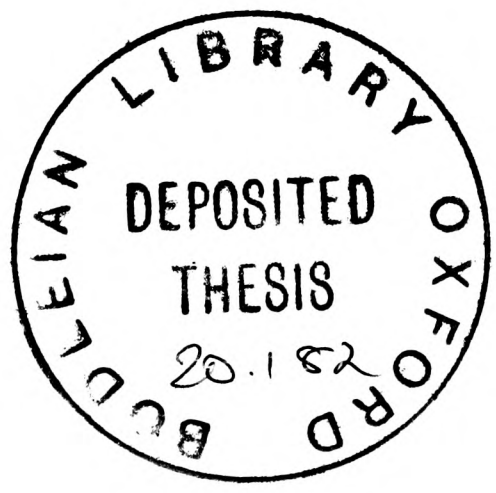
BREEDING BIOLOGY AND FEEDING ECOLOGY

OF

BLACK GUILLEMOTS

by

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Thesis for D.Phil. degree
at the University of Oxford,
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A pair of Black Guillemots in courtship.
Flatey Island, NW. Iceland. Summer 1976.

Photo: Magnus Magnusson.

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Abstract (Prepared for ASLIB)

Title: Breeding biology and feeding ecology of Black Guillemots

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Degree: D. Phil.

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Since 1974 a population study of Black Guillemots has been conducted on Flatey Island, NW Iceland. The main aspects are summarized below.

Population numbers and distribution. The population has been censused several years, also those of 20 islets near Flatey. Information was collected on past status. Great changes have occurred since turn of the century. Last major change began in 1967; the population started increasing of such a scale that it can only have resulted from massive immigration. These changes are thought to be due to rats and Mink.

Attendance and population structure. Data was gathered on timing of spring return to nesting areas, status of attending birds, sex ratio, area and nest-site fidelity, pair-bond maintenance, and post-breeding departure. Special attention has been given to the problem of censusing birds attending nesting areas.

Breeding biology. Breeding biology variables were quantified and studied on a seasonal basis; timing of laying, clutch size, interval between eggs, egg size, reproductive output, lengths of incubation and nestling periods. Supernormal clutch and brood experiments were conducted. I looked at length of replacement time of lost clutches, factors influencing timing of laying, its effect and that of clutch and egg size on breeding performance. Egg and chick losses were analyzed. Many interesting population phenomena seem to have been associated with the unusually rapid population increase.

Feeding ecology. Analyses were made of prey taken, feeding rhythm and areas, and factors influencing feeding rate and prey selection. Some information was collected on share of the sexes in feeding chicks, and kleptoparasitism. Study was made of chick growth, fledging condition and post-fledging survival.

Population dynamics. About 3300 birds were ringed, providing basis for determining age at maturity, adult survival, and mortality. Pre-breeding survival was calculated using data from ringing schemes. A population model was constructed for the population, showing magnitude of immigration. Ringing provided data on dispersal.

Abstract

The thesis is divided into 12 chapters, dealing with the breeding biology and feeding ecology of Black Guillemots (Cepphus grylle) on Flatey Island, NW. Iceland in 1974-1977.

Chapter 1 is introductory, stating aims and giving some background information, such as the literature on the subject, general distribution and habitat requirements of the species, description of the study area and general methods.

Chapter 2 outlines what is known about changes in the study population this century. These were considerable, the most recent trend being an unusually rapid increase since 1967. Explanations are offered as to the causes of these changes; Mink and rats are thought to be responsible.

Social structure of the population forms the subject of Chapter 3. The length of the period attending nesting areas over the year, was documented, from the birds'return in spring till their departure towards the end of the summer. The numbers of breeders and non-breeders attending in the pre-laying period were quantified, the seasonal occurrence at nesting areas and distribution of non-breeders in the breeding season, and the age of non-breeding nest-site holders. Sex ratio, area-, nest-site-, and mate fidelity were investigated quantitatively. Former breeders were very area tenacious, and tended to keep their mate and site in consecutive years. These bonds were influenced by a variety of factors, the most obvious one being the success of breeding the year before. Extensive ringing of chicks has provided some information,previously unknown, on the winter distribution of Icelandic Black Guillemots, but so far none on the whereabouts of adults outside the breeding season.

Finding nests of Black Guillemots is extremely tedious, and Chapter 4 deals with the problems related to counting birds to obtain information on population size. Counts present problems of how to carry these out and how to interpret the results. Various environmental factors influenced the numbers

of birds present at nesting areas, and there were great diurnal variations. Because of varying proportion of non-breeders present at different breeding stations, correction factors relating counts to breeding population, cannot be used to extrapolate to other populations. Suggestions are made of how to obtain greatest accuracy when censusing, but counts can only give relative figures for population size, which still should be useful when monitoring populations.

Chapter 5-9 have a running title, all dealing with different aspects of Black Guillemot breeding biology. The first, dealing with the timing of laying, gives circumstantial evidence that the 6-6½-week spread of laying dates in the population, was primarily the effect of the age structure, which has been greatly influenced by an unusually high influx of new breeders into the population.

Chapter 6 gives the basic breeding parameters, clutch size, egg size, and reproductive output. Egg size and laying date were the most important factors affecting breeding success, these in turn being correlated with age and/or experience of the breeders. Careful analyses were made of the causes for egg and chick losses. Seasonal effects dominated in all aspects of the breeding biology; there was a seasonal decline in clutch and egg size, breeding output was not only actually smaller in late-nesting birds, but also proportionally. The proportionally less success of late breeders was emphasized at the egg stage, while they were just as successful fledging their chicks as long as these hatched. Most of the egg and chick losses were attributed to parental behaviour.

Chapter 7 deals with replacement laying, investigating its natural frequency, and change of this with season and state of incubation of former clutch. The replacement of a lost clutch took about 2 weeks. Late breeders did not replace a lost clutch, and incubation of a former clutch decreased the likelihood of a replacement clutch.

The incubation period is dealt with in Chapter 8. Egg weight declined as incubation proceeded. The length of the incubation period was found to be correlated with ambient temperature. Length of the interval between eggs in 2-egg clutches, was

documented. Asynchrony at hatching was one factor which lead to failure; this was most apparent in clutches in which the eggs were laid greater interval apart than normal. If eggs in a clutch were large, the first egg (the a-egg) tended to be the bigger of the two, but the reverse if the eggs were small. An explanation of this is advanced; this may do with the overall fitness of the breeders and may turn out to have survival value.

In the chapter on the nestling period (Chapter 9), documentation was made of the size of chicks at hatching, the length of their stay in nest, growth rate, mortality, factors influencing length of their stay in the nest, and the chicks' condition upon fledging. Post-fledging survival appeared to be independent of the time of season at which the chicks hatched. Chick growth was related to their size for the first half of the nestling period, thereafter size did not matter. Chicks reached near adult weight 4 days before fledging, then their weight declined. This weight recession corresponded to a decline in feeding frequency towards the end of the nestling period, although chicks did receive some food right up to fledging.

The food eaten by chicks and adults was compared using data from same region and same period. This is given in Chapter 10, along with notes on behaviour of adults feeding young and the incidences of kleptoparasitism. The feeding areas were located 2-7 km away from the island. The sexes appeared to bring equal amounts of food to the young, except the first days of the nestling period. Then one sex may have done most of the feeding, while the other most of the brooding. At the height of summer, when there was continuous light, feeding took place at all times during the 24 hours, but the frequency was always highest in the morning. Various factors affecting the feeding rate and prey selection were identified, such as girth of the prey (rather than the length), the chicks' age, and brood size.

The main population parameters are documented in Chapter 11. Most Black Guillemots appear to start breeding when 4 years old. The pre-breeding survival was around 24% of those fledging. Annual adult survival was 87%. Most recoveries of ringed Black Guillemots

in Iceland and elsewhere, are made through activities of man; Black Guillemots are specially liable in getting entangled in fishing nets. The extent of this mortality in the Flatey region was estimated about 1% of the breeding population over a 2 month period. Although ignored in many population studies, immigration was very obvious and could not be overlooked in the present study. The rapid increase in the study population between 1967 and 1977, was estimated to be near exclusively due to immigration.

Chapter 12 deals with experiments with larger-than-normal clutch and brood sizes. Some discussion is devoted to why Black Guillemots most often have 2 eggs and some only lay a single egg in a clutch, while parents were capable of raising 3 chicks to fledging, hence increase the number of chicks fledged compared with those from 1- or 2-chick broods.

Chapter 1: General introduction

1.1 Main aims

During the last 25 years ecological research has increasingly become orientated towards examining adaptations in life histories of animal species (e.g., Crook 1965, Ashmole 1971, Kruuk 1972). The works of Lack (1954, 1966, 1968) have gone furthest in emphasizing the interrelations between all aspects of a species' biology among birds. In seabirds, to which group of birds the Black Guillemot (Cepphus grylle (L.))* belongs, these studies have been primarily concerned with breeding adaptations (e.g., Coulson (and et al.) 1956 et seq., Richdale 1957, Ashmole 1963, Nelson 1966, 1970, Simmons 1970, Perrins 1970).

The breeding and feeding ecology of Black Guillemots have been relatively little studied. There are probably two main reasons for this; firstly, Black Guillemots typically nest very dispersed, often solitarily, and secondly, their nest-sites are frequently inaccessible and hidden so that eggs and chicks cannot be reached without difficulty. Yet Black Guillemots should be highly suited as study species for exploration of adaptive themes in life histories since, in many respects, they show strategies which are different from those of many other seabirds, e.g. the five other N. Atlantic alcid species.

As already mentioned, the nest dispersion is unusual. Lack (1968: 130) mentioned that 98% of all seabird species were colonial. Black Guillemots usually nest in "loose" colonies, or solitarily. Showing a gradient from solitary to colony nesting, Black Guillemots should be ideal for studying the advantages and disadvantages of colonial nesting and the evolutionary reasons for colonality. Because of the dispersed manner of nesting, instead of using the term "colony" I have

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* Scientific names of bird species mentioned in this thesis, are given in Appendix I.

used phrases like "nesting area", "nesting group" or "nesting aggregation" in this thesis.

Black Guillemots most commonly lay 2 eggs in a clutch in contrast to the single egg clutch laid by the majority of alcids. Yet Black Guillemots frequently lay only a single egg, making them highly suitable for studying the factors influencing clutch size.

Black Guillemots are inshore feeders, and their chicks are fed to near adult size while in the nest. Again this contrasts with other alcids, the majority of which tend to feed further from the coast than do Black Guillemots, while some species take their chicks out to sea at an early age. Food, feeding pattern, and the relationship with the food supply should therefore warrant study.

In contrast to the ways in which Black Guillemots differ from other alcids, they also show many similarities to them. In common with many other seabird species, Black Guillemots have deferred maturity, are monogamous, show strong fidelity to nest-site and mate, are relatively long-lived, and the sexes share the breeding duties.

In the beginning of the study I basically wanted to find out as much as possible about the breeding and feeding of Black Guillemots, and to quantify various population parameters to learn something about the species' population dynamics. As my first field season progressed these ideas crystallized into the following aims:

1. Document the unusually rapid increase in numbers which had been taking place in the study population, and discuss possible reasons for this (Chapter 2).
2. Study attendance of birds at nesting areas, and factors influencing their attendence pattern in order to work out a reliable census method (Chapters 3 & 4).
3. Work out the basic features of the breeding biology, and identify some of the factors influencing reproductive output (Chapters 5, 6, 7 & 8).
4. Examine growth of chicks, and factors related to this (Chapter 9).
5. Describe the food and feeding strategy of young and

adults, and factors related to these (Chapter 10).

6. Compare population parameters with those of some other auk species for which comparable details are available, and construct a model for the study population (Chapter 11).
7. Discuss the evolution of clutch size in the species (Chapter 12).

Since my study was intended to cover only three field seasons, I could only expect to collect minimum data on population dynamics for the study population. Likewise the lack, at the outset, of a ringed, known-aged population was to prove a major obstacle when dealing with breeding biology phenomena.

1.2 Literature review

Until in recent years the literature on Black Guillemots has been very limited. This can be divided, albeit arbitrarily, into three main fields: (a) Anatomy, phylogeny, and taxonomy, (b) ecology and behaviour, and (c) ringing and censusing.

The most comprehensive works on ecology and behaviour, are those by Preston (1968), with an emphasis on social behaviour in an ecological context, Asbirk (1978a, 1978b, 1978c, 1979a, 1979b, 1979c) on breeding biology and behaviour, and Cairns (1978, 1979, 1980) on breeding biology. Other studies on breeding and feeding ecology of Black Guillemots include those of Hyde (1936, 1937), Winn (1950), Storer (1952), Kozlova (1957), Belopol'skii (1957), Uspenski (1958), Dennis (1966), Bianki (1967), Bergman (1971, 1978), Slater & Slater (1972a), Anderson & Rosenlund (1973), Slater (1974) and Olsson (1974). Works of varying detail are presently being carried out, or recently have been, by Barrett (pers. comm.) in Norway, Bergman (pers. comm.) in Finland, Broad (pers. comm.) in Shetland, Evans (pers. comm.) in Greenland and Britain, Nettleship and Gaston (pers. comm.) in Canada, Divoky & Boekelheide (1978) in Alaska, Ramsay (1976) in the Orkneys, and Unger (pers. comm.) in Sweden.

The closely related - some authors say conspecific - Pigeon Guillemot of the N. Pacific was valuable for comparison with Black Guillemots. The general ecology of this species

was described by Thoresen & Booth (1958), Drent & Guiguet (1961), Drent (1965), and Drent et al. (1964), while important contributions were made by Winkler (1947), Storer (1952), Ainley, Lewis & Higbee (1971), Aitchison (1972), Koelink (1972), and Follett & Ainley (1976). The ecology of the third Cepphus species, the Spectacled Guillemot of the N. Pacific, is virtually unknown. Most of what is known stems from the works of Austin & Kuroda (1953), and Nazarov & Labzyuk (1972).

Black Guillemots in Iceland, where the present study was carried out, have been the subject of four papers, Gudmundsson (1953), who dealt with the species´general biology in Iceland, Ingólfsson (1961) on taxonomy, Bardarson (1975) describing kleptoparasitism by Arctic Terns, and Petersen (1977) describing some ringing and morphological work relating to winter distribution. Excluding local species lists, the only other references to Black Guillemots in the Icelandic ornithological literature are found in general faunistic works (e.g., Faber 1822, Slater 1901, Hantzsch 1905, Saemundsson 1936a, and Timmermann 1949).

There has been an upsurge in life history studies on auks during the last 15-20 years. Particularly important have been the works of Bédard, Drent and co-workers, Manuwal, and Sealy on N. Pacific alcids, Bédard and Nettleship and co-workers on NW. Atlantic auks, and Ashcroft, Birkhead, Harris, Hudson, Lloyd, Tschanz, Ingold and their co-workers, and Williams on NE. Atlantic auks. Much of earlier works on auks were contributed by Russians, in particular Belopol´skii, Gerasimova, Kaftanovskii, Kartaschew, Krassovskii, and Uspenski. Other important early contributors, were Myrberget, Paludan, Southern, Storer, Tuck and Udvardy.

Work done on three auk species (other than Black Guillemots) have been particularly important to my study, that on Puffin (Ashcroft), Razorbill (Lloyd), and Common Guillemot (Birkhead), besides that on the much related Pigeon Guillemot (works of Thoresen & Booth, Drent and co-workers).

1.3 General distribution, and nesting habitats

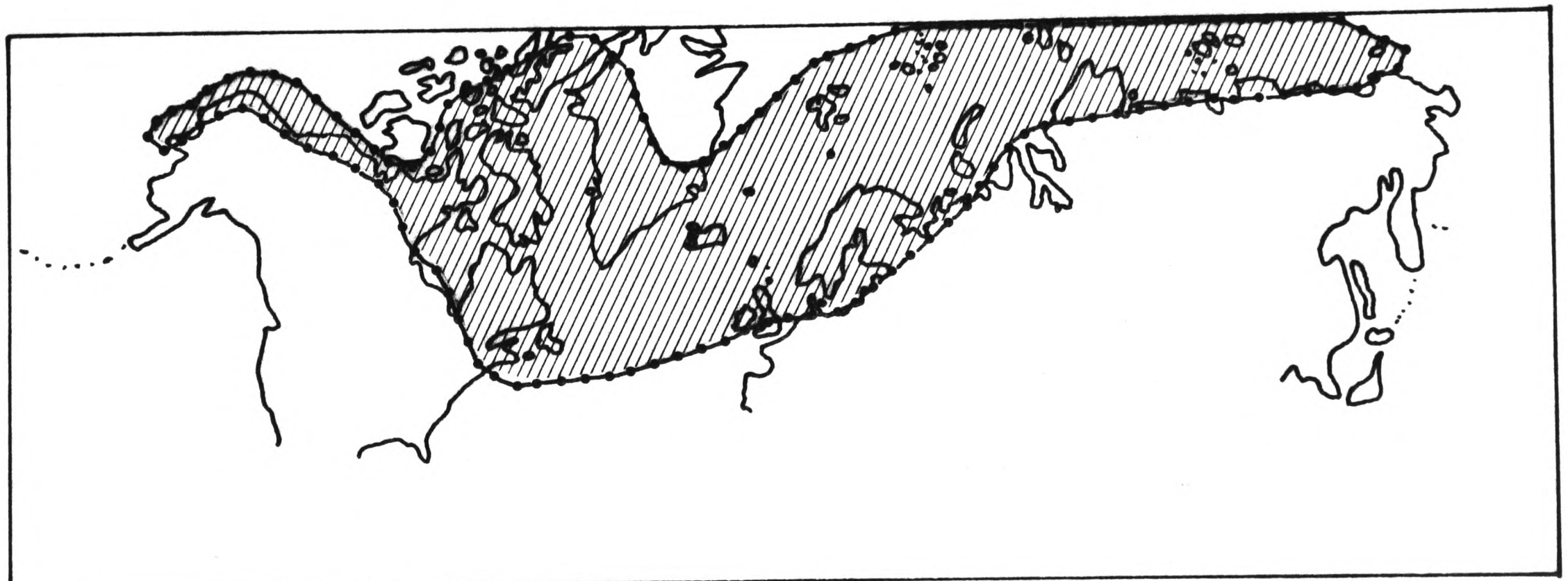
Black Guillemots are holarctic birds, nesting over large areas of the N. Atlantic and Arctic Oceans. Their eastern limit is Wrangel Island, but in the west, Cape Thompson, as shown in Fig. 1.1. In the N. Pacific Black Guillemots are replaced by a closely-related species, the Pigeon Guillemot, which some authors say is conspecific (Salomonsen 1944, Kartaschew 1960:67). I believe we have here a typical case of superspecies (vide Mayr 1969: 52).

Icelandic Black Guillemots have been thought to represent a separate subspecies, Cepphus grylle islandicus Hörring 1937. Although there has been some disagreement over how many subspecies there are of the species Cepphus grylle, all workers have recognized the validity of islandicus (Salomonsen 1944, Storer 1952, Ingolfsson 1961, Vaurie 1965: 515).

Black Guillemots are common along the coasts of Iceland the whole year round and are found breeding in most coastal parts of the country (Gudmundsson 1953). They are not common as nesters along the south coast which mostly does not meet the species' habitat requirements for breeding, because of extensive sandy beaches and lack of rocky areas (cf. Preusser 1976: 108).

The details of the breeding distribution of Black Guillemots in Iceland are still largely unexplored. As far as is known, no nesting aggregations are of a comparable size with those in high arctic Canada of ca 2000-10000 pairs (Brown et al. 1975: 191), or in Greenland of ca 2000 pairs (Salomonsen 1950: 390). The largest aggregations formerly known in Iceland were those at Ögur of ca 200 pairs (Löppenthin 1938) and at Ennishöfdi of 250-300 pairs (F. Gudmundsson, pers. comm.). Both these nesting groups are now reduced to very few pairs. The present study population is now the largest aggregation known in Iceland, with 417 pairs in 1977 (Chapter 2). All three localities are in NW. Iceland. In terms of numbers of individuals and wide occurrence of breeders, the Northwest appears to be the centre of Black Guillemot breeding distribution in Iceland. This pattern is broadly similar to that shown by three other alcid species, namely Common Guillemots,

Fig.1.1. The limits of the world breeding distribution of Black Guillemots.



