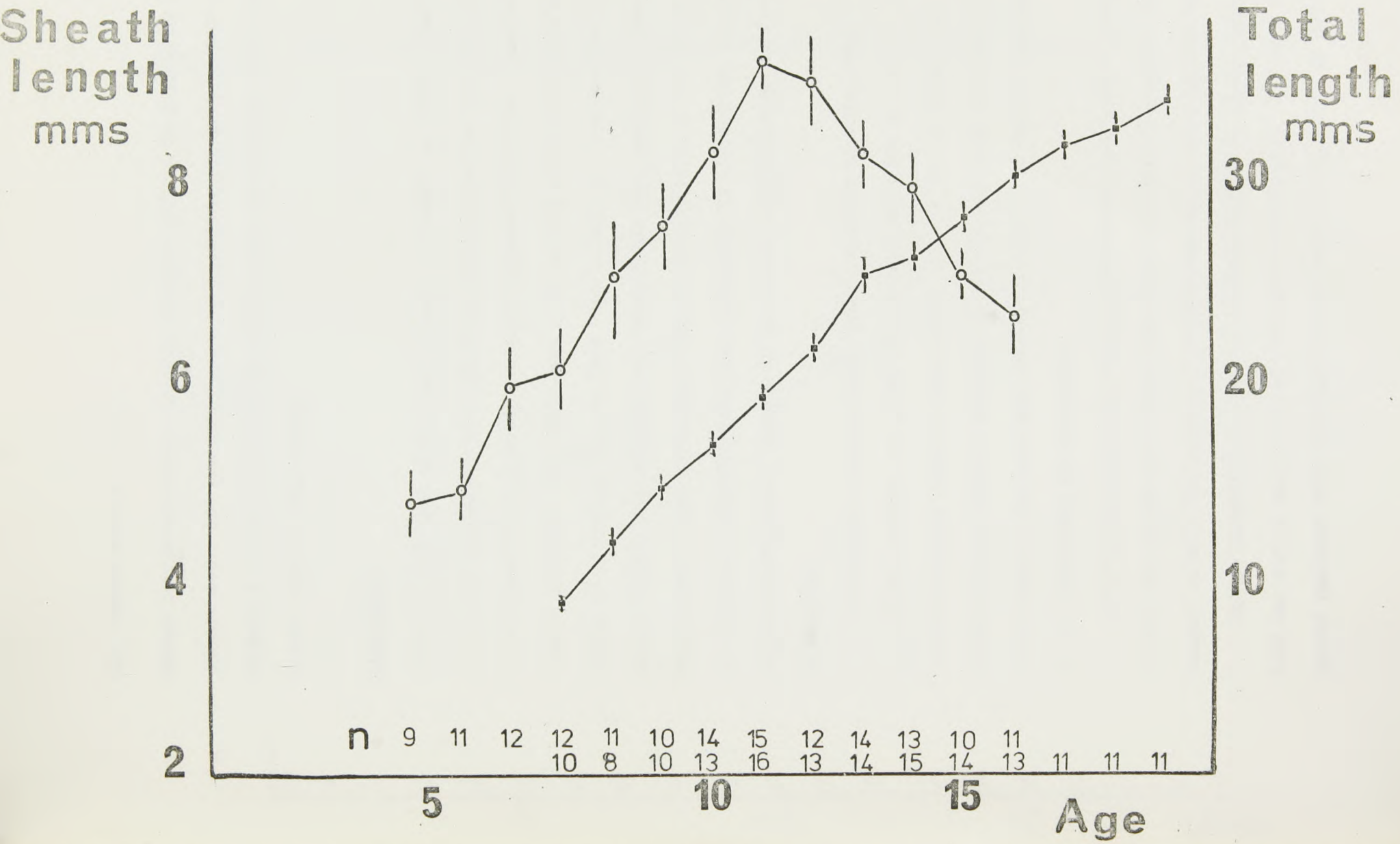
aalge Tuck 1960, Cerorhinca monocerata Richardson 1961, Cepphus grylle Winn 1950, Cepphus columba Drent 1965, Fratercula artica Harris 1976, Ptychoramphus aleuticus Thoresen 1964). Behavioural changes involving increased energy requirements and water loss by maturing tissues appear to be two main causes of weight loss at this time (Ricklefs 1967a; 1968a). Observation of Razorbill chicks before fledging showed they increased the amount of wing-flapping and other activities on the evening preceding fledging (pers.obs. and Lawman 1975a).

At fledging the Razorbill chicks weighed on average about 25% of adult weight. This is slightly lower than the weights quoted by both Brun (1959, 28%) and Plumb (1965, 30%) for Skokholm birds, possibly because these figures were based on the same three individuals weighed in 1958. The weight at fledging appears to differ in different latitudes. In the sub-arctic, Razorbill chicks, like those of both Common and Brünnich's Guillemots, fledge at a similar weight to those further south, hence considerably lighter relative to the adult weight. However, they require a nestling period of 20-25 days (Belopol'skii 1957; Kartashev 1960) because of the slower rate of growth associated with the colder climate and hence the extra energy required to maintain heat. Similarly guillemots breeding still further north have the same long nestling period and their chicks fledge at an even lower weight (Uspenski 1956; Belopol'skii 1957; Kartashev 1960; Tuck 1960).

II Feather growth

The feather sheath, like weight, increased in length from Day 1 to a peak on Day 11 (Figure 4.23). After this the sheath broke away from the base of the feather and decreased in length to 4.5 - 5.0 mm at fledging. The total feather length increased steadily from Day 7 to reach 40% of that of the adult at fledging.

Figure 4.23 Feather growth shown by measurements of inner primary covert (mm). Sheath lengths (o—o) and feather lengths (■—■) are given ± 1 standard error.


Sheath length mms
Total length mms
8
6
4
2
30
20
10
n 9 11 12 12 11 10 14 15 12 14 13 10 11
10 8 10 13 16 13 14 15 14 13 11 11 11
5
10
15
Age

III Tarsus growth

Tarsus length increased steadily to about 32.5 mm 16 days after hatching (Figure 4.24) and was fully grown at fledging, possibly because it is important for the chicks to be able to swim efficiently after fledging before they are full grown.

Discussion

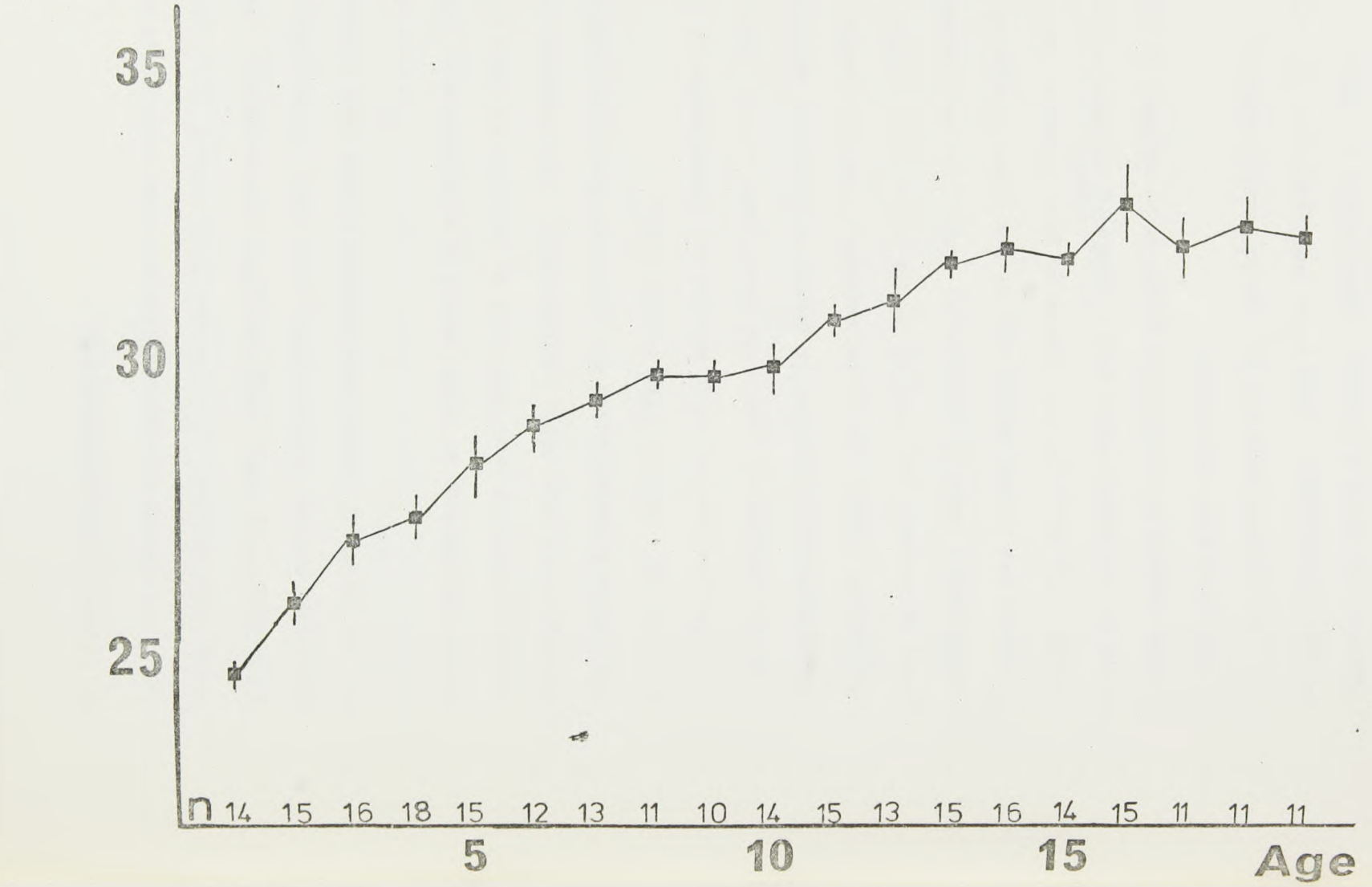
Weight is the most widely used measure of growth in young birds because it is easy to measure with relative accuracy even in very young chicks. It is biased as a recently fed young appears older than it actually is. Growth curves in this study were based on the average weight of all chicks of a certain age, so that those which had just been fed to some extent should have balanced out those which were awaiting a feed. Weight gave a good indication both of the condition of the chick and of changes in prevailing feeding conditions or differences in growth in successive years, presumably paralleled by differences in feeding conditions.

In Razorbill chicks sheath length could be measured from an early age (Day 2) onwards and gives a good representation of feather growth up to the age of about 11 days; after this it was of little use. Total feather length could be measured throughout the time the Razorbill chicks were in the nest and provided a measure of feather development in the later part of the period.

Although tarsus length could be measured throughout the nestling period, the length at hatching was about 76% that at fledging (adult length) so that the amount of growth observed in the nest was small.

In the Razorbill the growth observed whilst the chicks were on land was only a small part of the total development. The rest of the growth occurred when the chick was at sea, and the birds do not reach

Figure 4.24 Tarsus growth shown by mean lengths (mm ± 1 standard error) at different ages (days).



adult size until almost two years old.

2. Further analysis of growth

Growth in chicks of many seabirds has been represented by weight curves; these have included auks (Paludan 1947, Bédard 1969, Tuck 1960, Myrberget 1962, Winn 1950, Drent 1965, Thoresen 1964, Richardson 1961) and other species (Harris 1966a; Snow 1960; Nelson 1964). Differences in the growth of chicks from different sized eggs (Skoglund 1952) have been compared by the examination of their weight at a certain age and daily weight increments have been used to indicate the rate of growth (Spaans 1971; Dunn 1975; Koelink 1972). The amount of food provided by the adults also indicates the growth of the chick (Myberget 1962; Koelink 1972; Spaans 1971; Royama 1966).

The analysis of daily weights and measurements of body size show only the pattern of growth and development so that other quantitative measurements are required if growth in different individuals or successive seasons are to be compared. For this reason an attempt was made to estimate the rate of growth in Razorbill chicks based on measurements taken in the present study. In the Razorbill, weight increase was linear during much of the first 14 days of life (Figure 4.22). The slope of the regression line fitted to the points on this part of the growth curve gave a suitably accurate estimate of growth rate, though other methods of determining growth rate outlined by Ricklefs (1967b; 1968b) were also considered.

The growth rates for all chicks weighed during the three years are shown in Table 4.22. This shows that growth in 1973 progressed faster than in the other two years. Observations of feeding frequencies at Twinlet (see b4) also showed that in 1973 the chicks were receiving on average 1.7 as many feeds per day as in 1972. The growth rate of the

Table 4.22 Growth rates based on regression line fitted to chick weights from Day 1 to Day 14. X = Age in days
Y = Weight in g.

Year	Growth rate (g per day weight increase)	Growth equation	Sample size
1971	8.7	Y = 8.7 X + 56.7	716
1972	8.6	Y = 8.6 X + 55.4	425
1973	9.7	Y = 9.7 X + 58.8	299

Note Values of d : (* P< 0.05)

	1972	1973
1971	0.11	1.86
1972	-	1.99*

Table 4.23 Growth of chicks which failed to reach fledging age in 1971 compared with the mean. (X = Age of the chick in days, Y = Weight in g.)

	Growth equation	Sample size
Non-fledging chicks	Y = 4.9 X + 54.0	16
Mean	Y = 8.7 X + 56.7	716

Note Non-fleding chicks grew significantly slower than average
d = 4.60, P< 0.001

nine chicks which disappeared before fledging age or were actually found dead in the nest in 1971 was significantly slower than average (Table 4.23).

Growth rate and laying date

Chicks were grouped according to their laying period and growth rates were calculated for each group for the three years of the study. The results (Table 4.24) show no clear effect of laying date on growth. The slowest growth each year could occur amongst chicks hatched at any stage of the season. Hatching weight was closely correlated with egg size (see a) so that the early hatchlings were heavier than those later in the season, following the seasonal decline in egg size.

Weight at fledging was also examined in relation to laying date (Figure 4.25). In all three years the heaviest chicks at fledging were those that hatched earliest in the season. In 1973 fledging weights declined progressively with season, but in the other two years both middle and late chicks fledged at a similar weight, considerably below that of the early chicks. As chick weight was independent of egg size after about the first week of life (see a), the high fledging weight of early chicks may have reflected more frequent feeds by the adults concerned. This may have been associated either with more abundant food early in the season or with a greater efficiency on the part of the adults breeding early in the season. The older birds mainly bred at this time and these were possibly more efficient at feeding their chicks.

In late July and August, when most chicks were leaving the nest, feeding conditions may not have been so good as earlier in the season. By late July the second generation of Ammodytes lancea have not yet produced larvae and the single generation of A.marinus have mostly dispersed from the Irish Sea (Cameron 1959). Only A.lanceolatus was

Table 4.24 Growth of chicks from different laying periods.
(X = Age of chick in days, Y = Weight in g.)

Year	n	Growth equations: Early laying period	n	Middle laying period	n	Late laying period
1971	167	Y=9.6 X+52.3	317	Y=8.2 X+59.5	168	Y=8.8 X+54.0
1972	131	Y=8.4 X+58.9	177	Y=8.7 X+56.0	104	Y=8.8 X+52.5
1973	132	Y=9.4 X+66.3	119	Y=9.4 X+61.3	106	Y=8.5 X+61.0

Note Significance of different growth rates; values of d marked * are significant ($P \leq 0.05$)

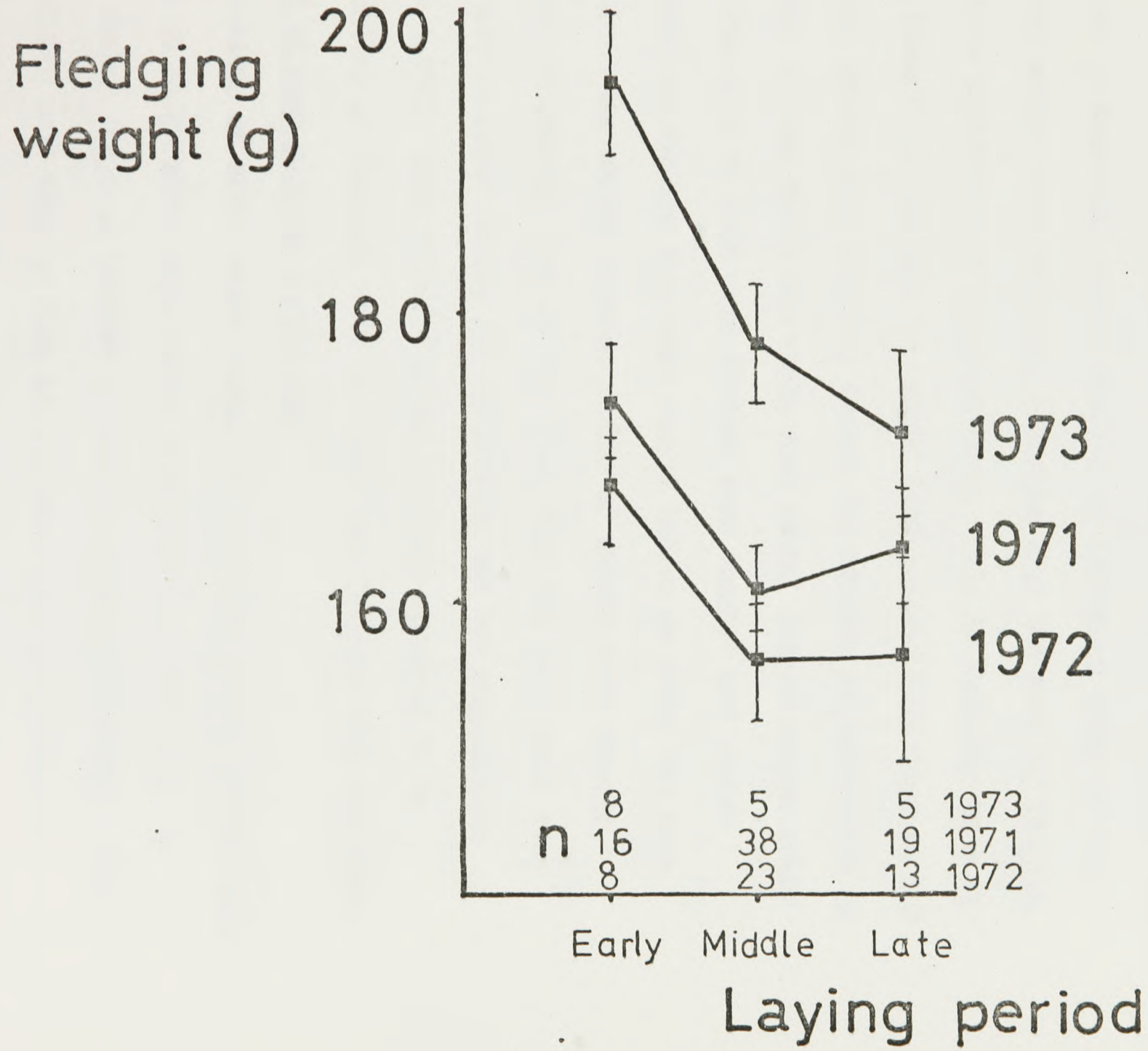
		1971			1972			1973	
		E	M	L	E	M	L	E	M	L
1971	E	-	2.50*	1.36	2.35*			0.70		
	M		-	1.01		0.89			2.82*	
	L			-			0.10			0.08
1972	E				-	0.60	0.67	3.05*		
	M					-	0.10		2.14*	
	L						-			0.19
1973	E							-	0.05	2.10*
	M								-	1.87
	L									-

Table 4.25 Number of birds ringed as chicks on Skokholm and retrapped as breeding adults in relation to the date upon which they were ringed. Date x = Day on which the maximum number of chicks were ringed.

Year	Ringed before date x	% Recovered	Ringed after date x	% Recovered
1963	36	2.8	120	1 8.3
1964	63	0.0	58	5.2
1965	82	3.7	73	6.8
1966	81	3.7	73	11.0
1967	62	12.9	137	5.8
1968	101	5.9	94	1.1
1969	112	0.9	150	4.7
1970	105	4.8	114	2.6
Mean		4.3 ± 1.5		5.7 ± 1.2

Note Difference in means is not significant. Wilcoxon matched-pairs signed-ranks test $T = +12$, $P > 0.025$.

Figure 4.25 Mean fledging weights (g ± 1 standard error) of chicks from different laying periods. Analysis of variance showed that the differences between the groups were significant only in 1973 ($F=2.47, P>0.05$, $F=1.05, P>0.05$ and $F=6.57, P=0.01$ for the three years respectively), although in each year chicks fledging early in the season were significantly heavier ($P\leq0.05$) than those fledging in the two later periods.


Fledging weight (g)
200
180
160
1973
1971
1972
n
8 5 5 1973
16 38 19 1971
8 23 13 1972
Early Middle Late
Laying period

present in abundance in larval and juvenile stages throughout the Razorbills' nesting period, yet this species appeared to be rarely taken. Thus feeding conditions may have been slightly easier for the birds rearing chicks early in the season, allowing a faster growth than was possible for those reared later in the season. Early young in many species grow more rapidly than late young (Rayfield 1958; Harris 1966a; Spaans 1971).

In a few cases, eg Manx Shearwater (Perrins 1966), early young not only fledge at a higher weight but also have a significantly better chance of surviving to return to breed. The survival of Razorbill chicks fledged at different times of the breeding season were compared, assuming that the date of ringing gave some indication of hatching date. This is probably true as young Razorbills can only be ringed during about 8-10 days in the nestling period (Day 4-12/14) though the ringing of Razorbills on Skokholm covered about six weeks each year. Chicks ringed every year from 1963 to 1970 were divided into 'early' and 'late' depending on whether they were ringed before or after the date upon which the annual maximum number of chicks were ringed. Although on average more of the late than the early young were retrapped in later years, the difference was not significant (Table 4.25). Thus post-fledgling survival appeared to be independent of fledging date in birds bred between 1963 and 1970.

Effect of nest site on growth rate

Observations of adult birds during the nestling period showed that chicks on ledge sites were always accompanied by at least one adult whilst those in boulder sites were often left alone. Thus both adults were able to fish at the same time for chicks in boulder sites but chicks on ledges could be fed by only one adult.

Chicks in open sites were on average heavier than those of similar age in boulder sites but there was no significant difference in the growth rates (Table 4.26). Thus the adults were able to increase the feeding rate to meet the chick's food requirements, even if only one bird was able to fish at a time.

Effect of prevailing weather on growth

Severe weather conditions may make fishing difficult for the adult birds; this apparently happens in the Puffin (Corkhill 1973). Any reduction in the number of feeds resulting from adverse weather conditions could be reflected in the growth of the chicks. For this reason the weights of chicks each day were compared with prevailing weather conditions.

The amount by which the weight of any chick on a given day deviated from the mean weight for that age was calculated by deducting the observed weight from the mean weight of all chicks of that age. The variation in these age-corrected weights on any one day were then related to the prevailing weather conditions and date by a stepwise multiple regression analysis. Date, wind speed, wind direction and cloud cover were used as independent variables (see Chapter 2iiie) but little of the total variation in weight was attributable to them (Table 4.27). In 1972 and 1973, 13% and 9% respectively of the total variation in weight was explained by significant correlations with date and wind direction but in 1971 only 3% of the variation could be explained, by correlations with cloud cover and date. Other factors such as the availability of food obviously had a much greater effect on the chicks' growth than the prevailing weather.

Table 4.26 Growth in chicks from nest sites on ledges and under boulders. X = Age in days Y = Weight in g.

	Growth equation	n
Boulder sites	$Y = 9.1\ X + 56.5$	151
Ledge sites	$Y = 9.1\ X + 58.0$	179

Note Difference in growth rate is not significant.
$d = 0.11$, $P > 0.05$.

Table 4.27 Results of regression analysis for the effect of weather on chick weight. Correlation coefficients (R) are given for the factors which on their own had a significant effect ($P \leq 0.05$); the combination of factors which most efficiently predicted the variation in the dependent variable is also given, with the percentage of variation explained (R^2)

Year	Singled independent factors	Combination of independent factors	
1971	Date + 0.49	+ Date - Cloud cover	3.2%
1972	Date + 0.33	+ Date + Wind direction	12.7%
1973	Date + 0.31	+ Date + Wind direction	8.9%

The variation from the average weight increased as the season progressed so that the chicks weighed late in the season deviated most widely from the expected growth pattern. This may also have reflected the possible deterioration in food supply which caused the early chicks to fledge on average heavier than the late chicks (see a.). Cloud cover also appeared to affect the chicks' growth with largest deviation from the mean growth pattern in clear weather.

d. Twinning experiments

Introduction

Apparent two egg clutches were regularly found in small numbers during the present study (see iih and Appendix VIII). If these had hatched successfully, what would have been the advantage, in terms of breeding productivity, to a bird attempting to rear two chicks? The results of preliminary experiments in 1972 suggested that Razorbills were probably unable to recognise their own eggs or chicks (Appendix LX). Therefore it was not expected that a total rejection of the chick by the foster parents would cause the failure of the experiment described below.

Experiments with artificial broods have shown that several species of seabirds can sufcessfully raise more than the usual number of young per nest to fledging (Larus glaucenscens Vermeer 1963; L. fuscus Harris and Plumb 1965; Creagrus furcatus Harris 1970c; Rissa tridactyla Coulson in Lack 1966; Sula bassana Nelson 1964; S. capensis Jarvis 1974; Puffinus puffinus Harris 1966a; Perrins et al. 1973; Fratercula arctica Nettleship 1972; Corkhill 1973; Ptycoramphus aleutica Manuwal 1972). In the Red-billed Tropicbird Phaeton aethereus,

two chicks were raised instead of the usual one, under natural conditions (Stonehouse 1962). Plumb's (1965) study of the Razorbill showed that some birds could raise a second chick. There was no evidence that the Razorbills on Skokholm were ever short of food. In 1973, in fact they apparently had little difficulty in feeding their single chick.

Method

In 1973 a second chick was introduced into 14 sites the day after the chick hatched. The introduced chicks were of the same weight as the original chicks; the twinned chicks in all 14 sites were weighed each day. Four sets of twins were watched throughout the day on July 2 and the frequency, timing and size of feeds brought to them were recorded. One adult in each pair was colour-ringed so that the share of duties and the time each bird spent away from the nest could be established.

Results

The introduced young were fed by their foster parents and there was no difference in survival to fledging between true and introduced chicks (Table 4.28). However, in only two out of the fourteen sites did both chicks survive to fledging.

Growth in the experimental chicks was still significantly slower than average (Table 4.29) and all surviving chicks fledged at a lighter weight than those in other colonies fledging at the same time (Table 4.30). Even the chicks which started off with a twin and lost it during the nestling period were heavier at fledging than the four twin chicks that fledged.

The average number of feeds brought to the sites with twins (Quarry) was compared with that to sites with single chicks (Twinlet) (Table 4.31). There was a peak in feeding between 0400 and 0500 , immediately after dawn in both colonies (Figure 4.26). The number of

Table 4.28 Survival of 14 true and 14 introduced chicks in twinning experiment 1972.

	True	Introduced
Died	1	1
Disappeared	5	5
Fledged	8	8

Table 4.29 Growth in twinned chicks compared with mean for 1973
(X = Age in days Y = Weight in g.)

	Growth equation	n
Twinned chicks	$Y = 4.4\ X + 60.1$	308
Control chicks	$Y = 9.7\ X + 58.8$	299

Note Difference in growth rates is significant $d = 4.92$, $P < 0.001$.

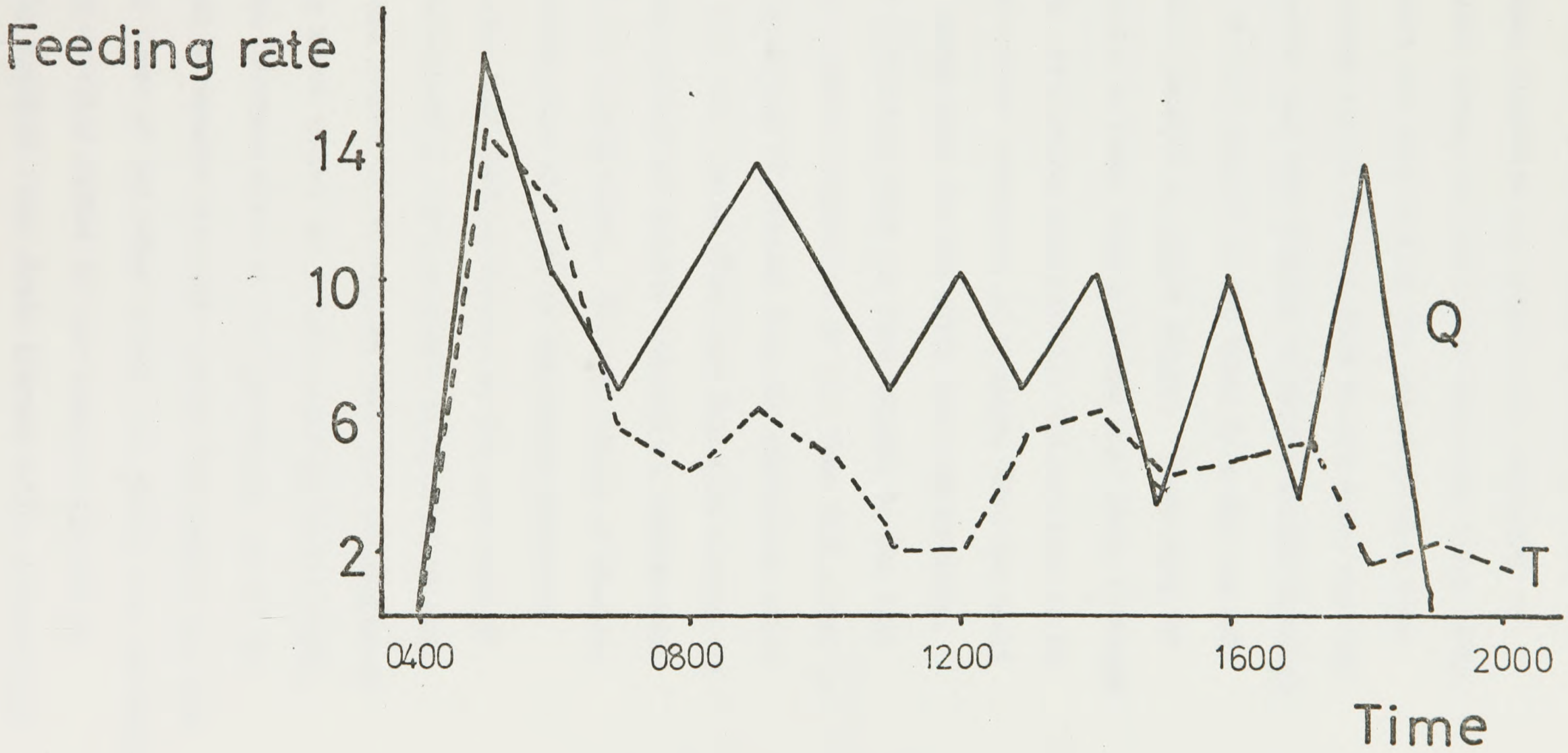
Table 4.30 Fledging weights of twins (g $\pm$ 1 standard deviation) compared with other chicks in same colonies. Differences are significant $P < 0.01$.

	Mean fledging weight	n
Control chicks	194.5 ± 10.4	18
Successful twins	129.5 ± 4.5	4
Single chicks fledging from a site given twins	159.4 ± 1.9	16

Table 4.31 Feeding regime for twinned (Quarry) and single (Twinlet) chicks. Means are given $\pm$ 1 standard deviation with sample sizes in brackets; all differences between twins and single chicks significant $P < 0.001$.

	Single chicks	Twin chicks
Absence preceding feed (minutes, dawn - 1000)	58.7 ± 39.1 (46)	35.7 ± 8.5 (15)
Total number of feeds/nest/day	4.7 ± 0.5 (6)	9.0 ± 1.2 (4)
Average estimated weight of each feed (g)	3.9 ± 2.3 (81)	4.4 ± 0.6 (27)
Total estimated weight (g) of food/nest/day	22.0 ± 2.2 (6)	40.3 ± 7.0 (4)

Figure 4.26 Hourly feeding rate (number of feeds/nest/100 mins. observation each hour) at sites with twins ——— (Q,Quarry) and single chicks - - - (T,Twinlet).



feeds to twins remained relatively high (0.5/nest/hour) for the rest of the day compared with single chick sites (0.2/nest/hour). The total number of feeds during one day to sites with twins was on average significantly higher than the number of feeds to the Twinlet sites, but the latter were open ledge sites where only one adult was able to fish for the chick at a time. The calculated average weight of each feed to the twins was also significantly greater than that brought to single chicks although the total weight of food brought to the twins in a day was only 1.8 times the amount brought to single chicks. Thus, when the adults had two chicks to feed, they collected more food, although not twice as much. As feeding rate normally did not seem to be influenced by the chicks' behaviour, it appeared that the adult birds with twins compensated for the extra food requirements.

There was no indication that the food brought to the twin chicks differed in species composition or size from that given to single chicks. The length of absence from the nests with twins before returning with food varied from less than five minutes to two hours; the long periods of absence recorded at Twinlet were never observed at the Quarry sites. The mean length of absence whilst fishing between dawn and 1000 at the Quarry sites was significantly shorter than that at Twinlet at the same time of day ($t = 9.4, P < 0.001, n=61$). Data on duties undertaken by each bird at the nest are scarce but it appears that the two adults at each of the Quarry sites shared the feeding equally (Table 4.32).