Note: (1) Drawn from Voous (1960: 171), with additional information from Dementiev et al. (1951: 232), Swartz (1966: 655-656), MacLean & Verbeek (1968), Divoky et al. (1974), Brown et al. (1975: 192), Kuyt et al. (1976), and Sowls, Hatch & Lensink (1978: 20).

Brünnich's Guillemots (Einarsson 1979), and Razorbills.

Although Black Guillemots are present along the Icelandic coasts outside the breeding season very limited information exists on the origin of these birds. Theoretically, they could comprise birds from outside as well as within the Iceland population. Black Guillemots have always been considered the most sedentary of Icelandic seabirds, but little evidence has been available from ringing or morphological studies to substantiate this. Very few Black Guillemots had been ringed in Iceland prior to the present study, so the movements of Icelandic birds outside the breeding season were virtually unknown. The state of knowledge on the origin of Black Guillemots occurring in Icelandic waters, and the movements of Icelandic birds, have been treated in a separate paper (Petersen 1977, see Appendix II).

Like most other truly marine bird species, Black Guillemots nest on or near the coast although in Spitsbergen they have been found nesting as far inland as 2-3 km (Birulya 1910). The primary requisite of Black Guillemots when nesting is a shelter, preferably where the incubating bird is not seen from the outside. Their preferred habitat is boulder areas or talus slopes, but they also make use of crevices in low cliffs.

In the present study area Black Guillemots nest primarily in boulder screes. Typically, Black Guillemots use natural holes or crevices for nesting, although they may excavate burrows themselves (Asbirk 1978b, c, pers. obs.), a habit which seems even more common in Pigeon Guillemots (Drent 1965). A characteristic of Black Guillemots which sets them apart from the truly colonial auk species, is their great flexibility in choice of nest-sites. There are numerous reports of unusual nesting places occupied by Black Guillemots. These include dense thorn bushes (Asbirk 1978b, c), piers (Witherby 1939, Armstrong 1940, Asbirk 1976, pres. study), stone dykes (Gudmundsson 1953, Asbirk 1976, pres. study), pile of gutters (Asbirk 1978b), buildings occupied by man (Th. Helgason, pers. comm.), disused buildings (Kuyt et al. 1976, pres. study), under driftwood (Gudmundsson 1953, Bianki 1967: 185, Preston 1968: 10, Divoky, Watson & Bartonek 1974, Kuyt et al. 1976, Asbirk

1978b, c), oil-drums (MacLean & Verbeek 1968), discarded oil stove (T. Tryggvason, pers. comm.), discarded trawler boilers (A. Gardarsson, pers. comm.), self-excavated burrows in soft, man-made turf-dykes (pers. obs.), permanently anchored ships (H. Arnason, pers. comm., pers. obs.), ditch excavations (pers. obs.), and nest-boxes for Eiders (T. Tryggvason pers. comm.). Unusual sites have also been reported for Pigeon Guillemots, in wharves and piling (Campbell 1977, Fisk 1978).

1.4 Study area

General descriptions of the geography of Iceland are found in Thorarinsson (1968, 1975), and a more detailed one in Preusser (1976). General descriptions of fauna and flora are found in Gudmundsson (1975) and Einarsson (1975), respectively. The basic features of the Icelandic climate, and a description of the present study area, are summarized below.

Iceland is located at the boundary of the subarctic and arctic zones (Sjörs 1963, Ashmole 1971). Its oceanic climate of rather mild winters and cool summers is considerably milder than that of other countries at similar latitudes. This is primarily an effect of the North Atlantic Drift (an extension of the Gulf Stream) which sweeps the south and west coasts. The Northeast and East parts, on the other hand, are washed by the cold East Iceland Current. There are thus considerable differences in sea temperature, and consequently in the whole climatic regime, between these two regions of the country.

The west coast of Iceland is dominated by two large bays, the more northerly of which is Breidafjordur. The bay stretches about 110 km from E to W and 60 km from N to S, but is indented by fjords. The innermost one-third of the bay is strewn with numerous small islands and skerries; there are thought to be some 2000-3000 of them. Navigating among these islands is extremely treacherous because of supernumary reefs and submerged rocks, general shallowness of the sea, strong and changeable currents, and ever-changing depth of the tidal waters. The tidal range is considerable, up to 5 m during

spring tides within a single diurnal cycle.

My main study area was Flatey, one of these islands, at 65°22′N; 22°55′W. The nearest part of mainland Iceland is towards the north, approx. 18 km away. Fig. 1.2 depicts the general geographic location of Flatey.

The island of Flatey forms a part of Flateyjarhreppur (=Flatey civil parish), an administrative partition, constituting some 536 islands (Skulason 1977:247) distributed over an area of approx. 650 km^2. The Flateyjarhreppur islands are traditionally divided among 7 farms, certain clusters of islands belonging to each farm. These farms are: Hergilsey, Flatey, Svefneyjar, Hvallatur, Skaleyjar, Svidnur and Bjarneyjar. The eight, Stagley, is long deserted. Fig. 1.3 shows the administrative boundaries, the farms and their approximate boundaries, and area used during present study. A thorough description of Flateyjarhreppur is given in Skulason (1935, 1942a), and Skaptason (1959). Four of these farms are still inhabited (Flatey, Svefneyjar, Hvallatur, Skaleyjar).

For centuries seabirds, their eggs and down as well as the birds themselves, have been of great importance to the islanders (Olafsson 1772: 335-341, Sívertsen 1840:182, Skulason 1942b,1970:182-184).To-day these islands are exploited every summer for their natural resources. Some of the traditional practices have greatly diminished, however, owing to changes in life-style. The most important resource now, is Eiderdown.

Flatey, the principal study island, is about 1.85 km long, 400 m at its widest but only about 30 m where narrowest. The total area is only 0.5 km^2, yet it is one of the largest islands in the Flateyjarhreppur. As its name implies, Flatey is a flat, very low island, its highest point being 16 m a.s.l. Vegetation is rather homogenous, principally hummocky grassland, coastal flats, and hayfields. Davidsson (1971, 1973) described plant communities on the island and presented a list of plant species. In 1920 189 inhabitants were living on Flatey (Preusser 1976: 322), but to-day only about 20 persons are resident the whole year round. During the summer months of June, July, and August a varying number

Fig. 1.2. The geographic location of Flatey Island (NW. Iceland), the principal study island, during the present study.

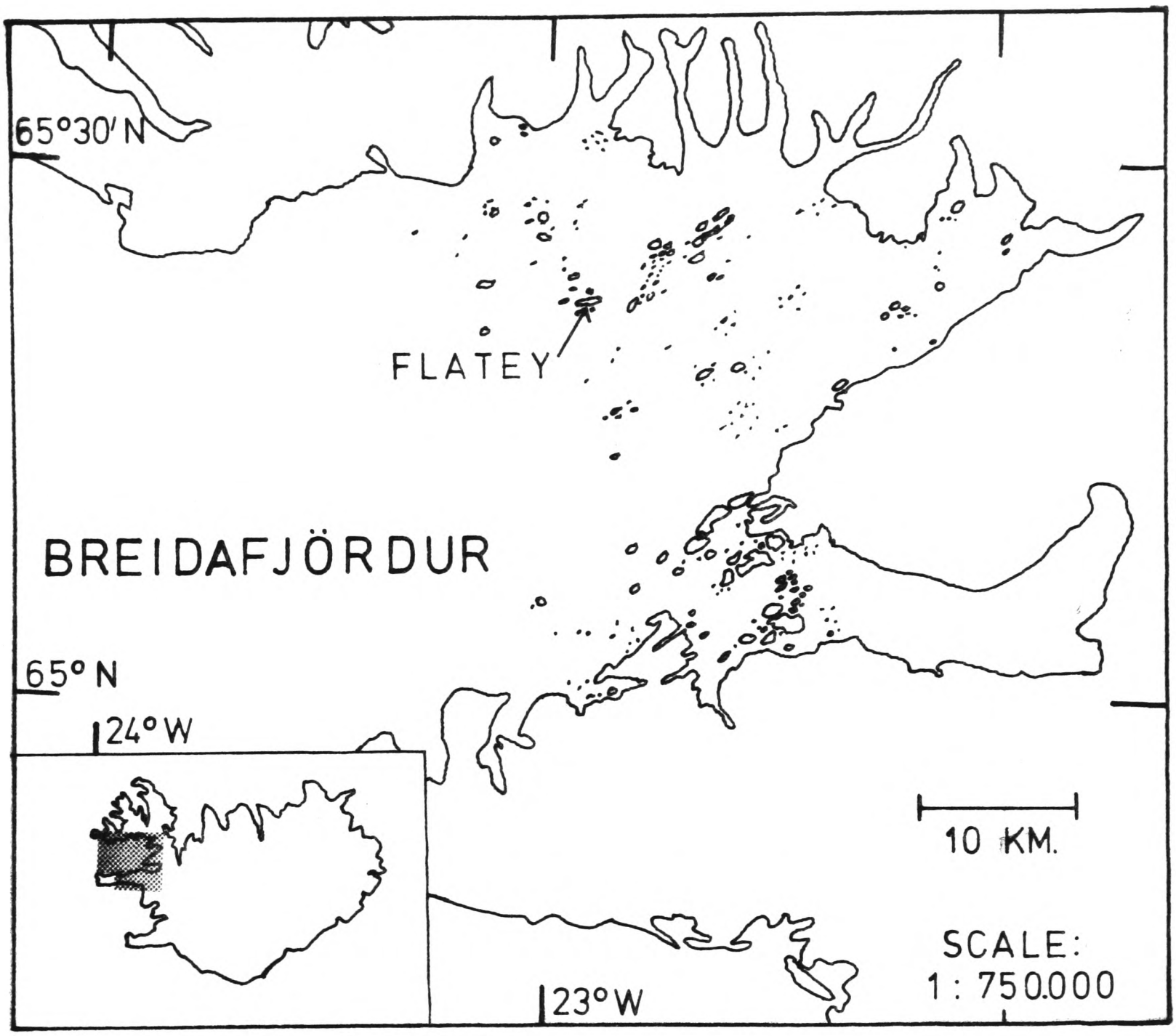
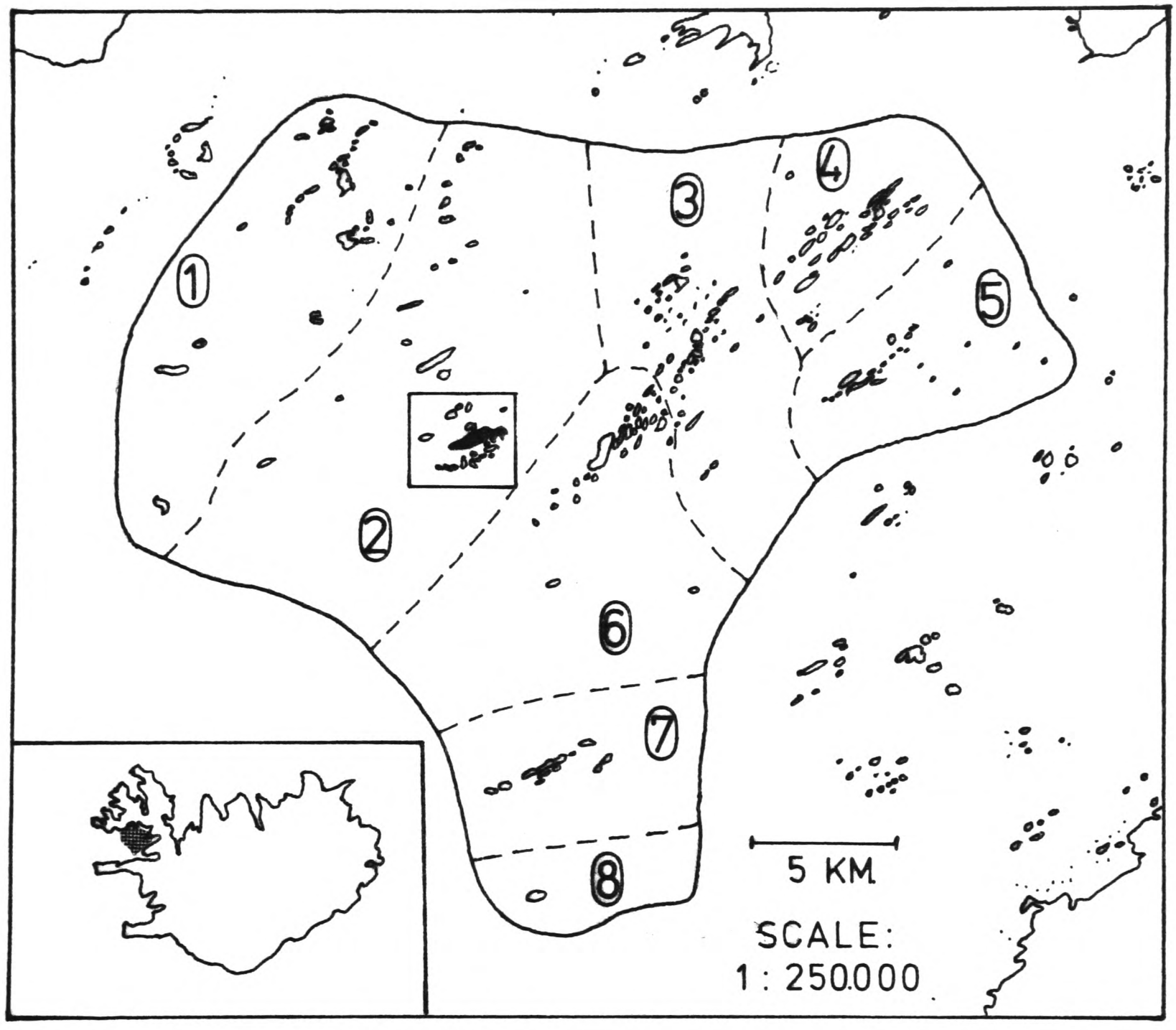


Fig. 1.3. The limits of Flatey civil parish (= Flateyjarhreppur) (unbroken line), the boundaries of the 8 farms which made up the parish, one of which long since deserted (broken lines), and limits of present study area (rectangle).



Note: (1) The figures indicate the farms: 1- Hergilsey, 2-Flatey, 3- Hvallatur, 4- Skaleyjar, 5- Svidnur, 6- Svefneyjar, 7- Bjarneyjar, 8- Stagley.

of up to 100 persons, summer visitors and permanent residents, stay on the island.

A number of islets in the immediate vicinity of Flatey were used for specific aspects of the study. Fig. 1.4 shows the spatial relationship of Flatey with these islets.

No faunistic, let alone ecological, papers have ever been published on the bird life of the Flateyjarhreppur islands, except two very general accounts by Skulason (1935, 1949), and an inaccurate species list of birds in an otherwise botanical paper by Davidsson (1971), all far from exhaustive. Recently I published a separate paper dealing with the nesting bird species of Flatey and some of the adjoining islets (Petersen 1979, see Appendix III). Because of the scarcity of material on the bird life of the Flateyjarhreppur islands, I am summarizing information I have collected in Tab. 1.I, giving a rough indication of numbers. In contrast to the lack of faunistic papers, the utilization of birds as a resource, and their methods of exploitation have been well documented, notably by Skulason (1935, 1942b, 1949, 1964, 1966, 1970, 1976).

1.5 General methods

Before the start of my study in 1975, a pilot study was carried out in summer 1974 (28.6.-14.7.; 1.8.-5.8.) in order to obtain some experience of the island and determine if a 3-year research programme was feasible. I looked at the breeding distribution of Black Guillemots on the island, colour-ringed breeding birds, marked nest-sites, and ringed as many chicks as possible. Unfortunately, no ringing had been done in this area before my study, except for 13 birds in 1973.

Disturbance by people was a potential hazard to the study, especially since the island was visited every summer by several thousand tourists, particularly from late June till early August. Because of this it was originally thought necessary to restrict access to certain study areas. In continuation of this idea, the easternmost part of Flatey (together with some islets south of the island) was declared a reserve by law in 1975. This area is completely closed

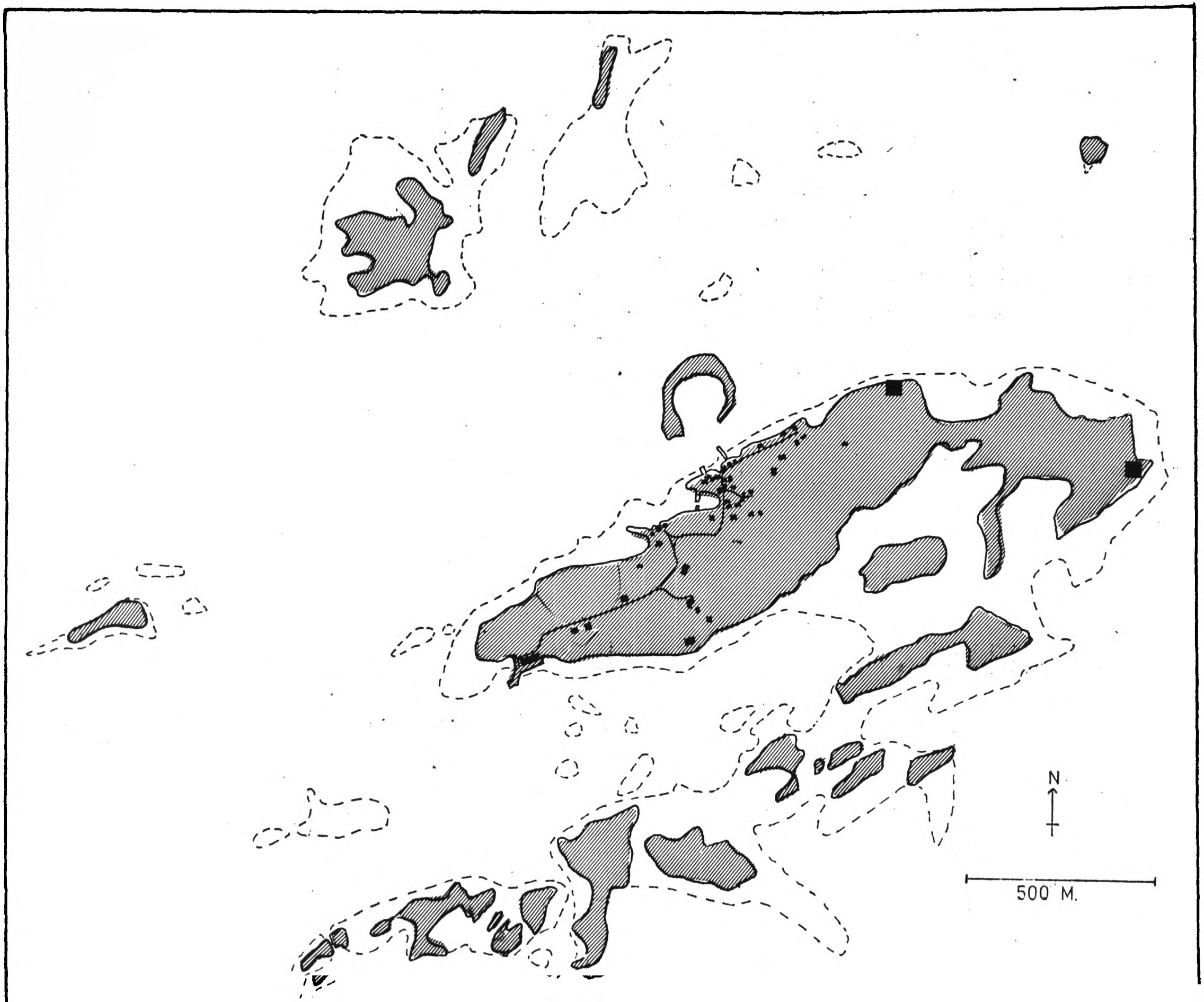


Fig.1.4. Main study island (Flatey), and neighbouring islands used for limited study darkened. The extent of the settlement area (small squares) and roads are shown. Broken lines show area uncovered at low tides. The two large squares indicate huts used for hide studies (see text later).

Tab. 1.I. A list of the breeding species of birds in Flateyjarhreppur, with notes on their relative abundance.

Red-throated Diver	:	4-5 pairs
Fulmar	:	Common
Cormorant	:	Common (Gardarsson 1979)
Shag	:	Common (Gardarsson 1979)
Grey-lag Goose	:	Widespread
Mallard	:	Widespread
Teal	:	Localized
Wigeon	:	Rare
Long-tailed Duck	:	Rare
Eider Duck	:	Very common
Red-breasted Merganser	:	Localized
White-tailed Eagle	:	Nested 1976 and 1977, first since 1894 (Petersen 1976c, 1978).
Oystercatcher	:	Common
Ringed Plover	:	Common
Snipe	:	Common
Redshank	:	Common
Dunlin	:	Widespread
Grey Phalarope	:	Rare, probably no more than 15 pairs
Red-necked Phalarope	:	Common
Great Black-backed Gull	:	Common
Lesser Black-backed Gull	:	Rare
Glaucous Gull	:	Ca 10 pairs
Black-headed Gull	:	Several small colonies
Kittiwake	:	Common
Arctic Tern	:	Very common
Black Guillemot	:	Common
Puffin	:	Very common
Raven	:	Ca 10 pairs
Wheatear	:	Not uncommon
Meadow Pipit	:	Common
White Wagtail	:	Common
Redwing	:	1 pr. in 1930 (Skulason 1931); 3 prs 1976; 4 prs 1977
Snow Bunting	:	Common

Note:(1)Four more species(Golden Plover, Whimbrel, Arctic Skua, Short-eared Owl) are known to have nested, and possibly also Whooper Swan and Barnacle Goose.

to visitors from 15th April to 15th August (Stjornartidindi B (1975) no. 395/1975). Later experience showed, that disturbance was negligible. Most people did not attempt to visit the eastern part of the island where 60-70% of all Black Guillemots nested. Moreover, most of the birds nested in boulder screes below the grassy edges of the island, or in stony outcrops, both terrains which deterred people from walking there. The islanders, knowing of my intentions, avoided disturbing the birds. There was a mutual agreement that no eggs, or chicks, should be taken, although by law Black Guillemots can be taken for food in areas in Iceland, such as Flateyjarhreppur, where fowling has been a tradition for centuries (Stjornartidindi A (1966) no. 33/1966). Black Guillemot eggs and chicks have always been taken on a minor scale anyway compared with Shags, Cormorants, and Puffins for instance (Skulason 1970: 182-194), even more so after the islands started to become depopulated after World War Two (see Preusser 1976: 322). In 1916 350 Black Guillemot chicks were taken in the islands in contrast to an annual harvest of up to 31200 Puffin chicks (Hagstofa Islands 1919, Skulason 1976).

I stayed on Flatey for three whole breeding seasons; 1975: 18.4.-21.6., 24.6.-14.7., 21.7.-30.8., 1976: 17.4.-28.8., 1977: 16.4.-30.8. . The whole island was used for quantifying basic breeding biology parameters, individual areas being selected for specific studies. It was already apparent in 1974 that most Black Guillemot nests fell rather conveniently into groups according to local topography. Fifteen such "nesting areas" were recognized, numbered I-XV, of which 13 can be said to be natural groupings. In the beginning of the 1975 field season wooden huts were placed at two of these areas, area IV on the island's north side, and at area IX at the eastern end (see Fig. 1.4). These huts were used for feeding observations and other hide studies.

The only studies on islands in the nearest vicinity of Flatey, were censuses conducted of their breeding populations, looking for any ringed birds, and ringing of birds (principally chicks) for studying inter-island movements.

For the purpose of this thesis the material used has been limited to that collected during 1974-1977, although the study has been continued. The only exceptions relate to data gathered through the ringing of birds and estimates of productivity of chicks. In all 2775 Black Guillemots were ringed during 1973-1979 (in 1973 by T. Tryggvason). The birds were given a numbered stainless steel ring(supplied by the Museum of Natural History, Reykjavik). During 1974 to 1978 chicks were given a combination of steel and colour rings specific for each year class but not for individual recognition. However, a distinction was made between birds ringed on Flatey and those ringed in island in its neighbourhood so these groups of birds could be spearated on sight. Breeders were also given colour rings in addition to the steel ring, in individual combinations for recognition. All captured adults were colour-ringed to begin with, but later, colour-ringing of adults was restricted to birds caught at nest-sites in the vicinity of the observation huts.

More detailed descriptions of methods and materials used will be given in the appropriate chapters. Many technical terms used throughout this thesis are explained in Appendix IV. The reader is asked to refer to the appendix when appropriate.

Chapter 2: Population numbers and nesting distribution of Black Guillemots on Flatey and nearby islands.

2.1 Introduction

Black Guillemots are, as noted earlier (Tab. 1.I. p.14), common breeding birds on islands of the Flatey civil parish (=Flateyjarhreppur). Almost every islands has nesting Black Guillemots, although their numbers are generally small on any one of them. Largest numbers are found on Flatey which, if viewed as one breeding station, now harbours the largest aggregation of nesting Black Guillemots known in Iceland.

No published accounts of sufficient detail exist on the past status of Black Guillemots in the Flateyjarhreppur. The only papers describing the past bird life of the region merely mention Black Guillemots as common breeders, of wide distribution, and of some use as food (Skulason 1935, 1949). In view of this paucity of published material for comparison I was fortunate to have at my disposal the observations of local naturalists, as well as two unpublished diaries. From this material, and my own, it has been possible to show that great changes have taken place in the numbers of Black Guillemots nesting on Flatey and some islands in the vicinity during the present century.

The main aims of this chapter, are: (a) to describe the numbers and nesting distribution of Black Guillemots, mainly on Flatey, with a primary objective of showing the abrupt changes in numbers which have taken place this century, and (b) to seek explanations for these changes.

2.2 Materials and methods

Various data, quantitative and descriptive, from before 1974 (when I came first to Flatey) have been incorporated into the present chapter. Most of this information was provided by Mr. J. Bogason, a former inhabitant of Flatey, now a research assistant at the Marine Research Institute in Reykjavík, Mr. H. Gudmundsson, a farmer on Flatey since 1965 and a keen, observant naturalist, and Mr. S. Gunnlaugsson, a former schoolmaster on Flatey. I have also used the unpublished diaries

of Richard Hörring and Finnur Gudmundsson, former Curators of the Zoological Museum in Copenhagen and the Museum of Natural History in Reykjavík from 1908 and 1942, respectively.

An estimate was made of the Black Guillemot population on Flatey in 1974. This was partly done from counts of nests with eggs or chicks, partly from counts of birds attending nesting areas. Accurate nest counts were made at only one nesting area (IX) out of the fifteen on Flatey, and also on two adjacent islets. Later experience of Black Guillemot censusing indicated the estimate for Flatey may have been too low. The censusing time was short, nest-sites were undoubtedly missed, the attendance cycle of the species had not been worked out, and no standardized counting procedures had been developed.

In the three principal study years (1975, 1976, 1977) a search was maintained throughout the summer in order to obtain accurate figures for the size of the Black Guillemot population on Flatey. Records were kept of the exact location of all known nest-sites. Since the sites were traditional, each was given an individual number which the site kept between years. This work, I believe, resulted in figures very near the true ones for the size of the population.

In the principal study years population estimates were carried out on 20 islands in the immediate neighbourhood of Flatey, in late July/early August. Counts were made of sites containing eggs or chicks as well as sites from which chicks had recently fledged. These nest-sites were not numbered like the ones on Flatey, and counts were usually made on only one occasion on each island. These counts would potentially not be as accurate as those for Flatey, and probably can only be referred to as minimum counts. But these islands are also of only very limited size (see Fig. 1.4, p.13) and the potential Black Guillemot nesting habitat lesser still. Therefore I reckon not many sites were missed.

During all the years 1974-1977 numerous visits were made to other islands in the Flateyjarhreppur. These were made for general observations on the bird life. Besides I gathered much information from the local people, many of whom had lived all their life in the islands.

2.3 Results

Black Guillemot numbers on Flatey

Of all the Flateyjarhreppur islands the numbers of nesting Black Guillemots have been most closely observed on Flatey itself, even prior to my visits to the island. As far as can be ascertained, changes in Black Guillemot numbers have also been more dramatic there than on any other island of the parish.

Figures for numbers of nesting Black Guillemots are available for the period 1940-1977, and these are shown in Fig. 2.1. Numbers were low during 1940-1966, only 1-5 pairs nesting each year. The information from the 1940's, supplied by Mr. J. Bogason, ties in with that from F. Gudmundsson who stayed on the island for 9 days in summer 1942, during which he only saw "a few birds along the shores of Flatey". From 1967 to 1977 there was a continuous and exceptionally rapid increase in numbers. H. Gudmundsson claims the biggest increase between years occurred in 1971 but no figures are available for 1968 to 1973. I estimated the breeding population to be 180 pairs in 1974. Later experience of Black Guillemot censusing prompted me to consider this as an underestimate. The calculated figure of 224 pairs is regarded nearer the true numbers for that year. The calculation was made by extrapolating from the 1966-67 and 1975-77 data, by assuming a constant rate of increase between years over the whole period. This is shown in greater detail later (Tab. 11.X, p.298). During the period of intensive study (1975-1977) there was a 39% net increase in the Black Guillemot population, involving an addition of 118 pairs to the 1975 level.

Information from before 1940 is of a descriptive nature only. In 1908 Hörring stated that Black Guillemots were "noticeably common" on Flatey and the islets south of it. S. Gunnlaugsson has remarked that they were very common during the first three decades of the present century (after which he moved from the island). Hörring's and Gunnlaugsson's information is therefore in general agreement. Unfortunately, no information is available for the 1930's. From the existing data from before and after that decade, a dramatic decline

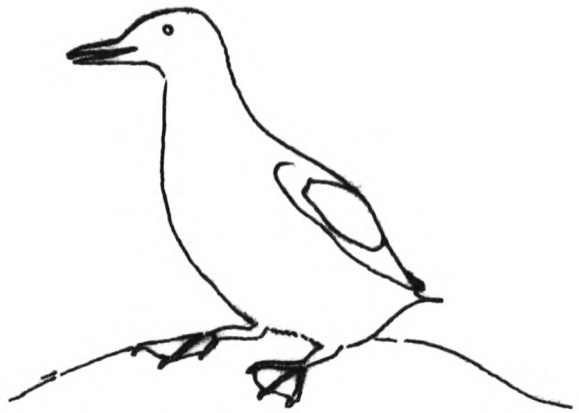


Fig. 2.1 The numbers of Black Guillemot pairs on Flatey in the period 1940-1977. The 1974 figure is calculated.

can be inferred. The reason for this decline and the later recovery of the population, is unknown, but explanations are offered later.

Numbers on nearby islands

The recent increase in numbers of breeding Black Guillemots, has not been limited to Flatey alone. In Tab. 2.I information is given for islands in the close surroundings of Flatey (those shown earlier in Fig. 1.4, p.13). A threefold increase occurred in Black Guillemot numbers on these islands from the 1940's to 1977. This was nonetheless much smaller increase than took place on Flatey over the same period.

Increases on other islands in the Flateyjarhreppur, but further away from Flatey, were noticed by local inhabitants in the approximate period 1970-1977. No quantitative data are available but increases are claimed to have occurred on islands within four island groups (other than that belonging to the Flatey farm). These were the islands belonging to the farms Hvallatur, Skaleyjar, Hergilsey, and Svidnur, located within approx. 15 km radius of Flatey (see Fig. 1.3, p.11).

Nesting distribution on Flatey

Fig. 2.2 gives the location of nest-sites used by Black Guillemots on Flatey in the 1940's, 1955-1965, and 1966-1967. During the 1940's four sites were in use all the years (arrows A-D). In some years of that decade a fifth site was also occupied. Its location varied between years, each site being used only 1-2 years in turn (triangles). During 1955-1965 the 2-3 nesting pairs used the same nest-sites which had been occupied every year in the 1940's.

The 1966 breeding season may be considered a turning-point. That year the number of breeding pairs was at its all-time lowest since 1940, one pair only, although information is lacking for some years in the 1950's. The 1966 site (site E in Fig. 2.2) was established only a few meters away from the old site B, after it had been destroyed by rockfall. These two sites may have been occupied by the

Tab. 2.I. Numbers of Black Guillemot pairs nesting on islands in the immediate vicinity of Flatey (within a 1.2 km. radius), in the period 1940-1977.

	Year (s):					
Name of island[1]:	1940/50[2]	1969[3]	1974	1975	1976	1977
Akurey	1	-	-	1	2	1
Langey	6(0)[4]	-	-	29	29	28
Kerlingarholmur	1	-	-	2	-	1
Kerlingarholmsflaga	0	-	-	0	0	0
"Midflaga"	0	-	-	0	0	0
Hadegisholmsflaga	0	-	-	0	0	0
Hadegisholmi	0	-	1	3	2	2
Geirsholmi	1	-	5	6	10	9
Innri-Mafey	3	-	-	3	4	7
Ytri-Mafey	3	-	-	6	-	6
Pjattland	0	-	-	1	-	1
Flatholmarif	0	-	-	3	-	1
Flatholmi	3	-	-	10	-	9
Lagmuli	0	-	-	0	-	1
Klofningur	3	-	-	3	3	9
Syrey	7	-	-	12	-	7
Syreyjarholmi	5	6	-	30	-	24
Selsker	1	-	-	1	1	0
Hafnarey	6	-	-	9	-	9
Hrolfsklettur	1	-	-	6	-	4
	36-41			125		119[5]

Notes:

(1) See Fig. 1.4, p. 13.

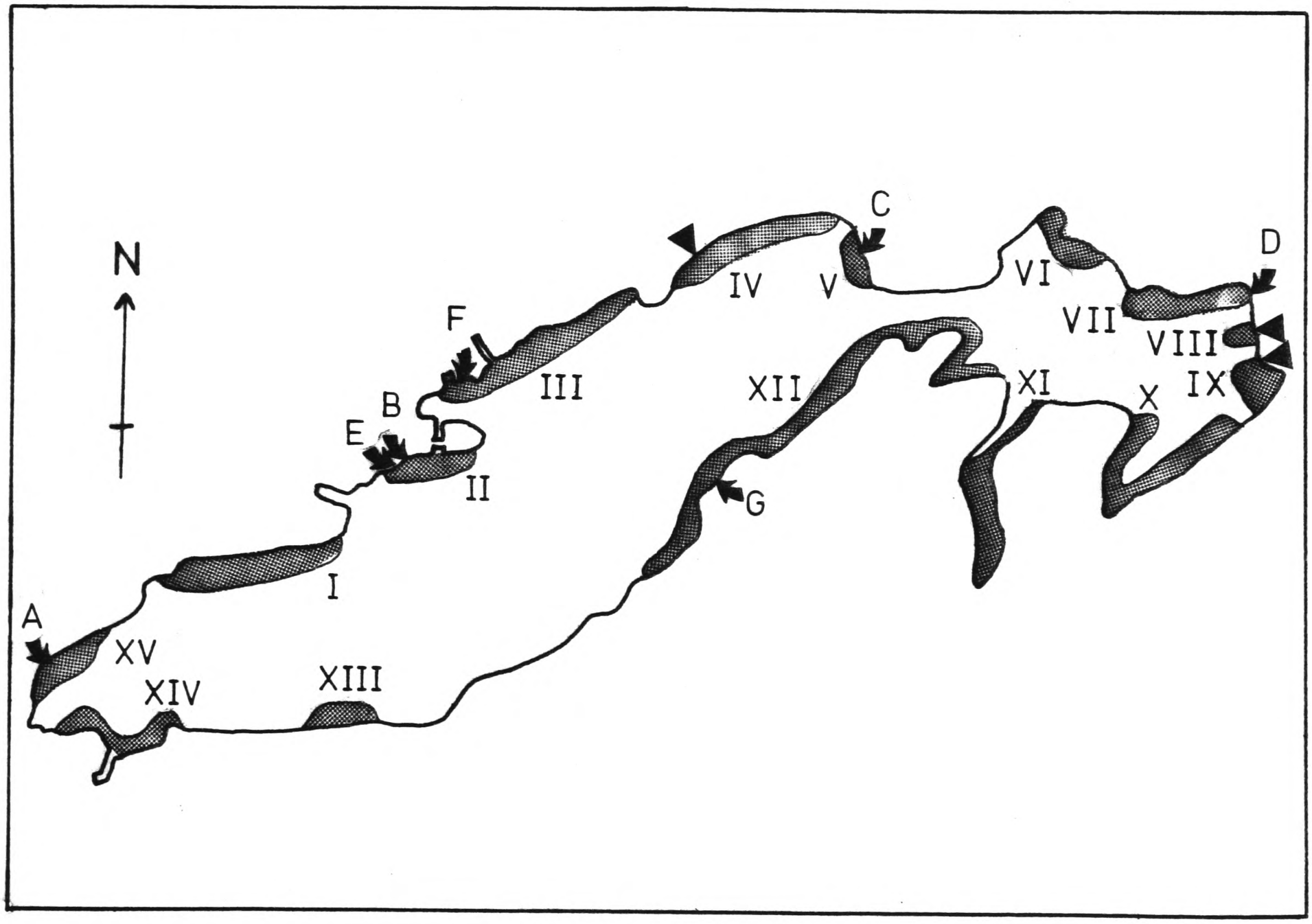
(2) J. Bogason, pers. comm.

(3) H. Gudmundsson, pers. comm.

(4) 6 pairs in 1942; 0 in 1945.

(5) The apparent small decline in 1977 was probably not genuine. There may even have been an increase. A combination of high tides and heavy winds in early June and again in early July, washed many eggs and chicks away. This was especially apparent in many areas situated directly facing the prevailing wind direction on these occasions.

Fig. 2.2. The location of nest-sites used by Black Guillemots on Flatey during the 1940's, 1955-1965, and 1966-1967, indicated by arrows and triangles.



Notes: (1) Sites A-D were used during 1940's, 1955-1965, sites A, C, and D in 1967, but site E in 1966 and 1967. Sites G and F were used in 1967.

(2) The shaded areas show the extent of the nesting areas as defined during the present study. The Roman numerals are the nesting area numbers.

same pair. Site E was still in use during 1974-1977, and was labelled no. 28 in the numbering system used during the present study. Eggs at this site were always laid among the very earliest in the population, perhaps indicating the oldest and most experienced pair was involved (cf. Chapter 5).

Six breeding pairs were on Flatey in 1967. They occupied the 3 old sites still usable (sites A, C, and D), the "new" site E, and two other (F and G). It is noticeable that these pairs did not nest together in the same area, but were scattered as solitary pairs over much of the island. All the sites used during 1940 to 1967 were located within the boundaries of the present nesting areas.

Fig. 2.3 gives the numbers and their distribution according to nesting area of Black Guillemot pairs during 1975 to 1977. An accurate nest count is also available for one area in 1974, nesting area IX, at which there were 33 nests, compared with 36, 36, and 35 in 1975-1977, respectively.

One nesting area (IV) contained far more nests than any other on the island, or about a third of the total population. This area was a boulder scree on the island's north side, where Flatey rises to its highest point (16 m a.s.l.). As most other islands in the Breidafjordur, Flatey slopes towards the south. Most of the habitat available for Black Guillemots - boulder screes, stony outcrops, and cliff crevices - is thus on the island's north side, and here the majority (ca 85%) of the pairs nested. Also most (ca 70%) of the population nested on the eastern half of the island, outside the human settlement (see Fig. 1.4, p.13). This distribution was largely influenced by the availability of suitable nesting habitats rather than humans, among whom Black Guillemots nested happily if not disturbed intentionally.