In six of the fourteen sites in the experiment, one of the two chicks appeared to receive few feeds though the reasons for this are not clear. In three of the other sites, both chicks were evidentally fed throughout the nestling period but one remained lighter in weight and probably received fewer feeds (Figure 4.27). Observations of the twinned chicks showed that they competed vigorously for food

Table 4.32 Share of feeding duties at sites with twin chicks in the Quarry.

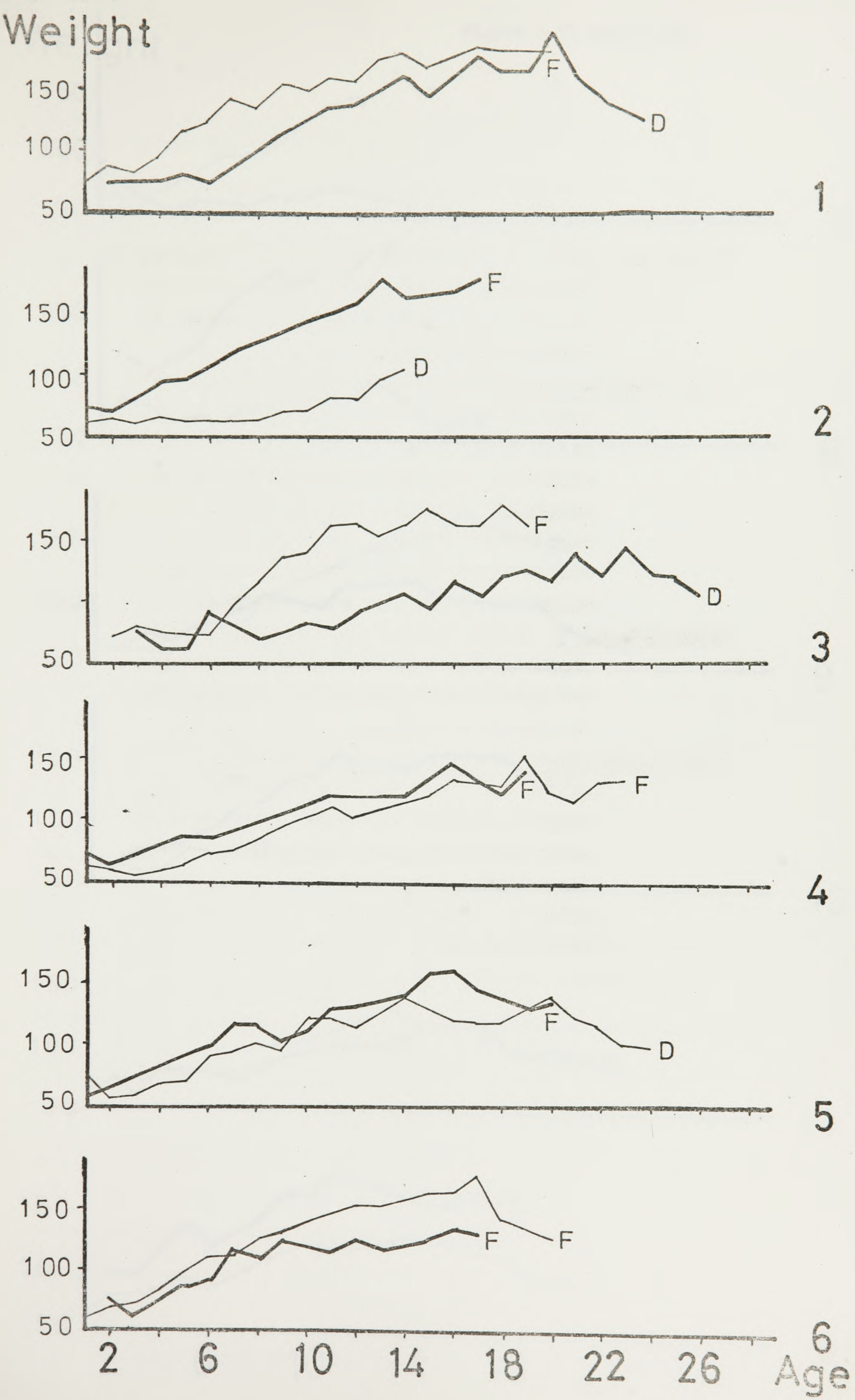
	Site number				
	2	4	6	10	Total
Total number of feeds by colour-ringed bird	3	5	4	0	12
Total number of feeds by unringed bird	3	1	5	2	11
Total number of feeds by unidentified bird	1	3	3	6	13
Total number of feeds observed	7	9	12	8	36

Figure 4.27 Growth of twinned chicks shown by weight (g) at different ages (days). The heavy line is the introduced chick. F=fledged, D=disappeared, X=found dead in site.

Sites 1,4,5,6, and 11 Both chicks remained almost equal in weight for most of the nestling period, until one chick fledged. The remaining one then lost weight until it too fledged (in 2 sites) or disappeared (3 sites) 3-5 days later. (The chicks that fledged were seen to do so, but those that disappeared were considered too loww on weight for normal successful fledging.)

Sites 3,9, and 12 Both chicks grew steadily but one was always lighter than the other; in each case the lighter chick disappeared 2-4 days after the other one fledged.

Sites 2,7,8, and 10 (and the two others not shown on the graph) One of the two chicks hardly increased atall in weight throughout the nestling period, whilst the other grew normally and fledged successfully. The under-weight chick died or disappeared either before (5 sites) or after (1 site) the other chick fledged.


Weight
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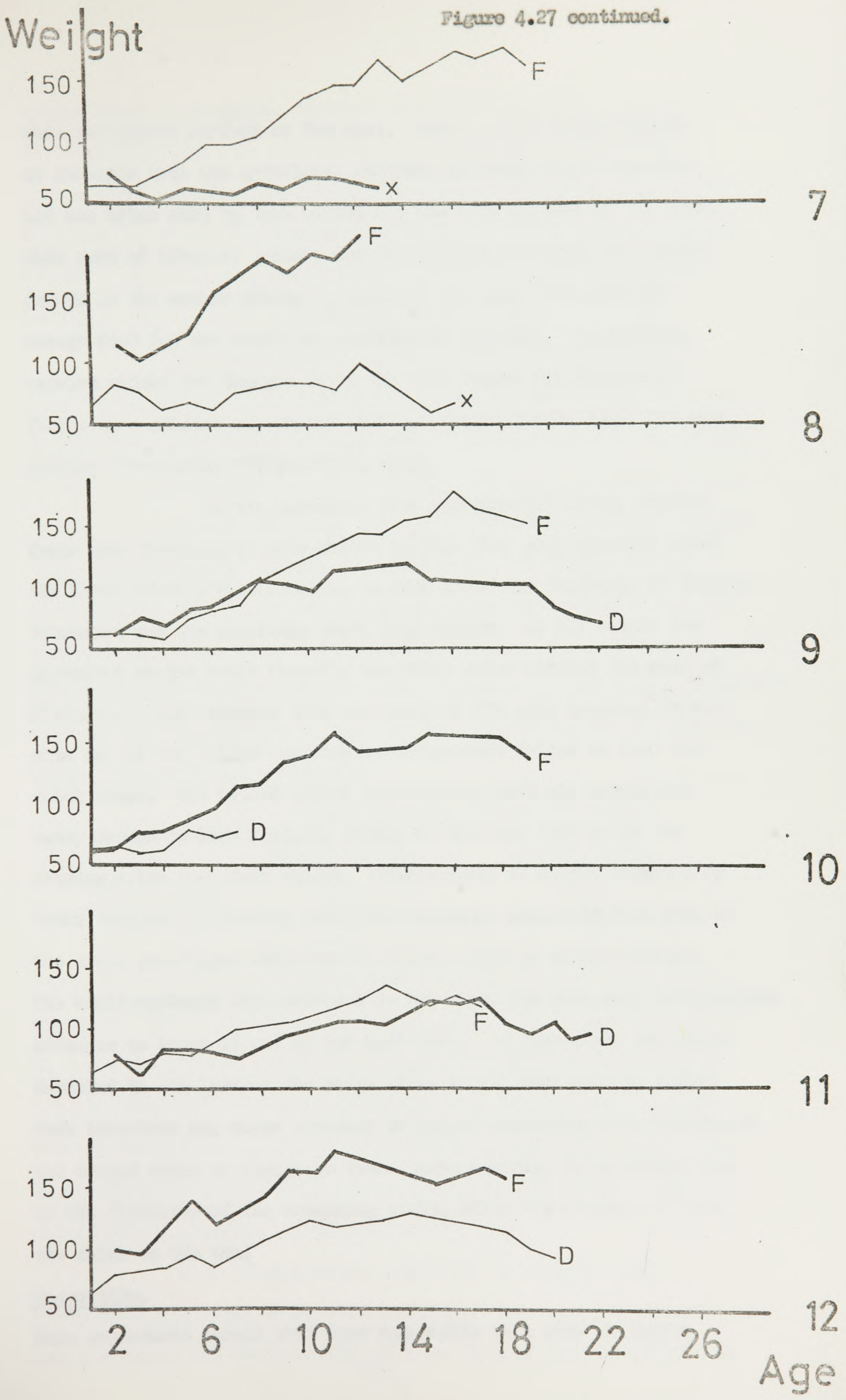
Age

Figure 4.27 continued.



when the parent arrived at the nest. Once a chick became larger or stronger than its artificial sibling, it would become dominant and was often able to take almost all the food brought to the nest. This sort of behviour quickly led to the loss of weight and slower growth in the weaker chick, in spite of the fact that more than enough food for one chick was arriving at the nest. Competition between chicks was thought to be the main reason for failure to fledge in a similar experiment with Razorbills (Plumb 1965) and with Puffins (Nettleship 1972;Corkhill 1973).

In the remaining five experimental sites, regular feeds were received by both chicks so that they grew normally until the first chick fledged. Then, in each case, the frequency of feeding decreased and the remaining chick lost weight. As all chicks are dependent on one adult (usually the male) after leaving the nest at fledging, it was assumed that one adult of the pair departed to sea with one of the chicks and the remaining adult failed to feed the chick alone. The second chicks were however both old enough and heavy enough to have fledged, either at the same time or on the evening after the first chicks. Observations of chicks deserted by their twin on the evening after its fledging, suggested that none of the usual pre-flight behaviour in either adult or chick occurred. The adult appeared disinterested in the chick and made only half-hearted attempts to bring it out of the nest site. In some cases the adult departed to sea leaving the chick alone in the nest for the night; such behaviour was never recorded in normal conditions. The failure of the second chick to fledge in these cases appeared to be mainly due to the inability of the remaining adult, often the female, to take the chick to the sea.

Discussion.

This experiment showed that some Razorbills were able to rear a

second chick to fledging. Whether this would have been possible had twins been put into open ledge sites (where only one adult at a time could probably have fished for the chicks) was not established. Observations on feeding frequency and growth rates in normal (single) chicks showed that food was especially abundant in 1973. Thus it is possible that the birds are not always able to rear twins.

In Plumb's (1965) study, if the author's assumption that the chicks which left the nest at a low 'fledging' weight after an extremely short nestling period had fledged successfully is correct, 14 chicks survived from the original 24. This gives a fledging success of 58%, compared with the usual 78% and a productivity of 1.17 fledged young per nest, compared with the usual 0.78. Similarly, in the present study only 57% of the chicks survived (92% normally) but the productivity increased to 1.14 chicks per nest. An accurate comparison of productivity however must take into account egg loss during incubation. Assuming the rate of loss is the same for clutches of one and two eggs, nesting successes are as follows:

	Number of young fledged per pair	
	Single clutch	Double clutch
Plumb (1965)	0.53	0.81
1973	0.73	0.83

Hence the overall gain in chick production if two chicks are raised instead of one is probably very small. If the habit were advantageous it seems likely that it would have been selected for and successful two egg clutches would be encountered. Possibly the collection of extra food to form a second egg in spring and the delay in breeding that this could infer is the critical factor which makes a larger clutch size impossible in the Razorbill.

Four other species which normally produce single young have been shown to be able to raise twins to fledging. The North Atlantic and South African Gannets (Sula capensis) both raised

twins, though the fledging weights of twinned chicks in both studies were significantly lighter than that of the controls (Nelson 1964; Jarvis 1974). Jarvis showed that the immediate post-fledging survival in S.capensis was related to fledging weight so that twinned chicks may have survived relatively poorly. The post-fledging survival of twinned S.bassana chicks may have been similarly reduced.

Manx Shearwaters successfully raised twins in two seasons and post-fledging survival rates of these were as high as that of the controls (Harris 1966a;Perrins et al.1973). The Swallow-tailed Gull is a nocturnal feeder and unique among gulls in having a cluthh of one. Experimental additions of eggs showedthat the birds could both hatch two eggs and raise two young (Harris 1970c). None of these twins have been recorded back at the colonies on the Galápagos Islands in later years so post-fledging survival may have been poor (Harris pers.comm.).

In the present study, the mean weight at fledging was significantly less in both the successful twins and other chicks raised for part of the nestling period as a twin (Table 4.30). In Plumb's experiment too, the average weight of the successful twin chicks at fledging - assuming the one that disappeared weighing only 97g did not fledge - was 159g, compared with that of controls 189g. (Statistical comparison is not possible on available published data.) In the Razorbill post-fledging survival appears to be independent of weight at fledging; time will tell if the twinned chicks in the present experiment survived after fledging.

Young Gannets and Manx Shearwaters fledge alone and must learn to fend for themselves. Weight at fledging is critical if fat reserves are needed while they learn to plunge-dive (gannets) or have to undertake a transequatorial migration (shearwaters). Razorbill chicks remain with the adult for at least several weeks after fledging so that weight may be less critical for survival.

iv. Breeding success

Breeding success in the study colonies was measured by:

1. Percentage of eggs laid (first eggs and replacements) that hatched = Hatching success.
2. Percentage of chicks hatched that fledged = Fledging success.
3. Percentage of pairs of breeding to breed that produced a fledged young = Nesting success.

Breeding success varied in the different years of the study (Table 4.33); the differences were not significant and in the following discussions data from all three years are combined.

a. Breeding success and laying date.

The breeding success of birds laying at different stages in the season are shown in Table 4.34. Although hatching success was independent of egg volume, more of the eggs laid early in the season hatched (on average 75% of those laid in Intervals 1 - 3) than those laid at the end of the season (63% in Intervals 4 & 5). Egg volume was correlated with laying date (iic), so that birds laying early in the season not only produced large eggs but also had had a high hatching success compared with those laying later in the season. The frequency of replacement of lost eggs also declined from 57% early on, to 3% of those lost in Interval 4 and none of those lost at the end of the season.

Fledging success remained fairly constant throughout the season, but chicks hatched from late eggs had least chance of fledging. Thus the overall nesting success was highest (83%) in pairs which laid for the first time in Interval 1, mainly because a large proportion of first eggs lost were replaced. Nesting success decreased seasonally so that only 56% of all pairs laying in Intervals 4 and 5 produced a fledged chick. A decline in nesting success with season has been noted in other seabirds (Harris 1969a; 1969c). This can often be at

Table 4.33 Breeding success (%) at the 14 larger study colonies

	1971	1972	1973	1971-73
Number (1st) eggs laid	257	236	242	735
Hatching success	73	68	71	70
Fledging success	92	96	93	94
Number replacement eggs laid	14	16	24	54
Hatching success	64	69	63	65
Fledging success	100	91	100	97
Overall nesting success	71	69	72	71

Table 4.34 Breeding success (%) in all study colonies in relation to laying date. For definition of terms see text (above and iia1).

	Laying interval				
	1	2	3	4	5
Total number of eggs laid	116	243	198	187	41
Hatching success (Eggs hatched/Eggs laid)	72	78	76	60	66
Replacement of first egg losses	57	51	32	3	0
Fledging success (Chicks fledged/Chicks hatched)	70	72	70	54	61
Nesting success (Chicks fledged/pairs breeding)	83	79	61	56	

least partly explained by relation to the age structure of the population.

b. Breeding success and age

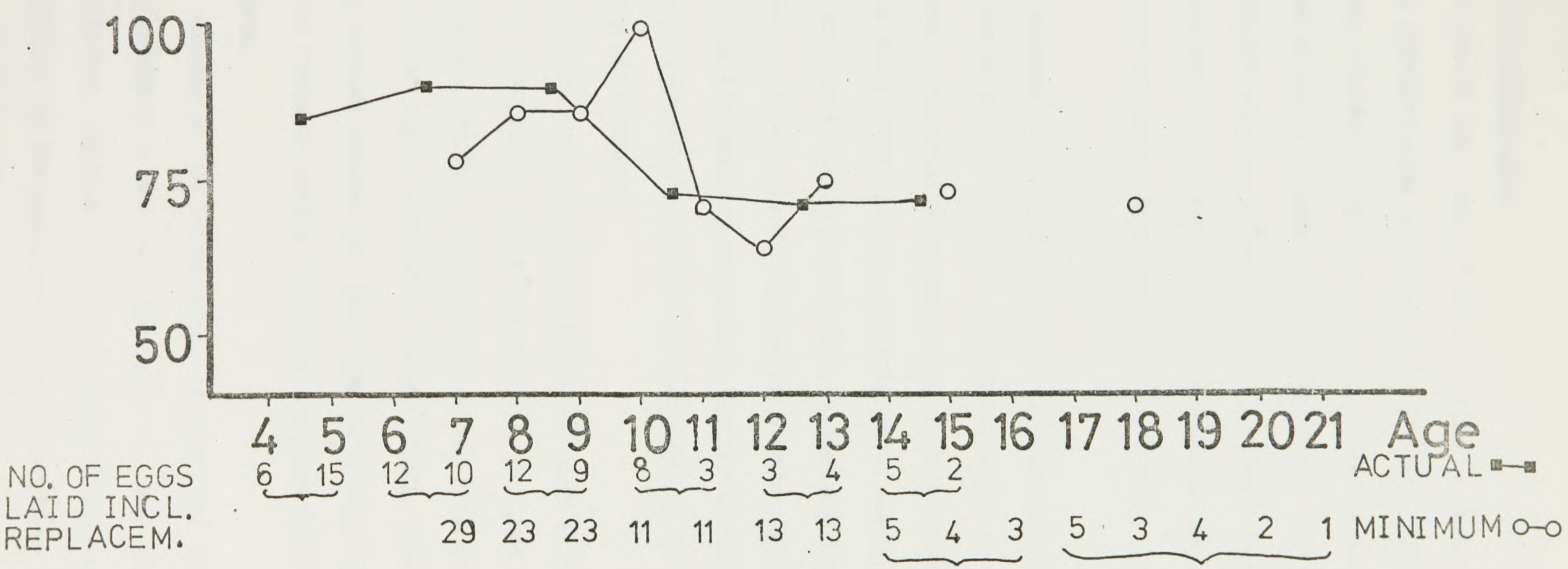
The seasonal decline in nesting success suggested that the birds laying late in the season were in some way less accomplished breeders than those laying earlier. As the youngest birds in the population not only produced relatively small eggs, but also laid late in the season (iif), the effect of age on breeding success was examined more closely.

The relationship between the two is shown in Figure 4.28, based on the number of fledged chicks produced by 48 birds of known age (ringed as pulli) and 71 birds of presumed minimum age (ringed as breeding adults when they were at least five years old). Sample sizes are small but success was relatively low in birds breeding for the first time at four years old; after this breeding was more successful and there is some indication that the birds were most productive between six and ten years of age. Other observations in this study suggest that breeding success may have been enhanced by experience gained with age.

An improvement in breeding success with age has been recorded in a number of species (Lack 1966). This may in turn lead to seasonal differences in productivity of the population as many young birds tend to lay late in the season (eg. Richdale 1957; Coulson & White 1958; Nelson 1966a). Differences in breeding success have been attributed to differential egg loss during incubation associated with the previous breeding experience and hence the age of the individual. In Lesser Balck-backed Gulls intra-specific interference can cause the loss of many clutches laid late in the season (Davis and Dunn 1976). Comparable information is available for several other species although in the Great Tit Parus major, birds of five years and older have a lower nesting success than those aged two to four (Perrins & Moss 1975).

Figure 4.28 Nesting success (% of birds producing a fledged chick) of known age birds.
■—■ 48 birds ringed as pulli and o—o 71 birds ringed as adults.

Breeding success in the youngest birds was probably lower than indicated as some eggs must have been lost immediately after laying before I could find them.



c. Breeding success and colony type

Breeding success was examined in both types of colony (Table 4.35); boulder colonies were separated into the most intensively studied colonies (those visited daily throughout the season) and the relatively undisturbed colonies (visited less frequently). The observation study colonies consisted mainly of ledge sites; records of breeding performance were available for these and for a number of sites in intermediate colonies (included in 'all colonies' group in Table 4.35).

Hatching success was highest in ledge colonies and lowest in the intensively studied boulder colonies indicating that, in spite of their apparent vulnerability to predation, eggs on open ledges survived better than those hidden under boulders. Comparison of the two groups of boulder colonies showed that disturbance may have increased egg loss, although the difference in hatching success was not significant. The low hatching success in boulder sites, compared with that in ledge sites, appeared to be mainly due to heavy predation of eggs by Jackdaws.

Fledging success was high in all study colonies though chicks survived best in undisturbed areas and worst in the more disturbed boulder colonies. Overall nesting success was high in ledge colonies where 80% of pairs produced a fledged chick. The difference in nesting success between the two types of boulder colony was not significant but frequent visits by humans may have slightly lowered breeding success.

Breeding success in the larger study colonies was examined further to see if the grouping or the positioning of the nest sites affected the birds' success. Neither hatching nor fledging success were significantly affected by the grouping of the sites (Table 4.36), nor was breeding success in central and peripheral sites of the larger

Table 4.35 Breeding success (%) in different types of study colony.

	Number of colonies	Number of eggs laid	Mean hatching success	Mean fledging success	Mean nesting success
Intensive study colonies	19	414	66.2 ± 18.1	91.1 ± 8.5	63.8 ± 25.4
Ledge colonies	12	183	79.0* ± 12.2	94.6 ± 8.6	80.1* ± 12.3
Undisturbed boulder colonies	5	94	70.6 ± 20.9	97.5 ± 3.4	72.9 ± 15.9
All colonies		815	71.7 ± 12.9	93.3 ± 5.0	69.3 ± 14.0

Note *Denotes significant difference ($P \leq 0.05$).
Means are shown ± 1 standard deviation.

Table 4.36 Breeding success in single and grouped sites in the Bluffs study colony in 1971.

	EGGS		CHICKS		PAIRS	
	Hatched	Failed	Fledged	Failed	Produced young	Failed
GROUPED	33	8	29	4	29	12
SINGLE	12	4	12	0	12	4
Fisher's exact probability test:	P = 0.25		P = 0.27		P = 0.26	

Note No differences are significant

Table 4.37 Breeding success in central and peripheral ledge sites in Twinlet, Guillemot Point and Wildgoose Bay in 1971.

	EGGS		CHICKS		PAIRS	
	Hatched	Failed	Fledged	Failed	Produced young	Failed
CENTRAL	31	9	29	2	29	11
PERIPHERAL	15	7	13	2	13	9
	$Y^2 = 0.25$ $P > 0.05$		Fisher's exact prob. test $P = 0.30$		$Y^2 = 0.63$ $P > 0.05$	

Note No differences are significant

ledge colonies significantly different (Table 4.37). Kittiwakes, by comparison, breeding at the edge of a colony not only had a lower breeding success than those in the centre, but also had a lower survival rate. Peripheral birds appeared to be of poorer quality and unable to obtain 'better' nestsites (Coulson 1968; Coulson 1971; Coulson & Wooller 1976).

d. Disturbance and other factors affecting breeding success

Disturbance of a breeding colony for whatever cause, gave potential predators an opportunity to approach eggs and young usually protected by sitting adults, so my presence undoubtedly slightly reduced breeding success in certain colonies. The speed of the birds' return to the nest following disturbance therefore partly determined whether or not they lost their egg or chick. Although there was much individual variation (some birds in the more frequently visited study colonies rarely left the site atall), it seems probable that the more experienced breeders, which were usually amongst the first to return to their sites, had least chance of losing an egg or chick as a result of disturbance.

These birds were often the most successful breeders for a number of other reasons too:

i. Being the older birds in the population, they tended to breed early in the season.

ii. They were often able to replace a first egg if it was lost.

iii. They laid relatively large eggs and produced large chicks on hatching which, for at least the first week of life (during which most of the nestling mortality occurred), were slightly heavier than average.

iv. Chicks produced early in the season fledged at a higher weight than those later in the season.

These facts suggest that accumulated experience with age, and the ability to start laying early in the season are important for successful breeding.

Chapter 4

C. BEHAVIOUR OUTSIDE THE BREEDING SEASON

Juvenile Razorbills (like other auks) leave the area of the breeding colony immediately after fledging; I never saw young Razorbills at Skokholm after they fledged. A boat trip on July 9 1973 between Skokholm, Skomer and Grassholm showed that some of the birds moved offshore at this time but appeared to remain in small groups. Razorbills seen on this occasion included four single adults each with a young bird, and one juvenile with three adults. The adults accompanying chicks were seen to dive and surface with fish in their bills. Normally a Razorbill swallows fish underwater so it seems likely that these adults were still feeding the young. Guillemots reared in the laboratory cannot catch fish until they are six weeks old (Oberholzer and Tschanz 1968). Paludan (1947) also records fishermen's reports from the south Baltic of Razorbill chicks, accompanied sometimes by two adults, seen far offshore in autumn. Meltofte (1972) saw only one pair of Razorbills (adult and young) 100 km northwest of Norway (61°N) on July 2, though sightings of Guillemots with their chicks in this area were quite frequent.

Ringing has shown that mortality in the first autumn of life is heavy and many young birds die soon after fledging, especially if there are strong autumn gales. While they are still with the adults, the young from the Pembrokeshire colonies remain in the Irish Sea, although they probably leave the feeding grounds used during the breeding season. First year birds start to migrate south at the end of August, reaching the Bay of Biscay in September, Iberia in October and the Mediterranean and Morocco in November and December. Many young Razorbills, especially from colonies in the north of Britain (and possibly from the Faroes and Iceland)

are shot or caught in fishing nets off the south coast of Norway in the first autumn of life; this does not appear to affect large numbers of birds from the Pembrokeshire colonies (Lloyd 1974).

The birds' behaviour after their first winter is difficult to establish due to the small number of ringing recoveries available. Birds of breeding age do not move far from the breeding colonies; those from Pembrokeshire remain in the Irish Sea and English Channel throughout the winter. Adults from other north European colonies are also dispersive, rather than truely migratory (Lonnberg 1938; Kartashev 1960).

When the adults leave the breeding colonies in July, they undergo a full wing and tail moult during which they are flightless (Salomonsen 1944; many field obs.). Flocks of up to a hundred apparently flightless auks were seen in the vicinity of Skokholm and Skomer during the present study and similar flocks have been recorded elsewhere in the Irish Sea in autumn (A.Taylor, G.A.Miles, P.Watson - pers.comm.). There is some evidence that birds from one colony, or several adjacent colonies, remain together for some time after the chicks fledge. In the 'wreck' of auks in the Irish Sea in the autumn of 1969 (NERC 1971), eight Razorbills ringed as chicks on Skokholm a few weeks earlier were recovered.

Studies of moult in captive Guillemots (possibly somewhat biased by ad lib food supply) have shown that flight feathers grow relatively quickly but body moult progresses more slowly (Birkhead and Taylor in prep.). Primaries can be replaced in 42-90 days and secondaries in less than 25 days, so that the birds are flightless for about 45-50 days. There is a little evidence that pre-nuptial moult starts earlier in the Guillemot than in

the Razorbill (Verwey 1923;Salomensen 1944). This may be an adaptation for the Guillemots' return to the breeding colonies in winter.

CHAPTER 5

SURVIVIAL AND AGE AT FIRST BREEDING

The breeding biology of several of the Atlantic auk species has been studied in both the east and the west of their range. Most studies have either been short-term, lasting two or three years, or have not involved many ringed adult birds so that relatively little has been learnt about the age of first breeding or annual survival. Adult survival rates have been calculated from ringing recoveries for these species.(Birkhead 1974a; Lloyd 1974; Mead 1974), but such data depend on birds washed ashore dead and ringing recoveries do not always give survival rates similar to those found in more detailed studies of marked populations (Grosskopf 1964; Perrins 1971).

Most of the ringing from which the data on survival in this study are derived, dates from 1963 when an intensive campaign of ringing nestlings was started. From 1968 onwards, all nestlings were given a coloured plastic ring denoting their year class so that the age of the birds could be determined from subsequent sight records. The plastic rings, like their metal counterparts, suffered from wear but provided valuable information on the return of young birds to the colony. Since 1970, full grown birds were given a laminated plastic ring on which large numbers were inscribed, enabling the individuals to be identified at considerable distances in the field (Table 5.1 and figure 5.1; see also Appendix IV).

Observations of ringed birds on Skokholm were made during daily visits to the cliffs during the present study and the work

Table 5.1 Number of Razorbills colour-ringed on Skokholm and Skomer 1968-73.

	Adults			* Pulli	
	Skokholm	Skomer	Colour	Skokholm	Skomer
1968	-	-	White	236	-
1969	-	-	Red	302	-
1970	85	17	Yellow	275	188
1971	61	27	Green	271	188
1972	51	26	Blue	215	272
1973	36	11	Orange	223	68
Total	233	81		1522	716

Note * Excluding those which died or lost their colour ring before fledging.
After 1970 chicks on Skomer were colour-ringed on the right leg and those on Skokholm on the left so that the natal colony was known at subsequent sightings.

Figure 5.1 Colour ringed Razorbills on Skokholm. The upper photograph shows a bird ringed as a pullus in 1968 (white colour ring) in the foreground and an adult-ringed bird (C50) in the background. Below, adult-ringed bird (C39) in the foreground - note also the metal ring, and white ring (1968 pullus) behind.





was continued by the staff of the Bird Observatory in 1974. In one study colony, The Bluffs, visited daily throughout the season, the birds became tame and there was a high probability of identifying all colour-ringed birds present. Only two records (out of a possible 86) relate to birds which were missed in one year but seen in the next (2%), compared with 19 out of 226 for the other colonies on Skokholm (8%) and 31 out of 118 for the study colony on Skomer (26%).

i. Fidelity to natal breeding colony

Nearly all Razorbills returned to their natal colonies to breed. Out of 477 ringed birds retrapped on Skokholm, only three had been ringed elsewhere. Two birds, aged two and seven years, had been ringed on Skomer only three kilometres away and the other bird, ringed as a pullus on the Calf of Man (265 Km north), was retrapped breeding on Skokholm in 1970 and recorded in all subsequent years of the study. One Razorbill colour ringed as a pullus on Skokholm in 1969 was found breeding on St Margaret's Island off Tenby (38 Km east; see Figure 2.1) in 1974.

A total of 22 birds ringed as pulli on Skokholm were positively identified on Skomer up to 1974 (Table 5.2) and two of these finally bred on Skomer; no sightings of Skomer ringed birds were made on Skokholm. Hence permanent emigration from the colony did occasionally occur, usually before breeding age. There were no records of birds moving colony once they had started to breed but, on the other hand, not all immature birds that visited other colonies necessarily bred there.

Table 5.2 Details of 22 colour-ringed Razorbills which were ringed as pulli on Skokholm and were known to have visited Skomer in their pre-breeding years. The number of sightings on Skomer are given in parentheses expressed as a percentage of the annual total of sightings (not corrected for ring loss) of birds in that age class.

Year of ringing	Year of sighting	Number of sightings
1968	1972	9 (26%)
1968	1973	1 (5%)
1971	1973	0
1971	1974	10 (42%)
1972	1974	1 (33%)

Note No pulli were colour-ringed on Skomer in 1968 (or 1969) therefore all white rings were of Skokholm origin; no red-ringed birds were seen on Skomer. The natal colony of birds colour-ringed in 1970 was not distinguishable - see Table 5.1. 1974 records supplied by C M Perrins and T A Birkhead.

Many, after visiting another colony, probably eventually returned to their natal colonies to breed. The sharp drop in older birds ringed on Skokholm and sighted on Skomer may be explained in this way.

ii. Return of young birds to the breeding colony

Young Razorbills can be distinguished from adults by plumage characteristics until the second autumn of life (Salmonsen 1944). In this study, two-year old birds could also sometimes be recognised by the lack of a white bill stripe; in some individuals the stripe was incomplete or faint (Chambers 1971) but this character was not a reliable indicator of age. Further, the bill of many two-year old birds may still be noticeably shorter, less deep and less ridged than that of older birds. In late July, some of the immature birds started the autumn body moult and white feathers appeared on the throat, giving the plumage a speckled appearance.

The calculations are complicated by unusual happenings in two years of the study. First, in 1969 a larger than usual number of ringed fledgling Razorbills from Skokholm were recovered shortly after leaving the island (see below) and therefore fewer must have survived to reach breeding age than in other years. Secondly, the return of birds in the spring of 1972 was disrupted by almost continuous rough weather (Lloyd 1973; see Chap. 3ii).

No colour-ringed one-year old birds were recorded on land in the present study and there were only three sightings of first year birds in the rafts of auks below the colonies, confirming that Razorbills rarely returned to the breeding colony when one year old (Lloyd 1974). Even the number of two-year old birds

coming to land was small (compared with the number that later bred). For each cohort of young, more birds returned to the colony each year from age 2 to age 5 (Tables 5.3 and 5.4).