Nest-site availability

The continued recruitment of new breeders into a breeding population is obviously dependent on the availability of nest-sites, if there are no other limitations. Hence the

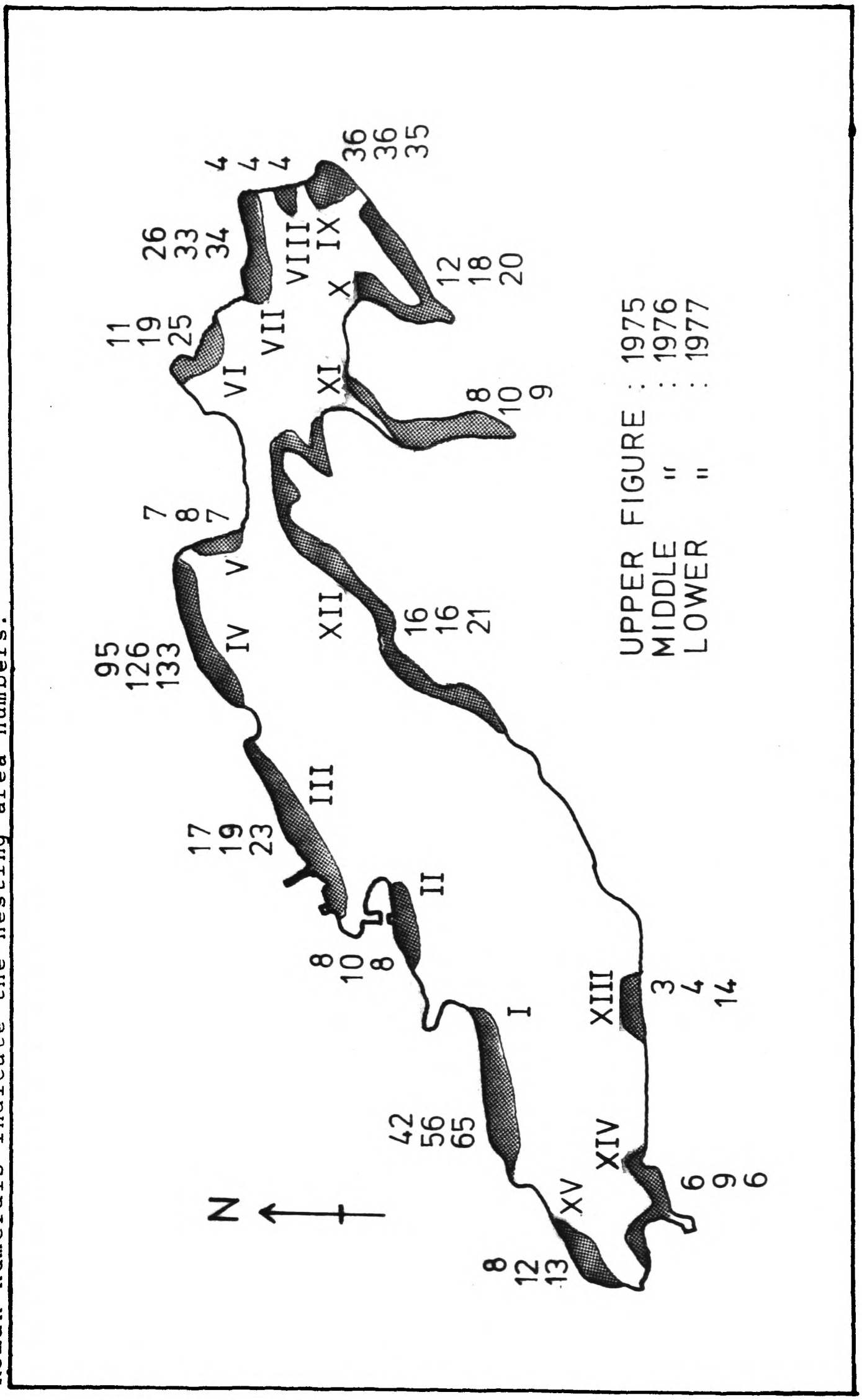


Fig. 2.3. Numbers and distribution of Black Guillemot nest-sites used during 1975-1977. Roman numerals indicate the nesting area numbers.

greater the number of potential nest-sites available, the larger could the breeding population become.

The increase in numbers of breeding pairs on Flatey was very much greater than in the surrounding islands. Flatey is the biggest of these islands (see Fig. 1.4, p.13), so judging by size alone, it is not surprising that the increase was greatest there. Yet it is difficult to tell where Black Guillemots could potentially nest, and my data on numbers of pairs per island (cf. Fig. 1.4, p.13 and Tab. 2.I, p. 22) clearly indicate that its size alone did not determine the availability of nest-sites. Topography must also be an important determinant of the "carrying capacity" of an island. Disregarding the size differences between islands, the finer details of topography varied between islands, hence presumably the numbers of potential nest-sites. In view of both size and topography Flatey has by far the greatest number of potential nest-sites for Black Guillemots, at least in my judgement, and is therefore able to hold a much larger breeding population than the other islands.

Similar differences in carrying capacity appeared to exist between different parts of Flatey. Visually to me these differences were rather obvious, and presumably were important in governing the amount of increase in numbers of breeders taking place between years, but this differed markedly, as shown in Tab. 2.II. Between 1975 and 1976 two (out of three) areas which showed no increase, seemed to me the least likely nesting areas to have vacant nest-sites. In this respect it must be remembered that, although the numbers of suitable sites is the upper limit to numbers of breeders, the distribution of the sites, and hence the density of breeders, could be important. The pattern of nest-site occupancy by established breeders may change somewhat from year to year, hence also the potential for newcomers to settle. Cairns (1978) made a series of measurements of Black Guillemot nest-sites on islands in the St. Lawrence estuary, and from these determined the number of sites "which could conceivably be useable by Guillemots" (p. 61). He found that at high-density areas a greater proportion of

Tab. 2.II. Changes in numbers of pairs breeding within nesting areas between years.

Nesting area	Nos. 1975	Change 1975-76 Nos.	%	Nos. 1976	Change 1976-77 Nos.	%
I	42	14	33	56	9	16
II	8	2	25	10	-2	-20
III	17	2	12	19	4	21
IV	95	31	33	126	7	6
V	7	1	14	8	-1	-13
VI	11	8	73	19	6	32
VII	26	7	27	33	1	3
VIII	4	0	0	4	0	0
IX	36	0	0	36	-1	- 3
X	12	6	50	18	2	11
XI	8	2	25	10	-1	-10
XII	16	0	0	16	5	31
XIII	3	1	33	4	10	350
XIV	6	3	50	9	-3	-33
XV	8	4	50	12	1	8
	299	81	27	380	37	10

potential nest-sites was occupied. Presumably this is why density was high, but the question remains as to why occupancy varied. Density of breeders has been shown to be important in relation to breeding output of many seabird species (cf. Coulson & White 1960). One reason why density may differ is in how far the rate of colonization has proceeded towards the maximum carrying capacity of the area. Another possible answer is that new recruits into an area may be attracted to the high density area in proportionally greater numbers than to the low-density area, other factors such as breeding output being constant.

On Flatey the net number of additional breeders in 1977 over 1976 was much lower than that for 1976 over 1975. Thus the increase appeared to be slowing down. (This has been confirmed in later years). One area was clearly an anomaly, showing a big increase in occupied sites between 1976 and 1977 while little change took place between 1975 and 1976. The sites at this area are entirely in man-made stone dykes, which are hardly available on other parts of the island. The increase in this area constituted 27% of the total 1976-to-1977 increase for the whole island. The reason for this rather sudden increase in the use of "artificial" nest-sites, was perhaps that natural sites were preferred earlier. With the increase in the population and subsequent decrease in the availability of natural sites, the unoccupied artificial nest-sites may have become increasingly attractive to potential newcomers.

2.4 Discussion

Possible reasons for population changes

It is clear that the increase on Flatey can only have resulted from a massive immigration of birds from somewhere else. Between 1966 and 1977 the population increased on average 3-4 times between years. This cannot have resulted solely from the production of young by the resident population, especially keeping in mind that Black Guillemots do no mature until they are several years old. Later (Chapter 11) some calculations are presented to substantiate this

point further in quantitative terms.

In view of this immigration one can ask where these immigrants might have come from. It seems to me rather unlikely that the immigrants were birds from surrounding islands since simultaneuous, although much smaller, increases occurred there at the same time, at least in a part of Flateyjarhreppur, if not the whole. Unfortunately, no ringing results are available which could point to the areas of origin of these presumed immigrant birds. A limited number of Black Guillemots have been ringed on the islands of southern Breidafjordur but none of these have turned up close to Flatey.

I suggest that immigrants to Flatey came from outside the Flateyjarhreppur, particularly from the mainland of Iceland, or islands close to the mainland, towards north of Breidafjordur. It is hypothesized that predation and general disturbance by feral Mink (Mustela vison) at Black Guillemot breeding stations has driven young birds away from their natal areas to settle in islands sufficiently far away from the coast where there are no Mink. Effects of Mink on wildlife (and poultry at times) are well known from Iceland (Gudmundsson 1952a, Thompson 1962, Gardarsson 1975, Elkington 1977), as from Sweden (Gerell 1972), and Norway (Folkestad 1978). Olsson (1974) documented the gradual decline of the Black Guillemot population in the Swedish archipelago over a period of 25 years. He considered Mink the main cause, noting for instance that breeding success of Black Guillemots was high on individual islands until these were reached by Mink. Anderson & Rosenlund (1973) reported a decline in the Black Guillemot population at Bohuslän (Sweden), Mink being partly responsible.

The most common nesting habitat of Black Guillemots in Iceland overlaps extensively with a favoured habitat of Mink, talus slopes along the coast. In such situations were two of the formerly largest Black Guillemot aggregations in Iceland, that at Ogur (Löppenthin 1938) and Ennishöfdi (F. Gudmundsson, pers. comm.), of some 250-300 pairs each. Both these are nearly deserted now, Mink being the most likely cause of their desertion.

The history of introduction, the establishment of a feral population, and subsequent spread of Mink throughout Iceland, as well as general biology, has been treated in Skírnisson & Petersen (1980). It is shown there that Mink have been increasing and spreading to all parts of the country up till now, reaching the most distant parts of Iceland at the middle of the 1970's, some 35-40 years after a feral population first became established in SW. Iceland.

A sizeable population of Mink had not become established on mainland areas towards north of Breidafjordur bay until about the mid-1960's (see Einarsson 1958-1978). I postulate that Mink had to become fairly common before beginning to have adverse effects on Black Guillemots. Hence it seems that as Mink became well established on the mainland they may have led to Black Guillemots starting to increase in numbers on Flatey in the latter half of the 1960's.

Important though Mink appear to have been in disturbing Black Guillemots away from their mainland haunts, this explanation alone is not sufficient to explain the observed pattern of increase in Black Guillemot numbers on Flatey. Another introduced mammalian predator, the Brown Rat (Rattus norvegicus) also appears to have been partly responsible. Interestingly enough, rats seem to have been the reason for the decline during the 1930's in Black Guillemot numbers, described earlier.

Rats were first seen on Flatey in the early years of the 19th century but were exterminated 7 years later (Sivertsen 1840). By 1897 rats had colonized Flatey again (S. Gunnlaugsson, pers. comm.). Hörring (unpubl. diary) noted that rats and House Mice (Mus musculus) were very common on Flatey in 1908. During the 1930's rats were very common but confined almost solely to the settlement area. When the island started becoming depopulated, rats started spreading to other parts of the island. During 1955-1965 rats did not seem to be as common as in the 1940's but still found all over the island. It was not until winter 1969/70 that real efforts were made to eliminate rats with poisoned bait. Large quantities were distributed, also the following winter.

Since February 1971 no rats have been seen on Flatey and same goes for House Mice.

It seems that rats were having effects on Black Guillemots, keeping down their numbers by eating eggs and perhaps chicks. It may be recalled that a claim was made that the biggest increase from one year to the next may have taken place in 1971, in February of which year the last rats and mice were exterminated. Rats have been reported having effect on seabirds elsewhere (Parslow 1973, Cramp, Bourne & Saunders 1974, Imber 1978).

There is seemingly, however, an inconsistency in this interpretation. As noted earlier there were large numbers of Black Guillemots early this century co-existing with high rat numbers. Contemporary reports indicate that rats were more or less confined at that time to the settlement area, living mainly on scraps and remains from fish which were common on drying racks. That practice mostly vanished when people started moving away from the island, and simultaneously rats started spreading further afield, as mentioned earlier. It therefore is concluded that rats, having an abundant food supply around human habitation, did not harass Black Guillemots as much as they appear to have done later.

It is possible to invoke food as a potential reason for the increase in the Black Guillemot population on Flatey, but there is little supporting evidence. There are no indications that food supply for Black Guillemots has become more favourable in the past two decades. However, there is very little data on this problem and therefore food may conceivably have increased undetected. If one tries to find indirect evidence through other seabird species in the area, there is very little supporting evidence for apparent large-scale changes in populations which can be linked to the food supply. Kittiwakes and Fulmars are increasing in the Flatey general area (Petersen 1979 and pers. obs.), but since this is a part of more widespread phenomenon (Fisher 1950, Nelson 1980: 190-191) their increase cannot per se be used as an argument. If anything Puffins have increased in numbers (H. Gudmundsson, pers. comm.) but this probably

represents a return to their former population level after exploitation lessened. The same can be argued for the Shag which is increasing rapidly (Gardarsson 1979). The Cormorant has apparently not changed very much in numbers over the past decades (Gardarsson 1979). Cormorants are benthic feeders like Black Guillemots and prey on much the same species, albeit normally bigger individuals (pers. obs.).

Chapter 3: Seasonal attendance at nesting area, and some features of the social structure of a Black Guillemot population.

3.1 Introduction

The seasonal pattern of attendance at breeding stations is very complex among alcids. This becomes particularly clear when censusing of populations is attempted (cf. O'Connor 1967, Birkhead & Ashcroft 1975, Harris 1976a). Besides variations due to a fluctuating environment, the situation is made more complex by the different status of birds in the population, in respect of age, deferment of maturity, and the proportion breeding.

Philopatry is a general feature among seabirds (Ashmole 1971: 270), especially the established breeders which may return year after year to the same breeding area, often to lay their eggs at precisely the same spot as in previous years. Outside the breeding season young birds tend to disperse more than the mature birds (Birkhead 1974, Lloyd 1974). Young birds appear in general to be less philopatric to their natal area than breeders (e.g., Nelson 1980: 128-129). They may breed elsewhere from their natal area, others within the general area but at varying distance from the exact spot where they were raised. Before reaching maturity young birds may spend one or more summers away from their natal area to which they may later return to breed when mature.

In this chapter I look at various data to elucidate some of the social features of a Black Guillemot population and their movements according to age and season. The main aims were to: (a) document the length of the period Black Guillemots regularly attended the nesting area during the year, (b) look at some aspects of the social structure of nesting area assemblies, in relation to age, sex, and breeding status, (c) quantify the fidelity of birds to their nesting area, nest-site, and mate, and (d) examine the movements of birds ringed on Flatey, based on reported recoveries. In a related exercise (Chapter 4) I deal more specifically with diurnal attendance and environmental fluctuations in the pre-laying period in

relation to the problem of censusing.

3.2 Materials and methods

Records were made of the time in late winter at which regular attendance at the nesting area began. These data and some other information from outside the breeding season, were collected by Mr. H. Gudmundsson of Flatey over a number of years.

Recoveries of birds ringed on Flatey include those reported up to 31.12. 1980 to the Museum of Natural History, Reykjavík.

Data relating to the proportion of non-breeders to breeders attending the nesting area, were collected only in the pre-laying period. The methods used are explained in more detail in Chapter 4.

Data on the occurrence of known-aged and colour-ringed birds were collected throughout the entire field season (April-August), whenever these birds were met with (sightings, re-traps). Information on non-breeders holding nest-sites, was obtained through observations from a hide.

Sex ratio of birds in the Flatey region in summer was studied by dissecting birds which were shot or drowned in Lumpsucker (Cyclopterus lumpus) fishing nets.

Nesting-area, nest-site, and mate fidelity were studied using ringed birds. An effort was made to record the sites at which these birds nested each year and to identify their mate. If a change was made from one year to the next I tried to infer the circumstances bringing about the changes.

3.3 Spring return to nesting area

Black Guillemots are seen off Flatey every winter (H. Gudmundsson, pers. comm., unpubl. Christmas counts at Museum of Natural History, Reykjavík). Usually they do not visit the immediate vicinity of nesting area in any numbers at that time of year. Single, or at most a few, birds may approach the island but their occurrence is irregular and behaviour normally passive, i.e. no sexual or agonistic displays. Their appearance in the immediate vicinity of

Flatey has normally been associated with good weather conditions. Such an association has also been noted in Fulmars to their breeding cliffs in Iceland (Gudmundsson 1952b).

Whether these winter birds off Flatey originated from the island, is unknown. Black Guillemots are common breeding birds of the inner parts of Breidafjordur bay (pers. obs.) which, being shallow and weakly saline, frequently get frozen over in winter. Hence these winter birds may come from these inner parts as well as Flatey, or even from further afield. The waters west of Flatey, which is at the edge of the Breidafjordur archipelago, never freeze in winter, and in this area Black Guillemots are always found in numbers throughout winter.

The behaviour of Black Guillemots in the pre-laying period contrasts markedly with that in winter. The start of mass occurrences below nesting areas with approaching spring, is usually very conspicuous. The levels of communal activities are very high and prominent behaviour patterns are exhibited, accompanied by the Black Guillemot's characteristic high-pitched calls. In accordance with this change in behaviour, I have defined the pre-laying period as the time from when Black Guillemots are first seen in numbers below the nesting area in late winter until egg-laying begins, in the third week of May (Chapter 5).

The first mass occurrences of Black Guillemots at Flatey were observed in late March/early April in years prior to the present study. In 1976 the first raft of attending birds was seen on 11 March, but on 7 March in 1977, or 9-10 weeks prior to start of egg-laying in the population. Black Guillemots seem to have been unusually early in 1976 and 1977 compared with earlier years. Weather does not seem to have been the cause, as the first three months of 1976 were very unfavourable (Vedurstofa Islands 1976); hence arrival should have been delayed rather than enhanced. In 1977 the weather was unusually good during January to March (Vedurstofa Islands 1977). It is also possible that the first rafts of attending birds were overlooked earlier when the population of Black Guillemots breeding on Flatey was smaller (cf. Chapter 2). With increasing population size there may also have been greater competition for nest-sites, leading to gradually earlier

arrivals. Such an effect was suggested in Kittiwakes (Coulson & Wooller 1976). Common Guillemots in Britain tend to return very early to their colonies (October/November), suggesting a strong selection pressure to return early, perhaps as a consequence of competition for breeding space (Birkhead 1976a: 149).

From the first day of raft formation Black Guillemots were normally seen every day below their nesting areas in large numbers. This is quite unlike the pattern of attendance by Puffins, Common Guillemots, and Razorbills which show a cyclic pattern with 4-7 days between peak numbers (Corkhill 1971, Lloyd 1973, 1976: 22-26, Ashcroft 1976: 204-211, Birkhead 1976a:154-155). In Black Guillemots the pattern of high numbers nearly every day could be disrupted by bad weather, as happened for instance in 1977. There was a cold spell with frequent rains from 12-18 April during which no Black Guillemots came to the nesting areas. Regular attendance was resumed on the 19th, immediately after the weather had improved. There were also day-to-day fluctuations in numbers of birds attending the nesting areas due to other environmental factors, e.g. tides, wind, and temperature (Chapter 4).

3.4 Status of attending birds

Proportions of non-breeders and breeders

There was a distinct surplus of birds attending nesting area over those which eventually came to breed in the area. This information is derived from counts of attending birds in the pre-laying period (Chapter 4) by subtracting the numbers of breeders as found through nest counts later in the breeding season (Chapter 2). Unfortunately, non-breeding Black Guillemots did not congregate into separate flocks at nesting area like, for instance, Common Guillemots at "club" areas (Birkhead & Hudson 1977). Non-breeding birds mingled freely with the breeders, both on land and on the sea. The size of the non-breeding segment could not therefore be estimated directly, except for yearlings which were identifiable by their speckled wing patch (verified by ringing).

The numbers of yearlings were always low in the pre-laying

period, 3.1% (1975), 2.4% (1976), and 1.1% (1977) of the total numbers of birds, being averages for many evening counts at the time of maximum attendance. Breeders accounted for 82.5%, 92.2%, and 86.4% of the attending birds in 1975, 1976, and 1977, respectively. By subtraction non-breeders 2 years and older represented 14.4%, 5.4% and 12.5%, respectively, and could include both mature and immature birds.

The seasonal occurrence of non-breeders

Non-breeding 1- and 2-year old birds, as identified through colour-ringed individuals, were present at nesting areas from long before the beginning of laying. These were thus birds which had been raised on Flatey. Yearlings were seen as early as 22 April, or a month before egg-laying. During late April to June, even into July, yearlings were in active moult, whereas nearly all older birds had already acquired full summer plumage by late April.

From recoveries of birds ringed as chicks on Flatey it is known that some immature Black Guillemots stayed hundreds of kilometers away from their natal area in the breeding season (May-August). The extreme record was a yearling, recovered 370 km (at sea) from Flatey (on 23 May). Most of the birds recovered in summer, had been drowned in Lumpsucker (Cyclopterus lumpus) fishing nets. This fishery is active mainly during April to July. Fig. 3.1 shows all the ringing recoveries which have been made in the breeding season, and their distribution. Of the birds ringed in the Flatey area and recovered in summer there were striking differences between birds of different age-classes in whether they were recovered close to or away from the Flatey area. This is shown in Fig. 3.2. Birds which were recovered away from Flatey were 1-3 years of age. As detailed later (Chapter 11) some birds bred for the first time when 3 years old, although the majority probably not until 4 years of age. Birds four years and older, as well as those ringed as adults were recovered only in the Flatey area. There was a significant difference between 1- and 2-year old birds on the one hand, and 4, 5, 6 year olds + adults in their distribution on re-

Fig. 3.1. The distribution of Black Guillemots, ringed during 1973-1979, recovered during the breeding season (May-August) and reported to the Museum of Natural History up to 31.12.1980. 30. August was taken as the dividing line between years. The figures indicate the month of recovery, the symbols age on recovery as indicated on the figure.

● = 1st year
○ = 2nd year
✶ = 3rd year
✡ = 4th year
■ = 5th year
□ = 6th year
▼ = Adults

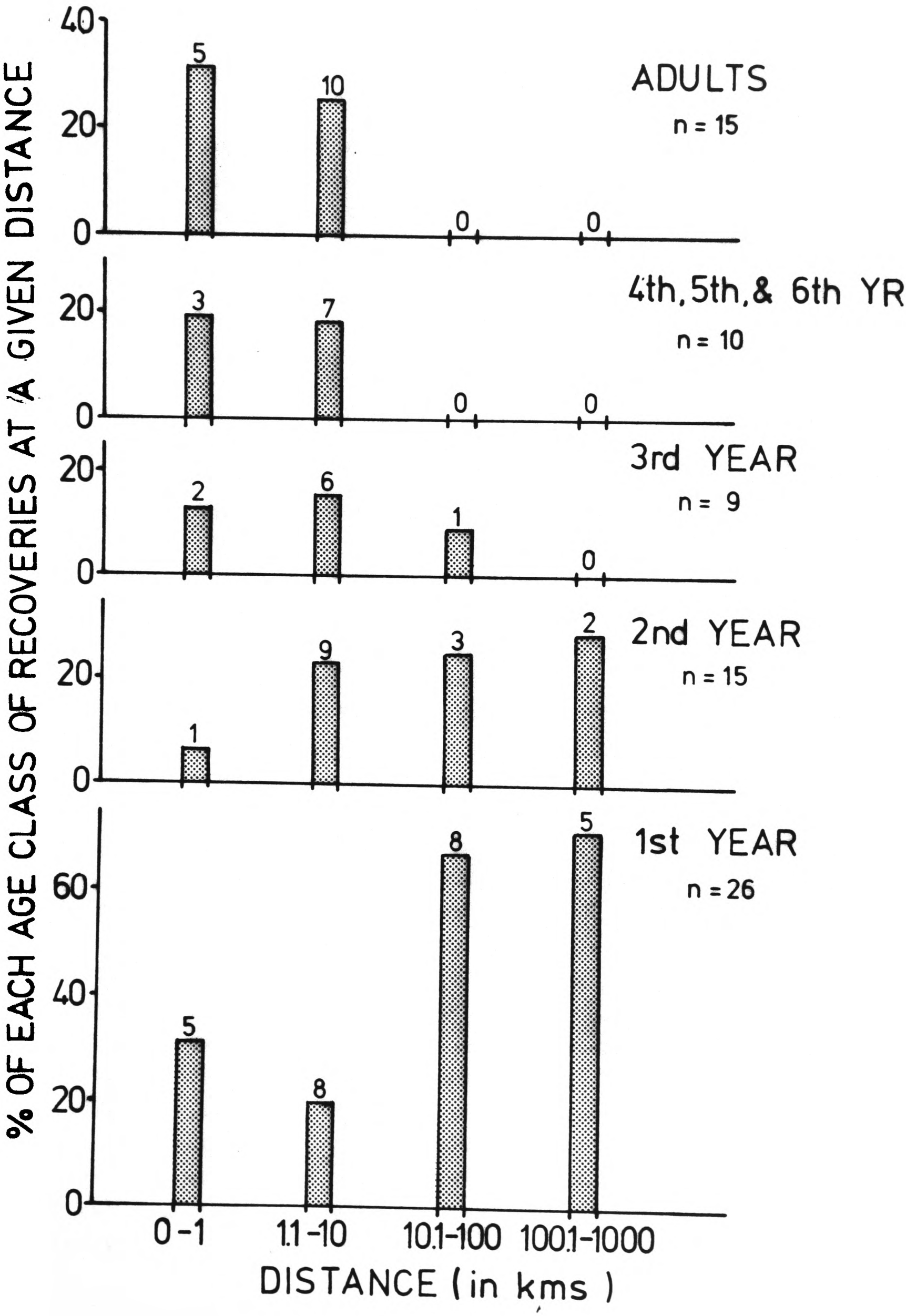
FLATEY

5 KM.

40 KM.

Fig. 3.2. Distance zones from Flatey at which Black Guillemots, ringed there, were later recovered in the breeding season (May-August). The numbers of birds recovered at each zone and at a given age, are presented above each column.

Note: (1) No account was taken of the different probability the birds had to reach a given age, but birds ringed as adults would have had the same probability as yearlings.


% OF EACH AGE CLASS OF RECOVERIES AT A GIVEN DISTANCE
ADULTS
n = 15
5
10
0
0
4th, 5th, & 6th YR
n = 10
3
7
0
0
3rd YEAR
n = 9
2
6
1
0
2nd YEAR
n = 15
1
9
3
2
1st YEAR
n = 26
5
8
8
5
0 -1
1.1 -10
10.1-100
100.1-1000
DISTANCE (in kms)

covery (P=0.00003; Fisher Exact Test). There was some indication that more yearlings were recovered away from the island than 2-year old birds (50% versus 33%) but the difference was not significant (P=0.15; Fisher Exact Test). These observations indicate that as maturity was approached Black Guillemots native to Flatey were more likely to be in the vicinity of the island than away from it.

I did not quantify by counting birds at nesting areas, the proportions of breeders and non-breeders in the egg and nestling periods mainly because of technical difficulties, i.e. the proportion of breeders hidden on nests was unknown. The non-breeding group, primarily made up of 1- and 2-year old birds but also some 3-year olds (which is the year when first recorded breeding, see Chapter 11) were certainly seen attending nesting areas.

Preston (1968) stated that there were long-term seasonal changes in the numbers of non-breeding Black Guillemots at their breeding station on Kent Island (New Brunswick), and that "there was continual decrease in the number of birds throughout...the summer months", with "the largest numbers of individuals...generally recorded early in the year, just prior to the beginning of laying" (p. 18). The same appeared to be the case in the Flatey population, as shown in Tab. 3.I, which shows that the percentage of non-breeders declined steadily as the season progressed.

Although yearlings and 2-year old birds were sighted as early as a month before the start of egg-laying, there were indications that many birds of these ages, native to Flatey and presumably returning after wintering elsewhere, did not return until the egg- or nestling periods (June-July), as significantly more birds were recovered away from Flatey in April-May than in June-July. This is shown in Tab. 3.II. Although these age groups were treated together there were indications that a greater proportion of 2-year old birds than 1-year olds returned to the natal area during any season. This is borne out by 81% (9/11) of 2-year olds, recovered in June-July, were found close to Flatey whereas only 67% (12/18) of the yearlings recovered at same time were found close to Flatey.

Tab. 3.I. Proportions of breeders and non-breeders (of ages 2 years +), drowned in Lumpsucker (Cyclopterus lumpus) fishing nets, with progressing season. Combined data for 1976 and 1977.

Time of season	Total n	Breeders(1)	Non-breeders	%non-breeders
1.-15.5.	4	2	2	50
16.-31.5.	18	14	4	22
1.-15.6.	22	18	4	18
16.-30.6.	9	8	1	11
1.-15.7.	13	12	1	8

Note: (1) The distinction between breeders and non-breeders was made by examination of the gonads and measurements of their size, and by examining for the absence or presence of Bursa Fabricii (cf. Petersen 1976a).

Tab. 3.II. Numbers of Black Guillemot chicks ringed on Flatey, recovered in their first and second year early or late in the summer, away from or in the Flatey region.

	Nos. of birds recovered:	
	in Flatey region[1]	away from Flatey
Early (April-May)	1(10%)	9(90%)
Late (June-July)	21(72%)	8(28%)
		P=0.003[2]

Notes: (1) This is an area of about 7 km radius around Flatey
(2) Fisher Exact Test
(3) One bird could not be assigned to either period

The data, presented in Tab. 3.III, show that significantly greater number of yearlings from June-July were ringed, thus known to be natal to Flatey, than from April-May.

The results from these two last analyses are interpreted to mean that as summer proceeded more and more immature birds returned to the natal area, and a greater number of two-year old birds than yearlings. These results are clearly in apparent contradiction to the earlier results that there was a gradual decline in non-breeders as the season progressed, but there is a likely explanation for this. Early in the season the non-breeders close to Flatey were predominantly from some other breeding localities, and moved away as the season progressed. The decline in non-breeders can only indicate that, since there is also a movement of birds to the island, there are more birds moving away than returning. This is not surprising, as non-breeders from elsewhere, being potentially from many breeding stations, could easily outnumber the birds native to Flatey. This is especially likely since the Flatey population has been increasing very rapidly (Chapter 2). Hence the immature population native to Flatey would not be in proportion to the breeding population, being the breeding output of up to some years previously.

Non-breeding nest-site holders

At one part of nesting area IV on Flatey an effort was made to discover all pairs which were holding nest-sites but not breeding. This was only done in 1977 since by that year, the last study year, the greatest number of birds was ringed. Besides those ringed as adults, potentially there could be birds aged 1-4 which had been ringed as chicks.

Four non-breeding pairs held sites in the study area, which was about 50x50 m, besides 20 breeding pairs. Thus 17% of the site-holders were non-breeders. Moreover there were 10 unused sites in the area from previous years.

Two of the eight non-breeders were 2 years old, ringed as chicks in 1975. A third bird, which was ringed as an adult in 1975 and had lost its mate from the year before, was paired to one of the 2-year old birds. These observations

Tab. 3.III. A comparison of the proportions of ringed and unringed Black Guillemot yearlings, drowned in Lumpsucker fishing nets off Flatey. Data from 1976 and 1977 combined.

	Nos. of yearlings that were:[1][2]	
	Ringed	Unringed
Early (1. May-7. June)	1(11%)	8(89%)
Late (8. June-15. July)	6(67%)	3(33%)

P =0.024[3]

Notes: (1) Only birds which could be identified by plumage. Several birds, found as skeletons in the nets (eaten by amphipods), were omitted.

(2) Only yearlings considered here since 2-year old birds (which were included in Tab. 3.II) could not be separated on plumage or by dissection, from still older birds if they happened to be unringed.

(3) Fisher Exact Test

were made in July and it was noted that both the known 2-year olds had very abraded (brownish) wing tips. None of the adults which were actively feeding chicks at this time, showed this condition, which therefore appeared to be useful for identifying 2-year old birds from older birds at this time of year. Of the 5 unringed non-breeders, three had such brownish wing tips and therefore possibly 2 years of age. Hence it is concluded that of the 8 non-breeders, 5 appeared to be 2 years old, one was an adult, and two were of unknown age, but most likely 3 years old.

Preston (1968: 28-29) noted the presence of site-holding pairs of Black Guillemots which did not lay eggs. He designated them as producing 0-egg clutches, on the reasoning that they were affecting the total reproductive output of the population. This is by no means so, unless it can be shown that these pairs were preventing other pairs from breeding, pairs which otherwise would have bred, and this was not shown in Preston's study.

3.5 Sex ratio

Published information for sex ratio in seabird species gives a highly variable picture of sex ratio (cf. Belopol'skii 1957: 152-160), most likely because of various biasses in the samples. My data on sex ratio were subdivided according to method of sampling. The basic data were for birds which had been shot on the feeding grounds or at nesting areas in the evening. I have no reason to believe that these results give anything other than an unbiassed picture of sex ratio. In collecting the sample, any bird which was met with was shot until a sufficient sample was obtained. The Black Guillemot is a monomorphic species so there should be no collection bias towards either sex, although it is always possible that behaviour of males and females differed somehow so to make one sex more liable to collection than the other (see later). The sample of shot birds included 22 (51%) females and 21 (49%) males so there was no deviation from a 1:1 ratio.

I also looked at sex ratio in birds in adult plumage

(2 years +) which had become drowned in fishing nets. When examined on a time basis, rather unexpected results showed up. Tab. 3.IV shows that birds from the latter part of the fishing season (latter half of June/first half of July) were nearly all males. These results clearly show the dangers of biassed samples. The reason for this unequal ratio is unknown but perhaps had to do with brooding of the chicks. To explain, the peak of hatching in the Flatey Black Guillemot population centred around the end of June/beginning of July. Chicks are brooded for 3-6 days (Rol'nik 1948, Kartaschew 1960: 73, Rol'nik & Kaftanovskii in Shilov 1968: 141). The peak of brooding coincided approximately with dominance of males in the nets. My scanty information on the share of the sexes in feeding of young indicated that one of the pair did most of the fishing in the first week of the nestling period. Of 19 trips at 5 nest-sites 84% of the trips were made by one member of the pair, but it is unknown which, and if always the same one, because of difficulties in sexing live Black Guillemots. The most obvious interpretation of the observations in Tab. 3.IV, is that females brooded the young while males did most of the feeding for young. But the reverse appears to be the case as R. Broad (pers. comm.) found, using ringed birds, that males did most of the brooding. Clearly many more data are required here, also on the length of the brooding period and development of thermoregulation.

It could be questioned whether the observed change in sex ratio had anything to do with breeders as birds caught in nests could potentially be breeders or non-breeders in adult plumage. Of the 66 birds in the sample 12 (18%) were considered non-breeders. This was found by dissection, non-breeders having inactive gonads and a Bursa Fabricii (cf. Stresemann 1934: 174-175). These non-breeders were from different stages of the breeding season, and cannot have resulted in the above changes in sex ratio.

3.6 Area fidelity

Fidelity to nesting area was very strongly developed in

Tab. 3.IV. Adult Black Guillemots, drowned in fishing nets, according to sex and time of season. N=66.

	Time of season (in fortnightly intervals):					
	1.-15.5.	16.-31.5.	1.-15.6.	16.-30.6.	1.-15.7.	Total
♀	2	10	10	1	0	23
♂	2	8	12	8	13	43

$X_1^2 = 11.4$, $P < 0.001$ (2)

Notes: (1) Data from 1976 and 1977 were lumped since on prior examination these were identical for both years separately

(2) Chi-squared test with Yates' correction.

the Black Guillemot, and is probably characteristic of the species, at least under undisturbed conditions such as on Flatey. A known breeder was only once seen attending another nesting area than its own, in spite of the very short distances between different nesting areas on the island. This was moreover after its breeding duties were over, and the area attended was next to the bird's natal nesting area, a distance of some 150 meters. The bird was also sheltering in lee from heavy seas. In contrast on hundreds of occasions were birds, ringed as breeding adults, sighted or retrapped at their former nesting area. I also made numerous excursions to islands around Flatey, but never saw Flatey breeders attending nesting areas there.

In contrast to adults, I frequently saw non-breeding 1- and 2-year old birds, natal to Flatey, attending nesting areas in other islands, and vice versa birds from elsewhere at Flatey. This could be verified since birds from other islands were ringed with different colour combinations from birds ringed on Flatey.

Two birds ringed as chicks and thus of known age, were later recorded nesting. Both were found within the respective nesting areas where they had been raised. This indicates a great fidelity to natal area once breeding is started. Yet in Denmark, a bird was recorded breeding 50 km away from where it had been ringed as a chick five years earlier (Andersen-Harild 1969). Birds natal to Flatey and starting nesting for the first time, may have settled down in surrounding islands, but no systematic attempt was made to look at this. Although 1- and 2-year old birds were seen attending nesting areas on other islands, they are likely to have been immatures. I certainly never saw any indications that they were breeding.

3.7 Nest-site tenacity

The occupancy of nest-site can be expressed in two ways, in relation to individual birds or individual nest-sites. The first describes the fidelity of birds to their former nest-site, and included only birds which survived for at least

two successive years. The latter is a measure of the turnover of birds occupying individual sites, and includes also birds which died in the intervening period between two breeding seasons.

Data relating to adults

A number of breeders (colour-ringed or with steel ring only) was recorded occupying the same nest-site in successive years. Thus 42 adults were found at the same site two consecutive years, 8 for 3 years, and 13 for 4 years, which was the longest possible occupancy within the study period. Storer (1952) recorded 23 Black Guillemots at same site up to 4 years in succession. Asbirk (1979b) recorded 70 birds at same site in 2 consecutive years, 15 for 3 years, 3 for 4 years, and 1 for 5 years. Similarly, Drent (1965) recorded 6 Pigeon Guillemots for 2 consecutive years at same site, 7 for at least 3 years, and 6 at least 4 years.

Nest-site tenacity was worked out quantitatively using only colour-ringed adults, as no systematic effort was made to follow adults marked only with steel rings. From a total of 91 "bird-years", 9 site-changes (10%) were made. Different individuals were involved in 7 of these changes, but one bird moved sites twice. These changes took place between seasons, not within season, though this was recorded once. That bird was ringed at site 1974.100, which it kept in 1975, moving the year after to 1976.99, changing sites that same summer to 1976.409, a site it held in 1977.

If site change did take place the distance moved was always short. The mean straight-line distance was 12.4 m (n=10, range=2.1-28.4 m). The new site was always within the boundaries of the same nesting area as the old site.

Preston (1968: 24) stated that destruction of the former nest-site and disappearance of the previous mate were typically associated with nest-site changes. Drent (1965) considered unusable sites the most important factor initiating nest-site changes in Pigeon Guillemots. Asbirk (1979b) considered nest destruction, change of mate, and interspecific competition the main causes for site changes in Danish Black Guillemots.

Very few nest-sites on Flatey became unusable from year to year, as the data in Tab. 3.V shows, only 2-4%. At the same time 16-23% of the sites used in one year were not used the next year despite still being usable, although a few were temporarily obstructed by seaweed. Of the 10 cases in which ringed adults were known to change sites, seven of the old sites were re-occupied by other Black Guillemots in later years, hence clearly acceptable for nesting. The remaining three sites had not become "physically" unusable, merely not used, whatever the reason.

Although some of the changes in nest-sites were associated with destruction of the previous site, factors such as death of mate, divorce, sex-related site tenacity, and breeding failure were also likely to be important.

Success in breeding was very important in governing if birds used the same nest-site the year after. The data relate to colour-ringed adults and to avoid any bias due to unequal weighing of results, only one bird was considered per nest although at some sites both members of the pair were colour-ringed. Tab. 3.VI shows that if birds bred successfully one year there was a greater probability that they used the same nest-site the next year than if they had been unsuccessful. Three explanations are plausible of these results: (a) divorce more common among unsuccessful birds, leading to at least one pair member moving to a new site, (b) unsuccessful pairs more likely to move as pairs to another site, and (c) unsuccessful birds more likely to die, and the surviving member of the pair moving to a new site. Various prerequisites had to be fulfilled in order to investigate each of these points independently. My sample sizes were therefore very low and mostly insignificant. The only significant result showed that change of site was more likely to take place after death of the partner, as shown in Tab. 3.VII. Fuller coverage of these points will be given in the discussion.

Data relating to sites

An analogous analysis to that in Tab. 3.VI, was carried out relating sites to breeding success in the previous season, irrespective of the birds occupying the sites. Former breeders

Tab. 3.V. Numbers of nest-sites which were not used from one year to the next.

Yr. x	Nos. of sites known to be usable in yr. x	Nos. of these not used in yr. x + 1, but judged still usable (1)	Nos. which had become destroyed by yr. x + 1
1974	138	32 (23%)	6 (4%)
1975	328	51 (16%)	7 (2%)
1976	429	77 (18%)	11 (3%)

Note: (1) At these sites no physical changes had taken place which could alter the suitability of the sites.