The survival of birds ringed as chicks in 1969 was especially low: none were seen on Skomer. This was possibly due to the heavy mortality of Razorbills in a local "wreck" during the autumn (NERC 1971) when ten (an unusually high number) Skokholm-ringed pulli were recovered within a few weeks of fledging. Sightings in 1974 were probably biased by a change in observers as few of the 1968 or 1969 ringed birds (which were almost certainly still alive) were reported. Excluding these observations, the average numbers of birds returning to the colony at successive ages are shown in Table 5.4 . Once the birds started breeding, loss of the colour rings increased (presumably because the birds spent more time on the ledges, so wearing the rings more than if they were at sea). In 1973, at least three 1968 young lost their rings during the breeding season. Ring loss must partly account for the relatively small number of sightings of birds of breeding age.

Records of known non-breeders (identified by colour ring and metal ring number) on successive days throughout the season, permitted an estimate of the amount of the season these individuals spent on land (measured by the difference between the earliest and latest records of individuals in different seasons). Generally, the youngest birds were on land for the shortest time, and the oldest birds for the most time, although the difference between three- and four-year old birds was not

Table 5.3 Colour ringed birds of known age seen after ringing, expressed as percentage of those ringed (corrected for ring loss); the actual numbers seen are given in parentheses.

Year of ringing as pullus	Year of sighting			
	1970	1971	1972	1973
1968	2.5(6)	10.6(23)	17.8(35)	11.9(22)
1969		1.0(3)	5.0(14)	12.9(33)
1970			2.9(8)	11.3(29)
1971				4.1(11)

Note Ring loss progressed linearly - after 3 years: 7%, 4 years: 12%, 5 years: 28%, and (predicted) 6 years: 40%
Chicks which lost their rings in the nest or failed to fledge are excluded above. It was not always possible to be sure that some of the colour ringed birds in a colony were not omitted or counted twice in these records (and those in Table 5.2), since several different colour ringed birds in each age class were often present on land or in flight at the same time. In some cases, the ring number on the metal ring was read and the bird individually identified; birds which had lost their colour rings were sometimes found in this way. In 1974 observations were biased by the change in observers; the % of colour ringed birds seen (corrected for ring loss) were 1.4, 9.6, 7.6, 7.3 and 5.9 for age groups 2-6 years respectively.

Table 5.4 Average (%) return to colony by birds, in their second, third and fourth years of life.

Age (years)	Excluding 1969 pulli	1969 pulli alone
Two	3.2	1.0
Three	11.0	5.0
Four	17.8	12.9

significant (Table 5.5). Birds aged four years or older and known to be breeding are omitted from this table.

Because of the variation in the timing of the breeding season in different years, the dates upon which individual colour-ringed birds were first seen on land in successive years are compared on a scale from 1 to 57 so that 25 represents approximately the middle of each laying season (Figure 5.2). The mean dates of return to the colony (given on the same scale) show that the youngest birds tended not to come to land until the nestling period; these birds remained in the colony for about two weeks and left as the chicks started to fledge. The three-year old birds first returned at the end of the incubation period, on average one week earlier than the two-year olds, but their departure also coincided with that of the fledging chicks. The four- and five-year old birds returned even earlier in the breeding season and at least some were present on the island throughout the incubation period; again their departure coincided with the start of fledging.

iii. Age at first breeding

Before colour ringing began at the Skokholm colonies, few Razorbills under the age of six years were caught as breeding birds (Table 5.6), though a few birds bred at four years of age. Most birds were caught on the nest and the youngest breeding birds were nervous and therefore not likely to be trapped.

Although the same problems in trapping young breeding birds existed in the present study, the necessary information was obtained from observations of colour-ringed breeding birds which could be indentified without being caught. Twenty individuals of known age were recorded breeding for the first

Figure 5.2 Comparison of dates of first sighting on land of immature birds of different ages. Date Index 25=10 days after the start of the middle laying period each year, arrows mark mean date of return with 1 standard error either side; ages are given in years with sample sizes in parentheses. The significance of diffrences in mean arrival dates in successive ages is as follows:

2 - 3 years d=3.08,P=0.01 with 21 d.f.

3 - 4 years t=3.45,P=0.002

4 - 5 years t=0.29,P > 0.05

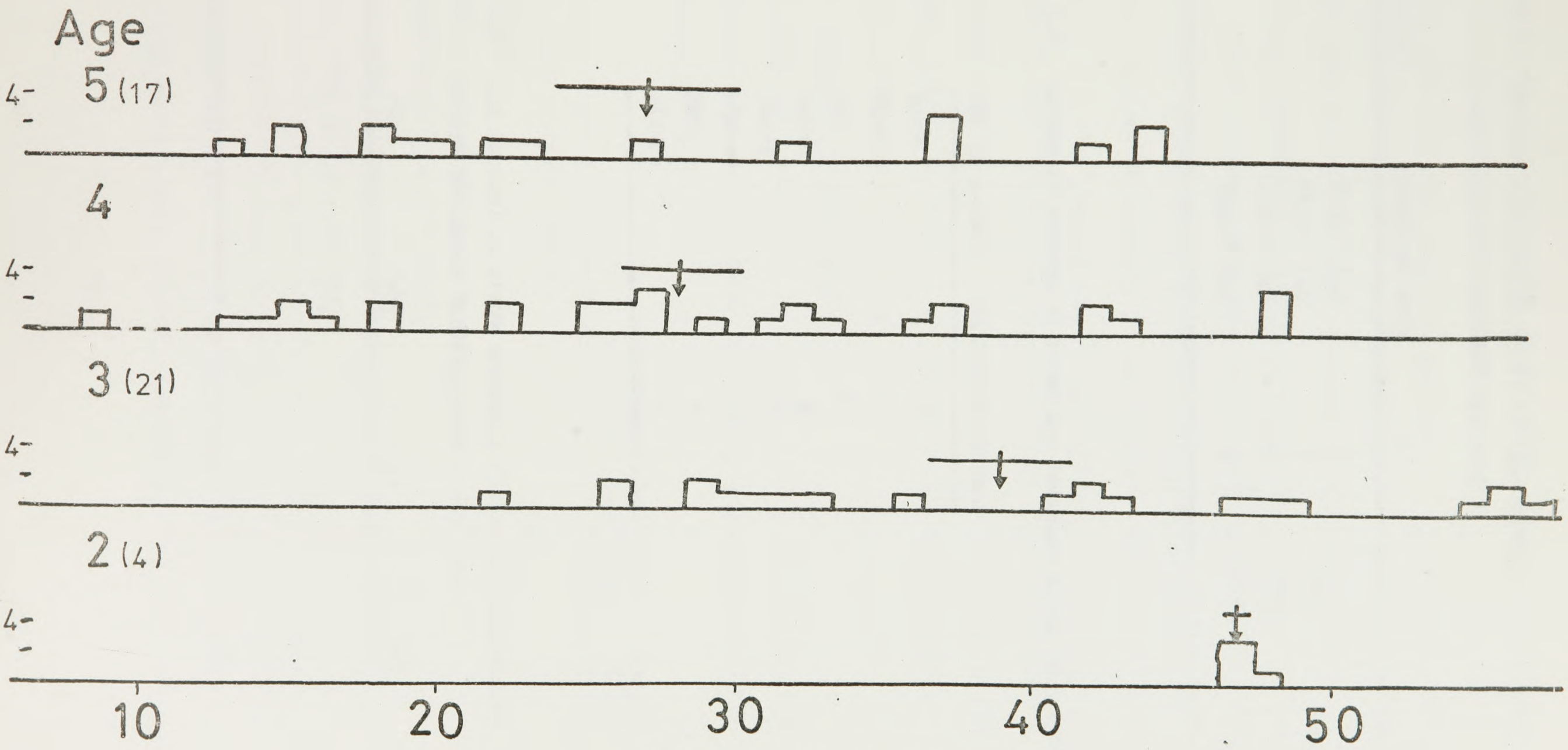

Age
5 (17)
4
4
3 (21)
2 (4)
10
20
30
40
50
Date Index

Table 5.5 Average duration of visit to land during pre-breeding years (days ± 1 standard deviation)

Age (years)	Length of stay	n	t	P
Two	12.6 ± 5.5	3		
Three	21.4 ± 5.5	7	9.3	<0.001
Four	21.0 ± 3.5	11	1.5	>0.05
Five	33.0 ± 7.3	4	25.0	<0.001

Table 5.6 Number of retraps of known age breeding birds 1963-1970.

Age in years	Number of retraps
Four	7
Five	12
Six	10
Seven	8
Eight	7
Nine	8
Ten	5
Eleven	1

Table 5.7 Age (years) at first breeding; figure in parentheses refers to Skomer breeding bird - see text.

Age	1971	1972	1973	Total
Four	3	(1)	4	7
Five	2	3	7	12
Six			1	1

time in the three main years of the study (Table 5.7); these showed that just over a third of the birds breeding for the first time were four years old and most of the rest were five. There was no evidence that males and females bred for the first time at different ages as has been reported in other seabirds (Richdale 1952; 1957; Coulson & White 1956).

There was evidence in the ringing data that relatively few young birds bred for the first time in 1972 (the year in which breeding was delayed by bad weather). Although at least 18% of the chicks ringed in 1968 were present at the colony in 1972, no colour-ringed four-year old birds bred on Skokholm. In 1973, however, despite the poor survival of the 1969 chicks which resulted in only 14% of them returning to the colony, four four-year old birds bred.

iv. Survival of adult birds

Sightings of individually colour-ringed adult Razorbills (Table 5.8) provided the following estimates of mean annual survival between 1970 and 1974:

	% Mean survival	Standard deviation	Sample size
All birds colour-ringed on Skokholm	80.7	2.8	6
Birds colour-ringed in The Bluffs study colony, Skokholm	89.0	6.1	9
Birds colour-ringed in The Inner Basin study colony, Skomer	92.1	4.7	6

The differences in estimates of survival for all Skokholm birds and the other two groups were significant ($t = 3.09$, $p = 0.01$ and $t = 5.10$, $p < 0.001$ respectively for The Bluffs and

Table 5.8 Sightings and retraps of birds colour ringed as adults.

	Year of ringing	Number ringed	Number of sighting/retrap 1971	1972	1973	1974
The Bluffs	1970	17	16	14	13	11
	1971	20	-	17	15	(11)
	1972	14	-	-	11	11
	1973	9	-	-	-	8
All Skokholm	1970	85	73	58	51	(34)
	1971	61	-	48	43	(26)
	1972	51	-	-	38	(28)
	1973	36	-	-	-	(22)
Skomer	1970	17	16	16	14	(8)
	1971	27	-	26	23	(15)
	1972	26	-	-	23	(21)
	1973	11	-	-	-	(8)

Note Observations in 1974 given in parentheses, biased by the change in observers, were excluded from calculations of mean adult survival.

Skomer birds), but survival of birds on The Bluffs did not differ significantly from that on Skomer ($t = 1.05$, $p > 0.05$). Sightings in 1974 were used to correct records for birds missed in previous years. Otherwise only the 1974 sightings for The Bulffs are included in the estimates of mean survival as the change in observers (after 1973) meant that many birds were missed outside The Bluffs.

On Skokhom the highest annual survival rate was recorded on The Bluffs where nearly 90% of the adults survive each year. On Skomer the estimate was higher than this (92%). Estimates based on ringing recoveries of birds ringed throughout the British Isles between 1960 and 1970 gave an annual survival figure of 89.0 $\pm$ 1.1% (Lloyd 1974). This agreed closely with the 89 to 92% annual survival of colour-ringed birds on Skokholm and Skomer and with Mead's (1974) analysis of ringing records, using only those birds "..... recovered after the heavy immature mortality and before ring loss had started." which gave 91.4 $\pm$ 4.0% annual survival.

v. Life table for the Skokholm Razorbills

Using these data and those on breeding success (Chapter 4 Biv), it is possible to construct a rough life table for the Razorbill on Skokholm. There was no evidence that pairs failed to lay in certain years, though it is possible some adults which lost their mates failed to remate in time to breed. Considering a population of 100 pairs, 100 eggs are laid and produce 66 fledged young. However, a quarter of the pairs that lose their eggs lay a replacement. Such eggs have a slightly lower overall success (63%) than the first clutches, but about 5

replacement chicks are raised by each 100 pairs. Hence 100 pairs of birds might be expected to raise 71 (66 + 5) young each year.

About 18% of the young birds may survive to breeding age (4 or 5 years) (Table 5.4), hence only about 13 young per 100 pairs (18% of 71) are likely to reach breeding age each year. This figure is a minimum since interchange between colonies is assumed to be negligible, although we know that a few Skokholm birds finally breed on Skomer. Nevertheless, if the population is to remain stable, recruitment seems insufficient in view of the data on adult survival; an annual mortality of 8 to 10% yields 16 to 20 adults dying from each 100 pairs per year. The evidence available suggests that survival of adults may exceed 90-92% in some years, but be considerably lower than this in others. There was no suggestion of a decline in adult survival with increasing age as has recently been demonstrated in the Kittiwake (Coulson and Wooller 1976). A longer-term study is essential if more accurate estimates and hence more reliable average figures are to be obtained for the Razorbill.

To summarise, colour-ringing on Skokholm showed that most Razorbills return to their natal colony to breed. There was no interchange of adult birds between colonies but some young birds from Skokholm were seen on Skomer and at least one remained there to breed. Other ringing records suggest that there is little permanent immigration or emigration at the Skokholm colonies. Similar studies of the Manx Shearwater Puffinus puffinus on Skokholm (Harris 1972) have shown that even short-

distance movements (to Skomer) are uncommon (o.15%) and very few birds (0.06%) move away from Skokholm to breed. Like Razorbills, young Shearwaters may visit other colonies during their pre-breeding years but eventually return to breed on Skokholm.

Few young Razorbills returned to the colony before their third and fourth year of life. The return of non-breeding birds followed a similar pattern to that described for other seabirds. Perrins et al (1973) found that the youngest immature Manx Shearwaters (two years old) returned to the colony latest in the season and stayed the shortest time, whilst the older immature birds returned progressively earlier each year and remained at the colony for increasing lengths of time. 30% of the Shearwater chicks ringed each year returned to the colony in pre-breeding years. Similar figures for other species of seabird studied are 38% for the Short-tailed shearwater Puffinus tenuirostris (Serventy 1967), 64% for the Waved Albatross Diomedea irrorata (Harris 1973) and 25-33% for the Storm Petrel Hydrobates pelagicus (Scott 1970). Compared with these, the 18% return of Razorbill chicks up to the age of four is low. In the Arctic Tern, where many young birds remain on the wintering grounds for the first two years of their life, only 5% of the birds ringed on the Farne Islands return to the colony in pre-breeding years (2 years old) (Coulson and Horobin 1976). Studies of attendance at breeding colonies throughout the season in the Razorbill on Skokholm and elsewhere (Lloyd 1973; Lloyd 1975 and 1976) have shown that the number of birds in a colony increases gradually to a peak in the nestling period. Colour-ringing of Razorbills on Skokholm has shown that this is due

to the return of non-breeding birds which are present in greatest numbers about the time of the nestling period. As soon as the chicks start to fledge, attendance at the colony decreases and becomes more variable and this coincides with the exodus of immature birds from the colony.

Just over a third of the Razorbills known to be breeding for the first time were four years old and most of the rest were five. This determent of maturity is characteristic of seabird species in which adult survival is also high (Table 5.9); Lack (1954) suggested that this had evolved because the care and feeding of the young and other breeding activities would impose too great a strain on young birds.

Table 5.9 The age at first breeding (years) of some seabird species.

Species		Age	Reference
Waved Albatross	Diomedea irrorata	6	Harris 1969d
Laysan Albatross	D.immutablis	7	Rice & Kenyon 1962
Black-footed Albatross	D. nigripes	5	Rice & Kenyon 1962
Royal Albatross	D.epomophora	(9 ♀ (8 or 11 ♂	Richdale 1952
Manx Shearwater	Puffinus puffinus	(5 or 6 (8 or 9	Perrins et al 1973 Brooke 1974
Sooty Shearwater	P.griseus	6	Richdale 1963
Short-tailed Shearwater	P.tenuirostris	(5 or 6 ♀ (6 or 7 ♂	Serventy 1967
Storm Petrel	Hydrobates pelagicus	4 or 5	Scott 1970
Leach's Petrel	Oceanodroma leucorhoa	3	Gross 1947
North Atlantic Gannet	Sula bassana	5 or 6	Nelson 1965b
Lesser Black-backed Gull	Larus fuscus	4 or 5	Harris 1970a
Herring Gull	L.argentatus	4 or 5	Harris 1970a
Kittiwake	Rissa tridactyla	(3 or 4 ♀ (4 or 5 ♂	Coulson & White 1956
Arctic Tern	Sterna paradisaea	4	Coulson & Horobin 1976
Razorbill	Alca torda	4 or 5	Present study
Guillemot	Uria aalge	3	Southern et al 1965
Puffin	Fratercula arctica	5	Ashcroft in prep.

CHAPTER 6

POPULATION REGULATION IN THE RAZORBILL

Theories on population regulation

In natural conditions, bird populations tend to be stable (Lack 1954). The number of birds lost each year through mortality is balanced by the number of young birds reaching maturity and entering the breeding population. Although the reproductive output of fledglings may be far in excess of the annual adult mortality, if the population is stable, sufficient young birds will die before they attain breeding age, for their numbers to balance the current year's adult mortality. Thus, for example, if losses of either nestling or immature birds are so high as to prevent enough birds reaching maturity to replace dying adults, the population will decline.

Lack (1954) has argued that, in a stable population, numbers are controlled by certain factors which operate in a density dependent manner. When numbers increase, the factors reduce the reproductive output of the population and/or increase the death rate, whilst in a declining population the factors favour a high reproductive rate and/or low mortality. In all birds the reproductive rate, evolved through natural selection, results in the greatest number of surviving young per pair. Hence the control of population density must be brought about by factors which affect the mortality. In many of the species which have been studied in detail, one of the most important of these factors is food availability, either during or outside the breeding season. A shortage of food results in density-dependent mortality of adults and independent young through direct competition. Lack did not consider that other factors

such as predation, disease and the availability of nest sites (which could also affect numbers in a density-dependent fasion) were sufficiently consistent to be important.

Wynne-Edwards (1955), on the other hand, whilst accepting that food ultimately limits numbers, suggested that the individuals in a population have the capacity to control their own numbers by 'restrictive adaptations' for low reproductive output. These adaptations, he maintains, are a common feature of the breeding biology of many seabird species in which the mortality is low and numbers must therefore be controlled or increase indefinitely. They are namely the egg clutches, single broodedness, failure to replace lost eggs, long incubation and nestling periods, reproductive cycles of more than one year and deferred maturity.

Ashmole (1963b) also shared the view that many seabirds are ultimately limited in number by food availability. As a result of his study of terns and noddies on Ascension Island, he suggested that food shortage actually during the breeding season itself can bring about density dependent variations in both reproductive rates and recruitment of young into the breeding population and hence regulate population size. The adult mortality in these tropical seabirds was so low that it seemed unlikely that it could affect numbers in a density dependent manner. This type of population control, Ashmole suggested, could also operate in temperate zone seabirds. Most populations are maintained at a level well below that at which competition for food occurs during breeding but, if numbers increase and food becomes critical, individuals which are least efficient at finding food

for the young will be the first to lose chicks, and hence the total reproductive output of the population will be reduced. Similarly, young birds will be prevented from breeding in such conditions so that the age of first breeding will be raised and the size of the population correspondingly reduced.

The main difference between the theories of Lack and Ashmole lie in the inferred food regimes prevailing at the breeding colonies. Lack believed that birds bred when food was abundant both for themselves and their chicks. Outside this period, inferior feeding may govern adult survival. In temperate zones, there is generally an increase in food available to many species during early summer; this must account for the relatively restricted breeding season of our seabirds in Britain and Ireland for example.

For the species studied by Ashmole, however, food was widely dispersed; a characteristic of tropical seas. Outside the breeding season the birds wander over a wide area to feed but have to come to land to breed. Not only are demands for food increased during breeding, but food must also be collected quickly from relatively close to the colonies. Thus, feeding conditions in the vicinity of a large breeding colony could become seriously depleted so that the birds reach the limit of their feeding capacity. This, Ashmole suggests, is responsible for the features characteristic of many oceanic seabird breeding cycles which Wynne-Edwards claims to be adaptations for low reproductive output.

Population regulation in the Razorbill

Food availability potentially limits Razorbill numbers in the

manner described above. As Ashmole suggested for other species, it is possible that food supplies may become critical during the breeding season when the birds concentrate in the vicinity of the breeding colonies and need extra food to produce eggs and rear young. Outside the breeding season, Razorbills are more widely dispersed and there is some evidence that their distribution overlaps less with that of the other auks than during the breeding season. This in itself reduces the chance of competition should food be limited in availability.

It seems likely that Razorbill numbers remain below the level at which dompetition for food could occur, by factors which act independently of population size. These include occasional incidents of unusually heavy mortality from which, as discussed below, the population takes a while to recover. This mortality sometimes takes the form of a natural 'wreck' (see NERC 1971) in which the number of birds involved can be increased by the effects of toxic chemicals in the body. Similarly, both oil spillage incidents and the effect of continuous chronic oil pollution in certain areas, especially during winter (Bourne and Bibby 1975), have killed large numbers of birds. Documentation of oil spills affecting birds (eg Bourne 1969; annual reports of The Advisory Committee on Oil Pollution of the Sea) shows that in the 1950s and 1960s mortality due to oil was especially heavy; doubtless before this large numbers of birds must have died undetected. Recently, however, although pollution in British and Irish waters is still a serious problem, fewer birds have died each year through oiling (eg RSPB-Seabird Group Beached Bird Survey

results (February); average 1.2 oiled corpses/mile in 1969 (Bourne and Devlin 1970), compared with only 0.4 oiled corpses/mile in 1976.). Earlier this century, human persecution must have provided an additional threat to Razorbill numbers.

Breeding success can be affected by factors such as predation or human disturbance, though these do not appear especially important in most British and Irish colonies. On Skokholm, breeding success during the present study was reduced by Jackdaws which took on average a fifth of all eggs laid. This is a relatively new source of mortality at the colony so that its effect on the population remains to be seen.

Finally, food availability appears to affect numbers indirectly by imposing limitations on reproductive output. Several of the ecological adaptations to breeding in seabirds outlined by Lack (1967; 1968) are found in the Razorbill. These include colonial breeding, deferred maturity, a single egg clutch, a comparatively long incubation period and young relatively well developed at hatching; these features can be related to the birds' exploitation of locally abundant offshore (ie out of sight of land) food supplies.

In the Razorbill and certain other auk species, such as Uria spp., the chicks undergo relatively rapid growth during a short nestling period and then depart to sea with the adults. This appears to be an additional adaptation to offshore, possibly mobile, feeding grounds and may also be associated with the deterioration of feeding conditions near the breeding colony. The mortality of young birds during the post-fledging

stage must be heavy so that the advantage that this behaviour infers must outweigh the relative safety of a chick reared on land. Hence, as Lack suggested for other species, much of the adaptations for breeding in the Razorbill appear to be related to overcoming the difficulties in its feeding regime, resulting in a relatively low reproductive output.

Razorbill population dynamics

Several features of the Razorbill's population dynamics - with comparatively low breeding productivity, deferred maturity and high survival of breeding birds - makes it particularly vulnerable to factors affecting either the breeding success, or the recruitment of young birds into the breeding population, or the adult survival. Even a slight increase in adult mortality can be detrimental to population equilibrium. If only ten 'extra' Razorbills die per 100 birds per annum, for example, the annual mortality is doubled (ie 100% increase). In a species such as the Blackbird Turdus merula, in which on average 44% of all breeding birds die each year (Lack 1966), ten extra dead per 100 represents an increase in mortality of only 23%. As survival of young Razorbills in their pre-breeding years is usually relatively low (in the present study only 18% survived to breed), there is little chance that an increase in adult mortality can be compensated for by increased recruitment. Moreover, the factors causing increased mortality in adults can be expected also to affect the survival of non-breeding birds.

A population takes at minimum several years to recover from a single incident of exceptionally heavy mortality.

Breeding productivity is always low (ie less than one young per pair per annum) and there is no evidence to suggest that Razorbills can breed before they are three years old. Thus any of the factors mentioned above that increase mortality or drastically reduce breeding success can have a significant and sometimes long-term effect on Razorbill population size.

Factors affecting breeding success are generally local in effect and even sometimes temporary. Others, such as human interference, are either considerably less important now than in previous times or local in their effect and easily identified and remedied; still others are unavoidable, such as 'natural' wreck mortality. It is the increase in mortality through both oiling and the effects of toxic chemicals that appear to play an especially important part in Razorbill population dynamics. Although the former has shown signs of allieviating in the past decade, there is no reason to suppose that marine pollution will not increase with the extraction of oil from below the seas of the continental shelf during the next few decades.

In conclusion, population parameters are variable (cf between 85% and 100% adult survival recorded in different years of this study): population levels fluctuate from year to year as a result. Long-term monitoring is therefore necessary if population trends are to be detected. Moreover, to obtain reliable results, at least some of the recommendations on census techniques suggested by this study must be adopted. A carefully planned programme of population monitoring in both Britain and Ireland, and an awareness of the main potential threats to the species are therefore probably the best methods of safeguarding Razorbill numbers at the present time.

APPENDIX I Latin names of birds and mammals mentioned in text. (mostly after BOU checklist 1971).

Birds.

Great-crested Grebe	Podiceps cristatus (Linnaeus)
Waved Albatross	Diomedea irrorata Salvin
Laysan Albatross	D.immutablis Rothschild
Black-footed Albatross	D.nigripes Audubon
Royal Albatross	D.epomophora Lesson
Fulmar	Fulmarus glacialis (Linnaeus)
Manx Shearwater	Puffinus puffinus (Brünnich)
Short-tailed Shearwater	P.tenuirostris Temminck
Sooty Shearwater	P.griseus (Gmelin)
Storm Petrel	Hydrobates pelagicus (Linnaeus)
Leach's Petrel	Oceanodroma leucorhoa (Vieillot)
North Atlantic Gannet	Sula bassana (Linnaeus)
Cape Gannet	S.capensis (Lichtenstein)
Red-billed Tropicbird	Phaethon aethereus Peters
Redhead	Aythya americana Eris
Eider	Somateria mollissima (Linnaeus)
Velvet Scoter	Melanitta fusca (Linnaeus)
Ringed Plover	Charadrius hiaticula Linnaeus
Quail	Coturnix coturnix (Linnaeus)
American Woodcock	Philohela minor (Gmelin)
Great Skua	Stercorariusskua (Brünnich)
Black-headed Gull	Larus ridibundus Linnaeus
Herring Gull	L.argentatus Pontoppidan
Lesser Black-backed Gull	L.fuscus Linnaeus
Great Black-backed Gull	L.marinus Linnaeus
Glaucous Gull	L. hyperboreus Gunnerus
Glaucous-winged Gull	L.glaucescens Naumann
Red-billed Gull	L.novaehollandiae Stephens
Kittiwake, Black-legged Kittiwake	Rissa tridactyla (Linnaeus)

Swallow-tailed Gull	Creagrus furcatus (Néboux)
Arctic Tern	Sterna paradisea Pontoppidan
Sooty Tern	S.fuscata Linnaeus
Great Auk	Pinguinus impennis (Linnaeus)
Little Auk	Plautus alle (Linnaeus)
Razorbill	Alca torda Linnaeus
Common Guillemot	Uria aalge (Pontoppidan)
Brünnich's Guillemot	U.lomvia (Linnaeus)
Black Guillemot	Cepphus grylle (Linnaeus)
Pigeon Guillemot	C.columba Pallas
Puffin	Fratercula arctica (Linnaeus)
Ancient Murrelet	Synthliboramphus antiquus (Gmelin)
Xantus' Murrelet	Brachyramphus hypoleuca Xantus
Cassin's Auklet	Ptychoramphus aleutica (Pallas)
Rhinoceros Auklet	Cerorhinca monocerata (Pallas)
Great Tit	Parus major Linnaeus
Jackdaw	Corvus monedula Linnaeus

Mammals.

Arctic Fox	Alopex lagopus
Rabbit	Oryctolagus cuniculus
Ringed Seal	Phoca hispida
Harp Seal	P.groenlandica

APPENDIX II Measurements of adult Razorbills.

Measurements of adult Razorbills (Alca torda islandica) were collected from the following sources:

a. Published measurements of museum specimens

b. Museum skins from the British Museum (Natural History), Tring and Liverpool Museum. Immature birds were treated separately and birds of unknown sex omitted.

These samples included birds collected throughout the year so measurements were biased by the variation in wing length through abrasion, and the change in bill dimensions associated with the loss of the horny basal ridge in winter.

The position of the measurements of bill length and depth that were made are shown in Figure 1; these measurements were consistently so that birds from different skin collections were comparable. Published wing measurements on the other hand were of little use for comparative purposes.

The published measurements of museum specimens and the measurements collected in the present study illustrate the large overlap in size of male and female birds (Table 1). Immature specimens were identified by the undeveloped structure of their bills (Salomonsen 1944). Razorbills collected in the first twelve months of life had small bills without a white stripe. Birds in their first winter had smooth bills; the first groove appears to develop by the time the birds are one year old. The white bill stripe was absent in most individuals until the second winter and, in some birds at least, did not develop until the third winter. This bears out observations of colour ringed two year old birds on Skokholm, some of which had no bill stripe (Chambers 1971). The main groove was present on the bill of most two year old specimens and thus probably developed during

Figure 1. Position of bill depth (A) and length (B) measurements.

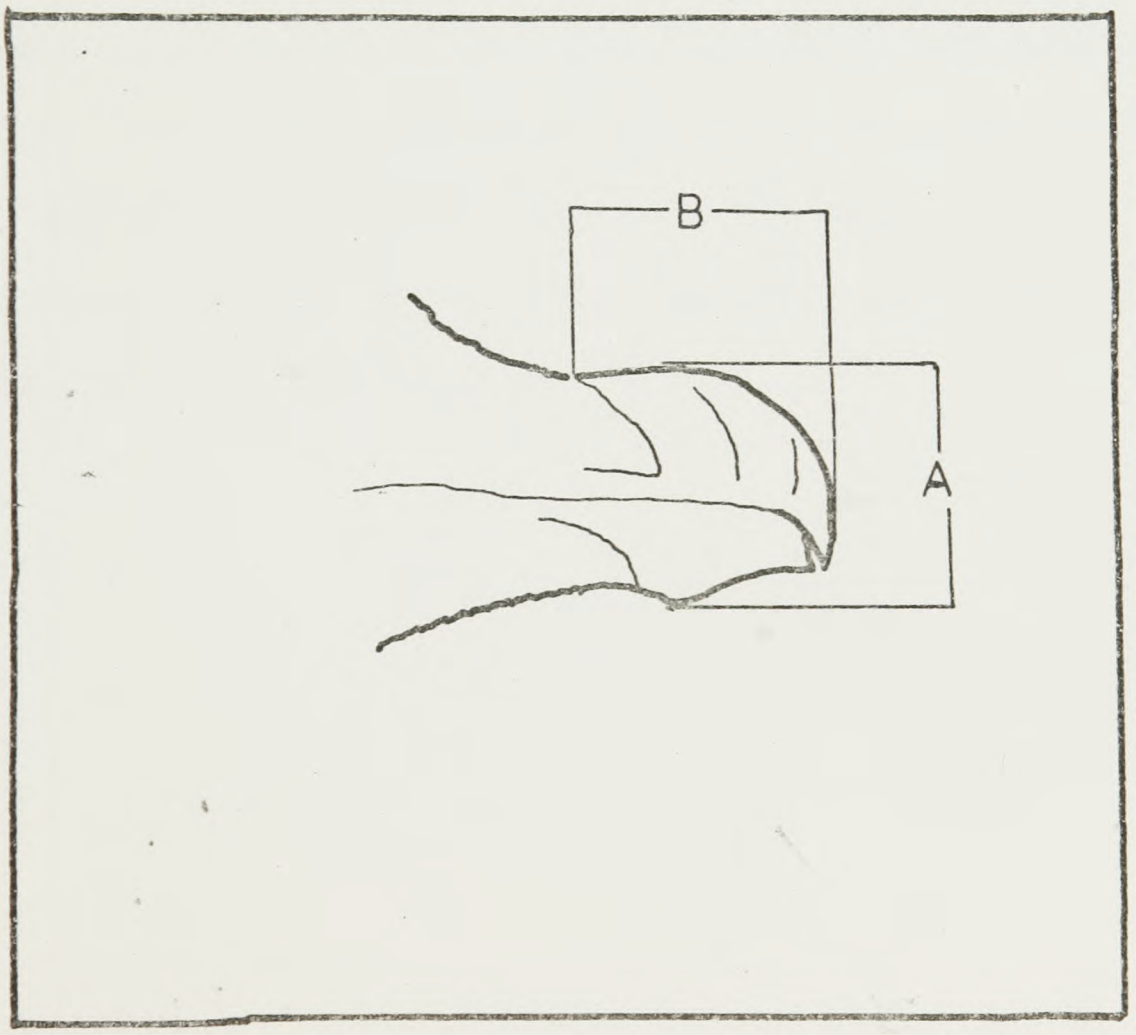


Table II.1 Range of measurements (mm) of adult Razorbills (A.t. islandica) from museum specimens (see text).

Source	n	Sex	Wing length	Bill length	Bill depth
Ticehurst 1936	31	♂♀	186-198	-	19-21
Witherby et al 1941	14	♀♀	185-200	29-34	20-22
	14	♂♂	185-203	30-35	21-23
Salomonsen 1944	3	♀♀	192-195	31-34	20-23
	4	♂♂	187-192	32-34	21-21.5
Løvenskiold 1947	?	♀♀	185-200	29-34	20-23
	?	♂♂	185-203	30-31	
Vaurie 1965	22	♀♂	181-202	-	19-22.5
Haftorn 1971	?	♀♀	185-200	29-34	20-22
	?	♂♂	181-203	30-35	19-23

the second winter of life. Figure 2 shows the bill structure of birds in approximately the first winter, first summer and second/third summer of life (see also Salomonsen 1944, p.21).

In both sexes, the bill of the first year birds was significantly ($P \leq 0.05$) smaller than that of the adults - on average 83% adult length and 67% adult depth (Table 2). Salomonsen (1944) also noted that the bill (and wing) of first year birds was shorter than that of the adults, although he suggested that second year birds were only very slightly smaller. Second and third year birds in the present study were still significantly smaller ($P \leq 0.05$) than adults in both bill length (94% adult) and depth (84% adult). Full grown male specimens on average had longer bills than the females, but the average bill depths of the two sexes did not differ significantly.

Figure II.2 Heads from Razorbill skins in Liverpool Museum, by courtesy of G.H.Green. Birds were in their first winter, first summer and 2nd. or 3rd. summer of life (right to left) respectively when collected.



Table II.2 Mean measurements (mm ± 1 standard deviation) of Razorbill skins from the British Natural History Museum, Tring and Liverpool Museum.

	Sex	Approximate Age in years	Bill length	n	Bill depth	n
IMMATURE	MALE	1	28.5 ± 1.7	6	14.7 ± 2.2	5
		2-3	30.9 ± 2.0	11	18.4 ± 2.6	10
		1-3	30.1 ± 2.2	17	17.2 ± 2.9	15
	FEMALE	1	26.0 ± 3.6	6	13.8 ± 2.2	5
		2-3	30.5 ± 1.8	6	17.3 ± 2.0	6
		1-3	28.3 ± 3.6	12	15.7 ± 2.7	11
ADULT	MALE	4+	33.4 ± 1.8	18	21.9 ± 4.5	14
	FEMALE	4+	32.0 ± 1.8	15	20.5 ± 0.6	14

Note All differences are significant ($P \leq 0.05$) except those marked N.S.; t values as follows:

Ages compared	n	Bill lengths	Bill depths
1Y♂ - 2/3Y♂	17	2.54	2.93
2/3Y♂ - adult♂	29	3.43	2.17
1Y♀ - 2/3Y♀	12	2.80	2.81
2/3Y♀ - adult♀	21	1.75 N.S.	3.10
Immature♀ - immature♂	29	1.71 N.S.	1.30 N.S.
Immature♀ - adult♀	32	3.56	6.45
Immature♂ - adult♂	30	4.91	3.32
Adult♀ - adult♂	33	2.25	1.11 N.S.

APPENDIX III Estimates of the numbers of auks breeding on Skokholm 1928-1973 from bird observatory records.

Year	RAZORBILL		GUILLEMOT		PUFFIN	
	Maximum spring count	Estimated number of pairs	Maximum spring count	Estimated number of pairs	Maximum spring count	Estimated number of pairs
1928		800		160		20,000
1929						
1930						
1931						
1932		"Steady				"No
1933		increase"		162		noticeable
1934				190		change"
1935				200		
1936				220		
1937		1,000		220		
1938						
1939						
1940						
1941-46		Apparent decrease during war				"No apparent change"
1947		670		110		
1948	800	730		110		8,000
1949		700		110		
1950		700		90-100		
1951		650		80-90		
1952						
1953						5-10,000
1954			180		5,000	
1955	1,500		150	50	5,000	6,000
1956	1,500		150		5,000	
1957	1,500		155		2,500	
1958	1,190		131		5,000	
1959		700	178	75	4,000	2,000
1960	795		180	30-40	2,900	
1961	1,200		125	60	3,250	
1962	930		157		2,500	Nos. > 1961
1963	400	343		60		
1964	1,200		270			
1965	1,200		240		3,000	
1966	400	500				
1967		546	116	"Small inc. over recent years"	2,000	No apparent change
1968		600		120		1,500
1969		650		120		2000-3000
1970		375		60		2,500
1971	967	480	176	70	1,900	
1972	653	470	268	105	2,800	2,000
1973	728	470	237	110	1,600	

APPENDIX IV Rings used on Razorbills.

a. Metal rings

Aluminium rings were used on Razorbills during the early years of ringing on Skokholm and similar rings were used for Manx Shearwaters and most other seabirds ringed on the island. Lockley estimated that these rings only lasted two years on Shearwaters once the birds had come to land (Harris 1964b). It seems unlikely that on Razorbills, breeding in rocky sites rather than earth burrows, the rings lasted any longer than this. Eeven before rings wear through and fall off they are often made illegible by abrasion.

In order to avoid this, a new "double-ended" ring was gradually brought into use for Razorbills and the other species. These rings were also made of aluminium and were 56mm in length (instead of the usual 25mm). The address and the ring number were engraved twice on the outer side of the ring and, when in position on thebird's leg, the inner inscription was protected by the large overlap. These rings lasted only a little longer than the earlier ones and, from 1958, were replaced by a third type of ring made of 'monel' (copper/nickel alloy) which was more resistent to wear. The original series used on the Skokholm Razorbills (304-/307-) were superseded by the standard Size 3 (SS-) rings from 1963 onwards. These lasted longer than the early monels but still tended to become illegible after about four years (see Figure 1 in Lloyd 1974).

In 1966 a special Razorbill ring (M-) was designed to suit the species' flattened tarsus; some of these rings had to be replaced during the present study (four to seven years after ringing), although the amount of wear depended to some extent on the nature of the bird's nest site. Birds living in rocky boulder sites tended to abrade their rings more quickly than those in ledge or earth-lined boulder sites. These rings bore the number longitudinally on the

outer surface which made reading the number through a telescope in the field difficult, as the bird had to turn round for both sides of the ring to be read. Also when rings were placed on young chicks, some turned round on the tarsus so that the number lay on the underside. Although this enabled the identification of a bird ringed as a pullus (the adult tarsus was too thick to allow a ring to turn round in this way), part of the ring number was often made illegible by wear

From 1973 yet another type of ring was introduced (Lloyd 1975c) The rings were even more resistent to wear as they were made of 'incolloy' (chromium/nickel alloy) which was harder than monel and therefore springy and slightly more difficult to close. The number was duplicated, on each side of the ring, so that the bird could be identified by seeing just one side of its ring. The address (for reporting a ringed bird) was inscribed once so that it lay on the top of the bird's tarsus when in position. So far these rings have proved most successful in the amount of wear they show after one year and in the ease with which they can be read.

b. Colour rings

The colour rings used in this study were made of 'darvic' plastic and secured with 'Tensol' cement glue once on the bird's tarsus. Rings of a single colour were used on pulli to denote year classes (see Chap.5ii); these were slightly thinner and narrower than those used on adults. The adult birds' rings were laminated (yellow on black) and engraved so that each ring bore one letter (J,C or X on Skokholm and A or T on Skomer) and two numbers (01-99). These were engraved twice on each ring so that it could be read from one side in the field. In this way every adult-ringed bird could be individually identified (see Figure 5.1).

Wear on colour rings was variable, depending on the type of nesting colony used by the bird. Colour rings on pulli wore through quickly once the birds had come to land (see Chap.5ii), but

the adults' colour rings usually lasted for two or three years before needing replacing. Many pulli lost their colour rings, but both types of colour ring would wear through almost completely on the under surface without actually falling off.

APPENDIX V Razorbill population census methods

a. Egg count

A population census can be made by counting all the eggs present in a Razorbill breeding colony. Ideally the egg count should be carefully timed to coincide with the time when most birds have laid and should also take into account rates of egg loss and replacement. Unfortunately the disturbance involved in such counts sometimes increases egg loss from exposed sites and large or inaccessible colonies egg counts are unfeasible.

Population census counts on Skokholm were traditionally conducted by this method. During the present study egg counts were made approximately one month after the start of laying when most (first) eggs had been laid but none had hatched. The counts were supplemented by eggs found after this date but sites from which an egg was lost immediately after laying were obviously missed. Such sites were probably more frequent outside the main study colonies, in areas infrequently visited. Egg counts for 1971-1973 were directly comparable with similar counts made by observatory staff in previous years.

Generally, however, there is often an error in this type of census due to a subconscious bias on the part of the observer who will tend, for example, to be especially aware of traditional nest sites not in use after visiting a colony, and thus form an impression of a decline in numbers. Some evidence of this is shown in the egg count on Skokholm in 1970, following the 'wreck' of auks (but mostly Guillemots) in the Irish Sea the previous autumn.

b. Maximum spring count

This census method is based upon the highest annual count of birds on the sea around the colonies in spring; on Skokholm this figure was occasionally recorded in the Bird Observatory annual report sometimes in addition to the egg counts (see Appendix III). Such counts involve few, if any,

immature birds and are relatively easy to conduct accurately. Interpretation of the counts is the main problem; if weather disrupts attendance patterns, the maximum spring count is meaningless. For example, the Skokholm breeding population remained between 470 and 480 pairs from 1971 to 1973 but the maximum spring counts were 967, 653 and 728 respectively.

c. From ringing records

The avai able ringing records for Razorbills on Skokholm were as follows (all from annual reports of the Bird Observatory):

Year	No. of Razorbill pulli ringed	Tot no. of Raz. ringed	No.of Raz. retrapped
1937	518*	603	11
1938	?	618	9
1939	?	320	10
1940	?	0	12
1946	?	295	6
1947	?	301	11
1948	?	374	18
1949	?	343	16
1950	?	144	6
1951	95	114	10
1952	124	162	10
1953	57	106	10
1954	?	149	16
1955	167	228	23
1956	202	254	28
1957	69	94	12
1958	199	215	6
1959	238	307	18
1960	252	289	4
1961	128	164	13
1962	0	0	1
1963	194	244	23
1964	176	261	30
1965	266	330	56
1966	226	251	29
1967	256	277	40
1968	239	263	57

Year	No. of Raz. pulli ringed	Tot. no. of Raz. ringed	No. of Raz. retrapped
1969	309	401	79
1970	276	327	78
1971	278	305	124
1972	219	242	172
1973	233	253	215

Note. * May include some birds ringed on Skomer and Grassholm.

These data were compared with the annual population estimates (usually based on egg counts) in order to attempt to predict population size in years when only the ringing totals were known eg. 1637-39, 1946, 1952-58 etc. - see Appendix II. The number of pulli ringed each year was not correlated with the estimated size of the breeding population for the eleven years for which both types of data were available ($r=0.10, P > 0.05, n=11$).

Theoretically, the number of 'accessible' sites in which chicks could be ringed should not have varied from one year to the next. Annual differences in breeding success were probably small and should have had little effect on these predictions. The variation in annual ringing totals therefore reflects both the population trends and the effort put into ringing Razorbills. For example, when the late Einar Brun studied the Razorbills on Skokholm (1958) he ringed only 199 pulli, in spite of his reputation for climbing and the fact that probably about 700 pairs of birds were breeding on the island.

An annual index of ringing effort was calculated by summing the number of adults retrapped and the number of adults newly ringed (ie total ringed minus those ringed as pulli). This was taken to represent an index of the effort put into catching Razorbills in any one year and should also reflect trends in pulli ringing totals. The latter prediction was supported by a strong

positive correlation between the pulli annual ringing total and the calculated Ringing Effort Index (REI) for the 21 years for which both types of data were available ($r=0.53, P=0.02, n=21$). The following multiple regression equation was calculated in order to express the pulli ringing total (Z) in terms of REI (X) and the estimated population size in pairs (Y):

$$Z=0.41X + 0.01Y + 181.37$$

This correlation however was not significant ($r=0.48, P>0.05, n=21$). Moreover there was no relationship between the estimated ringing totals from this equation and the observed ringing totals in the years where both REI and population estimates were available ($r=0.48, P>0.05, n=21$).

These results suggest that the relativelyaccessibility of sites in different years, was variable, ie the number of chicks ringed each year probably in fact depended more upon the climbing ability of the observatory staff and the current interest in Razorbills, than on the size of the breeding population on the island. Thus ringing records were of little use in estimating the number of Razorbills breeding on the island in different years.

d. Head count

Razorbill census counts usually consist of 'head' counts of all individual birds on the colony. Some of the 'Operation Seafarer' Razorbill counts were made by this method although the recommended counting unit was "apparently occupied sites". The final results of this survey were published as 'pairs' (Cramp et al 1974) and to obtain this figure the total numbers of apparently occupied sites and individual birds counted were added together. In the light of more recent information on how the total number of birds present in a colony compares with the number of occupied sites, this must have reduced the accuracy of the

published estimate of the size of the British and Irish population.

Examination of attendance patterns at breeding colonies show how variable the number of Razorbills present can be (Lloyd 1973). Census counts based on a single visit to a colony can be extremely inaccurate andtherefore of little value (Lloyd 1975b). In addition, Razorbills often have hidden nests or nest amongst Guillemots, sometimes in high densities, and are one of the hardest auks to census as a result. Reviews of these problems are given by Gibson(1950) and O'Connor (1967) and Birkhead and Ashcroft (1975) discuss the situation of Skomer.

Where birds nest on ledges in the open, all individuals can be counted. Provided consideration is given to the timing and frequency of counting, census counts of reasonable accuracy (eg 10%) can be obtained. Information on attendance patterns in cliff-nesting Razorbills in different breeding colonies throughout Britain and Ireland has been provided by an annual census co-ordinated by the RSPB and the Seabird Group. These data indicate that ideally a series of at least five counts should be made in the birds' nestling period, although little accuracy is lost if the counts are made in a longer time period, providing they are confined to the month of June (see Figure 3.3,Chap.3i).

Razorbill head counts need careful interpretation if a figure of actual breeding pairs is required. In ledge colonies the relationship between the number of breeding pairs is relatively easily worked out by observation. An attempt is made below to examine how head counts of birds in boulder colonies can be related to the breeding population by using the information gained from more easily visible ledge colonies.

During the present study of attendance (Chapter 3i), counts were made at a colony where the nest sites were hidden under boulders. Attendance at this colony was comparable to that at the ledge colony only when all sitting birds were discounted from the latter counts. Head counts made at colony A, an open ledge colony (see Chapter 3i), involved every bird in the colony; the number of occupied nest sites could also be counted in this colony and the number of breeding birds calculated. (Sitting birds were easily identified in Colony A by observations at dusk when all other birds had left the cliffs.) At colony B, a boulder colony, only birds sitting out on boulders could be counted and the size of the breeding population theoretically unknown.

Each daily count of birds in Colony A was compared with that at Colony B by subtracting the number of sitting (incubating or brooding) birds in the colony - which would have been out of sight in a colony like Colony B. A ratio of corrected total count at colony A to the number of eggs and/or chicks present was calculated each day during the period under review. The average value of this ratio indicated that 0.75 ± 0.06 birds were 'visible' for each sitting bird in colony A.

A daily estimate of the number of incubating or brooding birds present in Colony B was obtained by dividing the daily count at this colony by the constant 0.75. This gave an average estimate of the number of incubating/brooding birds (= breeding pairs or occupied sites) as 45.5 ± 3.3. Eggs present at the end of incubation (35th day) represented about 75% of those laid, excluding replacements. About 25% of all eggs lost were replaced (6% of those laid) and only 70% of these survived to the end of incubation (4% of those laid). Hence the number of breeding birds in a colony at hatching represents about 79% (75.4) of the original breeding population. The estimated breeding population of Colony B in 1973 was therefore between 53 and 62 pairs; the number of occupied sites actually counted in this colony was 55.

This procedure gave a satisfactory estimate of the size of the breeding population in a colony where not all birds could be seen or counted but there are several reasons why it cannot be more widely applied as a census technique.

1. The estimate of the average head count in both colonies was based on 16 days' counts. If only five counts had been made at Colony A in the nestling period (average count: 72.2 $\pm$ 11.2), the variation in the mean count indicated that the estimate could have been inaccurate by up to 11%; with 10 counts the error could have been reduced to 8% but a single count could have been 33% either side of the 'true' mean. In the boulder colony (B), the mean visible attendance during the nestling period was 34.2 $\pm$ 8.9. The accuracy of this figure would have been reduced to 18% and 25% respectively if only ten or five counts had been made and a single count could have resulted in a 57% error.

2. The information necessary for the correction for egg loss was obtained during a three-year intensive study which would not be feasible for general census work. Moreover, it seems unlikely that egg loss, replacement rate and hatching success are similar in different breeding populations; more information is needed on this before the correction factors calculated from this study can safely be extrapolated.

In addition to the problems involved in actually counting the birds or eggs in any colony by these methods, the interpretation of the figures obtained require a background knowledge of the colony and breeding biology of the species that can only be gained by detailed study over a number of years. 'Head counts' are affected by weather conditions which may have quite unpredictable effects on attendance (Chapter 3ii). The number of immature or adult non-breeding birds in a colony may vary from year to year with no change in total numbers present, so that 'head counts' do not give entirely accurate population estimates.

APPENDIX VI Method of estimating egg shell thickness.

The following expression was used to estimate the thickness of the shell (plus membrane) on a Razorbill's egg, given the length, breadth and weight of the shell.

$$m = \frac{S\pi}{6[LB^2 - (L-2T)(B-2T)^2} \qquad \delta T = \delta F \frac{dT}{dF}$$

$$\therefore \quad 8T^3 - 4(2B+L)T^2 + 2(2LB+B^2)T - \frac{m\pi}{6S} = 0$$

$$\frac{dF}{dT} = 2AT - 8T(2B+L) + 2(2LB+B^2)$$

Where: M= egg weight (g)

S= specific gravity of the eggshell (2.12 g/cc - see text)

L= length (mm)

B= maximum breadth (mm)

T= estimated shell thickness (mm)

Measurements of fragments of shell with the membrane intact showed that the thickness with membrane was 118.5% of that without the membrane. The estimates of shell thickness in museum eggs were corrected accordingly before comparison with shells measured in the field.

APPENDIX VII Results of chemical analyses of a sample of eggs from Skokholm Razorbills.

The following results were obtained by gas chromatography analysis for polychlorinated biphenyls in a sample of 9 eggs collected on Skokholm in 1972. The analyses were conducted by Dr P I Stanley, Pest Infestation Control Laboratory, MAFF (Tolworth, Surrey).

	Total weight of egg(g)	Weight of egg minus shell(g)	Weight of yolk analysed(g)	ppm PCB (Yolk)
1	81.76	59.66	10.24	61.0
2	44.44	35.02	6.44	268.0
3	41.55	32.50	6.50	237.0
4	60.75	49.85	6.66	92.0
5	45.90	36.25	6.35	243.0
6	64.98	55.00	6.12	45.0
7	32.40	41.78	6.75	151.0
8	58.11	45.02	5.98	45.0
9	43.90	33.55	6.46	56.0

Note All eggs except no. 1 were either crushed or broken. Results indicate the presence of arochlor 1,2,5,4.

APPENDIX VIII Two egg clutches

During the three years of the study, seven Razorbill nests were found containing two eggs. In each case, the sites had been checked before the start of laying and both eggs were laid in the current year. The events at these sites are summarised below.

I Far Bay 4

1971	May 12	Egg laid and incubated for at least 24 hours.
	June	Second smaller egg present, being incubated; first egg cold.
	July 15	Second egg disappeared, well after the date it should have hatched.
1972 and 1973		Site not used.

II Far Bay 16

1971	May 18	Single egg present, measured and photographed.
	June 12	First egg cold, buried under earth in site; second larger egg present and being incubated.
	June 24	Second egg hatched (therefore laid c.May 20), chick fledged.
1972		Single egg laid, similar in pigmentation pattern to first egg in 1971.
1973		Single egg laid.

III Nell's Bay

1971		Single egg.
1972	May 26	Two eggs present; smaller one cold, larger one being incubated. This hatched and the chick fledged successfully.
1973		Single egg laid, pigmentation not like either 1972 egg.

IV Wallsend Bay 6

1971		Single egg, C32 used site.
1972		C32 seen twice on land during the season but not caught on this site though it probably bred there.
	May 28	Egg laid and incubated.

	June 4-12	Second smaller egg laid, unincubated but later proved to be fertile. First egg failed to hatch - infertile.
	1973	Single egg; C32 known to be breeding elsewhere.

V Wallsend Bay 19

	1971	Single egg.
	1972	Single egg, similar in pigmentation to that of previous year.
	1973 May 23	C32 trapped in site, incubating the larger of 2 eggs present. (see Chapter 4Biie Figure 4.13). Pigmentation of both eggs unlike those laid in 1971 and 1972.

VI Frog and Scabbard 9

	1971	Single egg.
	1972	First egg chilled when the site became flooded; this was measured and removed. Second (replacement) egg laid but failed for the same reason. NB This would have appeared to be a two egg clutch if I had not removed the first egg.
	1973 June 12	First egg (laid some time between May 27 and June 12) found cold, wedged in a crevice in the site margin. This was measured, photographed and replaced in the site.
	June 13-18	Second (replacement) egg laid and incubated; identical in pigmentation pattern but (unexpectedly) larger in size than the first.
	July 6	Both eggs cold.

VII Wallsend Bay 2

	1971 and 1972	Single eggs.
	1973 May 12-13	Egg laid and incubated.
	May 22	Egg cold.
	June 10	Second (replacement) smaller egg present, being incubated.
	June 20	Second egg cold.

In three cases (Sites I, VI, VIII) both eggs were almost certainly laid by the same bird. The second egg in each case was produced as a replacement for the first which had become cold but had not been taken from the site. This conclusion was supported by the smaller size of the second egg and/or the similarity in pigmentation pattern between the two eggs.

In the other sites, the larger of the two eggs laid was incubated suggesting that a second female was involved. In Site II the female which laid first in 1971 appeared to be ejected by a second bird which laid and incubated an egg in the site.

There was no evidence in the present study to suggest that one female laid and incubated a two egg clutch, and in no case were two birds found incubating eggs in the same nest site when a two egg clutch was present. In spite of this, Razorbills have two brood patches and this has been suggested to indicate that they once laid two eggs (cf Cramp et al 1974).

APPENDIX IX Experiment to test the powers of egg and chick recognition in the Razorbill.

Introduction

Adult Guillemots have been shown to learn the characteristic calls of their chicks during the chipping period of hatching (Tschanz 1959). The first few days after hatching are especially important for the development of parent-chick recognition; the youngest chicks will shelter under any free adult. Puffin chicks cannot distinguish their own parents nor parents their own chicks (Myrberget 1962); this is also true of the Pigeon Guillemot (Koelink 1972). Razorbill eggs and chicks are highly variable in appearance and in 1972 a simple experiment was designed to test whether adults would adopt strange eggs or chicks.

Method

Eggs from different sites on The Bluffs were inter-changed during the incubation period to discover if a bird would incubate any egg it found in its nest. (This did not however establish if the bird could actually recognise its own egg.) Pairs of chicks of the same age were also inter-changed during the nestling period. The amount of handling in these exchanges was kept to a minimum and was no more than that involved in the usual daily weighing. The different ages at which the changes were made are given in Table 1.

Results

All eggs were incubated normally after being moved from their original sites. Hatching success was not reduced by the exchanges, compared with other (control) sites on The Bluffs (Table 2). Further trials showed that the birds would incubate a plaster model egg or a gull's egg instead of their own.

All eight of the chicks interchanged, apart from those swopped 15 days after hatching, were adopted and apparently

Table IX.1 Timing of exchanges of eggs and chicks in recognition experiment 1972.

Number of days after laying that eggs were changed	Number of days after hatching that chicks were changed
1 and 2	1
2 and 3	2
2 and 3	3
2 and 4	3 and 4
6 and 7	8
6 and 8	15
21 and 22	
21 and 23	
31 and 34	
33 and 34 - chipping	

Table IX.2 Hatching success of experimental and control eggs in egg swopping experiment 1972.

	Experimental	Control
Number of eggs hatched	6	33
Number of eggs unhatched	2	14
Total	8	47

Note Fisher's exact probability test: P = 0.3429

fed normally to fledging. Their growth rate was slower after the change (Table 3) and their weight at fledging also below average (Table 4). There was no marked weight loss after the exchange but growth continued with decreased daily gains in weight.

The two chicks exchanged at the end of the nestling period appeared not to be adopted by their foster parents. One had disappeared when the site was checked 24 hours after the change, and the other had done so by the following day. Their alertness and activity, characteristic of healthy chicks of this age, probably caused them to stray from or fall out of the site. These sites were within 2m of each other so that the possibility that the true parents accompanied their own chicks in successful fledging cannot be excluded. If the chicks had fledged alone and succeeded in reaching the sea, their subsequent survival would have been extremely unlikely.

Discussion

The results of the first part of this experiment showed that Razorbills would incubate any egg-like object they found in their nest; this indicates that their powers of recognition of their own egg are poorly developed.

Although most of the chicks exchanged were not rejected (or vice versa) by the strange adults, their growth was retarded. This suggests that the number of feeds was slightly reduced but the present study did not establish whether this was the fault of the chicks of their parents. Observations of normal chick-parent behaviour showed that Razorbill chicks were fed regularly, apparently without begging for food (Chap. 4iiib4). Thus failure by the adult to recognise an introduced chick may have caused a reduction in feeding rate.

The chipping eggs exchanged hatched normally and the chicks grew and fledged successfully with average rates of growth.

Table IX.3 Growth rates of chicks exchanged between sites in 1972, compared with unchanged chicks.
X = Age in days, Y = Weight in g.

		Growth equation	n
Experimental	Before	Y = 9.5 X + 49.9	39
	After	Y = 6.2 X + 60.8	70
Mean 1972		Y = 8.6 X + 55.4	425

Note Difference in growth rate before and after moving site is significant ($d = 5.03$, $P < 0.001$) but growth rate before the move is similar to the mean (control) $d = 1.74$ $P > 0.05$.

Table IX.4 Mean weight at fledging (g) in experimental chicks 1972.

	Fledging weight	n	S.D.
Experimental	146.8	8	10.3
Control	170.8	17	10.3
	$t = 5.33$	$n = 25$	
	$P < 0.001$		

The newly hatched chicks moved between sites however, grew more slowly than average. Hence, the chipping period in the Razorbill, as with the Guillemot, may be especially important in the development of parent-chick recognition.

Guillemots often breed in crowded conditions and birds arriving at the colony must locate their own chick, retrieve it from amongst other birds on the ledge and feed it as efficiently as possible. Vocal recognition by parent and chick appears to develop during hatching and is maintained until after fledging (Tschanz 1959; Oberholzer & Tschanz 1968) and plays a vital part in this. Razorbills usually nest in relatively uncrowded conditions and the chicks stay in the nest site and are thus comparatively isolated. Where Razorbills nest with Guillemots, the chicks are accompanied by one parent and therefore need not be retrieved from a crowd to be fed. Otherwise the adult has only to enter a nesting cavity to find and feed its chick; in either case there is no necessity for well-developed recognition. In burrow-nesters such as the Puffin or Pigeon Guillemot, there is a total lack of recognition between adult and young (Myberget 1962; Koelink 1972).

If a chick is dependent on its parent after fledging, as is the case with the Razorbill and Guillemot, the development of recognition during the nestling period could be important for survival. At one extreme is the Puffin in which although the chicks are not deserted by their parents before fledging (Harris 1976), they are independent afterwards so that recognition is unimportant. The reverse is true of the Guillemot and the Razorbill appears to occupy an intermediate position. Some degree of parent-chick recognition is retained though it is of little use during the nestling period and is probably essential at fledging and in the post-fledging period.

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OBSERVATIONS ON THE INCUBATION AND FLEDGING PERIOD OF THE RAZORBILL *ALCA TORDA*

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INTRODUCTION:

One of the aspects of the biology of the Razorbill that has been studied in detail is the length of the incubation and fledging periods (Brun 1959, Keighley and Lockley 1947 and 1948). Some further observations were made on these stages of the breeding cycle during 1970 and 1971 as part of a study of the breeding biology of the species on Skokholm Island, Pembrokeshire.

METHOD:

In 1970 six breeding colonies were chosen from the areas on the north and west coasts of the island. These were all made up of nest sites on ledges which could easily be observed without disturbing the birds. Two visits were made each day between June 20th and July 17th in order to determine the hatching date of each egg. During the period when the birds were fledging, an evening watch was kept at one of the colonies and the others checked the next morning. Since young Razorbills only leave the island at nightfall the morning visits established which birds had departed the previous evening. Observations were made on a total of 55 nest sites.

In 1971 nine study areas were kept under observation and the sites checked daily during the laying period in May and early June for new * an estimate of the length of the incubation period to within 24 hours. This gave Daily observations during fledging allowed the duration of the fledging period to be measured for the chicks in most colonies. Observations on the Purple Cliff sites were abandoned during the laying period because of heavy egg predation by the Herring Gulls (*Larus argentatus*) breeding nearby.

RESULTS:

Of the 49 eggs under observation in 1970, 44 hatched and from these 31 chicks were known to have fledged successfully (Table 1). Eight of the others had not left the nests by July 17th when observations ceased. Three eggs were lost before hatching, although others must have done so before observation began, and two eggs were unhatched by July 17th—one was still being incubated and the other deserted. Of the five chicks lost before fledging, four disappeared from the ledges and one was seen to be thrown off the ledge by two non-breeding birds when left alone by the parents. This gave an overall fledging rate of

* eggs + again in late June and July in the hatching period.

86.1%, not including the eight 'late' chicks which may have fledged successfully after July 17th (Table IV).

In 1971 the egg losses over the whole incubation period were recorded: thus an estimate of the hatching, fledging at total breeding success was obtained (Table II). The hatching success in 1971 was 70.4% and 91.2% of the chicks fledged. 145 chicks left the cliffs from 226 eggs laid, giving an overall breeding success of 64.2%.

TABLE I

THE FLEDGING SUCCESS IN 1970

Colony	No. of chicks hatched	No. of chicks fledged
Crow Point	2	2
Purple Cove	2	2
Little Bay	5	5
Wildgoose Bay	6	5
Dents	6	5
Twinlet Bay	15	12
TOTALS	36	31

TABLE II

THE HATCHING AND FLEDGING SUCCESS IN 1971

Colony	No. of eggs laid	No of eggs hatched	No. of chicks fledged
Near Bay	10	8	7
Far Bay	18	16	14
Twinlet Bay	28	21	18
Purple Cliff	23	9	8
Wallsend Bay ...	28	21	19
Bluffs	53	42	38
Warden's Rest ...	14	7	7
Widgoose Bay	24	18	18
Quarry	14	10	9
TOTALS	212	152	138
Replacement eggs ..	12	7	7
2 egg clutches ...	2	0	0
TOTALS	226	159	145

TABLE III

Observer	Year	Place	Incubation period in days			Fledging period in days		
			N	Range	Mean	N	Range	Mean
Paludan	1947	Denmark	7	35-36	35.5			
Keighley & Lockley	1947	Skomer				16	10-18	15.2
„	1948	Skokholm	18	33-36	34.3	18	12-18.8	15.7
Brun	1958	Skokholm				20	16.21.5	18.0
Plumb	1964	Skokholm	29	34-39	36.2	34	14-24	18.5
Bedard	1969	Gulf of St. Laurence, Quebec, Canada.	9	36-39	36.9	30	16-22	18.2
Present study	1970	Skokholm				37	14-21	16.9
„	1971	Skokholm	92	28-43	34.6	73	14-22	17.4

TABLE IV

	Keighley & Lockley	Brun	Plumb		
	1948	1958	1964	1970	1971
	Skomer	Skokholm	Skokholm	Skokholm	Skokholm
No. of eggs laid	50	31	86	—	226
No. of eggs hatched	18	20	59	36	159
Hatching success	36%	65%	69%	—	70%
No. of chicks fledged	18	19	46	31	145
Fledging succes	100%	95%	78%	86%	91%
Total success	36%	61%	53%	—	64%

Two sites, both in Far Bay, were found with two eggs. In both cases these eggs were different in colour and amount of pigmentation and only one was being incubated. It seems likely therefore that they were not laid by the same bird. Only one egg hatched out of the four laid. Twelve cases of eggs being lost and replaced were recorded. The period between loss and replacement was about fourteen days. In all cases the second egg was smaller in length and breadth than the first although apparently similar in colour and amount of pigmentation. Egg losses were mostly due to predation by gulls and Jackdaws, especially if the site was left unattended for any length of time. All the 14 chicks lost were less than ten days old and only two more than four days old. Nine disappeared, probably taken by gulls or crows, three were found dead in the nest and two were drowned after heavy rainfall. The Twinlet Bay colony was the only one used in both years' observations. The fledging rate of 80% recorded in 1970 is slightly less than that observed in 1971 (85.7%). The Wildgoose Bay colony includes both ledge and boulder nest sites but only the former were used in the 1970 study.

The first chick was seen on June 19th, 1970. The peak of hatching occurred between June 24th and 27th that year and a peak in the fledging on ~~July~~ July 12th. In 1971 the first egg was found on May 1st and

the first chick hatched on June 7th. The peak of laying occurred on May 15/16th and peak of hatching on June 21/22nd. The length of incubation period in 1971 varied from 28 to 43 days with a mean of 34.59 days (N=92). The length of the fledging period in 1970 was between 14 and 21 days, mean 16.92 (N=37) and in 1971 from 14 to 22 days, mean 17.37 days (N=73). There is no significant difference in the length of the fledging period between the two years. (t= -1.3687 with 108 degrees of freedom).

The eggs were incubated by both adult birds in turn. The length of the spells at the nest site varied between individuals but changes were generally observed from two to four times during daylight hours. When not incubating the adult bird would sit beside its mate, preen itself and its partner or leave the site for periods of anything up to three hours, sometimes returning only to relieve the sitting bird.