Tab. 3.VI. The difference in use of previous year's nest-site between successful and unsuccessful breeders, all of which were alive in both years.

	Same site used in yr. x + 1	Same site not used in yr. x + 1
Successful in yr. x	52(84%)	2(22%)
Unsuccessful in yr. x	10(16%)	7(78%)

$X_1^2 = 13.19$, $P < 0.001$ (1)

Note: (1) Chi-squared tes with Yates' correction

Tab. 3.VII. Maintenance of nest-site in relation to death of former partner.

	Site maintained	Site not maintained
Both members of pair alive	18	0
One member died in intervening period	1	3

$P = 0.003$ (1)

Note: (1) Fisher Exact Test

may have stayed at their former site, divorced and moved, both moved, one or both died, etc. in the intervening period. The results given in Tab. 3.VIII, were similar to those in Tab. 3.VI; if breeding was unsuccessful one year, there was a greater probability that the site was not used the following year than if breeding was successful. The explanations are obviously the same as before, with one exception though. The previous set of data related to colour-ringed birds which were alive in both years, hence only these birds' mates may or may not have died. In the data on sites, both pair members could have died. Given the same mortality for both the sexes, the figure for successful birds not using same site again (45%) was double that for sites not used again by previously successful birds (22%), as would be expected.

Taking into account birds which died inbetween years, it is possible to calculate the occupancy of individual nest--sites from data on colour-ringed birds. Of 113 "nest-site-years" 22 (19%) of the birds died, 9 (8%) moved sites, and 82 (73%) maintained same site. Thus every year about 3/4th of the nest-sites contained the same birds as the year before. This means there would be a complete turn-over every 19 years. But this varies according to the outcome of breeding. Using data in Tab. 3.VIII 92% (439/476) of the sites in which breeding was successful, were used again the year after, only 65% (87/133) of the sites where breeding was unsuccessful.

3.8 Pair-bond maintenance and mate fidelity

A rather small sample of pairs was available for analysis of pair-bond maintenance between years. Both pair members needed to be colour-ringed and the nest-site they occupied in two consecutive years also had to be known. The data included 16 pairs over 26 "pair-years". Besides birds paired for only one season, 2 were mated for at least 3 years, and 4 for four years. Of the 26 pair-years, 5 (19%) cases were recorded in which the pair-bond was not maintained, giving 81% pair-bond maintenance. Yet, this is not the true picture of mate fidelity since in 4 of the 5 pair-bond breakages the previous mate was known or presumed dead. The fifth case

Tab. 3.VIII. The effect of breeding success in one year on the subsequent use of the same site.

	Site used in yr. x + 1	Site not used in yr. x + 1 (but judged still usable)
Successful in yr. x	439 (84%)	37 (45%)
Unsuccessful in yr. x	87 (16%)	46 (55%)

$X_1^2 = 68.55$, $P<0.001$ (1)

Note: (1) Chi-squared test.

involved the only recorded divorce. True mate fidelity was therefore 95% (21/22). The divorce rate of 5% was similar to that of 7% found by Asbirk (1979b) in Danish Black Guillemots, but this was from even a smaller sample than mine. In Puffins Ashcroft (1976: 26) showed that 13.3% of the pairs changed mate between years, of which 5.0% were divorces. The former figure is directly comparable with mine of 19% for Black Guillemots.

3.9 Post-breeding departure and winter distribution

Adult Black Guillemots attended nesting areas for a much shorter period of time after fledging of the young than before laying in spring. During the post-fledging period there was a gradual decline in adult numbers. No counts were made to document this decline but the overall trend was obvious. Fledging of young peaked in the first days of August (Chapter 9), and by 20 August very few chicks were still in nests, with few adults attending nesting area. One extremely late chick was recorded on 28 August. It had only completed about half of its nestling period, and hence would not have fledged until about middle September.

The adults went into moult soon after fledging of their young, but continued to attend nesting areas for about a week, as indicated by observations on three colour-ringed birds. It seemed that breeders most often had stopped breeding duties before going into moult, but this may vary according to when the chicks fledge. One colour-ringed adult with a chick still in nest on 16 August, had started moulting.

Six of seven adult-plumaged birds (which could be breeders or non-breeders), collected on 26 July, had not commenced body moult but one bird had just started. Body moult starts earlier in Black Guillemots than wing moult (unpubl.). A month later, on 23 August, twelve adult-plumaged birds were in heavy body moult, 7 of these were also flightless, 3 still with the old wing feathers unmoulted, and 2 intermediate.

From the first week of August onwards I noticed moulted

body feathers on land at the nesting areas. The attending birds also began looking very tatty, with loose, displaced feathers. From 4 August I began seeing adults with greyish cheeks and chins, in the region where body moult first starts (unpubl.).

Adult-plumaged birds, starting their 3rd winter or more, kept away from the island after having stopped attending nesting areas. They may already have started to disperse by this time. In Kandalaksha Bay (White Sea) adult Black Guillemots move away from the nesting areas right after fledging of their young. They are not seen for 1-1½ month in which time moult takes place (Bianki 1967: 199). Adult-plumaged birds (and possibly yearlings) appear to congregate in small moult flocks at this time, as indicated by one observation on 26 August. On a short stretch of water about 25 km south of Flatey I saw 4 such flocks of about 25, 25, 20, and 30 birds, and these birds were completely flightless. Flocking was otherwise quite unusual among Black Guillemots apart the nesting area assemblies. On the feeding grounds in summer they were normally well spaced out.

Yearlings, starting their second year, appear to leave nesting areas and begin moult in mid-July, or somewhat earlier than older birds. One yearling, collected on 26 July, was 1-2 weeks advanced in body moult, at which time adult-plumaged birds had hardly commenced moult, as seen earlier. Another yearling, ringed as a chick in 1974 and collected on 23 August 1975, was much further advanced in moult than adults collected on the same day (see above). If this is the general rule it means that by their 2nd autumn moult, then a little more than 2 years old, the birds have worn their feathers for longer time (1-2 months) than older birds. Their wing feathers, just before moult, should therefore be more abraded than those of older birds. This fits in with what has been said earlier (see section 3.4).

Upon fledging young Black Guillemots were completely independent of their parents and they were still unable to fly. Fledglings were seen walking to the water on several occasions, all of the departures being made around midnight

and they vanished out to sea alone. During boat trips around Flatey many newly-fledged young were seen and none of them was accompanied by adult birds. Chicks from same nest also often fledge on separate days and the adults continue to feed the remaining chick (Chapter 9). Fledglings appeared to leave the vicinity of Flatey rather quickly as recoveries indicate; from 29 August (26 km away), 14 September (102 km), ca 20 September (65 km), 21 September (34 km), 26 September (102 km), October (105 km), 2 November (310 km), and 12 November (663 km). Considerable time was spent in late July-August 1977 searching for fledglings on the sea within a wide radius of Flatey, but unexpectedly few were seen. Three fledglings, which were caught, were all unringed as were a few others whose legs could be checked at close quarters. This was rather unexpected since about 80% of all chicks fledging from Flatey, by far the biggest breeding station in a wide area, were ringed and a great proportion of chicks in 16 neighbouring islands.

Assuming a similar growth rate of primary wing feathers after fledging as before, by extrapolation the primaries of fledglings should have reached adult length about ten days after fledging, i.e. when about 44 days old (cf. Chapter 9). This is slightly less than the 2 weeks estimated by Asbirk (1978a : 44). Several fledglings were seen taking off the water, albeit with difficulty. The earliest of these records is from 3 August. According to my observations of fledging dates in the Flatey population (Chapter 9) this bird would only have fledged an absolute maximum of 14 days previously.

Very little is known about the distribution of Icelandic Black Guillemots outside the breeding season (September-April). Existing knowledge up to the beginning of September 1977 has been reviewed earlier (Petersen 1977), when only 5 recoveries of Flatey-ringed birds had been reported from outside the breeding season, including two from Greenland. Now (up to end of 1980) 15 recoveries have been reported, four of them from Greenland. These were all birds ringed as chicks and recovered before their presumed attainment of maturity.

They were all recovered well away from Flatey, as shown in Fig. 3.3. Immature birds natal to Flatey appear to disperse out of the Breidafjordur bay rather quickly, at first mainly towards the southern fjords of the NW peninsula (Vestfirdir), and perhaps the southern parts of Breidafjordur, around the Snaefellsnes peninsula. Some birds later find their way around the NW peninsula to the Hunafloi bay of North Iceland or across to Greenland. In my earlier review it was hypothesized that a sizeable proportion of Icelandic Black Guillemots may visit Greenland in winter, which earlier was not considered likely as they were regarded so sedentary (see Timmermann 1949: 599, Gudmundsson 1953). With the additional recoveries since then, about a quarter of the recoveries come from Greenland, but this may apply only to immature birds.

No adults native to Flatey, whether ringed as chicks or adults, have been recovered outside the breeding season. Hence nothing is known of their winter distribution. One adult ringed on Sugandisey Island, southern Breidafjordur, was recovered 6 years later (on 4 October) in SW Iceland, a distance of 200 km by sea from where it bred. It is likely that most Flatey breeders stay in the Breidafjordur area in winter.

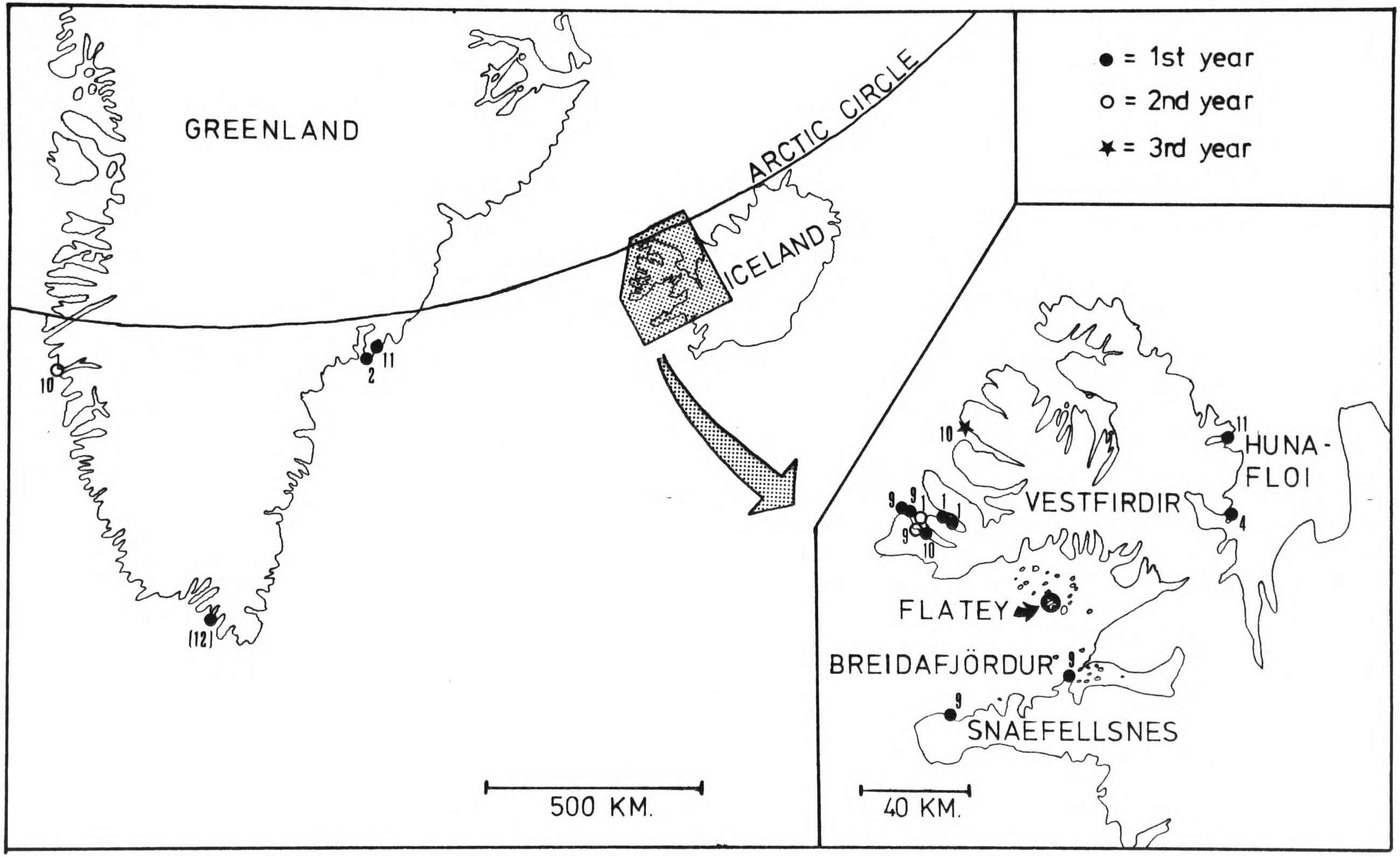
3.10 Discussion

The occurrence of non-breeders at nesting area

After migration or dispersal in winter adult Black Guillemots return to their breeding stations for the summer. So do many individuals which are not going to breed that season. If birds return to breeding stations at all, then age, degree of maturity, and breeding condition, may influence the timing of their return, the proportion of age classes returning, and the length of their stay at the breeding station (cf. in other auks, Lloyd 1976: 113-116, Ashcroft 1979).

The non-breeding population which accumulates at breeding stations together with the breeding segment, can be divided into three potential categories: (a) immature birds, incapable of breeding since they are not sexually mature, (b) non-breeding adults which may have bred before, perhaps

Fig. 3.3. Distribution of Black Guillemots, ringed on Flatey and recovered out of the breeding season (September-April). The figures indicate month of recovery and symbols the age on recovery. All the birds were ringed as chicks.


GREENLAND
ARCTIC CIRCLE
ICELAND
● = 1st year
o = 2nd year
★ = 3rd year
10
2
11
(12)
500 KM.
10
11
HUNA-
FLOI
VESTFIRDIR
4
FLATEY
BREIDAFJÖRDUR
9
SNAEFELLSNES
40 KM.

incapable of breeding in certain years, this category growing by an increasing number of failed breeders as the breeding season progresses, and (c) non-breeding adults which have never bred before. The last category in particular constitutes what is known as the "floater" population (sensu Manuwal 1974), i.e. birds capable of breeding if they had the opportunity. The existence of such a population seems to have been examined in only one alcid species, the Cassin's Auklet (Manuwal 1974), but most likely exists in most other auk and colony-nesting seabird species (cf. Petersen 1976a). Unfortunately floaters and other non-breeders (except yearlings) are not easily detected, as they look much the same as breeders.

There is a certain difficulty in doing an experiment like that by Manuwal (1974) who looked for a floater population by removing breeding pairs, and observing the subsequent re-settlement of the area by new breeders. The success of such an experiment could depend on when in the season it was performed. If done too late no birds may breed although they could pair and defend a nest-site. If done too early it is difficult to tell if the presumed floating birds were going to breed somewhere else, but simply preferred the artificially vacated sites because they were in some way more suitable. One reason why individual birds which would be categorized as floaters, may not breed one year, is if they pair with an immature bird. This is probably what happened in the case of the adult which was known to have bred before, later pairing with a known 2-year old bird.

The occurrence of immature Black Guillemots at nesting areas long before the start of egg-laying in the population is an unusual feature compared with Common Guillemots, Razorbills, and Puffins. In these species young, immature birds do not begin to arrive at the colonies until around the beginning of egg-laying, each year class arriving progressively earlier with increasing age (Myrberget 1962, Lloyd 1974, Birkhead & Hudson 1977, Ashcroft 1979). Furthermore, yearlings of these species do not normally visit the breeding colonies (Lloyd 1974, Petersen 1976a, Birkhead & Hudson 1977, Ashcroft 1979).

Although yearling Black Guillemots were seen as early as in the pre-laying period, it is interesting to note that more and more birds seemed to return as the breeding season progressed, as in the other alcid species cited above. This species difference is probably related to the earlier onset of maturity in Black Guillemots compared with the three other species (Chapter 11).

Winn (1950) on Kent Island (New Brunswick) recorded (on one occasion) in July, about 50% more Black Guillemots attending the nesting area than could be accounted for by the number of breeders. Preston (1968: 18), at same study locality, estimated that 45-50% of the birds present during the period of maximum numbers were non-breeders but of these yearlings were few. De Korte (1972) found 16 pairs and 10 unpaired birds in spring at one breeding station in Spitsbergen but only 9 nests on later visits. Extremes for the proportion of non-breeders would be 24% (10/42) and 57% (24/42) by the former figure assuming not all nests were found. Finally, Ramsay (1976) found non-breeders average 65.9% of all birds attending various Orkney breeding stations. This was in July-August, and presumably many nests in which eggs were destroyed before censusing took place, were not included. The percentage of non-breeders is therefore likely to have been somewhat lower, possibly around 50%. This is estimated by taking account of my study population where an average 21% of all breeding pairs completely lost their eggs or chicks each year.

Although various biasses are bound to be attached to these literature references, I think it is safe to conclude that the proportion of non-breeders at Flatey in the pre-laying period, was much lower than at these three other localities, where there are presumed long-established, stable populations, contrary to the situation on Flatey. There the proportion of non-breeders was 7.8-18.2%, compared to around 50% at the other localities.

In an expanding population as on Flatey, one would expect no constraints such as nest-site limitation to be operating, and birds to start breeding as soon as they were mature. That being the case, one would expect relatively fewer non-breeders

than in stable populations. There would also be fewer non-breeders since they are the products of previous years when the population was smaller. In view of this no serious attempt was made to examine if a "floating" population existed, since there were also many unoccupied nest-sites which had been used for breeding in earlier years. But in spite of this there may still be some competition for the "best" sites, since sites are likely to vary in quality.

Nest-site and mate fidelity

As was the case with Black Guillemots, other alcid species are highly philopatric, particularly the adults. For Puffins, Ashcroft (1976: 29-31) never recorded burrow-owners moving permanently to other colonies. They were most often seen in same subsection of their respective colonies. Lloyd (1976: 47) showed that 5% of Razorbills, ringed as adults and later retrapped, were found at colonies other than where they had been ringed. But only 0.6% of the birds retrapped at the study island (Skokholm) had been ringed somewhere else (Lloyd & Perrins 1977). On the other hand, Harris (1976b) recorded the rather unusual case of mass immigration of Puffins to Isle of May (Scotland) - birds which had been ringed as young somewhere else - and many of them bred there.

Pronounced nest-site fidelity is also the general rule among alcids, although this has but rarely been expressed quantitatively. Ashcroft (1976: 24) recorded about 95% site fidelity in Puffins, Birkhead (1977b) 95% in Common Guillemots. Site tenacity of 90% in Black Guillemots on Flatey is considerably higher than that of 68% recorded by Preston (1968: 24), that of 78% by Bianki (1967: 185), or 56% and 79% recorded by Asbirk (1979b). The relatively rarity of sites becoming completely unusable in my study, appears to be the reason why site tenacity was higher than in these other studies. This is likely to vary according to local conditions. In Denmark, for example, Asbirk (1979b) found 43% of all his nests were under fish-boxes and driftwood, objects which are likely to shift rather often.

The difference in site fidelity between successful and unsuccessful birds has three plausible explanations as mentioned

earlier. To examine if divorce was more common in unsuccessful breeders than successful ones, both members of a former pair had to be alive. Only one divorce was observed and that pair had been unsuccessful the year before, but two other unsuccessful pairs did not divorce. On the other hand, none of 16 successful pairs divorced. Hence from this scanty information it appears that divorce might be more likely in unsuccessful pairs than those that were successful.

Both pair members had to be alive in two consecutive years and mated to each other in both years, to examine whether birds were more likely to move to another site as a pair, following unsuccessful breeding the year before. Of 2 unsuccessful and 16 successful pairs, no such change took place. Thus it did not seem that this kind of movement took place.

The question whether unsuccessful birds were more likely to die, was examined by analyzing the survival of unsuccessful and successful birds. Of 79 successful birds 6 (8%) died in the intervening period between two breeding seasons, but none of 19 unsuccessful birds. Although these sample sizes were very low and not significant, proportionally more successful breeders died between years.