This pattern was maintained after hatching, one adult staying with the chick while the other collected food. The periods between feeds varied from 17 minutes in one case observed to 4¾ hours in another and may well be longer. The chicks were closely brooded for the first few days after hatching, which in some cases made it difficult to establish the exact date of hatching. Later the chick was left alone for increasing lengths of time while both parents were absent, presumably searching for food.

Fledging occurred in the evening when the chicks were about 17 days old. As light faded after sunset the young birds became increasingly agitated. They were joined at this time by one adult. The other parent was nowhere near the nest but possibly present in the rafts of birds at the foot of the cliffs. The parent may play a part in determining the exact time at which the chick launches itself from the ledge. The young birds at this age are unable to fly as their wings have no primary feathers although the coverts are well developed. The timing of the leap may be critical as apparently there should be enough light to enable the chick to reach the sea (which in the cases of nest sites not directly above the water may mean a series of drops from one rock to the next) but not light enough for the predatory gulls to be able to see them. The parent, having followed the chick from the ledge, waited patiently at the foot of the cliff while the fledgling floundered among the rocks calling incessantly and occasionally being answered by the parent. Once united the adult and chick swam out to sea together.

DISCUSSION:

The figures obtained for the lengths of the incubation and fledging periods of the Razorbill compare quite favourably with similar estimates obtained in other studies. Table III.

The breeding successes observed are given in Table IV together with those for the present study. The choice of nest sites in these studies and the amount of disturbance caused are important when con-

sidering these figures. Nest sites among boulders, although less easily observable, are usually more accessible and thus useful for daily chick weighings which were carried out in the 1958, 1964 and 1971 studies. Frequent visits to these sites must involve greater disturbance of the birds and result in increased predation. Observations on the ledge sites made without disturbing the birds are thought to give a better indication of the true egg and chick losses but one would expect these losses to be higher than those in the more sheltered sites. The 1971 nest sites were mostly hidden, as were thirteen of Brun's nineteen sites in 1958 and this may have contributed to the high breeding successes observed on these occasions.

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ATTENDANCE AT AUK COLONIES DURING THE BREEDING SEASON

Clare Lloyd

Introduction

The number of birds present at a colony during the breeding season varies throughout the day and from one day to the next. This type of fluctuating attendance has been described for several species of seabirds that have been studied, but this paper is confined to the three species of auk--the Razorbill *(Alca torda)*, Guillemot *(Uria aalge)* and Puffin *(Fratercula arctica)*—all of which breed on Skokholm. Estimates of the breeding population of these species, especially the first two, are usually made by counting the birds visible on the breeding cliffs. It is essential to know how many non-breeding birds one would expect to find on the ledges at the different times of the season and whether the numbers of birds vary with the time of day or season or with other factors such as the prevailing weather conditions. The timing and pattern of the return to the colonies in spring is also important as counts early in the season involve breeding birds only because most of the younger immature birds do not arrive until the breeding season is well under way; this is discussed more fully later. The aim of these counts was to record the return to the colonies in the spring and the pattern of attendance during the breeding season and to consider the effect of this behaviour on census counts.

As part of a more detailed study of the Razorbill on Skokholm, daily counts were made of the birds present around the island during the pre-laying period in the spring of 1971 and 1972. Guillemots were also counted and the numbers of Puffins within a mile of the island were estimated. During the nesting period of 1972, daily counts were made of Razorbills and Guillemots at one of the mixed colonies on the west coast of the island. These counts were made from a hide and involved the minimum amount of disturbance.

Pre-laying period

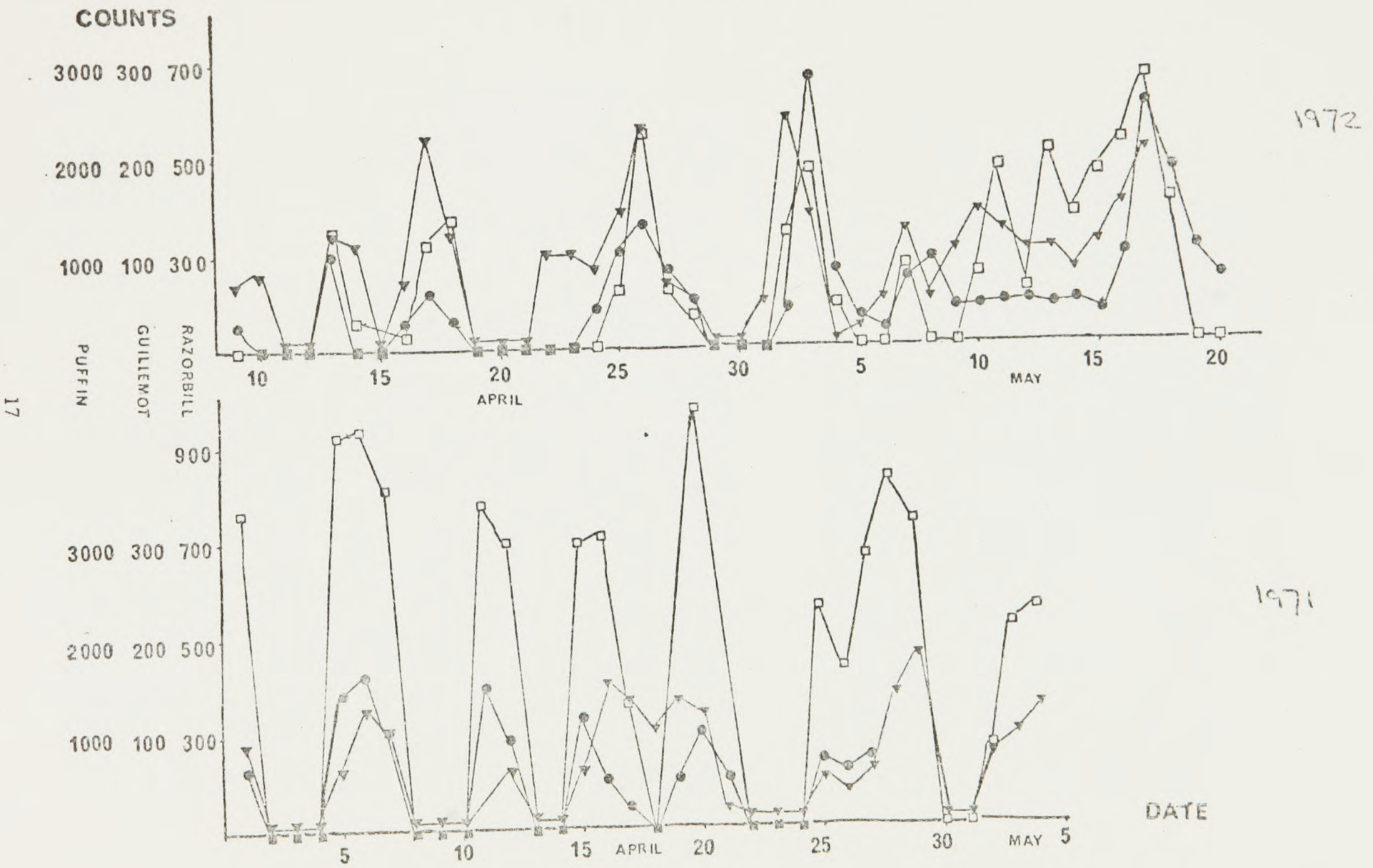
Auks are rarely seen during winter in the vicinity of the breeding colonies (Greenwood 1972). Occasionally birds will approach land in the early morning especially in the late winter months (December to February). Razorbills have been recorded from Skokholm in December (Harris—*pers. comm.*) and from Lundy at Christmas time (Perry 1940); Guillemots were also recorded on the Skokholm cliffs from December onwards by Lockley (1953). During March the numbers of auks build up within sight of land and the Razorbills

and Gillemots form rafts and long strings offshore. The birds are most numerous in the early morning although as the season progresses the numbers build up later in the morning and the birds remain near the island for longer periods in the afternoon. Bédard (1969) recorded early morning peaks in Razorbill numbers during the pre-laying period (May) at colonies in the Gulf of St. Lawrence. Perry (1940) working on Lundy noted that the Razorbills " tended to leave the cliffs earlier than the Guillemots and Puffins. And even in May they might all have gone out to sea by four o'clock in the afternoon". Puffin numbers are lowest in the early morning but increase to a late afternoon peak (*pers. obs.* and Corkhill 1970). This routine is established for each species in March and lasts until the start of the laying period in May.

The results of the daily counts are shown in figure 1. The three species are well synchronised in their attendance and the daily counts for each species are closely correlated. The number of birds present fluctuates widely from day to day but in 1971 a distinct rhythm in peak attendance was observed and further analysis (by autocorrelation) showed that this followed a four day cycle. No such pattern of regular attendance was found in 1972 when the numbers present were low until late in the season.

In order to establish if weather factors were affecting the numbers of birds present, detailed records of the sea conditions, visibility, wind speed and direction were made throughout the breeding seasons and maximum and minimum temperatures, rainfall and sunshine obtained from the Observatory records kept for the Meteorological Office. Extreme weather conditions involving strong winds, rough seas and heavy rainfall resulted in the reduction of the number of birds around the island and tended to break up the rafts. No such effect was observed on overcast or foggy days. Puffin attendance was less affected than that of Razorbills or Guillemots by rough weather. The effect of less extreme weather conditions was more difficult to establish and here the discussion is limited to the more accurate counts of Razorbills. In 1971 there was a significant negative correlation between the numbers of Razorbills recorded and the wind speed ($r = -0.46$, $p < 0.01$) although no similar relationship was found for temperature or wind direction. In 1972 the spring Razorbill counts were not related to any of the weather factors measured. The spring was very late that year and the weather conditions cold and stormy. The Razorbills appeared to be less synchronised and the counts remained low compared with 1971 until late in the season although there was no change in the size of the breeding population between the two years. This suggests that there was no day in 1972 upon which all the breeding birds gathered at the colony. Guillemot counts were about the same as in the spring of 1971 in spite of a large increase in the breeding population. Intra-specific synchrony for all three species was also

Figure 1 - Graph to show counts of Razorbills □—□ Guillemots ▼—▼ and Puffins ●—● during the Springs of 1971 and1972.



affected; this is indicated by a decrease in the amount of correlation between the counts from 1971 to 1972.

Fluctuating attendance at the breeding colonies in spring has been described for the Puffin by Lockley (1953) who suggested that the birds were subject to an internal rhythm which caused them to leave the island every few days to feed. Myrberget (1959) working at a Puffin colony in Norway found that attendance was related to weather and Corkhill (1970) recorded a five day cycle of attendance for all three species of auk at the Skomer colonies in 1969 and 1970.

The function of the synchrony observed between the different species and between individuals of the same species is complex. In most seabird species the optimal nesting period is relatively short and if the maximum number of individuals are to breed successfully the birds must be synchronised. The cyclic pattern of attendance at the colonies contributes to the development of this synchrony which is first established during the pre-laying period. This fluctuating behaviour may in turn be the result of a proximate factor such as day length or sea temperature which affects the birds at this time.

Nesting period

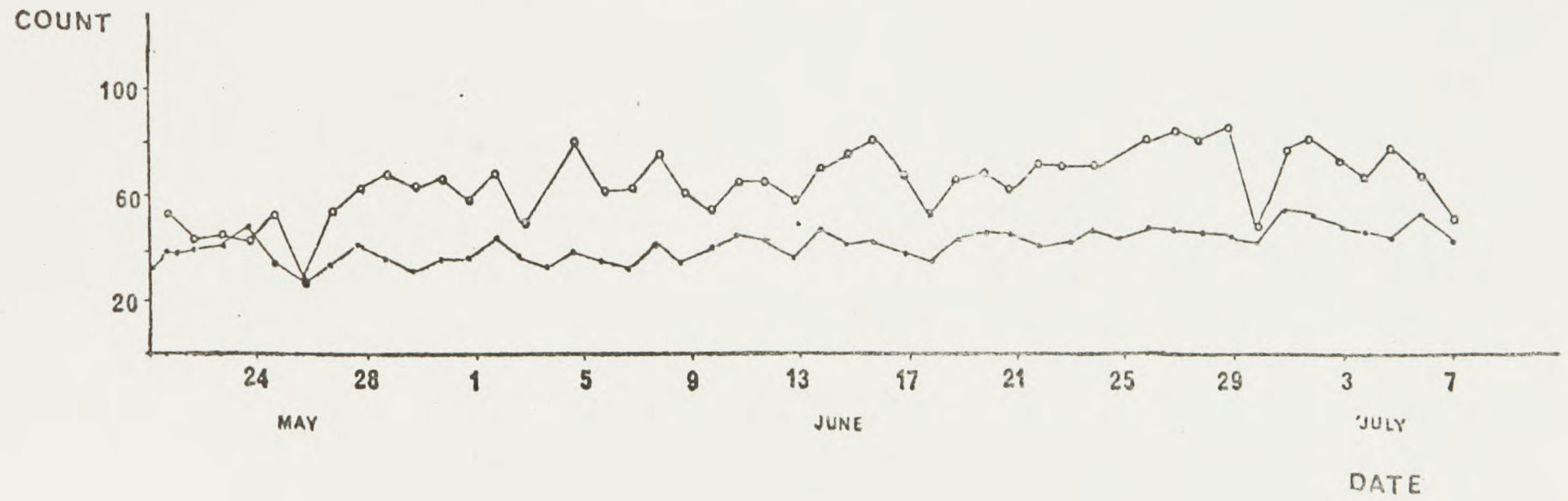
Puffin attendance at the colonies during the nesting period was also recorded by Lockley (1953) and further data collected during the fledging period is given by Myrberget (1959) and Roberts *et al.* (1967). Myrberget working in northern Norway recorded a daily peak late in the afternoon at the beginning of the season. The duration of this peak attendance increased as the season progressed and from June onwards a second smaller peak formed in the morning. Maximum counts throughout the season formed peaks every 3 to 12 days, on average every 6.3 days.

Tuck (1960) recording diurnal changes in the numbers of Brünnich's guillemots *(Uria lomvia)* at Cape Hay colony, Hudson Bay, noted good attendance during the early breeding season throughout the day and especially at night between 12.00 and 04.00. A diurnal rhythm was also maintained by Brünnich's guillemots on Jan Mayen in conditions of 24 hours of daylight (Cullen 1954).

Bédard (1969) collected similar data for a colony of Razorbills in the Gulf of St. Lawrence. The numbers of breeding birds built up steadily during the laying period and remained high throughout incubation and fledging. A decrease in daily attendance began in the late fledging period and accelerated during the departure of the young. Similar synchronised occupation of the breeding colonies has been recorded for Black guillemots, *Cepphus grylle* (Kosimies 1949) and Pigeon guillemots, *Cepphus columba* (Drent 1961).

The results of the daily counts of Razorbills and Guillemots at the Skokholm colony are shown in figure 2. After laying in late May it was possible to estimate the number of non-breeding

Figure 2 – Graph to show counts of Razorbills 0—0 and Guillemots •—•
at Twinlet Bay during the 1972 breeding season.



Razorbills present but this was not possible for Guillemots. Thus counts of breeding birds include the incubating or brooding birds and their mates when present at the nest. Counts of non-breeders include birds present at the edges of the colony and may contain some off-duty birds and failed breeders. Observations of incubating behaviour in the Razorbill indicate that in cliff colonies off-duty birds usually sit beside the mate in the nest site or leave the colony entirely.

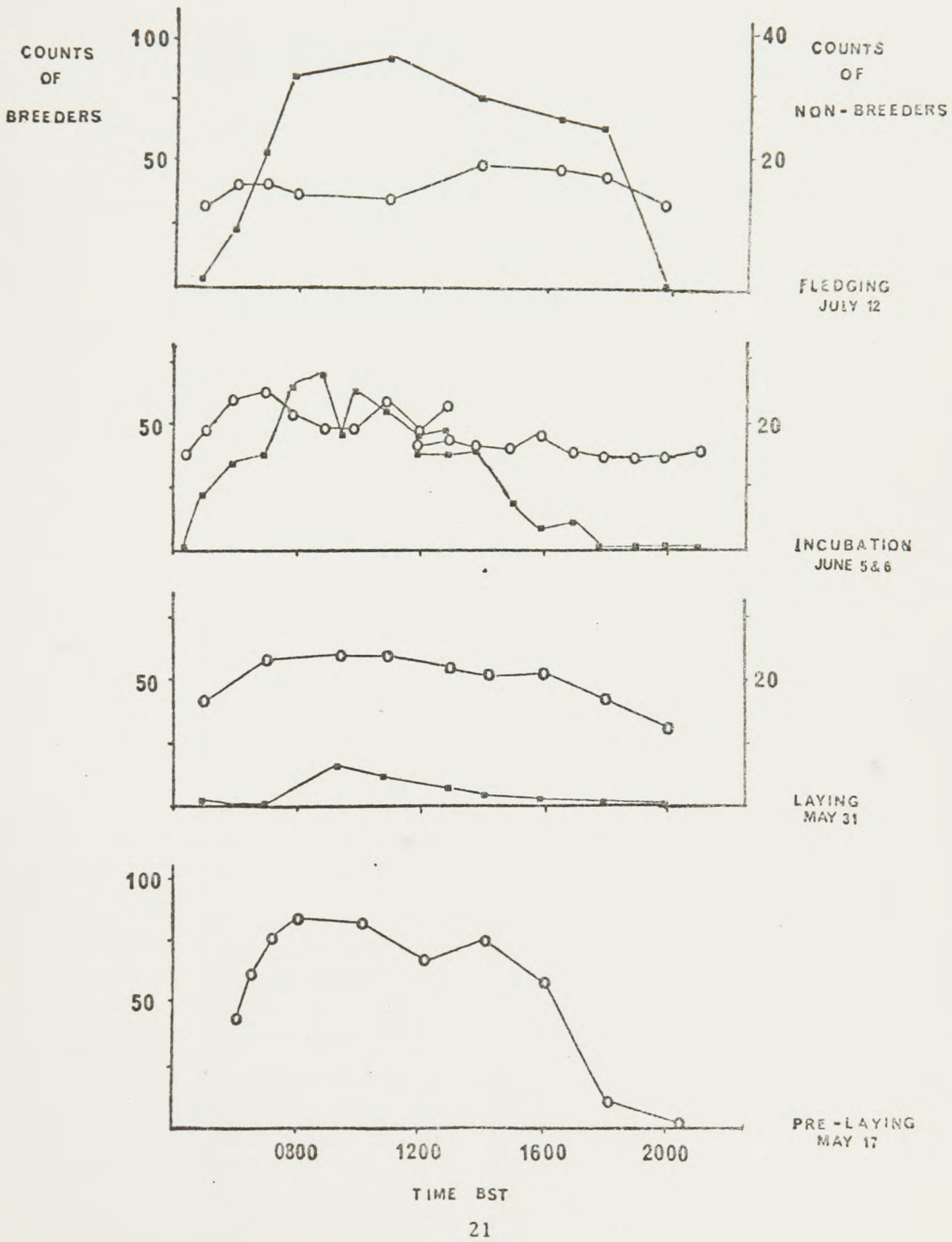
Razorbill numbers fluctuated widely during the pre-laying period but increased steadily after the onset of laying to a peak (80-85) birds in late June. This coincides with the maximum attendance of non-breeding birds. Guillemot attendance rose gradually between laying and fledging periods, probably due to the arrival of immature birds.

The diurnal variation in numbers of Razorbills is shown in figure 3 based on counts made during the pre-laying, laying, incubation and fledging periods. The diurnal pattern of Guillemot attendance is relatively constant throughout the day and there is a tendency for the birds to remain on the cliffs for a longer time in the evening than the Razorbills.

The Razorbill counts are high early in the season before breeding and prospecting birds could be distinguished; the numbers build up swiftly after dawn to a peak about 08.30. During the laying period the counts of breeding birds become more stable. The low counts at dawn and dusk are due to the presence of incubating birds which remain alone on the sites overnight. Once incubation is under way the return of the mates after dawn to relieve the sitting birds produces a well marked peak between 06.00 and 08.00. Attendance remains high throughout the day as the sitting birds are rarely alone for long. During the fledging period one of the adults is frequently absent and this lowers the count. During the week of peak fledging the number of birds decreased rapidly (cf. Bédard 1969). The proportion of "non-breeders" increases at this time due to the influx of ex-breeders. Observations of colour ringed birds have shown that it is not unusual for one bird of a pair to return to the cliffs after the chick has fledged.

The counts of non-breeders in the laying and incubation periods must include prospective breeding birds although laying in the colonies concerned was nearly over by the beginning of June. Later during incubation these counts are supplemented by a small number of failed breeders. The counts increase to a peak of 25-30 birds in late incubation and fledging when maximum numbers of immature birds are present; non-breeders at this time represent up to 40% of all the birds. Late in the season when birds whose young have fledged are present, the proportion of "non-breeders" rises as high as 70-90%. The diurnal peak in numbers occurs later in the morning with the progress of incubation as the birds stay longer on the cliff. Table 1 shows the counts of non-breeders

Figure 3 - Graph to show diurnal changes in counts of breeding o—o and non-breeding ▪—▪ Razorbills, Twinlet Bay 1972.



expressed as a percentage of the total number of birds present for the different parts of the season.

Table 1—Non-breeding birds expressed as a proportion of the total number of birds present.

Period of Season	Composition of Non-Breeders Counts	% of Non-breeders
Laying	Mostly prospective breeders	10
Incubation	Failed breeders, few off-duty breeding birds	20—30
Hatching	Maximum numbers of	40
Early fledging	immature birds	
Late fledging	Ex-breeders, few immatures	50
Post-fledging	Many ex-breeders	70—90

The effect of weather on these counts was evaluated by multiple regression analysis carried out on a 1906A computer. During the pre-laying period the size of the counts increased gradually with the progressing season and the only important weather factor was wind speed. Little of the variation in the numbers of breeding birds during incubation and even less of the variation in the counts of the non-breeders was attributable to the prevailing weather. There was a significant correlation between the numbers of breeding birds present and the cloud cover ($r = -0.374$, $p < 0.05$), good attendance being recorded on sunny days during incubation; this effect is also observed in the attendance of Guillemots at the Skomer colonies at this time (Birkhead—*pers. comm.*). The weather had most effect on the birds during the fledging period when wind speed and, to a lesser extent, cloud cover were especially important. There were significant correlations between the number of non-breeding birds present and both sea conditions and wind speed at this time ($r = -0.595$, $p < 0.02$ and $r = -0.577$, $p < 0.05$ respectively). Thus the weather was most effective in determining the numbers of non-breeders present at the time of the season when these counts consisted mainly of immature birds.

Throughout the incubation and fledging periods the numbers of non-breeders were closely related to those of breeding birds. This indicates that the two parts of the population are being affected

by the same external factors although to a differing extent. The peak in diurnal attendance of non-breeders at the colony appeared to be timed so as not to coincide with the maximum number of breeding birds.

These observations are confined to one colony and to only two breeding seasons; frequently the data are too scarce to permit discussion of all three species. More counts at different colonies and for different seasons are essential before reliable results, applicable to seasonal breeding censuses, can be obtained.

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Oiled seabirds successfully cleaning their plumage

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Notes

Oiled seabirds successfully cleaning their plumage Although the literature on the effects of oil on seabirds is extensive, there is apparently no record of oiled birds in the wild cleaning themselves. On the islands of Skomer and Skokholm off the coast of Pembrokeshire, a large number of seabirds (mainly auks and gulls) have been colour-ringed; this enables them to be recognised for study purposes. Here we present some observations of colour-ringed seabirds which were oiled and subsequently cleaned themselves.

Three incidents involved Great Black-backed Gulls *Larus marinus* on Skomer. In the first of these a male bird was heavily oiled on the head and breast during the discharging by the tanker *Malmghüs* of bilge washings in St Brides Bay between 20th and 24th April 1972. The bird was in bad health and in a distressed condition. On 2nd May it was seen with only a trace of oil on its plumage but still appeared sick. By 20th July the bird was apparently fully recovered, with no trace of oil on its plumage. It did not attempt to breed, however, although it had done so in the two previous years.

In the second case, also in April 1972, a male gull was oiled on the breast and underparts. This bird was clean in ten to fourteen days and later bred successfully. In the third case, a female gull with a clutch of three eggs was involved. It was oiled on the breast and underparts, but did not appear sick and continued to incubate, cleaning itself within eight days. The eggs failed to hatch after the normal incubation period and were found to contain partly developed embryos, which may have died as a result of oil from the female's plumage contaminating the eggs, or from a film of oil sealing the pores and suffocating the embryos. The same effect has been recorded in oiled terns *Sterna* (Rittinghaus 1956) and has,

in fact, been used as a method of gull control in New England (Kadlec and Drury 1968).

During mid-April 1973 oil began to come ashore on Skomer, and on 15th April 39 out of 682 Guillemots *Uria aalge* (5.7%) at a colony on the north coast had small amounts of oil on their plumage (estimated size range 2-70 square cm). Among those oiled were a colour-ringed bird and its mate, both with patches of oil approximately 25 square cm in area on the breast. Guillemot attendance at this time of year is irregular, and the birds were not seen again until 24th April, when both returned with no trace of oil, apparently behaving normally. On that date no other birds at the colony had oil on their plumage and, since there was no apparent reduction in numbers, it seems possible that more of those previously oiled had also managed to clean themselves. The colour-ringed Guillemot and its mate produced an egg in early June, but this was later knocked from the ledge by a falling chick of Herring Gulls *L. argentatus*.

In early May 1973 observations of oiled Razorbills *Alca torda* were made on Skokholm, the fate of ten individuals with small patches of oil being recorded (table 1). As expected, birds with smaller patches of oil cleaned themselves more rapidly than those with larger patches (Mann-Whitney *U* test, $P = 0.012$). All birds with patches of oil of less than 5 square cm bred successfully, though one was still slightly oiled two days after its egg was laid. One Razorbill with a 10 square cm patch of oil on its breast later laid an egg which was cracked and abandoned about one month after laying. It was not possible to determine whether oil on the plumage was responsible for this breeding failure.

The ability of wild birds to clean oil from their plumage depends upon the amount, type and toxicity of the oil and on its distribution over the plumage. Birds must be able to remove oil from their plumage, restore the feather micro-structure and water repellency (RUROS 1970) and survive the toxic effects of oil ingested during this process (Bourne 1969). In addition the time of year, local food availability and weather conditions are probably important, since

Table 1. Fate of ten Razorbills *Alca torda* with different-sized patches of oil, Pembrokeshire, May 1973

Number of birds	Approximate size of oil patch (square cm)	Number of days to clean	Breeding
1	10	—	Failed
3	4	8, 16, 16 (mean 13.3)	Successful
6	2	2, 2, 4, 4, 5, 5 (mean 3.6)	Successful

an oiled bird is under greater stress during cold and bad weather.

Gulls are noted for their ability to digest unnatural food items and probably have very resistant digestive systems. This may account for their ability to remove successfully relatively large amounts of oil from their plumage, and also their better success in rehabilitation efforts (Clark and Kennedy 1971). Auks are apparently less robust and more vulnerable to the effects of digested oil. However, the incidents described here have demonstrated that in some circumstances they can remove small amounts of oil from their plumage successfully. In addition, if the oil is removed before egg-laying, the birds' breeding biology is apparently not disrupted.

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Exceptional evening roosting movements of Black Terns

During 6th-8th August 1971, at Shellness, Isle of Sheppey, Kent, I saw a series of outstanding roosting movements, from sunset to dusk, of Black Terns *Chlidonias niger* (*Kent Bird Rep.*, 20: 60). The birds, which had probably spent the day feeding several kilometres out to sea, flew in from the north-east in groups of 30-100 to a roost on a stretch of tidal mud. During daylight hours, only up to about 100 could be seen feeding offshore in the Swale estuary, but the evening arrival in three-quarters of an hour on 6th included 1,130 Black Terns with about 2,000 Common or Arctic Terns *Sterna hirundo/paradisaea*; during the same period on 7th some 600 Black and 300 Common or Arctic were counted, but by 8th the Black Tern roost was down to 150. A few Sandwich *S. sandvicensis* and Little Terns *S. albifrons* were also involved. Several groups of Black and Common or Arctic Terns were seen to circle up high from the roost area, calling excitedly, and move away south or south-west; this would explain, at least partly, the drop in numbers each evening.

Movement and Survival of British Razorbills

by Clare Lloyd

This study of the results of ringing Razorbills in Britain brings further evidence of the wealth of information that can be drawn from the Bird Ringing Scheme—even when the recovery rate is as low as 3%. Records are grouped by age-classes and distance from the ringing site, and illustrate a migratory tendency in younger birds but a random dispersive movement for those of three years' old and more.

AT A TIME when serious concern is felt about the decline of British auk populations, it is important to quantify the extent of changes in mortality patterns and find the reasons for them. This paper describes the movement and survival of British Razorbills *Alca torda britannica*, based on ringing recoveries, and evaluates changes in the contribution of certain mortality factors.

The reports of ringed birds, both dead and alive, provide some evidence for the movements of the species although care must be taken in the interpretation of such records. For a seabird species such as the Razorbill, most of the records are of the recovery of dead birds. Mead (1974) has described the distribution of Razorbill recoveries and compared it with that of the Guillemot *Uria aalge* and the Puffin *Fratercula arctica*. Such data are subject to several biases, among the more important of which are the following:

(1) The chance of a bird dying is different in different areas. This is due to the presence of localised causes of mortality such as hunting, shooting, oiling and other forms of chemical contamination.

(2) Whether or not a bird is found depends considerably on the cause of death. If a bird is killed by man it is more likely to be examined and the ring detected. Thus a bird shot or caught in a fishing net is almost certain to be handled, whereas only a few oiled birds are picked up. If a bird is oiled or dies naturally at sea, the chance of its being washed ashore depends upon the proximity of the nearest land and prevailing winds and currents. This is further complicated by a tendency for dead birds to sink to the sea-bed (Hope Jones 1970).

(3) The chance of a dead bird being found on the shore-line varies with the density of the human population of the area, and whether or not the ring is reported depends on the standard of education.

(4) Birds of some ages are more likely to be recovered than others. This is usually a result of different patterns of movement in birds of different ages. If individuals of one age group tend to collect in an area where they are especially vulnerable, they will provide more recoveries than birds of other age groups which are more widely dispersed. Similarly, birds which use relatively land-locked inshore areas such as British coastal waters, are more likely to be washed ashore when dead.

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Some mortality factors affect young inexperienced birds more than adults in the same area. Thus there are many recoveries of first-year Razorbills, but few of adults, from areas with heavy shooting pressures, such as southern Norway. (The age is estimated from 1 July on the year of ringing as a *pullus*, so that a first-year bird is not yet one year old.)

(5) Rings used on seabirds are likely to become worn and lost with increasing age (Coulson and White 1955). Razorbills only come to land in the breeding season but birds which are not old enough to breed spend some time on land during the breeding season (see discussion below). From the age of return to the colony onwards, ring wear increases markedly due to abrasion on the rocks at the breeding site. This increases the chance either that the ring will be lost before recovery, or that the inscription will be illegible when the dead bird is found. The number of recoveries of older birds, and hence estimates of the life span, are thereby reduced. This is discussed fully by Mead (1974).

Ring wear

Harris (1964) gives data on ring wear in Manx Shearwaters *Puffinus puffinus* on Skokholm Island, Pembrokeshire. He suggests that the inscription on the aluminium rings used up to 1958 became illegible after

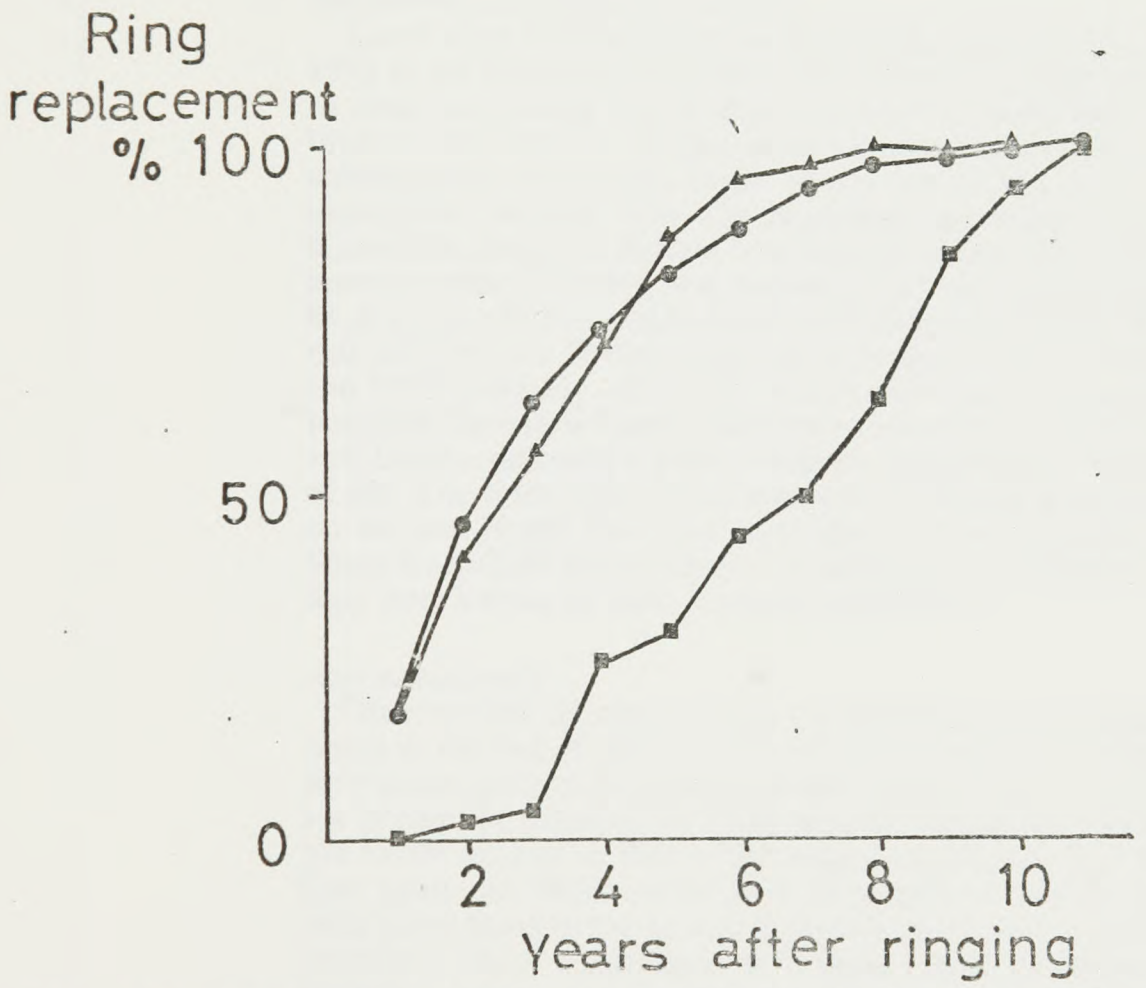

Figure 1. Wear in different rings. Percentage of rings from series ●—● AV–, AT–, AX–, ▽—▽ SS–, ■—■ 30– that had to be replaced in successive years after ringing.

two seasons on land, thus decreasing the chance of recovery. These 1958, when monel rings came into use. These (series 304-/307-) were superseded by standard size 3 (SS-) rings in 1963 which were in turn replaced by a special Razorbill ring from 1966. Figure 1 shows the average life of the first three types of ring used on Skokholm between 1923 and 1966. The curves are based on the time (in years) after ringing as an adult that a bird was re-ringed on being retrapped. Where a bird was retrapped several times but not re-ringed, the most recent date of capture was used as this gives an indication of the life of the ring. Of the aluminium rings 81% had to be replaced after five years' wear, and the SS- monels wore less well, 87% being replaced after the same length of time. The earliest monels (304-/307-) were more resistant to wear and only 31% were replaced after five years. The figures are somewhat biased by the different amounts of retrapping in each year and the assessment of wear of the rings, but this is unlikely to alter significantly the differences shown in Figure 1.

Recoveries available for analysis

There were 695 recoveries of Razorbills under the B.T.O. scheme from 1923 to 30 June 1971. Of these, 69 records were rejected as they referred to rings only being found (thus the date of death was unknown), young birds which failed to fledge, oiled birds released after rehabilitation and subsequently recovered, birds controlled at the place of ringing, and incomplete records. The 626 remaining recoveries represent 3% of all Razorbills ringed in Britain and Ireland during this time. A much higher recovery rate of 19.4% was reported for Norwegian ringed Razorbills, a large proportion of which were shot (Holgersen 1951). The slightly lower rate of 2.3% for British birds up to August 1952 (Landsborough Thomson 1953) probably reflects the more severe ring loss in early years. Landsborough Thomson found that recoveries of Razorbills from South Wales and Lundy indicated a more southerly movement of birds in the first year of life. The birds from the colonies in northwest Scotland were recovered on the east North Sea coast from Denmark north to the Lofoten Islands. Some Razorbills were recorded in subsequent summers at colonies where they were known to have hatched or had bred.

Age at recovery

Observations of ringed birds on Skokholm show that Razorbills first breed at the end of their fourth, or more usually their fifth, year. Ringing only takes place at breeding colonies, and although some immature birds are present at colonies for short periods during the breeding season, they are rarely caught, so that a bird ringed as adult or 'f.g.' is usually at least four years old. Birds in the first 12 months of life are considered separately from those in the second to fourth years, and records of birds of four years and older are grouped with those ringed as adults. These age categories are referred to throughout this paper and are different from those used by Mead (1974).

TABLE I. CAUSES OF RECOVERY OF RAZORBILLS WITH RESPECT TO AGE, 1930-1965.

CAUSE	AGE			
	1st-year	*2nd/4th-years*	*Adults*	*All ages*
Oiling	9.1	19.1	29.7	18.4
Shooting	23.4	17.3	5.2	15.8
Killed	22.3	20.0	7.7	16.9
Found dead	45.2	43.6	57.4	48.9
Total number of recoveries	197	110	155	462
Relative oiling intensity	16.8%	30.4%	34.1%	
Relative shooting intensity	34.1%	28.4%	8.2%	

The number of recoveries due to each cause are expressed as a percentage of the total number of recoveries. See text for explanation of the 'relative intensity' of shooting and oiling.

CAUSES OF RECOVERY

Eleven reports of recovery did not include any details of death; 47.8% of the rest were reported as 'found dead' or 'dying', although this category contains birds shot, oiled and killed but not reported as such, and a few miscellaneous recoveries such as birds reported falling dead on the deck of a ship in a storm. Also included are birds caught and released alive away from the place of ringing. It is assumed that if a Razorbill is caught in this way it is already ill and therefore unlikely to survive. Oiling accounted for 19% of the other recoveries; 18.2% were netted, caught, 'taken' (assumed dead) or killed; and 14.9% were shot.

The distribution of recoveries due to these four causes with respect to month is shown in Mead's Table XI. Table I below gives the cause of death for recoveries in three age groups. Only records of birds ringed up to 1965 are used as these are assumed to have a negligible number of present-day survivors. A large number of recoveries of all ages are reported 'found dead', and the proportion of recoveries due to oiling increases with each age category; the reverse is true of recoveries due to shooting and those reported killed. This pattern reflects both a decreasing tendency with age for a bird to be caught or shot, as well as the distribution of the birds of different ages. The regional effects of, for example, shooting off the coast of southern Norway, produce many recoveries in certain areas, whereas it is possible that the birds are equally well represented in other areas, such as northern Norway, but tend not to be recovered there due to the small amount of shooting or the deserted coastline. Because of these biases it was found necessary to establish in which areas the birds were vulnerable to such localised causes of mortality before considering the distribution of the recoveries.

The categories of birds killed or found dead were too heterogeneous for this type of analysis. The recoveries due to oiling and shooting, which together accounted for 34.2% of recoveries of birds ringed up to 1965, were examined for regional differences in intensity. In order to detect any changes in shooting and oiling pressures with time for each area, the recoveries were grouped into decades and divided according to eight geographical regions (Table II, and Birkhead (in press).). The relative

oiling intensity was then obtained by expressing the number of recoveries due to oiling as a percentage of the total number of birds found dead and oiled. This calculation, also used for the British Cormorant *Phalacrocorax carbo* (Coulson and Brazendale 1968), was repeated for Razorbill recoveries due to shooting. This time the oiled birds were omitted and the recoveries expressed as a percentage of the total found dead and shot. The relative intensities obtained for each region were independent of the factors which produce large numbers of recoveries in certain areas and so reduce the proportion of recoveries due to other causes.

When comparing the figures directly, allowance should be made for the fact that the probability that a dead bird will be discovered, examined and reported is different for the various regions involved. The percentages obtained are useful as indices for the comparison of shooting and oiling pressures in different areas and their change with time, and indicate neither the actual number of birds dying there due to either cause nor the relative importance of the two pressures.

TABLE II. CAUSES OF RECOVERY OF RAZORBILLS WITH RESPECT TO REGION AND DATE

		Period of ringing							
Region	*Cause*	*Up to 1940*		*1941-50*		*1951-60*		*1961-70*	
Britain: East coast	O	2						13	61.9%
	S								
	FD	1		1		4		8	
Britain: Northwest coast	O			2		1		2	15.4%
	S	1							
	FD			2		4		11	
Britain: Southwest coast	O	2		1		12	25.0%	13	22.4%
	S								
	FD	6		2		36		45	
English Channel	O			7	43.8%	10	38.5%	26	53.1%
	S							2	8.0%
	FD	7		9		16		23	
Biscay	O			1	7.7%	2	8.0%	5	26.3%
	S	1		2	14.3%	4	14.8%	3	17.6%
	FD	6		12		23		14	
Portugal	O								
	S			1		1		2	
	FD			1		4		6	
Mediterranean and Morocco	O			1				2	16.7%
	S	1		2		2		7	41.2%
	FD	2		1		5		10	
Belgium and Norway	O			1				11	50.0%
	S	10	76.9%	8		16	80.0%	29	72.5%
	FD	3		1		4		11	
Total	O	4	13.8%	13	30.9%	25	20.7%	72	36.0%
	S	13	34.2%	13	30.9%	23	19.3%	43	25.1%
	FD	25		29		96		128	

Key to causes: O=Oiled S=Shot FD=Found dead.
Percentages are 'relative intensities', given for samples of 10 or more records. See text for explanation.

From Table II it is evident that oiling has been a constant threat to Razorbills in the English Channel, Irish Sea and Bay of Biscay, a result also obtained by Bibby and Bourne (1972). The more exposed Atlantic coast of western Iberia appears to have remained the least contaminated. The relatively low standard of education in the human population of the area, associated with the low probability that a dead ringed bird will be reported, possibly contribute to this effect. More recently oiling intensity has increased in the North Sea, also on the north European coastline from Belgium to Norway, and in the Mediterranean. This may also be partly due to an increasing tendency for birds found dead to be reported as oiled as a result of the publicity given to marine pollution.

Shooting pressures are low in British waters, but elsewhere the amount of shooting has remained approximately constant, and it is heaviest on the north European coast, especially in Norwegian waters. Portugal appears to be free of any significant shooting pressure (possibly for the same reasons mentioned above), but the intensity seems to have increased since 1961 in the Mediterranean.

AREAS OF RECOVERY

A full analysis of the recovery pattern of birds from the Irish Sea and northern British colonies, with detailed maps for the recoveries of different age groups in each season, are given by Mead (1974). A summary of the movements based on the distribution of these recoveries is given below. The main colonies at which Razorbills were ringed are shown in Mead's Figure 1. These colonies are considered here in three groups.

South Irish Sea colonies

It appears that a majority of first-year birds remain in the Irish Sea during August after fledging in July. A few first-year birds disperse north to the west coast of Scotland, and five were recovered on the Atlantic coast of Ireland; most move south to the English Channel and Bay of Biscay by September. In October and throughout the winter many are reported from the Bay of Biscay, possibly due to the relatively high shooting pressure in the area. Recoveries from the west coast of Spain and Portugal occur from October onwards. Those from the Mediterranean are first reported in November and are most numerous in December. There are a few recoveries from these southerly latitudes in spring, and those from the English Channel increase slightly at this time. Some first-year birds winter in and around British coastal waters and a few reach Holland, Denmark and Norway.

The autumn recoveries of second-year birds are mainly from the English Channel, North Sea and Scandinavia, with a few from the Irish Sea. The Bay of Biscay and Mediterranean appear to be important wintering areas for these birds, which may in fact remain there during their first summer. The small number of Razorbills of all ages, especially first- and second-year birds, recovered between April and July may be due to the milder weather and abundant food supply. The available records indicate that some first-year birds at least leave their southerly wintering

grounds, although they do not return to the breeding colonies. (See Mead 1974 Table IV). The latest recovery in the Mediterranean of a Skokholm-ringed first-year bird is in April, and there has been only one subsequent recovery (of a second-year bird) in the area until December.

There is little indication in the recoveries of the whereabouts of the birds at this time although the Razorbill is a coastal species and is rarely seen far from land. The few records of Razorbills on the Atlantic islands of the Canaries (Bannerman 1963) and the Azores (Hartert and Ogilvie-Grant 1905), and the lack of records from Madeira (Bannerman 1965) and the Cape Verdes (Bannerman 1968), indicate that the birds do not move out into the Atlantic or farther south to the west coast of Africa.

The recoveries of third- and fourth-year birds are distributed between the Irish Sea, Bay of Biscay, English Channel and southern North Sea. The records of older birds, including those ringed as adults, are most frequent from the Irish Sea, English Channel and north Bay of Biscay throughout the year with the exception of the breeding season when few birds are recovered. The number of birds dying in these areas is probably even greater than is indicated by the recoveries, because of the heavy oiling pressure and associated low probability of report.

The mean distances of recovery during the winter months (November to February) from the colony are as shown below. (The distances are shown in miles as these were the units in which all but the most recent recoveries were recorded, and given ± one standard error.):

	Miles	*Kilometers*	*Number*
First-year birds	611.5±29.9	983.9±48.1	99
Second-year birds	582.0±49.4	936.4±79.5	30
Third- and fourth-year birds	444.6±60.7	715.4±97.7	18
Adults	328.8±43.6	529.0±70.2	39

There is a good correlation between age and mean distance from the colony during winter ($F=10.06$, $p<0.01$, $R=-0.996$, $p<0.01$). The first-winter birds are found farthest from the colony and birds from the older age classes are on average recovered progressively farther north.

North Irish Sea colonies

The youngest and oldest age groups are best represented in the recoveries from these colonies although the samples from each are small. The general pattern of migration appears to be similar to that of the birds ringed farther south. There is a tendency for north Irish Sea birds to produce fewer recoveries from the south Iberian Peninsula, Mediterranean and Morocco. This difference is not significant ($\chi^2=1.24$, $p<0.50$), and is probably due to the smaller number of recoveries. Significantly fewer birds from the north than from the south Irish Sea colonies are recovered east of the Straits of Dover ($\chi^2=5.70$, $p<0.025$). The lack of recoveries of birds from the Norwegian coast is surprising in view of the shooting there. As with birds from the south Irish Sea colonies, the mean distance from the colony during the winter months decreases with age ($F=2.86$, $p<0.05$, $R=-0.975$, $p<0.01$).

Northern colonies

The first-year birds account for more than half the recoveries; nearly two-thirds of the records are reported, mostly shot, from the Norwegian coast, especially during the autumn. South Norwegian waters are important moulting areas both for first-year birds from these colonies and for immature birds from the Irish Sea colonies. This is reflected in the tendency for birds ringed at Scottish sites to produce significantly more recoveries during their first year to the north and east of the colonies than do similar birds from the Irish Sea ($\chi^2=26.4$, $p<0.001$). The birds cross the North Sea after leaving the cliffs on fledging, and the earliest record of a first-year bird off Norway is in August; there are five birds ringed as *pulli* at Fair Isle and in Sutherland recovered during September off Norway. The sudden decrease in records from this area during the winter months indicates that the first-year Razorbills move south to winter with the birds from the Irish Sea colonies off Biscay, Iberia and North Africa. One bird ringed as a *pullus* on Fair Isle in 1968 was reported 'caught' off Agadir, Morocco, in May (3,400 km. south).

The few recoveries of second- to fourth-year birds are from the North Sea, except for one from the Bay of Biscay. The records of adults from these colonies are scattered, although there is a concentration of reports to the south of the colonies during the winter months (November–February). The northern adults are recovered significantly farther from the place of ringing than the Irish Sea birds at this time ($t=4.10$, $p<0.01$). This is a result of the isolated position of these colonies, but also indicates a tendency for northern birds to winter farther away from the breeding grounds.

The distribution of recoveries was also considered in relation to the regional causes of mortality discussed above. From Table I it is evident that the relative oiling intensity of adults is significantly greater than that of younger birds ($\chi^2=21.0$, $p<0.001$). The total numbers of recoveries due to oiling for first-year and adult birds were compared with those reported found dead, which are assumed to be relatively unbiased in their distribution. Significantly more adult birds than one would expect are oiled ($\chi^2=9.13$, $p<0.01$). There is no reason to suppose that oiling affects only adult birds throughout the year, although there is a possibility that this is so during the moult. The greater proportion of adults in the recoveries due to oiling is more likely to be due to the fact that first-year birds spend relatively little time in areas of high oiling intensity.

Similarly, the relative shooting and oiling intensities indicate that a high proportion of first-year birds are shot. There are remarkably few recoveries of adults from Norwegian waters during autumn, although first-year birds, especially from northern breeding colonies, provide as much as 72% of all recoveries from Norway between July and October. Comparison of the 'shot' and 'found dead' recoveries for adult and first-year birds also shows that a significantly greater proportion of first-year birds is shot ($\chi^2=21.1$, $p<0.001$). This bias in shooting towards the younger birds has also been found in the Woodpigeon *Columba palumbus* (Murton

1961), Dunlin *Calidris alpina* (Martin-Löf 1961), Black-headed Gull *Larus ridibundus* and Lesser Black-backed Gull *L. fuscus* (Lack 1943), and Cormorant (Kortlandt 1942). The possibility that the adult Razorbills are absent from Norwegian waters during autumn should not be ignored. The few recoveries of adults at this time are from farther south in the North Sea. In spite of the bias towards young birds in the Guillemots shot off Norway (Birkhead, in press), the small number of adults recovered indicates that the eastward movement from British east coast colonies may also involve mainly first-year birds. The adult Guillemots, like the Razorbills, are recovered mainly on the west side of the North Sea and farther south at this time.

In conclusion, the Bay of Biscay is an important wintering ground for Razorbills, especially for first- and second-year birds from the Irish Sea colonies. Some of these move south to Portugal and North Africa and into the Mediterranean as far east as Italy. The English Channel and Irish Sea are areas of moult and pre-migratory concentration; they are also rich feeding grounds and support a large number of birds throughout the year. A first-year Norwegian ringed Razorbill recovered during January in Co. Cork (Holgersen 1971), and another ringed in 1961 at Arkhangel, U.S.S.R., and recovered in February 1964 near Rhyl, Flintshire (Hudson 1965) show that the Irish Sea may support birds of a more eastern origin.

The south Norwegian waters are important feeding and moulting areas for many Razorbills from the north and east of Britain, as well as for immature birds from Irish Sea colonies and northern Norway, the Faeroe Islands, Baltic Sea and Helgoland (Holgersen 1951). The shooting pressure in this area contributes to the high recovery rate recorded for Scandinavian birds mentioned above. Recoveries of Norwegian ringed birds suggest that the wintering areas extend into the south Baltic. These may be joined by British birds and by birds of the nominate race *Alca torda torda* whose breeding distribution is confined to the Baltic (Salomonsen 1944).

AGE AND RANGE OF RECOVERIES

The pattern of recoveries indicates a wider movement of immature birds throughout the year with a tendency for most adults to be reported from the vicinity of the breeding colonies during the winter months. In order to establish more accurately the age at which most Razorbills return to the breeding colonies, the recoveries were considered in relation to distance from the place of ringing. Recoveries from a group of ringed birds with a negligible number of present-day survivors (such as those ringed as *pulli* up to 1960), show that approximately 97% of the mortality occurs during the first five years. For this reason the recoveries of birds ringed only up to 1965 were used in these calculations as they should represent a relatively complete set of records.

The movements of Razorbills from colonies outside the breeding season can be analysed as for other seabird species, such as the Cormorant (Coulson and Brazendale 1968). These movements are basically migratory or dispersive. If dispersal is considered as a random movement with respect

to distance from the colony, the resulting distribution, as sampled by recoveries, can be described mathematically with fewer records at progressively greater distances from the place of ringing. Thus the distribution resulting from a truly dispersive movement is predictable, whereas migratory movement, resulting in a clumped distribution, is not. For this reason the recoveries of British Razorbills were grouped into zones of equal distance from the ringing site. One hundred mile* intervals were chosen (miles being the units in which most recoveries are recorded), providing in most cases meaningful sample sizes.

If one assumes a random dispersal from the colony, the number of recoveries in each one hundred mile zone represents a constant proportion of the birds available for recovery in that zone and beyond. The situation is analagous to the mortality observed in each year of a bird's life. A constant mortality rate can be calculated for adults assuming the number of birds dying at any single age represents a constant proportion of all the birds alive at that time. This average annual mortality is calculated from the number of recoveries occurring at each age (Lack and Schifferli 1948). A similar rate, based on the proportion of recoveries in each distance zone from the site of ringing, can also be estimated. This value (R) represents the rate of dispersal of birds away from the colony. A high value of R indicates a heavy loss in each zone, few recoveries from the more distant zones, and thus a low dispersal rate. Conversely, a low value of R is associated with relatively fewer recoveries in each zone, a spread of all the records over a wider area, and a high rate of dispersal.

It should be noted that the method used here is slightly different from the analysis of Coulson and Brazendale (1968) for the Cormorant. They based their estimates on the number surviving in each zone and calculated a value (r) which represents the reciprocal of the value used here, although its interpretation of dispersal is similar. Finally, the method they used to calculate this survival rate was based upon an average of the proportion surviving in each zone (Lack 1943); the estimate used in this paper is obtained from the more refined expression used to calculate mortality rates by Lack and Schifferli (1948). The difference between the two methods is discussed more fully by Birkhead (in press).

When dealing with biased data such as recoveries, the overall trends rather than the exact numbers indicate the distribution of the birds. For example, the Razorbill is a coastal species, with recoveries confined to a relatively narrow zone off the west coast of the British Isles and the Continent coinciding with the continental shelf. In the discussion of dispersal this especially affects the more distant zones, with a higher proportion of oceanic water, where Razorbills are recovered in only a small part of the total area available. As the expected number of recoveries is based on mortality occurring throughout each zone, there is a tendency for fewer recoveries than expected to be reported from the most distant zones. The amount of each zone occupied by land is also important; in the present discussion, because of the position of Britain on the northwest side of Europe, approximately half the distance zones 400 miles or

*100 miles=160.9 km.

more from the colony are occupied by land. The biasing effect of the relatively isolated colonies, such as Shetland and Fair Isle, which tend to produce more distant recoveries, is to some extent balanced by colonies in land-locked areas, such as the Irish Sea, where short-distance recoveries are more frequent.

In order to detect any differences between the movements of Razorbills from different age classes, each age group was considered separately, although it was found necessary to combine the third- and fourth-year recoveries because of the small numbers involved. Birds ringed as adults were included in the fifth-year and older age class. The number of recoveries expected in each one hundred mile zone, assuming a constant dispersal rate R, was calculated and compared by a chi-squared test with the number actually reported from each zone. The differences were significant for the first- and second-year birds ($\chi^2=64.60$, $p<0.001$ and $\chi^2=16.25$, $p<0.025$ respectively) but not for the older age groups ($\chi^2=2.03$, $p<0.750$ and $\chi^2=14.63$, $p<0.100$ for third- and fourth-year, and fifth-year and above age classes respectively (Table III)).

Thus, during the first two years of life, the birds are truly migratory; but from the third year onwards, their distribution is more typical of a dispersal away from the breeding colonies. The rates of dispersal of the three colony groups, based on the movements of adults (i.e. ringed as adults or as *pulli* and recovered three or more years later) are as follows:

Northern Irish Sea colonies	35.4%
Southern Irish Sea colonies	31.3%
Northern colonies	20.7%

TABLE III. NUMBER OF RECOVERIES FOR DIFFERENT AGE CLASSES EXPECTED IN EACH NUMBER ACTUALLY OBSERVED.

Distance zones in miles	*Age of recoveries in years*							
	0-1		*1-2*		*2-4*		*4-5 and above*	
	Obs.	*Exp.*	*Obs.*	*Exp.*	*Obs.*	*Exp.*	*Obs.*	*Exp.*
0-100	21	38.6	6	14.7	13	11.0	50	44.2
101-200	22	30.9	10	11.5	5	8.1	16	30.8
201-300	37	24.7	12	9.1	5	6.0	30	21.5
301-400	7	19.7	8	7.2	4	7.7	11	15.0
401-500	26	15.7	12	5.6	5		12	10.4
501-600	21	12.6	5	7.9	2		9	7.3
601-700	19	10.0	4	.	4	9.2	8	5.1
701-800	15	8.0	2		1		3	6.0
801-900	12	6.4	7	6.6	3		3	
901-1000	4	5.1	0		0		1	
1001-1100	3	4.1	2	6.3	0		1	5.7
1100	5	16.2	1		0		2	
Total	192		69		42		146	
R	20.1%		21.2%		26.25%		30.3%	
χ^2	64.60		16.25		20.03		14.63	
Level of significance	P<0.001		P<0.025		P<0.750		P<0.100	

Although the values are not significantly different from the dispersal rate of third-year and older birds in Table III ($\chi^2=4.08$, $p<0.50$), the Scottish birds have the lowest value of R and move more widely than those from the Irish Sea, probably for the reasons discussed above.

The return of young birds to the colony is confirmed by observations at breeding sites. Birds in their first year of life, although easily identified in the field, are rarely seen at Skokholm (pers. obs.). Both the recoveries and the recaptures of birds at this colony indicate a tendency for most birds to return at the end of their third year. It is usual for a bird to return to the natal colony to breed, and then to retain the same site year after year. Of the 430 birds known to have been ringed as either adults or *pulli* and retrapped on Skokholm from 1933 to 1971, only two, aged two and seven years, had been ringed on the island of Skomer two miles away, although during recent years a few colour-ringed birds from Skokholm have been seen on Skomer. One other bird ringed as a *pullus* on the Calf of Man was retrapped breeding on Skokholm in 1970, and was seen again in 1971 and 1972. The 73 retraps of birds ringed as *pulli* on Skokholm contain only two second-year birds and one third-year. Colour-ringing at this colony has shown the number of second- and third-year birds present to be higher than is indicated by retrapping. This is because these birds are non-breeders, making infrequent landfalls, and are thus less likely to be caught. Few birds are recorded breeding before the fifth year of life.

Counts of Razorbills present at one of the Skokholm colonies throughout the 1972 breeding season indicate a gradual build-up of immatures from early in the incubation period to a peak at the time of hatching (Lloyd 1973). Observations of immature colour-ringed birds show that the fourth-year individuals are present for most of this period, the third-year ones for slightly less, while the few second-year birds visit land for the first time late in the incubation and early nestling periods. This increase with age in the numbers of birds present and the duration of their attendance at the colony in pre-breeding years has also been described for the Manx Shearwater (Harris 1966, Perrins *et al.* 1973).

MORTALITY RATES

The distribution of recoveries with respect to age up to 1965 is shown in Table IV. An estimate of the annual survival and hence the mortality of Razorbills was made by Haldane's (1955) method of analysis, using the data shown in Table Va and b. The recoveries during the first year are omitted from Table Va in order to avoid the effect of the especially heavy mortality observed during this stage of life. The use of only the more recent records is favoured because the rings used on Razorbills during the last 12 years were made of the alloy monel, which is more durable than the earlier aluminium rings, and thus the bias due to ring wear and loss is decreased, though not eliminated. The relatively low number of recoveries after the fourth year in Table Va tends to reduce the survival estimate of these birds. The annual survival of $57.0\pm4.8\%$, calculated from data for birds ringed as *pulli*, is clearly unsatisfactory in

TABLE IV. DISTRIBUTION OF RECOVERIES FROM BIRDS RINGED UP TO 1965 WITH RESPECT TO AGE

Time after ringing (in years)	*Age at Ringing*	
	Pullus	*Adult*
0-1	194	23
1-2	75	25
2-3	31	19
3-4	15	23
4-5	15	6
5-6	8	10
6-7	8	3
7-8	5	6
8-9	1	3
9-10	1	3
10-11	0	4
Total	353	125

TABLE V. DISTRIBUTION OF RECOVERIES FROM BIRDS RINGED BETWEEN 1960 AND 1970 WITH RESPECT TO AGE

(a) Pulli ringed birds—excluding first-year birds.

		Age at recovery in years									
Year of ringing	*Total*	*1–2*	*2–3*	*3–4*	*4–5*	*5–6*	*6–7*	*7–8*	*8–9*	*9–10*	*10–11*
1960	13	10	0	1	0	0	1	1	0	0	0
1961	8	4	1	0	1	1	0	1	0	0	
1962	10	5	1	1	1	2	0	0	0		
1963	15	6	1	2	3	1	2	0			
1964	13	5	4	1	1	1	1				
1965	10	5	2	1	2						
1966	18	5	2	1							
1967	12	9	3								
1968	3	2	1								
1969	2	2									
Total	94	53	15	7	8	5	4	2	0	0	0

(b) Adult ringed birds—including first year after ringing.

Year of ringing	*Total*	*Years after ringing*									
		0–1	*1–2*	*2–3*	*3–4*	*4–5*	*5–6*	*6–7*	*7–8*	*8–9*	*9–10*	*10–11*
1960	5	0	0	0	1	2	0	1	1	0	0	0
1961	8	1	1	3	1	1	0	0	0	1	0	
1962	7	1	1	1	1	0	0	1	2	0		
1963	5	0	0	0	2	1	1	0	1			
1964	14	2	4	4	1	0	3	0				
1965	16	4	2	1	7	1	1					
1966	12	4	3	3	1	1						
1967	5	0	1	2	2							
1968	18	6	10	2								
1969	4	2	2									
1970	2	2										
Total	96	22	26	16	16	6	5	2	4	1	0	0

the mortality it infers. Similar calculations using the birds ringed as adults (Table Vb), which had therefore survived at least the first four or five years of life, gives a survival rate of $89.0 \pm 1.0\%$.

Survival estimates of a species can be checked by long-term studies of single populations. The values obtained by this method are frequently higher than those calculated from recoveries. The reasons for this have been discussed by Grosskopf (1964) and include biases due to ring loss and differential mortality within the population, as mentioned above. Survival estimates from the return of ringed birds to a colony can also be affected by emigration, which tends to increase the apparent mortality. Such studies are often limited to breeding birds; it is possible that these survive unusually well compared with the non-breeding individuals which may be less fit (Perrins 1971). Survival may also vary in different parts of the birds' range (Soikkeli 1967). Finally, there is no way of estimating the effect of such studies on the birds, and it is possible that being caught and ringed during the breeding season and then recaptured in following years may affect survival. Colour-ringing reduces this type of error by removing the need for recapture.

The average adult mortality of 11% for the Razorbill is being checked by the study of a colour-ringed population on Skokholm. This survival is of the same order of magnitude as that noted for other seabirds with single egg clutches, for example 90% for the Manx Shearwater (Perrins *et al.* 1973), 91-95% for the Fulmar *Fulmarus glacialis* (Dunnet 1963), 91% for the Short-tailed Shearwater *Puffinus tenuirostris* (Palmer 1963), 94% for the Gannet *Sula bassana* (Nelson 1963), and 88% for the Guillemot (Birkhead in press).

The Razorbill is a relatively long-lived species. The oldest bird known was ringed as an adult on Skokholm in 1948 and recovered 20 years later. The oldest record of a breeding bird is one ringed as an adult and last retrapped breeding on Skokholm 18 years later. Birds of ten years and more are quite frequently recorded. They do not breed until at least the fourth year, and more usually the fifth, so that the expected mortality is low. Assuming an overall breeding success of about 64% (Lloyd 1972) and an annual mortality of 10%, only 20 chicks need to survive *per annum* to breeding age from 100 pairs to maintain a stable breeding population. This indicates an average annual mortality rate of about 25% to the end of the fourth year of life.

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SUMMARY

This paper deals with recoveries of British Razorbills reported between 1923 and 1971. The factors affecting the recovery of ringed birds and the resulting biases in

their distribution are discussed. The recovery rate for Razorbills is 3%. The causes of recovery are described and a relative shooting and oiling intensity are calculated for different regions. The records are analysed with respect to age and month of recovery for birds from each of three groups of colonies. The records in each age class are then grouped according to distance from the place of ringing, and a randomly dispersed distribution is established for the third-year and older birds. Analysis suggests that the birds are migratory during the first two years and afterwards disperse randomly from the breeding colonies. This is discussed in relation to observations at the colony on Skokholm Island, Pembrokeshire. The average annual mortality estimates from the recoveries of birds ringed as adults is 11%. This figure is compared with similar estimates for other seabird species.

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MARINE POLLUTION BULLETIN

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Seabird Mortality in the North Irish Sea and Firth of Clyde Early in 1974

Heavy mortality of guillemots in the Irish Sea was recorded in 1969 and was the subject of a detailed enquiry. Organochlorine contamination was thought to be a contributory factor, although this could not be conclusively established. These persistent pollutants remain in the environment and further mortalities might be expected if they were indeed responsible. In January, 1974 there was a further heavy loss of seabirds in the area and, this time, investigators were prepared and the incident was carefully monitored.

In the autumn of 1969, great public concern was caused by a mass mortality of Guillemots (*Uria aalge*) with smaller numbers of Razorbills (*Alca torda*) along the west coast of Britain, and by the discovery of unexpected amounts of organochlorines and heavy metals in some of the bodies. While it seemed likely that this mortality was precipitated by a combination of stresses, such as food shortage (though this could not be demonstrated) and gales, it was postulated that it might have been made worse by pollution, and especially by the liberation of the lipid-soluble organochlorine as the birds consumed their fat (Holdgate, 1971).

If this was so, and these compounds remained in the ecosystem, it might be expected that the mortality would recur at intervals. The Royal Society for the Protection of Birds Seabird Group beached bird survey, which detected the original disaster, was therefore maintained partly to provide continuing surveillance, with concentration of the routine surveys into five weekends between September and March from 1971, to more easily obtain comparable results (Bibby & Bourne, 1972). By the time the next large incident of this type occurred in January, 1974 more than 1,600 km of shore in Britain and Ireland were being covered in each survey.