As argued earlier (see Tab. 3.VII, p. 55) if one member of a pair died, the surviving partner was more likely to change site than if the bird did not die. This was the only significant finding for movements related to unsuccessful and successful birds. One further point is worth raising in this respect , for which there are no data. The nest-site bond may be stronger in one sex than the other, and this could influence the rate of site-change upon death of partner.

Both site tenacity and pair-bond maintenance were lower in Black Guillemots than species like Puffins and Common Guillemots. Divorce as a reason for not keeping a site or a mate, did not seem to differ in frequency from that of those two species, as shown earlier. On the whole it is likely that Black Guillemots nest in a habitat which is more subject to changes than e.g. Puffins, Common Guillemots, and Razorbills. Black Guillemots would therefore have to find a new nest-site more often. But site and mate tenacity in Black Guillemots were also lower because of lower annual survival in that

species, 81-89% (Preston 1968: 24-26, Asbirk 1979b, Chapter 11), compared with 89-96% in Common Guillemots, Razorbills, and Puffins (Birkhead & Hudson 1977, Lloyd & Perrins 1977, Ashcroft 1979).

There are several options facing birds which are unsuccessful in any one year. As long as both members of the pair survived to the next year, should they nest at same site, divorce, move together to a new site, or divorce and move? These questions touch upon which is stronger, attachment to former nest-site or the pair-bond ? Of 5 unsuccessful pairs which survived to the following year, one divorced, while 4 did not and bred at same site again, and so did one member of the pair which divorced. Judging from these results, it rather seems that to a Black Guillemot it is more important to maintain former site than former mate. Preston's (1968: 31) results indicate that the average clutch size of females which changed site, increased following the change. If these birds changed mate at the same time, was not controlled for. Nevertheless, making change would be advantageous for the birds,if increased clutch size leads to increased chick production. If divorce is the crucial factor determining if a nest-site is maintained or not, one could say that successful pairs have no "reason" to divorce. On the other hand, mortality may be higher among successful pairs. This seems likely if one accepts that breeding is a strenuous, energy-draining process. Presumably this would have greater effects on successful breeders than unsuccessful ones, most of which were relieved from breeding duties in the incubation period, some even before the eggs had ever been incubated (Chapter 6). This fits in with Asbirk's (1979b) results that parents fledging no chicks had higher survival than those which fledged 1 or 2 chicks. Nonetheless separation of pairs following unsuccessful breeding was much more important as a reason for not maintaining former nest-site than any differential mortality of successful and unsuccessful breeders.

The question posed earlier can be approached by looking at the gain birds are likely to make in terms of breeding success upon separating and changing sites. Asbirk's (1979b) data fit my predictions very well. Birds which retained its

mate had an overall breeding success of 45%, whereas birds changing mates only 36%. On the other hand, birds which changed sites had breeding success of 43% while birds retaining same nest-site had 36% breeding success.

Chapter 4: Attendance of Black Guillemots at an Icelandic breeding station: The problem of censusing.

4.1 Introduction

Accurate censusing of auks is difficult to achieve (O'Connor 1967, Corkhill 1971, Lloyd 1973, 1975, Birkhead & Ashcroft 1975, Harris 1976a, Birkhead 1978), and Black Guillemots are no exception (Cramp, Bourne & Saunders 1974, Nettleship 1976, Cairns 1979). There are two main reasons for this: (a) Black Guillemots usually nest either sparsely, singly, a few in a place, or in loose aggregations, and (b) their nests are normally hidden so that nest counts are either impractical (involving a great deal of work) or may give biassed results.

In view of the difficulties in counting nests, as a compromise the birds attending breeding stations have to be counted in order to obtain estimates of population size. Counts of birds present various problems which can be summarized under two main headings: (1) Factors affecting accuracy of counts, and (2) problems related to interpretation of results.

Seabird breeding stations are attended by a variable number of non-breeding birds (cf. Chapter 3). Since most of these cannot be separated by plumage from the breeders, any bird counts will inevitably include non-breeders as well as breeders. Only yearlings can be separated by plumage from older birds. The difficulty therefore arises of how to obtain an estimate of the breeding segment of the population. Ramsay (1976) touched upon the problems involved, with regard to interpreting the results of "Operation Seafarer" in Britain (Cramp, Bourne & Saunders 1974).

Two main factors are likely to affect the accuracy of counts: (a) Environmental factors, and (b) the diurnal and seasonal rhythms of the birds. A third factor, topography, may also affect accuracy, but careful choice of limits to census areas can greatly reduce or eliminate any such effects.

Environmental factors are known to affect attendance of seabirds at their breeding stations but quantitative data have

only begun to emerge in the past decade (see Lloyd 1973, Dott 1974, 1975, Birkhead & Ashcroft 1975, Slater 1976). There are no quantitative data for Black Guillemots, nor Pigeon Guillemots, Cepphus columba, but Preston (1968: 10) made some general statements.

As in many other seabird species, there are pronounced diurnal and seasonal rhythms of attendance by Black Guillemots at their breeding stations. The present work was done in the pre-laying period when no birds were hidden in nest-sites making accurate counts easier. This stage of the season was also recommended as the best for censusing Black Guillemots by the Seabird Group (not dated), and Nettleship (1976), and for Pigeon Guillemots by Ainley & Lewis (1972). My data are therefore restricted to that period, and changes in attendance which occur at other times of the season, were not dealt with (but see Chapter 3).

The diurnal pattern of attendance by Black Guillemots was not described in detail until recently (Ramsay 1976, Asbirk 1979b, Cairns 1979) although the general pattern was known (e.g., de Korte 1972). Keith (1937) and Suomalainen (1939), independently it seems, were the first to comment on the regular diurnal rhythm by Black Guillemots at their breeding stations. Koskimies (1949) drew attention to the importance of time of day at which censusing had to be made, as did Blomberg & Kjellberg (1972). Bjarnov (1958) commented on the absence of Black Guillemots from their nesting stations in the afternoon. Detailed information also exists for the closely-related Pigeon Guillemot (Drent 1965, Ainley & Lewis 1972), in which the attendance pattern is essentially the same as that of Black Guillemots.

There are relatively few population estimates for Black Guillemots in the literature. Some of those are difficult to interpret, especially those based on counts of birds, since standardized methods have not been employed. Cairns (1979) presented correction factors for Black Guillemots in order to relate counts of birds to size of the breeding population. In most cases little can be said (in quantitative terms) about past changes in Black Guillemot populations either locally or

over wider geographical areas. Exceptions exist for very small populations, particularly where nest-counts have been employed.

The original aim of the present exercise, was to develop a method, by which a reliable estimate of true numbers could be obtained and to relate numbers attending a breeding station to the number of breeding pairs. In the course of the study, the diurnal rhythm of attendance was described in detail, and effects of environmental factors on numbers evaluated.

4.2 Methods

Counts

Counts were made of all Black Guillemots on sea and land in the vicinity of one of their nesting areas (nesting area I) on Flatey. Nesting area I was chosen for study since this was the most discrete nesting area on the island, minimizing any potential effects from intermingling of birds from other nesting areas on the island or nearby islands. The area also held a reasonable number of breeding pairs.

Nearly always it was immediately clear if birds were attending the area or not. The few potentially doubtful cases included birds some distance offshore in the afternoon when no birds were in the immediate vicinity of the nesting area. These birds were excluded since they were invariably feeding, whereas birds attending nesting areas were not.

Yearlings, distinguished by their mottled wing patch (verified by ringing), were counted separately from birds in adult plumage (2 years and older). I am primarily dealing with the latter group of birds which included potential breeders and non-breeders.

At certain critical times, i.e. when establishing the arrival (or departure) of first birds to (from) the nesting area, and when detecting times of peak attendance, counts were usually made every 20 minutes. At the beginning of the study counts were generally made more frequently when the basic pattern of the diurnal cycle was being established. Counts were made on one occasion in other parts of the island to look at synchrony in attendance.

The data were collected in the following periods: 21.4.-23.5. 1975, 18.4.-25.5. 1976, and 17.4.-13.5. 1977. The study

area had 42 breeding pairs in 1975, 56 in 1976, and 65 in 1977 (see Chapter 2). The numbers of nesting pairs were found by careful nest searches throughout the whole breeding season (May-August).

Weather data were obtained from Flatey weather station, taken at 0900, 1500, and 2100 hours G.M.T. Weather data at other times (wind force, sea condition), were collected by myself using the same meteorological standards. Tide levels were obtained from nautical tables (Sjomaelingar Islands 1975, 1976, 1977).

Analysis of environmental factors

Effects of nine factors on numbers of adult-plumaged birds attending, were tested using multiple regression technique. Factors included in the program, were:

y- Log ratio of the number of birds at 1950 hours to the number later involved in breeding. I used this ratio to be able to combine the data for all three years into the program at the same time, as number of breeders varied between years.

x1- Date. 17 April=1, 1 May=15, 11 May=25, etc.

x2- Air temperature (in C°), as mean at 0900, 1500, and 2100.

x3- Wind force (on Beaufort scale) as mean at 0900, 1500, 1900, and 2100.

x4- Total precipitation (in mm) from 0900 to 0900 the next day.

x5- Wind direction. Dummy variables, using lee=1, on shore=2. Prevailing wind direction beween 0900 and 2100 was entered. The nesting area faces NNW. On shore wind (to the nesting area) was taken as the half circle from WSW to N to ENE, lee the other half.

x6- Sea condition, as mean at 0900, 1500, 1700, 1900, and 2100, estimated in steps of 0 to 9, 0 being absolutely flat, calm sea.

x7- Length of low-tide period. This is the length of time from extreme low tide, halfway towards extreme high tide that same day, or any part there of within the period 0900-1950. There could be either one or two such periods within this time span, depending on the state of the tidal cycle. If there were two periods, only the latter was entered.

The times, 0900 and 1950, were chosen so as to correspond approximately to 50% of the birds having left and returned to nesting area, respectively.

x8- Height of extreme high tide. Introduced to allow for varying height (in m) of tidal cycles on different days. If two high tides a day within the 0900-1950 time period, height of the second tide was used.

x9- Length of time from last low-tide period. Taken as the time from middle of the chosen low-tide period till 1950. Introduced to account for the ever-changing occurrence of the tidal cycle during the day.

4.3 Results

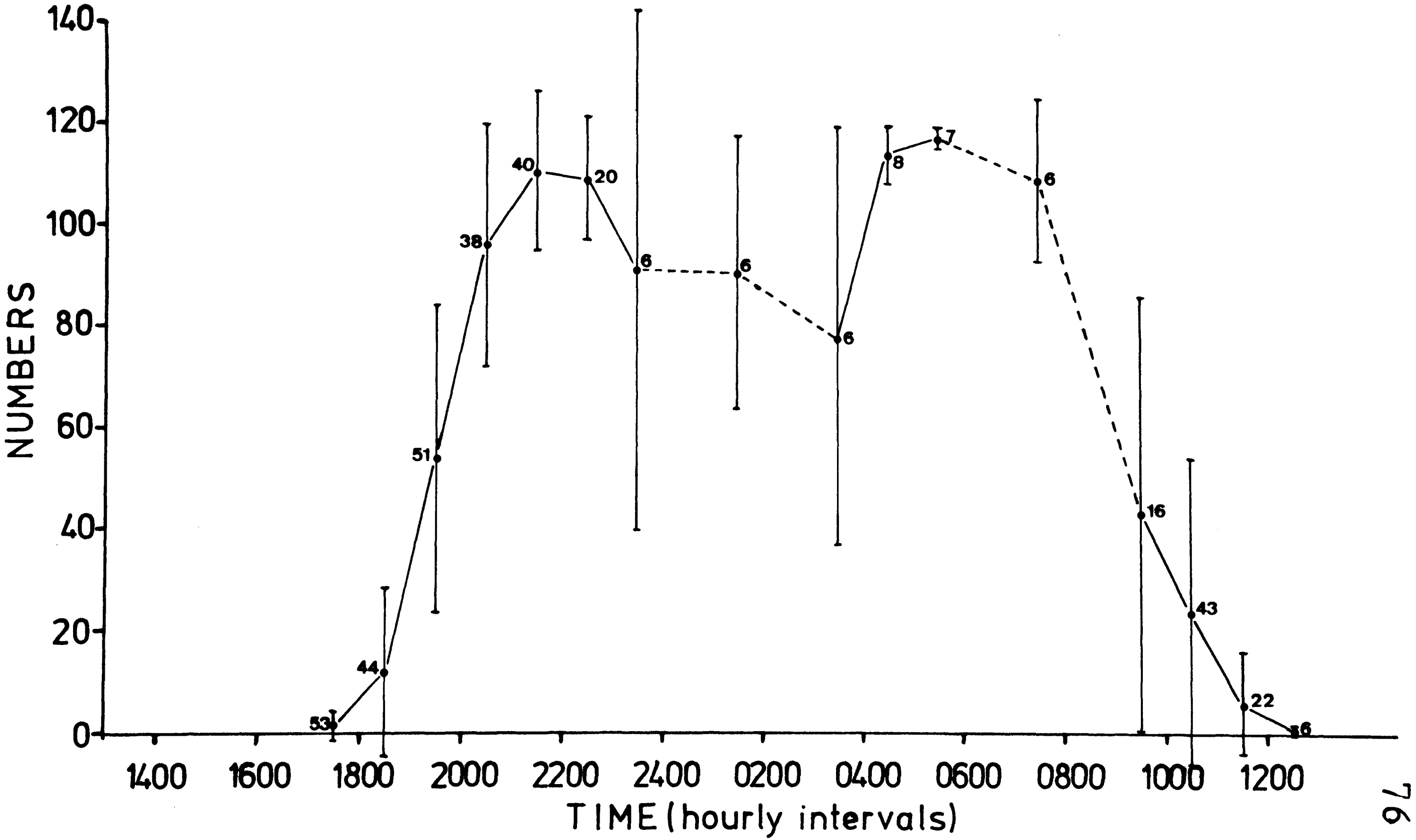
Diurnal rhythm of attendance

Fig. 4.1 shows the diurnal cycle in attendance by adult-plumaged Black Guillemots at Flatey. There were two pronounced peaks during the 24 hour cycle, one in the evening, one in early morning. The peak numbers of birds were a little greater in the morning but not significantly (t_{45}= 1.18, n.s.). The evening peak was much shorter than the morning one. Pronounced peaks of attendance in morning and evening have also been shown for Black Guillemots in other regions (Ramsay 1976, Asbirk 1979b, Cairns 1979) and Pigeon Guillemots (Ainley & Lewis 1972). Yet, at one of his study areas Cairns (1979) found a more or less continuous decline from morning to evening, and so did Drent (1965) in Pigeon Guillemots.

The figure shows very well the considerable variations which occurred over short time intervals, indicated for instance by the rapid build-up in numbers in the evening. Also, as shown by the standard deviations, there were considerable variation within the same hour from day to day. This was not the result of difficulties in making accurate counts. Numbers were low, considering numbers at colonies of some other alcids, and it was very easy to make an accurate count on any one occasion. Various factors, dealt with later, were responsible for these daily fluctuations.

Especially great variations occurred during the darkest period of the 24 hour cycle, approximately 2300 to 0400. These

Fig. 4.1. The diurnal rhythm of attendance of adult-plumaged Black Guillemots at one nesting area on Flatey. Based on data from 1976 only, from 18 April till 27 May. Numbers were grouped in hourly blocks, except 0001-0400 and 0601-0900, which are three hours each. Sample size and one standard deviation are given at each sample hour.


NUMBERS
140
120
100
80
60
40
20
0
1400
1600
1800
2000
2200
2400
0200
0400
0600
0800
1000
1200
TIME (hourly intervals)
53
44
51
38
40
20
6
6
6
8
7
6
16
43
22
6

variations were mainly due to marked differences in attendance in late April/early May compared with late May. At this time of year the light regime is rapidly changing in Iceland; sunset was about 2½ hours later on 27 May (1976) than 22 April (Saemundsson 1976). Early in the season most birds left the vicinity of the nesting area during total darkness. There is much more information - mainly qualitative - available for this early period than given in the figure. Data-collecting was limited by the difficulty of obtaining accurate counts because of poor visibility. After about 10 May it never became pitch dark at these same hours, by which time Black Guillemots started staying below the nesting area throughout the night. But there was always a slight decline in numbers from the preceding evening's peak, perhaps marking the departure of non-breeders.

Attendance was synchronized in different parts of the island. Fig. 4.2 shows how numbers built up in different sections of the island on one evening. The rate of increase was proportional to numbers nesting at each of the four regions considered. Note the apparent discrepancy at 2140 hours in one of the regions. This was due to flowing tides having covered a much greater area than earlier in the evening, resulting in the attending group of birds becoming more spread out and beyond the limits of the censusing area. This is a good example of how carefully the limits of the censusing area have to be chosen.

The attendance pattern of yearlings was irregular, and numbers usually low on any one occasion. In 1976 during counts on 372 occasions (those given in Fig. 4.1), 5-10 yearlings were present on 14 counts, 1-4 on 125 counts, and none on 233 occasions. On average 0.9 yearlings were present at each count. Their pattern of attendance did not show any clear consistency, although high numbers were usually associated with high numbers of older birds. Yearling numbers did not build up and decline like that of older birds. This was partly because yearlings were coming and going, and partly because there were but few individuals at all times. Yearlings were usually not present when older birds were absent from the nesting area.

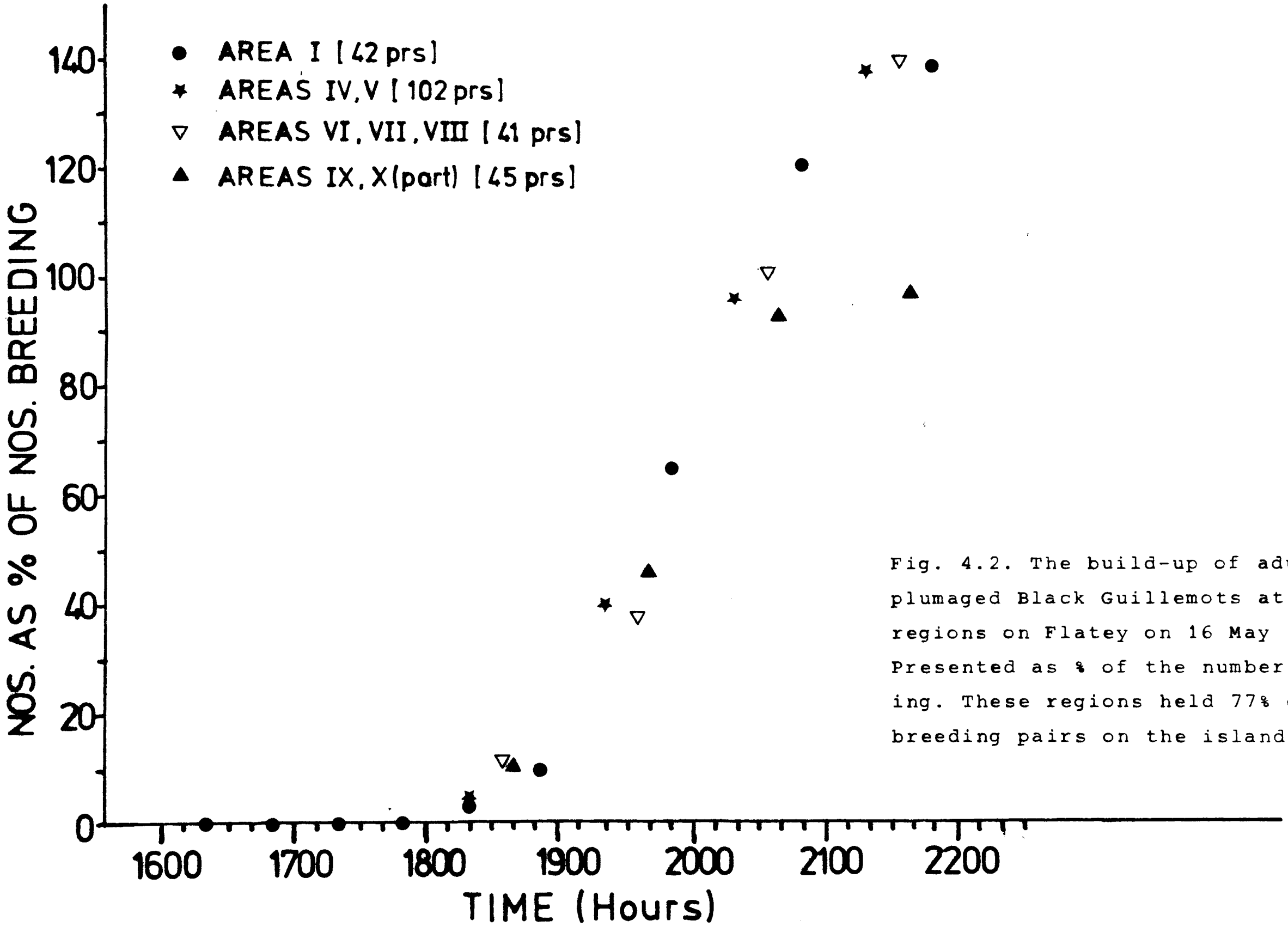


Fig. 4.2. The build-up of adult--plumaged Black Guillemots at 4 regions on Flatey on 16 May 1975. Presented as % of the numbers breeding. These regions held 77% of all breeding pairs on the island.