The Incident

The routine survey of January 26–27, 1974 revealed an increase in the usual level of mortality from Caernarvon in North Wales around the northern Irish Sea to Buteshire in south-west Scotland and the east coast of northern Ireland, as shown in Fig. 1. Guillemots were again the main species affected, with fewer Razorbills, and a wide variety of other species, especially Shags and Cormorants (*Phalacrocorax aristotelis* and *P. carbo*) as shown in Table 1. The way in which mortality increased in this area in this year, compared with the relatively unaffected east coast of Scotland and the previous year in both areas, is also shown in Table 2. Only 11% of the auks from the north Irish Sea were oiled in January, 1974 compared with 81% of the much smaller total for the equivalent survey of the previous year. As in 1969, many of the birds were extremely thin and there was a considerable proportion of young birds, though on this occasion the old birds were past the moult and the young ones were now, of course, almost fully grown.

During the terminal stages of the disaster, A. G. Stewart heard that oiled birds were coming ashore in Ayrshire between 26–30 January, and organized an additional beach survey there during the weekend of 2–3 February. By this time oil was already present on the beach at Girvan, Ayr, Prestwick, Troon and Seamill, and more was still coming ashore from Culzean to north of Dunure. None was seen at sea during an aerial survey of the east side of the Firth of Clyde as far south as Ailsa Craig, so that it seems likely that the slick, which was composed of heavy fuel oil, originated somewhere south of Arran, where oiled birds also came ashore on the south-eastern beaches. The majority of the badly affected ones, mainly Razorbills with many Guillemots



Fig. 1 Distribution of dead birds (total, followed by number per km) found around the Irish Sea and Firth of Clyde during the January, 1974 beached bird survey. The mortality in the Firth of Clyde was subsequently much increased when oil pollution also affected the birds.

TABLE 1

The number and species of dead birds found in the northern Irish Sea and Firth of Clyde during the January 1974 beached bird survey.

	km	Divers	Grebes	Fulmar	Gannet	Cormorant and Shag	Wildfowl	Waders	Gulls and Terns	Auks	Others	Total
Buteshire	52				1	21		1	16	5		44
Ayrshire	34			1		22	8	5	16	33		85
Kirkcudbrightshire	13							1	6			33
Co. Antrim	17					1	1	1	1			6
Co. Down	33					81			1			82
Cumberland	240	1		3	4	11	38	24	93	582	1	757
Lancashire	108	1	2			9	19	17	54	79	1	182
Cheshire/Flint/Denbigh	15								1			1
Anglesey	27				1	10			8	5		24
Caernarvonshire	33		1			11	8	3	17	67	1	108
Total	572	2	3	4	6	166	74	52	213	799	3	1322

TABLE 2

Comparison of bird mortality and incidence of oil pollution in the north Irish Sea and the east coast of Scotland in 1973 and 1974.

Species	East Scotland				North Irish Sea			
	1973		1974		1973		1974	
	Birds/km	Oiled	Birds/km	Oiled	Birds/km	Oiled	Birds/km	Oiled
Auks	0·06	40%	0·13	39%	0·16	81%	1·38	11%
Phalacrocoracidae	0·02	29%	0·04	0%	0·04	9%	0·29	12%
All species	0·56	15%	0·56	14%	0·50	34%	2·29	11%

and Eiders (*Somateria mollissima*), came ashore between Girvan and Prestwick, while there were also many oiled gulls and waders on the Culzean–Croy shore with smaller numbers at Ayr, Prestwick, and Troon. Most of the oiled birds came ashore on 28 January, and a few were still present into March, though elsewhere the mortality had returned to normal levels by the time of the next routine beach survey on 23–24 February. The 818 known casualties are listed in Table 3, and it was thought the full total was a little over a thousand.

More ringed auks and especially Phalacrocoracidae were recovered in the area of mortality in January, 1974 than at this time in any of the previous seven years; the number is compared with the average for this period in Table 4 and their distribution has been plotted by Mead (1974a). Most of the recoveries (61 or 91%) were made between 9 January and 20 February. Many of the birds had been ringed on the Great Saltee or Lambay in the south-west Irish Sea, and 88% were under 4 years old. A similar northward displacement of debilitated birds or bodies was recorded in the autumn of 1969 (Mead, 1974b). While the auks at least may disperse north regularly at this season (Bourne, 1971), it seems doubtful whether this movement normally occurs on such a large scale or lasts until January, unless the birds are short of food or weakened and unable to make headway against the prevailing south-west winds and northward drift of surface water.

An experiment to investigate the fate of marked bird bodies by the RSPB Research Department in the same area as the wreck chanced to coincide with the closing stages. A total of 300 dead Herring Gulls (*Larus argentatus*) and 19 dead auks were thrown overboard at intervals from the ferry between Liverpool and Douglas on the Isle of Man on 29 January. Only 24 (7·5%) of the bodies were subsequently reported compared with 58% for a similar experiment the previous year (Bibby & Bourne, 1974). The extremely unsettled weather with strong but variable winds which may have taken a long time to drift the bodies far and then landed them on unfrequented shores may help explain the poor recovery rate. Weakened birds are likely to swim or drift close to the shore before they die, so their recovery rate may be higher, but even so this observation suggests that the 1,600 bodies reported (compared with 12,000 in 1969) represent only a fraction of the mortality.

TABLE 3

Oiled birds recorded in Ayrshire in January–February, 1974.

Species	Alive	Dead	Total
Razorbill *Alca torda*	98	170	268
Guillemot *Uria aalge*	43	58	101
auk sp.	–	2	2
Herring Gull *Larus argentatus*	103+	3	106+
Eider *Somateria mollissima*	52	31	83
Black-headed Gull *Larus ridibundus*	70+	–	70+
Oystercatcher *Haematopus ostralegus*	36+	–	36+
Kittiwake *Rissa tridactyla*	32	1	33
Common Gull *Larus canus*	18+	1	19+
Cormorant *Phalacrocorax carbo*	12	5	17
Redshank *Tringa totanus*	14+	–	14+
Red-breasted Merganser *Mergus serrator*	6	6	12
Mute Swan *Cygnus olor*	7	4	11
Others	25	21	46
Total	516	302	818

The numbers followed by + are minimum estimates of birds seen together at one time. The other species included nine Shags *Phalacrocorax aristotelis*, eight Curlew *Numenius arquata*, five Black Guillemots *Cepphus carbo*, four Shelduck *Tadorna tadorna*, Gannets *Sula bassana*, and Great Northern Divers *Gavia immer*, three Great Black-backed Gulls *Larus marinus*, two Black- and Red-throated Divers *Gavia arctica* and *G. stellata* and Goldeneye *Bucephala clangula*, and one Mallard *Anas platyrhynchos*, Glaucous Gull *Larus hyperboreus* and Little Auk *Alle alle*.

TABLE 4

Number of ringing recoveries from the Irish Sea area in 1974 compared with the previous seven years.

Species	Average: 1967–73		1974	
	January	February	January	February
Cormorant	2·6	2·4	6	4
Shag	4·0	6·0	43	24
Razorbill	0·1	0·1	1	4
Guillemot	0·6	0·4	2	3

Post-mortem Examinations

Two Guillemots, two Razorbills and a Red-throated Diver (*Gavia stellata*) were investigated by D. Taylor and E. Wheeldon at the University of Glasgow Veterinary School, and a Guillemot and two Shags with the help of Mrs H. M. Hanson at Monks Wood Experimental Station. Some details of these and other specimens examined are also recorded in Table 5. In general, the birds were 20–40% underweight compared with breeding adults, with loss of most fat deposits, though the pectoral muscles were not always as wasted as in 1969; they also had fluid or frothing in the lungs. The Diver and Razorbills were oiled, which explains their death. Guillemot M4417 had blood on the bill and trachea and water in the lungs, and may have drowned after a blow on the neck. (It was the heaviest bird received at Monks Wood, five others ranging between 470–610 g (average 553 g). Guillemot B289, found dead on the beach at Kilcreggan, was only a little lighter, and the only significant finding was fluid in the lungs. Guillemot B283, found beached beside the River Nith at Glencaple, was much lighter (about 40% underweight) with a congested carcass and patchy discoloration of the kidney; a gram-negative coccobacillus pathogenic to mice was isolated from the liver. The two Shags M4118/9 were also about 30% underweight compared with breeding females in summer; their intestines were congested with haermorrhage and the kidneys full of urates and apparently malfunctioning, while in one the heart was congested. Together with the Razorbills they had nematodes in the gizzard, but this is not unusual.

Toxic Chemical Analyses

Details of 22 specimens which were analysed for organochlorine insecticide and PCB residues are given in Table 5. In half of them estimates are available for muscle as well as liver. In general, the Guillemots showed lower liver values and perhaps slightly higher muscle ones (at least compared to whole body values:

TABLE 5

Toxic chemical residues in ppm. wet weight in seabirds collected January–February, 1974.

No.	Species	Age/Sex	Origin	Weight	Oil	Tissue	PCBs	DDE	Dieldr
B287	Red-throated Diver	ad.m.	Dumbarton	1248g	+	liver	123	19·1	5·0
						muscle	41	17·1	1·6
C1	Cormorant	f.	Ayrshire	–	0	liver	23	0·4	1·9
						muscle	5	0·2	1·6
B276	Shag	imm.f.	Ayrshire	1270g	+	liver	10	2·5	0·9
M4118		imm.	Bute	1105g	0	liver	7	1·2	1·1
M4119		imm.	Bute	1160g	0	liver	8	1·4	1·6
B273	Eider	ad.m.	Ayrshire	2470g	+	liver	4	0·6	1·0
B274		ad.f.	Ayrshire	1420g	+	liver	16	4·1	1·6
C2		ad.m.	Ayrshire	–	0	liver	18	1·3	0·8
						muscle	7	1·2	0·8
C3		ad.f.	Ayrshire	–	0	liver	35	5·4	2·8
						muscle	3	0·2	0·4
C4	Guillemot		Ayrshire	–	0	liver	16	0·5	0·1
						muscle	3	0·2	0·0
C5			Ayrshire	–	0	liver	143	22·3	1·0
						muscle	23	0·4	0·6
M4117		imm.	Bute	730g	0	liver	13	3·1	0·6
B279		imm.	Ayrshire	630g	+	liver	98	7·1	–
B290		imm.	Arran	538g	+	liver	126	13·9	1·3
B289		ad.f.	Dumbarton	634g	++	liver	41	6·6	1·2
B284		ad.f.	Dumbarton	660g	0	liver	33	8·6	0·5
						muscle	6	1·7	0·1
B283		ad.m	Solway	576g	0	liver	18	6·3	0·0
						muscle	3	1·1	0·0
B291		imm.	Solway	575g	0	liver	6	1·2	0·1
						muscle	1	0·2	0·0
B292		imm.	Solway	561g	0	liver	40	3·2	0·5
						muscle	8	1·3	0·2
B277	Razorbill	ad.	Ayrshire	445g	+	liver	63	4·1	1·6
B285		ad.f.	Dumbarton	415g	+	liver	98	11·8	0·8
						muscle	16	1·8	0·2
B288		imm.f.	Dumbarton	443g	+	liver	20	3·0	1·3

B, analysed by Dr J. A. Bogan, Glasgow University.
C, analysed by Dr G. Best, Clyde River Purification Board.
M, analysed at Monks Wood Experimental Station.
ad., adult; imm., immature (normally first year).
Ayrshire birds normally found near Troon, Buteshire birds from Isle of Cumbrae, Dumbartonshire birds from Rhu, Helensburgh Kilcreggan.

Holdgate, 1971; Parslow & Jefferies, 1973) than in 1969, which may indicate that the 1974 birds died sooner, before so much organochlorine material, liberated from lipids, had accumulated in the liver. Among the other species examined, the Eiders, Cormorants and Shags had fairly low muscle organochlorine levels, but two to twelve times these amounts in the liver. The Razorbill whose muscle was examined had a rather high PCB level, and the Red-throated Diver rather high levels of all three organochlorine materials in both liver and muscle, for a bird which was still alive and had only begun to show a limited amount of concentration in the liver. It is notable that the species feeding inshore in the Firth of Clyde (the Eiders, Phalacrocoracidae and the Diver) show comparatively high dieldrin levels compared to most of the auks, which normally feed further out to sea. Some auks from the Firth of Clyde also had levels of dieldrin several times higher than any reported during the 1969 bird-kill, however, when unfortunately none of the birds from that area was investigated for dieldrin.

The livers of two Shags and a Guillemot (M4117–9) were also tested for certain heavy metals at Monks Wood, where all analyses were carried out by M. C. French, Miss C. Brown and L. Sheppard. They were found to contain 4·1–5·1 ppm mercury, 10–23 ppm copper, 0·11–0·31 ppm cadmium, 30–79 ppm zinc and under 0·2 ppm lead, wet weight.

Discussion

The initially cold and continuously stormy winter 1973/74 may provide an explanation for this seabi mortality. The distribution of the bodies was very simil to that found in 1969, though there were only about tenth as many, and other species were represented well as the auks on this occasion, especially the Phal crocoracidae, which are also already known to be pro to sudden high mortality at intervals (Potts, 1969). now seems increasingly clear that the locations in whi bodies wash up must be due more to the pattern atmospheric and oceanic circulation up the west coast Britain than to any particular features of the plac concerned, except where oil pollution intervened duri the terminal stages of both the 1969 and 1974 wrecks the Firth of Clyde. It seems as difficult to assess t potential role of toxic chemical pollution in increasi the vulnerability of the birds now as it was in 196 The post-mortem results remain inconclusive; the bir appear to have died of a variety of causes, and the on frequent findings are wasting and perhaps fluid in t lungs, which could well be due to a terminal heart renal failure, or to a fall in plasma proteins. As in 196 relatively high levels of PCB were present in the bird and in addition it is notable that elevated levels dieldrin were found in the birds from the Clyde. Wha ever the effect of these man-made compounds may b their presence is surely undesirable.

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TURNING THE TIDE AGAINST POLLUTION

'But there's no room for complacency'

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Good news on the fight against sea pollution comes this month in the annual report on the survey into seabird deaths round our coasts. But the authors of the report on the RSPB/Seabird Group Beached Bird Survey 1973–74, warn there is no room for complacency.

This is the report by Clare Lloyd, RSPB research biologist, and Bill Bourne, research director of the Seabird Group:

FOR THE fourth year in succession, comparatively few dead birds were found during beach surveys — an average of only 0·56 per kilometre. In the late 1960s it regularly exceeded one per kilometre. The proportion of birds oiled also fell to 21 per cent compared with 28 per cent last year. It appears that the efforts of over 500 observers patrolling over 1500 kilometres of beach are beginning to be rewarded by an improvement in the situation at sea. Let us hope that the situation will be maintained.

However, oiling incidents still occur. Thirteen involving the deaths of 60 birds or more were reported in the last 12 months. The worst was on the Firth of Clyde in which at least 820 birds died. In the same area only weeks before, 1322 birds — mainly guillemots, razorbills, some shags and cormorants — died in a pollution incident involving toxic chemicals. This was similar to the pollution disaster in the autumn of 1969 when more than 12,000 birds were killed. Examination of 22 bodies showed they contained similar amounts of manufactured toxic chemicals.

Three oil spills occurred on the Cromarty Firth, an area which has caused continual trouble. There have been 13 incidents since November 1969. The first two affected 140 swans, 21 of them whooper swans. Forty died despite efforts to save them by the Scottish Society for the Prevention of Cruelty to Animals. It is to be hoped that the new Cromarty Firth Port Authority will take a close look at the situation.

During the international survey in February, 14 Slavonian grebes were found in the Channel Islands and another 59 grebes recorded by the survey in France. This represents unusually heavy mortality for species considered rare in western Europe.

One of the worst cases of pollution occurred with the grounding of the 210,000 ton Royal Dutch Shell supertanker Metula in the mouth of the Strait of Magellan off the southern tip of South America on 9 August, just before 50,000 seabirds were due to return to their breeding islands on the strait. A total of 54,000 tons of oil polluted 40 miles of coast before she was refloated on 25 September. Much of the oil was swept out to sea and comparatively few birds affected. It was a leak of similar proportions from the Torrey Canyon which caused the death of at least 10,000 birds in the approaches to the English Channel in 1967. Many of these were washed ashore far away, and there are more birds in southern seas.

Oil pollution is clearly becoming an increasing problem off South America and South Africa. It is to be hoped that the improvement of the situation in the better-watched seas and the current energy crisis will not be allowed to cause complacency.

Table 1 Results of the priority beached bird surveys in winter, 1973–74

	Sept	Nov	Jan	Feb	Mar	**TOTAL**
Kilometres covered	1888	1835	1915	1931	1603	9172
Total no. corpses found	509	532	1885	1154	814	4894
Corpses per kilometre	0·27	0·29	0·98	0·60	0·51	0·53
Percentage oiled	6	19	21	25	23	21
Corpses per km 1972–73	0·41	0·35	0·36	0·50	0·39	0·40
Percentage oiled 1972–73	22	29	35	26	29	28

Table 2 Dead birds found on the international beached bird survey, 23–24 February 1974

	France	Germany	Scotland		England					Ireland	Channel	**UK & Eire**	**Grand**
	N	W	W	N & E	NE	E	SE	SW	NW	Wales	E	Isles	**Total**	**Total**
Kilometres covered	505	152	160	344	278	219	178	90	344	197	53	69	1931	2588
Divers	—	—	—	2	1	1	—	1	3	—	—	2	10	10
Grebes	59	—	—	—	—	—	—	—	1	—	—	14	15	74
Fulmar	3	—	2	6	—	—	—	—	5	—	—	—	13	16
Gannet	16	1	2	11	—	—	2	2	—	2	1	—	20	37
Cormorant/Shag	46	—	19	18	1	1	2	3	13	18	3	27	105	151
Eider	}	5	5	7	—	1	2	—	—	—	—	—	15	20
Scoters	}	3	—	1	—	—	3	1	4	13	—	—	22	25
Other wildfowl	5	2	2	20	—	7	1	—	53	—	1	1	85	92
Waders	4	1	3	7	2	10	—	—	35	3	—	1	61	66
Gulls	179	12	31	128	22	31	9	3	106	29	2	7	368	559
Razorbill	108	6	33	16	13	3	8	10	19	16	1	32	151	265
Guillemots	23	5	39	47	26	4	19	7	92	35	—	1	270	298
Puffin	11	—	—	1	1	—	1	—	—	—	—	3	6	17
Other species	27	2	1	4	2	—	—	3	2	1	—	—	13	42
TOTAL	481	37	137	268	68	58	47	30	333	117	8	88	1154	1672
Birds/kilometre	0·95	0·24	0·86	0·78	0·24	0·26	0·26	0·33	0·97	0·59	0·15	1·28	0·60	
% oiled	36	76	26	27	65	19	79	(33)	11	25	(13)	11	25	
Birds/km. 1972-73	3·27	—	0·38	0·66	0·17	0·32	0·09	0·26	1·20	0·30	0·15	0·21	0·50	
% oiled 1972-73	82	—	11	24	43	53	(24)	81	18	27	(69)	—	26	

Figures in brackets are from small samples

Dunnock *Prunella modularis*, Twite *Acanthis flavirostris* and House Sparrow *Passer domesticus*. Other species, notably gulls but also the Fulmar, have started to increase.

Some seabird species have had considerable effects upon the vegetation. On Skellig Michael much of the southern slopes was clothed by tussocks of *Armeria maritima* but, probably as a result of extensive burrowing by Puffins and Manx Shearwaters, these have recently died and have been replaced by *Spergularia rupicola*. If there is any further undermining of the ground, resulting in soil erosion, these colonies will be in jeopardy. A similar situation appears to have occurred on Little Skellig at the end of the last century when very large numbers of Puffins were nesting on the rock and numbers of Gannets were low. Since then Puffin numbers have declined to only a few pairs whilst Gannets have steadily increased.

In recent years, a number of expeditions have been mounted to study these breeding seabird populations. The problems of counting were investigated in some depth so that an assessment could be made of status changes in these populations. Although it is impossible to determine the status of breeding species such as Storm Petrel or Manx Shearwater where there is much interchange of birds between colonies, the numbers of Fulmar, Gannet, Kittiwake and the three common *Larus* species have certainly greatly increased in the last 10 to 20 years. The status of auks is rather more obscure since counting techniques are still far from adequate, but there appears to be great fluctuations in numbers on different islands, with major declines of Razorbill, Guillemot and Puffin on Inishtearaght in 1969 but small increases on neighbouring Inishnabro.

Although the colonies are now relatively secure from direct exploitation by humans, they are faced with the dangers of increased pressure of disturbance from tourists, and a very real threat of oil pollution from the neighbouring oil terminal in Bantry Bay. This bay and adjacent ones hold the bulk of the auk populations of south-west Ireland in August and September when they are flightless in moult. There has already been a number of oil spills, fortunately during late autumn and winter. It will take only one oil spill in late summer to be a very serious threat to these auk colonies.

Seabird studies in the Irish Sea

C. S. Lloyd

Since 1963 the island of Skokholm, off the Pembrokeshire coast of South Wales, has been one of the main sites for seabird research in the Irish Sea. The projects carried out on Skokholm have been mostly longterm, detailed studies often confined to a single species. They do, however, bear an important relationship to the more generalized types of seabird studies elsewhere in the Irish Sea, such as the national beached bird survey and annual seabird census organized by the R.S.P.B. and Seabird Group.

A study of the Razorbill *Alca torda*, carried out between 1970 and 1974, is a good example of how a detailed examination of the breeding biology and survival in one species can contribute to these surveys. On Skokholm the Razorbills nest in mostly inaccessible ledge sites or in easily accessible boulder colonies where adult birds and their chicks can be caught for ringing. From 1968 onwards the chicks were colour-ringed to indicate the year of their birth and after 1970 the adults were also individually colour-ringed. Sightings of young birds when they returned to the colony in subsequent years showed that many birds first bred at four years old. Similarly, records of colour-ringed adults in successive years of the study established that the annual survival was about 90 per cent. An attempt was made to describe the population dynamics of the species and factors regulating the population considered. Population levels appear to be restricted by the heavy mortality, due to oiling and other forms of chemical pollution which affect many birds, especially during the winter months. The results of beached bird surveys provide the main evidence for this.

Part of the study of the breeding biology of the Razorbill on Skokholm involved daily counts of individuals in two study colonies. The patterns of diurnal and seasonal attendance were important in determining suitable census methods. Information on attendance at Skokholm colonies indicated the period, when attendance was least variable, best suited to census counts. The results have been used to recommend counting techniques for the national seabird census. These censuses take place annually at about 60 study colonies throughout Britain and Ireland and are aimed at detecting population change in the three main species of auk, the Kittiwake *Rissa tridactyla* and the Fulmar *Fulmaris glacialis*. During the Operation Seafarer survey in 1969 the estimated number of Razorbills breeding in Britain and Ireland represented a very minimum of 60% of the world population of the species, so that accurate monitoring of the population is most important.

Population studies of Cormorants *Phalacrocorax carbo* breeding on the Saltee Islands

D. Cabot

During the period 1960–74 the Cormorant Colony on Little Saltee, Co. Wexford has fluctuated between 270 and 320 nests with a mean of 290 ± 19. Clutch size varied between 3·06 to 2·18 eggs with a mean of 2·67 (s.e. 0·021). There was no correlation between clutch size and colony size. Clutch size has been declining since 1969. Using data from the study together with some survival rates obtained by Kortlandt (1942) a population model based on Leslie Matrix Analysis showed a 1·08 annual rate of change with birds breeding in their fifth year and survival rates of 0·39 (1st year); 0·78 (2nd year); 0·84 (3rd year) and 0·89 (4–13 years). During 1960–74 a total of 3861 pulli were ringed with a 16·6% recovery rate. The annual survival rate was $0{\cdot}45 \pm 0{\cdot}017$ using the Haldane (1954) method. The percentage recovery of 1st year birds has progressively declined since 1960.

i) First impressions

Reports from various quarters suggest that 1975 may see a much-needed improvement in the low population levels of some of our summer migrants. Quite early on Dungeness Bird Observatory reported the best spring arrival for several years of Whitethroats, Sedge Warblers and Redstarts, and encouraging reports of Whitethroat abundance have come from localities as far apart as the New Forest an Rothesay. Several members of the Acrogroup have reported Sedge Warblers in higher numbers than in any spring since 1970, and Reed Warblers, although late, are also more abundant. B.T.O. staff report more Redstarts in the woods around Tring. Hirundines, generally speaking, appear to be down—and late to arrive. Christopher Perrins reports that in the famous Swift Tower at Oxford the first eggs were unusually late. Those members of the Tit Study Group who await the next tit irruption, may like to know that in the Wytham wood study at Oxford (the longest-running population study of its kind in the country) the number of occupied boxes is an all-time high, but broods are small. Good survival of the broods in the weeks after fledging would add to an already high population level. As this is a year in which the beech mast crop will be minimal, a food shortage seems likely and tits could, without actually irrupting, be much more mobile than usual. It might pay to stock up with peanuts.

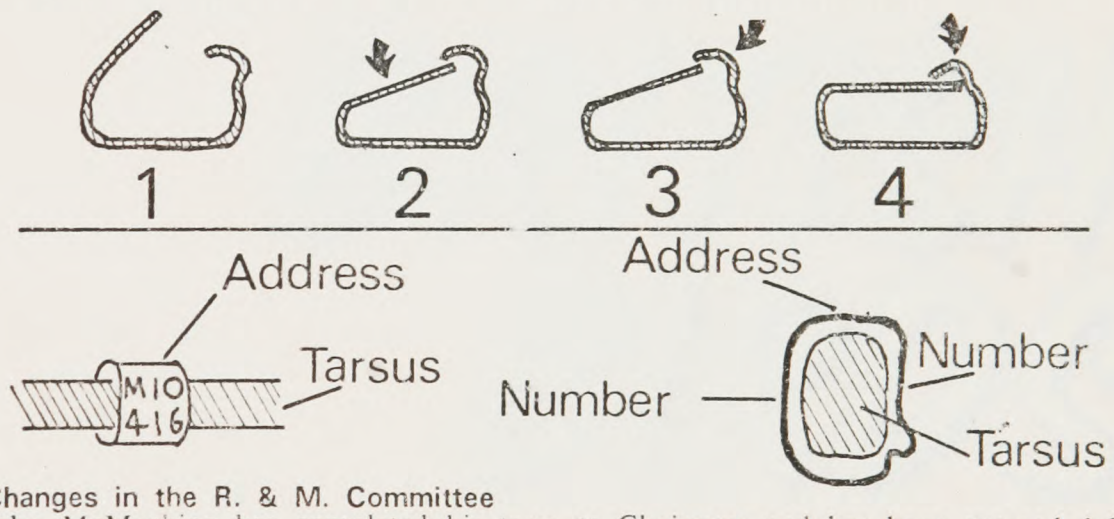
j) Report on Bird Ringing

The report for 1973 accompanies this bulletin. We had hoped to distribute the 1974 report with the December bulletin, and it seems possible that it could be ready on time. However, the present state of our finances will not allow us to publish two reports in one financial year (each edition now costs over £1,000). We therefore plan to issue the 1974 report in July 1976.

k) Razorbill "special" rings

Clare Lloyd has supplied the following notes: "These rings have been specially designed to make reading ring numbers (through telescope or binoculars) easier. The ring number is stamped on the ring twice so that the whole number (one letter, 5 figures) is visible from either side when on the bird. The address should lie on top of the tarsus not underneath, where it will wear away. (Beware: if chicks are ringed when very young the rings can turn round on the tarsus.)

The rings now being supplied differ from earlier models (not all of which may have been used up) in that the metal is Incaloy rather than monel and that the little "hook" is now on the short arm of the ring. Incoloy is a more springy alloy than monel, so that the rings are rather more tricky to close. Three separate pressures are required, as indicated by the arrows in the figure. It is hoped that the Incoloy will prove more resistant to wear.



l) Changes in the R. & M. Committee

John McMeeking has completed his term as Chairman and has been succeeded by Dr. Barrie Watson, 83 Buckingham Road, Shoreham-by-Sea, Sussex, BN4 5UD. Giles Bepler, Ian Stewart, Peter Morgan and Peter Stanley all completed their service on the committee and have been succeeded by:

Ike Hawthorn, 41 Bowling Green Road, Newbury, Berks., *Eric Meek*, 7 Shaftoe Way, Dinnington, Northumberland, *Andrew Ramsay*, 14 Camesky Road, Caol, By Fort William, Inverness-shire, and *Chris Reynolds*, 203 South Avenue, Abingdon, Oxon.

Thanks to all retiring members for their services: welcome to the newcomers.

m) Courses

Gibraltar Point 30th August—6th September: full but there might be a cancellation.
Spurn 4th-11th October: vacancies, details from Bob Spencer.

BRITISH BIRDS

Timing and frequency of census counts of cliff-nesting auks

Clare Lloyd

INTRODUCTION

Following the national census of coastal seabird colonies (Operation Seafarer) in 1969-70, a census has been carried out annually, as a population monitoring scheme, at about 50 colonies throughout Britain and Ireland. The species counted at these sites include the Razorbill *Alca torda* and the Guillemot *Uria aalge*. At most colonies the annual census is obtained from a single count, although counts on as many occasions as possible throughout the breeding season are specifically requested. Regular counts at a colony give information on attendance patterns, which is of vital importance to the timing and frequency of future census work. This is especially true of the auks, for which census counts involve the individual birds on ledges in a colony ('head counts') rather than the number of occupied nest sites. In this paper the results of regular counts of Razorbills and Guillemots at breeding colonies are presented and discussed with reference to population census techniques.

Counts made regularly throughout the day at a breeding colony on Skokholm Island, Dyfed (Lloyd 1973), showed that numbers increased after dawn to a peak attendance between about 08.00 and 10.00 hours; similar patterns of attendance have since been recorded at other colonies. Comparison of different days' counts from Skokholm showed that the actual level of attendance was less variable at this time than during the rest of the day. In the present study, therefore, most counts were conducted between 08.00 and 12.00 hours.

RESULTS

Fig. 1 shows the pattern of attendance of Razorbills and Guillemots at one of the study colonies, at Handa Island, Sutherland, where a resident warden was able to visit the cliffs each day.

For all colonies counted throughout the season, the amount by which attendance varied during the different parts of the breeding cycle was calculated (table 1 and appendix). The variation in attendance during the nestling period was used to estimate the error of the mean that could be expected if either one, five or ten counts had been carried out. These errors are shown in table 2 for colonies where more than ten nestling period counts were available. Fig. 2 shows the order of error to be expected from successive numbers of Razorbill counts during the nestling period.

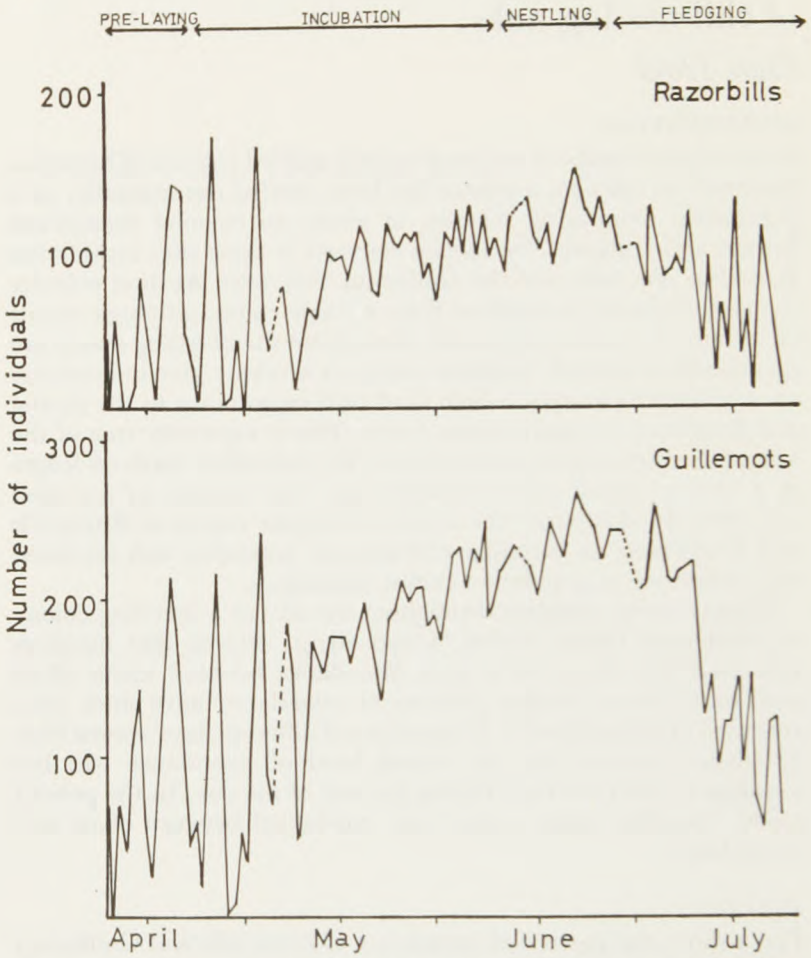


Fig. 1. Daily counts of Razorbills *Alca torda* and Guillemots *Uria aalge* on Little Stack, Handa, Sutherland, April-July 1973. Dotted lines cover 48-hour periods

DISCUSSION

(1) *Timing of counts*

Attendance of Razorbills and Guillemots at the colony on Handa followed the same basic seasonal pattern as that at other colonies for which similar information was available; it also agreed well with published observations for the species (Tuck 1960, Harris 1965, Bédard 1969, Lloyd 1973, Birkhead and Ashcroft in press).

The number of birds in the colony fluctuated from day to day throughout the season. Daily attendance became less variable as

Table 1. Variation in counts of Razorbills *Alca torda* **and Guillemots** *Uria aalge* **at different stages of the breeding season, at Bartlett Nab, Bempton, Humberside, in 1973**

X = Mean count during each period; SD = Standard deviation of mean; N = Sample size; C = Coefficient of variation, or SD expressed as percentage of X. Similar data for Bempton in 1972, 1974 and 1975, and for seven other colonies, are given in the appendix on pages 512-513

	RAZORBILL				GUILLEMOT			
	X	SD	N	C	X	SD	N	C
Pre-laying	27.7	9.8	15	**35.5%**	222.3	110.2	15	**49.6%**
Incubation	22.1	8.7	21	**39.4%**	302.8	53.2	21	**17.6%**
Nestling	25.8	5.6	14	**21.5%**	288.4	35.7	15	**12.4%**
Fledging	25.2	9.0	26	**35.6%**	210.0	67.6	26	**32.2%**
June	27.7	7.4	21	**26.9%**	271.1	32.4	21	**12.0%**

incubation progressed and appeared to be most stable during the nestling period (from when the eggs were starting to hatch until the first chicks left the ledges, a period of 18-20 days). After this, numbers decreased steadily and daily fluctuations became large.

A comparison of the coefficients of variation of mean counts at different stages of the breeding cycle also showed that counts tended to vary least in the nestling period.

Ideally, therefore, census counts should be made during the nestling period when attendance is most stable. The timing of breeding can, however, vary considerably from one year to the next (Lloyd in prep.), so that planning counts to coincide with the nestling period can be difficult. The month of June usually covers the late incubation, nestling and early fledging periods at most colonies. The coefficient of variation of mean counts during the month of June showed that attendance varied little more than during the nestling period alone. Hence, although census counts late in the breeding season should be avoided, counts made during June usually coincide with a period of relatively stable attendance.

(2) *Numbers of counts*

Even during the nestling period, attendance changes from day to day and a single visit to a colony can produce Razorbill and Guillemot counts as much as 46% and 26% respectively away from the mean number in the colony during the 18-20 day period. If further counts are undertaken, the estimate obtained can be considerably more accurate (table 2). The error is greatly reduced by conducting between five and ten counts, although the improvement resulting from more than ten hardly justifies the extra effort. Estimated

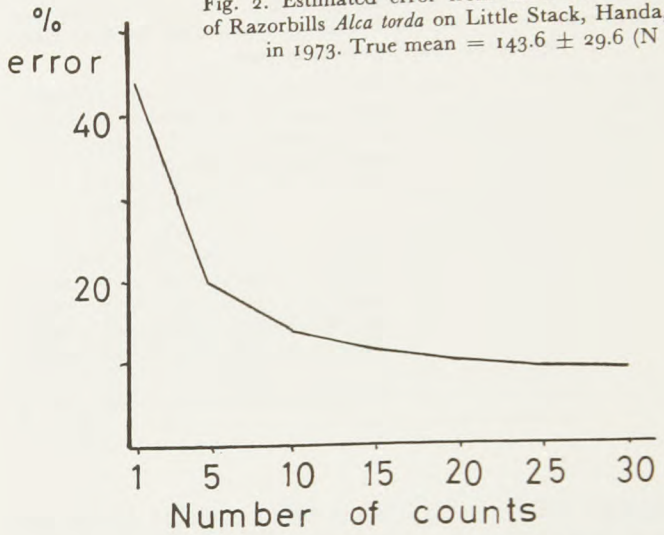


Fig. 2. Estimated error from different numbers of counts of Razorbills *Alca torda* on Little Stack, Handa, Sutherland, in 1973. True mean = 143.6 ± 29.6 (N = 16)

errors for different numbers of counts during June are similar to those for the nestling period.

Data collected so far have shown that the order of error from different frequency of counting varies from one colony to another, although it tends to be similar in successive years at any one colony; this was true both for counts during the nestling period and for those in June as a whole. This suggests that one season of regular counting (at least ten visits) may be necessary to determine the pattern of attendance during the nestling period or the month of June. The order of error to be expected from fewer counts can then be estab-

Table 2. Estimated percentage error (95% confidence limits) of the means of different numbers of counts of Razorbills *Alca torda* and Guillemots *Uria aalge* in 1973, comparing the nestling period (NP) and the month of June as a whole

		RAZORBILL			GUILLEMOT		
		1 count	5 counts	10 counts	1 count	5 counts	10 counts
Handa	NP	43.9%	19.5%	13.7%	19.2%	8.6%	6.0%
(Sutherland)	June	40.8%	18.1%	12.7%	20.2%	9.0%	6.3%
Bempton	NP	46.1%	20.5%	14.4%	26.4%	11.7%	8.2%
(Humberside)	June	55.9%	24.8%	17.5%	24.9%	11.1%	7.8%
Skokholm	NP	17.2%	7.6%	5.4%	23.2%	10.3%	7.2%
(Dyfed)	June	24.2%	10.8%	7.7%	21.6%	9.7%	6.8%
Skomer	NP	19.8%	8.8%	6.2%	12.9%	5.7%	4.0%
(Dyfed)	June	48.0%	21.3%	15.0%	13.7%	6.1%	4.3%

lished for the colony and used in subsequent years to interpret figures collected during less frequent visits. It must be emphasised, however, that at least five and preferably ten visits are essential for a census of acceptable accuracy.

These findings enable a quantitative assessment of the accuracy of previous census counts. Those made during the national survey of 433 Razorbill and 490 Guillemot colonies in 1969 and 1970 (Cramp *et al.* 1975) were, almost without exception, based on one head count at each colony. Therefore, these counts can be considered to be accurate to within only 46% for Razorbills and 26% for Guillemots. Furthermore, 9% of the counts in 1969-70 were carried out as early as May and 24% as late as July. (The breeding seasons in these years appeared 'normal' in their timing.) Mean attendance in the present study was nearly twice as variable in the incubation period (May) as in the nestling period (June) and nearly three times more variable in the fledging period (July and August). Thus the especially early or late counts in the Operation Seafarer survey cannot be expected to be truly representative of numbers. Similarly, though the annual counts at the sample of colonies since 1969 have usually been carried out during the nestling season, or at least at some time during June, at more than half the colonies, single visits are still used to provide a census figure. Only relatively large population changes are detectable at these colonies.

Finally, although some information is now available on how the accuracy of census counts in the Razorbill and the Guillemot can be improved, little is known of how the counts may be interpreted in terms of actual changes in the breeding population. For example, comparison of the numbers of incubating or brooding birds and apparently non-breeding birds in part of one of the colonies in the present study has shown that average numbers can vary by as much as 2.1 to 3.3 Guillemots or 1.8 to 3.3 Razorbills per occupied site in three successive seasons. These differences were not apparently related to the overall 27% increase in Guillemots and the stability of the Razorbill population during this time. Similar orders of variation were recorded at some of the other colonies. To what extent a change in number of non-breeding birds can be expected to affect the nestling period head count, and hence the census figure for the colony, urgently needs further consideration.

ACKNOWLEDGEMENTS

I am very grateful to T. R. Birkhead, R. A. Broad, C. J. Evans, A. Grieve, S. C. Madge, D. Mower and Miss Ethel Young who collected the data for the annual seabird census organised by the Royal Society for the Protection of Birds and the Seabird Group. Data for Skokholm were collected whilst I was supported by a grant from the Natural Environment Research Council. I am also indebted to Dr C. J. Cadbury, Dr M. P. Harris and Dr C. M. Perrins for criticism of the manuscript.

SUMMARY

Regular counts of the numbers of Razorbills *Alca torda* and Guillemots *Uria aalge* in a colony throughout the breeding season give valuable information on the variation in attendance. Counts of this kind were made at six of the colonies covered by the annual population monitoring scheme. Most counts were made between 08.00 and 12.00 hours to avoid variation due to diurnal attendance patterns. Counts were least variable during the nestling period and only slightly more variable at other times during the month of June. Providing this month coincides with the nestling period for most birds in the colony, census counts can most conveniently be carried out in June. An error of 17% to 46% in Razorbills and 13% to 26% in Guillemots must be expected if only a single count is made at a colony; with five or ten counts this error is considerably reduced (5% to 17% for Razorbills and 4% to 8% for Guillemots with ten counts). The accuracy of counts made during Operation Seafarer in 1969-70 and the annual census at a sample of colonies since are assessed.

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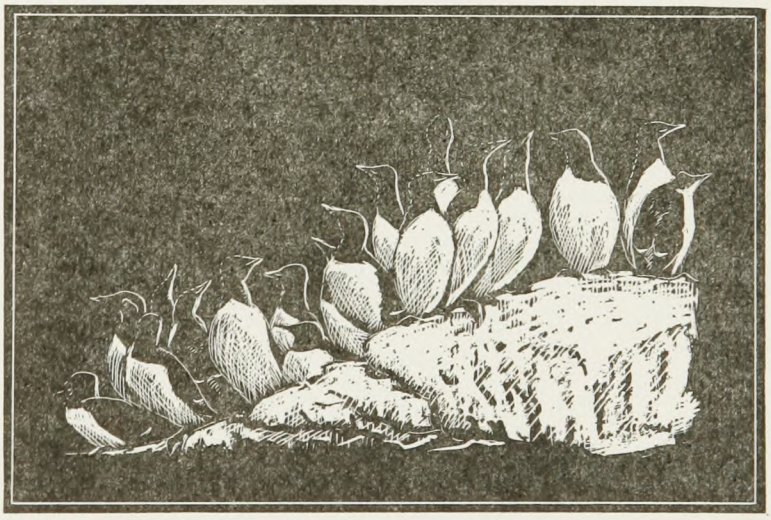
Appendix. Coefficients of variation of mean counts of Razorbills *Alca torda* **and Guillemots** *Uria aalge* **at eight colonies at different stages in the breeding season**

PL = Pre-laying period; IP = Incubation period; NP = Nestling period; and FP = Fledging period. Coefficients of means from samples where $N < 5$ are shown in brackets

		RAZORBILL				GUILLEMOT			
		PL	IP	NP	FP	PL	IP	NP	FP
Fair Isle (1) (Shetland)	1972	179	36	18	(114)	19	18	9	118
	1973	38	37	(18)	(24)	65	25	(7)	58
Fair Isle (2) (Shetland)	1972	–	–	–	–	–	27	(9)	(60)
	1973	–	–	–	–	73	33	(10)	65
Fair Isle (3) (Shetland)	1973	–	–	–	–	137	21	(8)	(88)
Yettna Geo (Orkney)	1974	(111)	21	(16)	–	(84)	13	(8)	–

		RAZORBILL				GUILLEMOT			
		PL	IP	NP	FP	PL	IP	NP	FP
Handa (Sutherland)	1973	97	34	21	53	65	36	9	12
	1974	–	–	11	–	–	–	14	–
	1975	–	19	12	–	–	11	12	–
Bempton (Humberside)	1972	–	35	24	54	–	14	11	56
	1973	35	39	22	36	50	18	12	32
	1974	31	28	29	23	33	8	12	10
	1975	97	18	17	–	82	12	10	–
Skokholm (Dyfed)	1972	78	16	9	–	99	14	9	27
	1973	81	20	8	22	79	12	11	14
Skomer (Dyfed)	1973	96	22	9	15	–	–	6	–
	1974	–	22	–	–	–	–	–	–

Miss Clare Lloyd, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL



BIRDKILL

From BIRDS magazine

Volume 6 33-34

1976

Five hundred dead seabirds are washed up on a beach; hundreds of geese are found dead near their grazing grounds; waterfowl are found paralysed and dying. Why? Apart from protecting birds, the RSPB has an important role to play in detecting threats to them in this country and overseas. Each year, research scientists piece together a jig-saw of facts on "birdkill" incidents. The object is to detect trends, particularly in pollution, and to forestall what could be bigger disasters in the future. Clare Lloyd, research biologist, looks at the pattern of events of the last 12 months.

A TOTAL OF 8450 birds have been found dead in birdkill incidents in Britain and Ireland since last June. This is a high figure and the true one must be far higher. This year disease joined pollution as one of the main causes of death.

The RSPB and the Seabird Group have also continued to measure more routine mortality in seabirds through regular surveys of birds washed up on beaches. About 650 volunteers covered a total of 10,756 kilometres during the five winter priority surveys. This is the greatest distance covered

The results given in Table 1, show that on average 0·3 dead birds were found for each kilometre of beach covered. Just under a third (31 per cent) of all the corpses found were oiled. Last season, more birds were found dead (0·5 corpses/kilometre) although only 21 per cent were oiled. Our recorders also noted that 17 per cent of the 1962 beach visits yielded some trace of oil pollution.

The international survey was carried out as usual during February. This year, results were received from seven different countries (Table 2). In Britain, the highest number of deaths were recorded on the coasts of east Scotland and north-west England. More than one dead bird was found every two kilometres.

Pollution was heaviest in southern England where at least half the victims were oiled. Mortality was high in northern France and Belgium and especially high in West Germany with more than four dead birds per kilometre. The smallest number of corpses was found on the coasts of the west of Scotland, southern Ireland, the Channel Isles and Bay of Biscay bordering the open Atlantic. A black guillemot, found on the Belgian coast during the international survey, was only the fifth on record for Belgium.

The heavy mortality and oiling on the Dutch and German coasts was partly due to oil spillage which killed at least 1290 seaducks. In December, before the international survey, another 1128 oiled corpses, mostly scoter, were found on only 13 kilometres of Dutch coastline following an oil spill from a tanker. At home more than 2800 seabirds died in eight oiling incidents during the year and at least another 230 in a winter storm "wreck" in the northern Irish sea.

Unlike last year when there were many oil-spill deaths, the mortality rate was low on the Cromarty Firth. But on the Pembrokeshire (Dyfed) coast in early September, at least 100 young Manx shearwaters and 75 young gannets were washed ashore dead after gales and an oil spill from an unknown source. Eighty grey seals, including pups were also affected.

More serious pollution occurred in Pembrokeshire in early May just as 165,000 seabirds on the nearby islands were preparing to breed. The *Esso Tenby*, damaged during a storm, spilled 20 tons of fuel oil. About 650 auks and nearly 1000 kittiwakes were affected, although the Department of Trade, having established that the slick was small, did not attempt to disperse it.

Then at the beginning of June, a leaking tanker, the *Anangel Friendship* was ordered out of Milford Haven oil terminal, sending a slick towards the islands of Skokholm and Skomer. Only a few birds were affected because although some oil drifted ashore, most dispersed quickly.

More cause for alarm came with oil spills in Bantry Bay, south-west Ireland. Two thousand six hundred tons of crude oil gushed out of the tanker *Universal Leader* in October. Less than 20 birds died, but three months later, a second smaller spill of crude oil from the *Afran Zodiac* killed 150 birds, mainly guillemots.

Soon after the international survey in March, French observers noticed an unusual number of dead fulmars. Thirty dead birds were found near Calais alone. Meanwhile, eight fulmars were found dead on the north Norfolk coast in Britain. Specimens were collected for analysis but the cause of the deaths was never established.

In late May, nearly 500 birds, including many shags from the Farne Islands, were found dead on the Northumberland coast. At the same time, unusually high levels of toxin were found in the local shellfish, due to a sudden increase, or "bloom" of a species of plankton. A similar "red tide" outbreak with higher toxin levels, killed hundreds of shags in the same area in 1968. Some of the dead gulls may have been affected by botulism.

Botulism, or "limberneck", caused by bacteria found naturally in soil and water, killed more than 4000 birds, mostly gulls, at 16 different sites in Britain between June and September. The bacteria thrived in the hot summer weather, particularly in rotting rubbish and evaporating pools favoured by feeding and bathing gulls. The poison results in paralysis, especially of the neck, so that the head droops and the bird may

Table 1 Results of the priority beached bird surveys in winter, 1974–75

	Sept	Nov	Jan	Feb	Mar	**Total**
Kilometres covered	1847	2249	2310	2565	1785	10756
Total no. corpses found	753	699	866	1019	685	4022
Corpses per km	0·41	0·31	0·37	0·40	0·38	0·37
Percentage oiled	23	12	39	27	22	25
Average 1971–74						
Corpses per km	0·3	0·3	0·6	0·5	0·5	0·5
Percentage oiled	17	22	31	32	30	28

Table 2 Dead birds found on the international beached bird surveys, January–March 1975

Kilometres covered	France Biscay 250	Channel Isles 60	Ireland SE 31	England SW 146	Wales 269	Ireland N 73	England NW 348	Scotland W 579	Scotland N&E 466	England NE 236	England E 178	England SE 179	France N 471	Belgium 242*	Nether-lands 134	West Germany E 433	Total 4095
Divers	2	—	—	—	—	—	4	—	3	—	1	—	3	—	—	27	40
Grebes	1	—	—	—	—	—	—	—	—	—	2	—	1	2	1	7	14
Fulmar	—	—	—	1	2	—	5	3	17	1	—	—	—	—	3	19	51
Gannet	8	—	—	3	1	—	2	7	11	3	—	2	11	6	6	21	81
Cormorant/Shag	—	1	2	1	16	1	6	24	23	1	—	4	4	—	—	—	83
Eider	2	—	—	—	—	—	3	—	4	2	—	—	26	1	15	1181	1206 +
Scoters		—	—	—	5	—	10	—	1	1	—	—		23	10	84	134 +
Other wildfowl		—	—	—	2	2	12	9	22	2	1	—		1	4	59	142**
Waders	—	—	—	—	4	1	23	11	23	4	4	—	—	2	14	52	138
Gulls	20	2	—	19	33	4	75	45	171	25	11	10	143	80	58	216	912
Razorbill	3	—	2	9	12	15	16	12	19	3	5	5	45	33	12	13	204
Guillemots	—	1	5	21	14	4	29	11	99	25	7	1	41	32	9	67	366
Puffin	2	—	—	—	—	—	—	—	2	1	—	—	—	—	—	—	5
Other species	4	—	—	2	1	—	5	3	2	—	—	—	16	11	1	10	55
TOTAL	42	4	9	56	90	27	190	125	397	68	31	22	290	191	133	1756	3431
Bodies/km	0·17	0·03	0·29	0·28	0·33	0·37	0·58	0·20	0·87	0·27	0·17	0·13	0·62	0·79	0·99	4·06	
% oiled	57	[25]	[78]	75	16	[7]	14	14	27	41	48	[68]	40	74	80	79	
Average 1967–73																	
Bodies/km	—	—	—	0·43	0·42	0·37	0·81	0·77	1·88	1·56	0·62	0·76	3·94	4·29	4·78	2·67	
% oiled	—	—	—	69	41	65	24	10	45	48	64	73	74	77	72	80	

Note: [ ] *Less than 30 birds found.* **Includes 164K NE France, 15K SW Netherlands, 63K Belgium* ***Includes some eider & scoters found in France*

drown. The largest number of deaths from botulism was recorded on the Firth of Forth where more than 1500 gulls died in June and at least another 500 in August.

On the Norfolk Broads, at least 300 black-headed gulls, swans, wildfowl and various other waterfowl were affected as drought conditions reduced water levels. Maggots reared on corpses affected by botulism and used by anglers, helped spread the disease. Hundreds of cage birds also died after being fed on maggots.

Problems were reported with Trithion, a seed-dressing introduced to replace dieldrin, banned earlier last year. Newly-sown grain treated with Trithion killed 200 pink-footed geese on the Humber estuary and 500 geese, mainly greylag, in Angus, after unusually wet weather had made sowing conditions difficult. Swans, geese and other wildfowl are particularly at risk from Trithion if they feed on freshly-sown wheat fields. Trithion has now been withdrawn from use in Scotland where most geese winter. A close watch is being kept this winter on geese in areas where this dressing is still in use.●

CLUES FROM WINGS

COLLECTING BIRDS' wings may seem a strange occupation. And during the past ten years, Bill Bourne has amassed more than 3000. But the wings are more than just a collector's obsession.

Surprisingly, wings can yield a great deal of valuable information, vital clues on bird-kill incidents. Where the beached bird survey supplies a good indication of amount, character and distribution of mortality, wings can go one further. Experts like Bill Bourne, research director of the Seabird Group, can assess factors such as age, sex and origin of bodies — extra details which help point to potential threats to certain species. Why wings? Simply because they are lightweight and easy for collectors to dry, label and post. Bill Bourne reports on the results of the exercise so far.

The value of this procedure was soon demonstrated when we were sent 1223 wings collected during the *Torrey Canyon* disaster in the spring of 1967. Two other large consignments of 476 and 548 wings also yielded valuable information about the *Hamilton Trader* oil pollution incident and Irish Sea birdkill in the spring and autumn of 1969. In addition to those originating during these major disasters we have also been sent 3016 wings during ten years, rising to 740 in 1969, and 755 in 1970, which were undoubtedly bad years in many respects, and 406, with hard weather early in the year, in 1972. The total normally lies between 100 and 200 annually.

The largest number of wings have been sent in during the late winter, rising from 92 in December, 301 in January, 888 in February and 761 in March. The numbers then fall rapidly to 103 in April, 227 in May (when there were some nasty oil pollution incidents), 29, 55 and 33 in June, July and August and up to 100 a month during the rest of the year. The largest number of wings was sent from eastern Scotland (1351), followed by north-east and north-west England (450 and 433). Between 100 and 200 were sent from East Anglia, south-east and south-west England, and Wales, and less than 100 from the west of Scotland and Ireland, where there are comparatively few observers who find few dead birds.

Guillemots were by far the commonest species reported, including 847 of the southern race *Uria aalge albionis* breeding in England and Wales, and 545 of the northern race *U. a. aalge* breeding in Scotland and more northerly countries. Nearly half the southern birds were immature, but less than a third of the northern ones. Since the total population of the southern subspecies in Britain is only about 10,000 pairs — whereas there are hundreds of thousands of the northern form to the north — the toll on the race *albionis* is clearly serious. The loss of 545 razorbills out of a population of about 100,000 pairs breeding in Britain is also notable. The next commonest victims were the herring gull (203) and puffin (152), which is less serious. There were smaller numbers of wings from 66 other species.

We now have a good knowledge of what can normally be expected to occur on our beaches for future reference, and it will clearly be useful to obtain further samples of wings during future disasters to see what has been killed. Meanwhile, with the rise in postal charges it no longer seems useful to continue the routine survey. Instead, we only propose to ask for wings from exceptional incidents.

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AN ESTIMATE OF THE WORLD BREEDING POPULATION OF THE RAZORBILL, *Alca torda*, L.

C.S. Lloyd

Introduction

The Razorbill, *Alca torda* is confined to the northern Atlantic, breeding on the west coast from about 73°N (West Greenland) to 43°N (Maine) and in the east from about 78°N (Spitsbergen) to 49°N (Brittany) (Voous 1960). The Razorbill and Guillemot *Uria aalge* suffer heavy mortality through oil and other pollution at sea (e.g Bourne and Bibby 1975) and declines have been reported in many breeding populations since the War (Cramp *et al* 1974). Available estimates of various populations are given in Table 1. Due to extreme difficulties in counting Razorbills accurately, the figures must be regarded as very approximate, but they do form a basis for comparison with counts in the future which, it is hoped, will be considerably more accurate.

Most published counts are expressed as "pairs" although there is sometimes doubt as to how these figures were obtained. In order to use comparable figures for all areas, I have converted the few counts given as "individual birds" (actually the better counting unit) to pairs. Observations of birds present at one breeding colony in South Wales in 1972 and 1973 showed that on average a count of 100 birds on the cliffs during the main part of the breeding season (June) represented 56 breeding pairs; about 35% of the birds on land at this time were non-breeders and a small

number of off-duty mates were also present throughout the day (Lloyd 1973; Lloyd in press). Observations at other colonies in Britain and Ireland since have given broadly similar results. Thus, where counts of birds are clearly indicated, I have multiplied these by 0.56 to obtain an estimate of the number of pairs.

West Greenland, Canada and U.S.A.

Bédard (1969) gave a total of 47,000 pairs of Razorbills in the western Atlantic colonies but some of the counts included were outdated. A more complete survey of these colonies given by Brown et al (1975) totals 20,644 pairs. However, counts at 33 of the 59 colonies they listed, which account for 39% of the total, were pre-1967. Earlier counts are available for 14 of the colonies covered by Nettleship et al in 1967-74 and these suggest extensive changes in the last 10 to 20 years. Numbers had apparently declined at seven colonies and remained stable (3) or increased (4) at the rest; there had been an overall reduction of about 50%. The best documented change in the north American Razorbill population has occurred in the colonies on the north coast of the Gulf of St.Lawrence where regular surveys at 7 sites have shown a decline from 16,216 individuals in 1960 (Moisan 1962) to 14,950 individuals (92%) in 1965 (Moisan and Fyfe 1967), to only 4,320 individuals (27%) in 1972 (Nettleship and Lock 1973). Much of this decline has been tentatively attributed to the effect of toxic chemicals in the birds' diet.

Spitsbergen

"Small numbers of Razorbills bred in southern Spitsbergen up to 1958" (Løvenskiold 1963), though there has been no recent count. At least eight pairs bred on Bear Island in 1970 (Brun 1970) where "very small numbers" had been reported in 1932 (Bertram and Lack 1933).

Russia

The only available estimate for the breeding population in northern USSR is outdated and no records have been found for the White Sea where the species also breeds (Voous 1960).

Iceland

No precise information is available although Hachisuka (1927) reports Razorbills to be more common in the south; however "although the Razorbill is a fairly common bird..... it is less numerous than both the Common and Brünnich's Guillemots" - Uria aalge and Uria lomvia - (F.Gudmunsson in litt 1973). The population has been tentatively estimated here to total 5,000 pairs.

Faeroe Islands

Equally little is known of the population of the Faeroe Islands but in 1974 Guillemots outnumbered Razorbills by an estimated 100:1 on the cliffs and 100-150:1 on the sea (B.Olsen in litt 1974).

Norway

Brun (1969) gives details of all colonies in Norway in about 1968, but by 1970 numbers had declined by 33% at least one colony in southern Norway (Runde) which previously held 12% of the total population (Brun 1971). Brun suggested that this order of decline could be expected for other colonies in the area, due to pressures from oil pollution and hunting,

and to birds becoming caught in fishing nets.

Finland

Merikallio (1958) suggested that the Razorbill breeding population was half what it was in the 1930s as the cold winters of 1939/40 and 1941/42 had a disastrous effect on the birds (von Haartman 1947; see also Lloyd in press).

Sweden

Wöhlex (1919) reported 7,500 pairs of Razorbills breeding in the largest colonies on the islands of Stora Karlsö in 1918, although this figure may have been greatly exaggerated. About 1,500 pairs are estimated to have bred there in 1975 (V.Olsson - in litt.). Human disturbance and adverse weather conditions ~~predation by mink, Mustela vison~~ are the main causes of the low numbers (Olsson 1974).

Denmark

The Danish birds were also affected by the cold winters. Paludan (1947) gives the following counts of birds breeding at Christiansø in the south Baltic: 1939 - 318 pairs (Salomonsen 1943 gives 2,200 pairs), 1940-161 pairs, 1941 - 175 pairs, 1942 - 59 pairs, 1943 - 64 pairs. Numbers appeared to recover at this and other Baltic colonies and Kartashev (1960) gives a count of 318 pairs which may have declined since (see Table 1).

Germany

Twelve pairs of Razorbills bred on the island of Helgoland in 1939, though by 1956 these had declined to a single pair (Vauk 1957); this colony is now extinct (GRPBourne in litt.).

Britain and Ireland

Operation Seafarer in 1969/70 gave a total of 144,000 pairs of Razorbills. This consisted of 108,736 pairs and 35,147 individual birds - approximately 19,682 pairs, but excluded two colonies of "Order 1" (1-9 pairs), 6 colonies of "Order 2" (10- 99 pairs), 3 colonies of "Order 3" and 3 colonies of "Upper Order 3" (100- 999 pairs), 1 colony of "Low Order 4" (1,000- 9,999 pairs) and 1 colony of "Order 5" (10,00 - 99,999 pairs). Together these accounted for an estimated minimum 17,310 pairs. Thus the total population was probably in the region of 145,730 pairs. Results from an annual monitoring scheme at about 50 sites since suggest that numbers are currently stable.

France

About 50 pairs of Razorbills bred at Les Sept Îles in Brittany before the "Torrey Canyon" oil spill in 1967, but these were reported to have declined to only 50 pairs (Monnat 1969) and unfortunately the colony has shown little sign of recovery since.

Discussion

At least 70% of the world population of Razorbills breeds in Britain and Ireland; the coasts of Canada/New England and Norway also hold 9% and 12% respectively of the total. By contrast, of the order of 10% of the world population of the far more numerous Puffin Fratercula arctica also breed in Britain and Ireland (Harris in press), although all these figures must be regarded as approximate since auks are

notoriously difficult to count accurately. Throughout much of its range, the Razorbill like the Puffin, is reported to have declined in numbers in recent years, though the timing and magnitude of these declines are impossible to assess in the absence of reliable early counts. As counting methods improve, the value of regular population censuses at even a small sample of breeding colonies increases. These are at present conducted in Canada by the Canadian Wildlife Service and in Britain and Ireland through the Royal Society for the Protection of Birds and the Seabird Group. In Britain we are responsible for a large proportion of the world's Razorbills and monitoring is essential if local declines and their possible causes are to be identified before colonies become extinct.

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I am very grateful to the Seabird Group for permission to use unpublished "Operation Seafarer" data and to A.Pape Møller, V. Olsson, A. Petersen and B.Olsen for supplying updated estimates of Razorbills in Denmark, Sweden, Iceland and the Faeroe Islands respectively, also M.P. Harris for an estimate of the proportion of all Puffins breeding in Britain and Ireland. The latter provided helpful criticism of an earlier draft of this paper.

Summary

Available estimates of Razorbill populations in both east and west Atlantic countries are presented. Razorbills, like other auks, are notoriously difficult to count accurately so the counts are only very approximate. About 70% of the world population of the species breed in Britain and Ireland and

most of the rest in North America and Norway (9% and 12% respectively). The importance of regular population monitoring is stressed.

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TABLE 1 An estimate of the world breeding population of the Razorbill *Alca torda*. Nomenclature after Salomonsen (1944).

Country	Subspecies	Approx. no. of breeding pairs	Reference	Year of Census *1
Greenland	*A t pica*	567(417)*2	(Joensen & Preuss 1972. Salomonsen 1950/51)	1965 1936,1949
Canada	*A t pica*	20,636(4,688)*2	Brown *et al* 1975	1928-74
Maine	*A t pica*	28(28) *2	Brown *et al* 1975	1971-74
N USSR	*A t pica*	2,200	Gerasimova 1961	
Norway	*A t pica*	25,440*3	Brun 1969; 1971	1968-70
Sweden	*A t torda*	4,000	V.Olsson-*in litt* 1975	
Finland	*A t torda*	875	Lippens & Wille 1972	
Denmark	*A t torda*	200	Franzmann 1974	
Iceland	*A t islandica*	5,000		
Faeroe Islands	*A t islandica*	5,000	B. Olsen - *in litt* 1974	
Britain & Ireland	*A t islandica*	144,000*4	Cramp *et al* 1974	1969-70
France	*A t islandica*	100	Brien 1970	
Estimated total		208,046		

Notes: *1 Year of census, when known to be different from that of publication.

*2 Count includes an estimated number of pairs from counts of individual birds; estimates are given in parentheses where relevant.

*3 Maximum, assumes a 33% decline in only 12% of the population - see text.

*4 Minimum - see text.

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TIMING OF SEABIRD BREEDING SEASONS

Following reports from some seabird colonies in 1975 that several features of the breeding season, especially its timing, were peculiar, participants in the RSPB-Seabird Group annual seabird census, and other ornithologists were asked to provide information on the timing of breeding. The species involved were the three common auks, the Kittiwake and Fulmar, some observers were able to comment on whether or not there was anything unusual about the 1975 breeding season and for a few colonies detailed records of the timing of the birds' breeding seasons were available from previous years. Otherwise the amount of published information on what constitutes a normal breeding season for some of our most abundant seabird species is very small.

In 1975 the birds' arrival and the start of laying appeared to have occurred late at a number of colonies. Fulmars were unusually late in laying at the Farne Islands and nine other colonies for which dates of laying were available. This may have been associated with the red-tide mortality on the Northumbrian coast about this time which killed at least 43 Fulmars.

Numbers of Kittiwakes built up exceptionally slowly at four colonies in the Irish Sea and at other colonies, where only information on the date of hatching was available, breeding also appeared to be late.

Razorbills and Guillemots laid late at several west coast colonies from the Solway to north Devon. At Hermaness NNR, and other Shetland colonies Peter Kinnear and Brian Sage

noted that very few Guillemots produced chicks, although there was no sign of a decline in numbers of birds present. Similarly at Foulseugh, Kincardineshire and The Lamb, Firth of Forth, Bill Bourne and Bob Smith respectively saw exceptionally few young Guillemots. Puffins returned very early to several east coast colonies but Mike Harris noted no abnormalities in the timing of breeding but the season was unusually prolonged.

In northern Norway, seabirds breeding on the Lofoten Islands had a bad year in 1975. None of the 25,000 pairs of Kittiwakes on Vedoy laid eggs and, although several thousand puffins usually breed on the island, no birds were seen carrying fish at the time when most eggs should have hatched. Breeding success was also very low in the other auks and tern which probably indicates a large scale food shortage or inavailability on offshore feeding grounds. The weather was unusually bad throughout the summer in Norway and this may have affected fishing condition. Similarly in Scotland the birds may have suffered in the sudden spell of cold weather in late April and early May which brought snow to many areas.

Little is known of the timing of seabirds' breeding seasons but information is easily collected. Can you please help by being observant when you visit seabird colonies? Record the presence or absence of each species early and late in the season, or whether each has eggs or chicks, and any other details on the timing of breeding. Send the information including the date, location of the colony and your name and address to me (RSPB, The Lodge, Sandy, Bedfordshire SG19 2DL). Any information from previous years would also be most valuable.

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