The effects of environmental factors on attendance

Results from the multiple regression analysis are given in Tab. 4.I. The significant variables explained 50% of the variation in numbers attending. To test for significance of added variables, those that were significant on their own, were added according to descending F-value.

Wind force (x1) was the most important variable. Wind force and sea condition (x6) are obviously highly intercorrelated, as the latter did not explain significantly more of the variation in bird numbers although wind can also have direct effects on the birds. This could cause birds to seek more sheltered places away from the censusing area. This was observed but only became obvious in exceptionally rough weather, rarely recorded during the observation periods. For the same reason I believe, wind direction (x5) did not emerge significantly in the analysis, as these movements to somewhere else were principally all-or-nothing, not gradual.

Air temperature (x2) contributed significantly to the effect on numbers of birds attending. The colder it was, the fewer birds arrived at the nesting area. This could have been a date effect, as Preston (1968: 18) stated that a gradual decline took place in numbers from just before egg-laying through the summer. No such date effect (x1) was detected in the present analysis.

It was not surprising that tides should have affected numbers attending the nesting area, in a species which obtains all its food in the shallow littoral zone around Flatey (Chapter 10). Preston (1968: 10) suggested that tides influenced the activities of Black Guillemots on Kent Island. Test-runs of the multiple regression program using "flow" and "ebb" as dummy variables, indicated that these tidal conditions were very important in affecting Black Guillemot numbers. An attempt was made to discover more precisely how tides affected bird numbers, hence independent variables x7, x8, and x9. When flow-tides occurred at 1950 hours, there was a long period of low-tide hours in the afternoon and a short one, if any, in the morning. Numbers attending were negatively correlated with length of the low-tide period

Tab. 4.I. Results from multiple regression analysis of the effects of environmental factors on Black Guillemot numbers attending one nesting area. The number of independent variables = 9 (x1 - x9). Number of observations = 54.

Independant variable	F-value	% explained	Significance
x1 Date	1.6	3.0	n.s.
x2 Air temperature	5.1	8.9	<0.05
x3 Wind force	16.2	23.8	<0.001
x4 Precipitation	3.5	6.4	n.s.
x5 Wind direction	2.9	5.2	n.s.
x6 Sea condition	10.8	17.1	<0.01
x7 Length of low-tide period	10.8	17.2	<0.01
x8 Height of highest tide	1.3	2.4	n.s.
x9 Time from last low-tide period	9.7	15.7	<0.01

	F-value	% explained	Significance of added variable
x3 + x7	19.4	43.2	<0.001
x3 + x7 + x6	13.7	45.1	n.s.
x3 + x7 + x6 + x9	10.1	45.2	n.s.
x3 + x7 + x6 + x9 + x2	9.6	50.0	<0.001

Regression equation: $Y = 0.03(x2) - 0.18(x3) + 0.11\ (x6) - 9.31^{-4}(x7) - 4.8^{-5}(x9) + 0.87$

(x7) in the afternoon. This suggests that low numbers were associated with a long period of low tide in the hours prior to attendance of nesting area. Length of time since that low-tide period (x9), being negatively correlated, suggested that the greater the length of the low-tide period, the smaller were the numbers of birds attending in the evening that day. Height of tide (x8) did not have significant effects, which is not surprising. The range of tide levels included in the program was small (2.87- 4.63 m), probably because the Flatey region is very extensive and shallow.

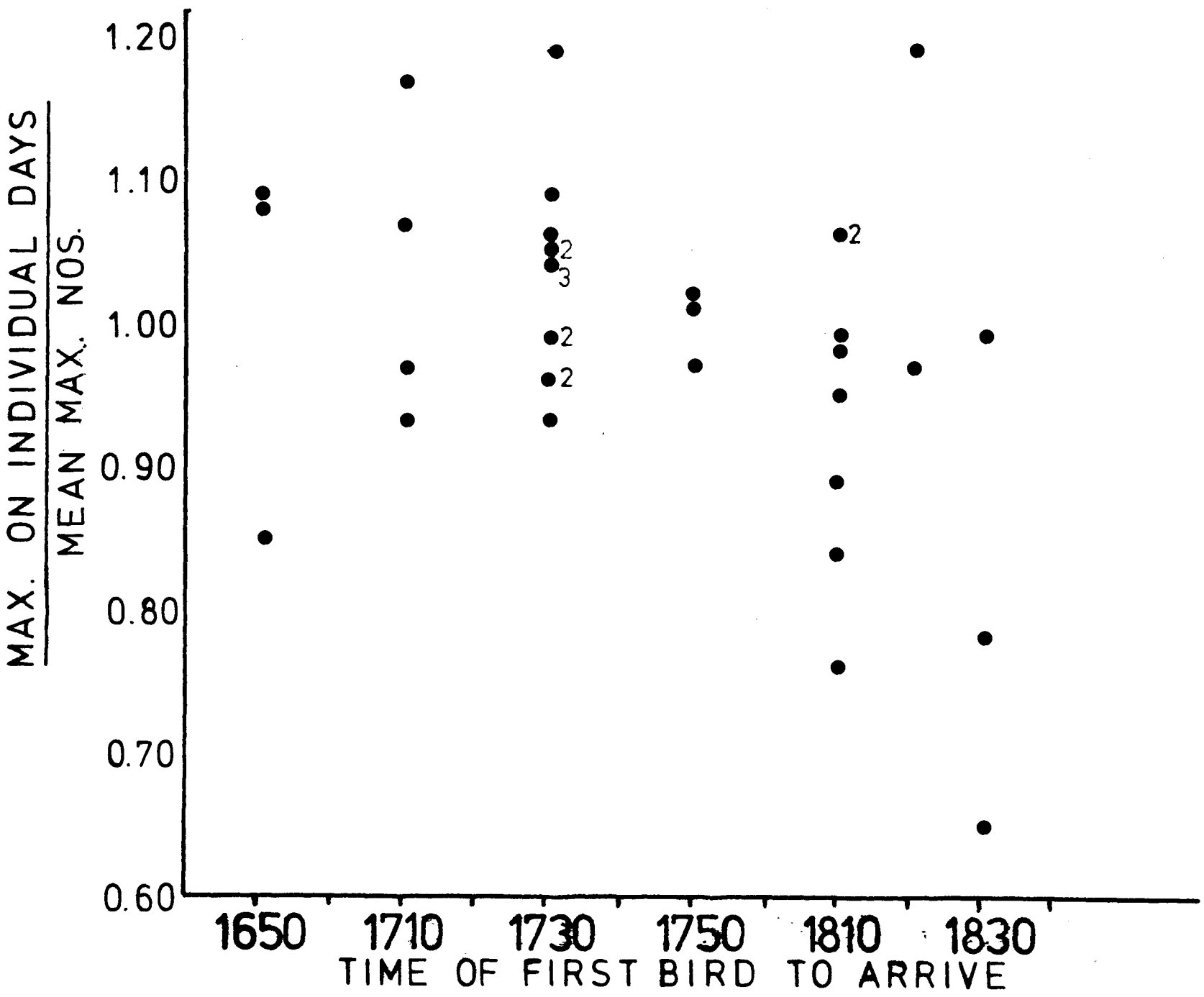
Suggestions for censusing

Fig. 4.1 showed clearly that times for censusing Black Guillemots have to be chosen with care. The afternoon was obviously unsuitable since no birds were seen at the nesting area between about 1200 and 1700 hours. It is self-evident that any censuses have to be carried out during times of peak attendance, in the evening or in the morning. I chose to concentrate on the evening period since the morning one occurred over longer period of time, with presumably corresponding greater variations. Peak numbers were maintained for a longer period in the morning by Black Guillemots also in the Orkneys (see Ramsay's (1976) Fig. 1: 35).

There were basically two types of variations involved, in the numbers of birds which arrived, and the time at which peak attendance was attained. The numbers of birds that were going to arrive at the nesting area on any one evening, could be predicated by the time at which the very first birds arrived from the feeding grounds. The earlier birds started returning to the nesting area, the greater the maximum numbers later that evening, but only up to a certain time, namely 1730 hours as shown in Fig. 4.3. The later after 1730 the first birds arrived the fewer were going to arrive that evening.

The number of birds present at 1950 hours reflected maximum numbers which arrived that evening (r_{26}=0.42, $P<0.05$), but there was no relationship between the time maximum numbers were attained and maximum numbers attending that evening (r_{23}= 0.23, n.s.). It was found that the timing of peak attendance

Fig. 4.3. Arrival times of first Black Guillemots to nesting area in relation to the numbers of birds eventually arriving that evening at the time of peak attendance. Data for 1975-1977 combined.



Notes: (1) Ratio of maximum number of birds attending on individual days to mean maximum numbers for all days, was used so as to combine information for all 3 years

(2) Regression was calculated for 1730 onwards: $r_{29} = -0.46$, $P<0.01$; $y = -2.315^{-2}x + 1.151$.

varied from 2000 to 2330 hours on different evenings. Presumably this would not apply without corrections to other latitudes.

With this information in mind the census results were analyzed with the eventual aim of finding how many counts were needed for reliable estimates of numbers to be made. Two analytical procedures were considered: (a) counts which aimed to find the maximum, or peak, numbers of birds attending, and (b) spot (or individual) counts made any time within the span of maximum numbers. Counts at no fixed time during the evening period of attendance were considered impractical, as the variation on different evenings would be so great as to make the results meaningless.

Tab. 4.II summarizes the variation in maximum numbers of birds on various days, and a comparison is made with the numbers of birds later involved with breeding at the nesting area. Each year 3-17% more birds attended the nesting area, on average, than accounted for by numbers of breeders. On the days of greatest attendance, numbers attending were 23-39% more than the numbers of breeders. Conversely, when attendance was lowest 6-33% fewer birds were present than accounted for by breeders. Hence the extreme variation between different daily maxima was 34-84%, depending on the year. Within the 95% confidence limits the annual variation was only 9-12%.

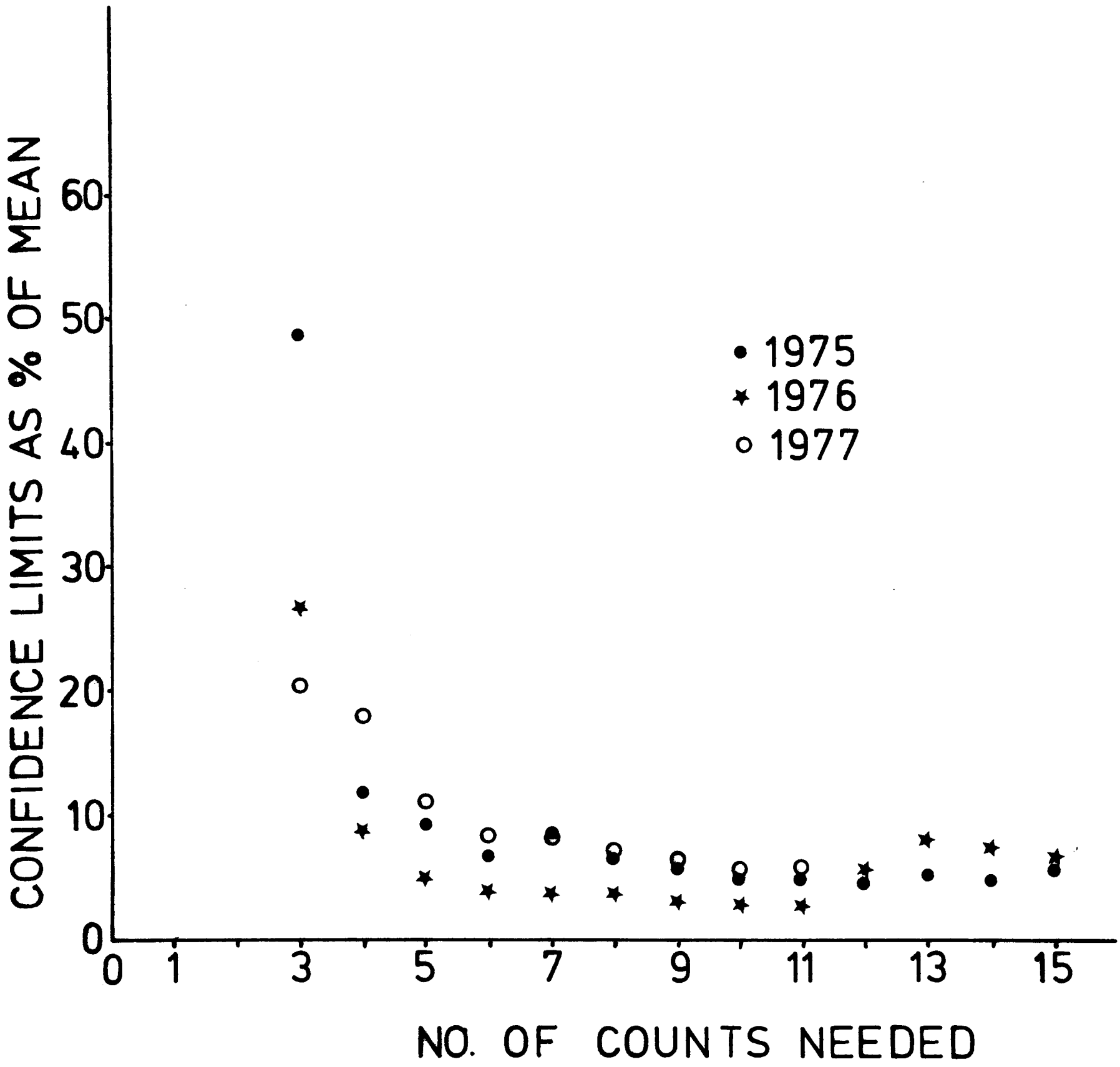
Fig. 4.4 gives an indication of the numbers of counts needed for a given accuracy. Very little accuracy was added beyond six counts.

Several counts aimed at getting maximum numbers may not be as practical as spot counts on one occasion between 2000 and 2330 hours. If that is the case the variation associated with the count becomes much greater. Tab. 4.III shows that despite the large sample sizes, the standard deviation was greater than that for the data in Tab. 4.II, although differences within the 95% confidence limits were similar. This results from the greatly variable numbers within a very narrow time span. Such variation, it seems, is much more pronounced in Black Guillemots than in other auks (cf. Birkhead & Ashcroft 1975). The difference is accentuated since the numbers of Black Guillemots are normally

Tab. 4.II. Day-to-day variation in maximum numbers of Black Guillemots attending a nesting area in evening in the pre-laying period.

Year	n	range	mean	SD	95% conf. limits	No. of breeders
1975	15	78-117	98.6	9.8	93.1-104.1	84
1976	30	75-138	115.6	13.2	110.5-120.7	112
1977	11	122-164	144.5	12.3	136.1-152.9	130

Fig. 4.4. The numbers of counts needed for a given accuracy, presented as the confidence limits as % of the mean. The counts were aimed at detecting the peak or maximum attendance on a given evening. Data for different years treated separately.



Tab. 4.III. Variation in numbers of Black Guillemots at the nesting area, from counts made at no fixed time between 2000 and 2330 hours.

Year	n	Range	Mean	SD	95% conf. limits
1975	78	43-117	85.8	13.5	82.6- 89.0
1976	103	33-138	105.2	20.0	101.1-109.3
1977	34	27-164	131.7	25.5	122.6-140.8

rather low compared with other auks. If the spot method is the only one applicable 40-50 counts would be needed to obtain 10-12% accuracy, i.e. a similar level to that obtained by four maximum number counts. Of course extreme fluctuations in numbers can be avoided by choosing the right tidal and weather conditions, hence lowering the number of counts needed for reasonable accuracy. Preferably, counts should be made on calm days when there is a long period of high tide in the afternoon. Counts should be made every 20 or 30 minutes. Counts can be made at least a month before the start of laying in the population. This method may not be very practical over large geographical areas if censusing teams are limited in man-power as is usually the case. The method is applicable to limited areas, perhaps associated with other aspects of research.

4.4 Discussion

Censusing

One of the original aims of the present exercise was to find a method by which numbers of Black Guillemots attending breeding stations could be related to the numbers of breeders. As shown maximum number counts usually gave higher figures than accounted for by the numbers of birds later involved with breeding in the area. These extra birds are non-breeders which inevitably are present in a species which does not become mature until it is several years old. Day-to-day fluctuations were, I suggest, primarily due to non-breeders, rather than breeders which may be expected to have a stronger urge to return to the nesting area. Yet environmental conditions on several occasions were such that not even all breeders could be accounted for during peak attendance.

Although censuses of auks have been geared towards times of peak attendance and made at standardized times of day, it is clear from my results that such counts do not necessarily give comparable results. At a given time on different days, bird numbers may be increasing, at peak level, or declining. Instead of counting at a standard time counts aimed at getting maximum numbers give greater accuracy. This may not apply to other auk species, since with most of these the numbers present

are so great that just making counts may be difficult. Hence any variations due to such difficulties may outweigh variations due to different timing of peak attendance.

The percentage of non-breeders (including yearlings) in the study population was probably unusually low compared to other populations (Chapter 3), being on average 18.2% (1975), 7.8% (1976), and 13.6% (1977) at times of maximum attendance. Because of the highly variable numbers of non-breeders, dependent on the state of the population in question (cf. Petersen 1976a) the percentage of non-breeders in the Flatey population cannot be used to extrapolate to other populations where the number of breeders is unknown. One cannot therefore use any standardized correction factors to calculate the size of breeding segments from standardized maximum counts. The same conclusion was reached by Cairns (1979). But these counts should be useful for monitoring populations in order to detect changes, despite the fact that an unknown proportion of non-breeders will always be present. Although accurate figures for the size of the breeding segment are highly desirable, the next best result is to get relative figures.

Factors affecting attendance

Fewer birds returned to their nesting area when the weather was cold, and when the wind was strong. Birds expend greater energy during colder weather. According to formula in Kendeigh (1970), and Owen (1970) who stated that there was a linear relationship between existence metabolism and ambient temperature, a Black Guillemot would need about 110 kcal/day at the lowest temperature in the analysis (-4.3°) but about 87 at the highest (+8.2°), for existence. This is 26% more energy which has to be obtained through feeding. Thus temperature may have direct effects in this way. This may be the reason why, on colder days, fewer birds attended the nesting area and those that did, came later; they may have been forced to feed for longer periods to satisfy their needs. But temperature could also have indirect effects through cooling of the sea, which presumably could be more rapid in such shallow waters as around Flatey. This may in turn have affected the availability of preferred prey for the

birds.

Windy conditions could also affect feeding efficiency of Black Guillemots. Wind causing turbulence may affect the birds directly so each dive would be longer, and indirectly through influencing the prey species, e.g. resulting in movements to deeper waters. Potts (1969) suggested a similarly induced reduction in the feeding efficiency in Shags. Slater (1976) found a negative correlation between wind speed and numbers of Common Guillemots attending the colony, and Birkhead (1976b) found a negative influence of sea conditions on feeding rate in same species.

Slater (1976) found a strong tidal effect upon attendance in Common Guillemots in the pre-laying period but not later in the season. A tidal effect is perhaps rather surprising in an offshore feeder like the Common Guillemot, but not unlikely in Black Guillemots. They are inshore feeders, living largely of bottom-living fish and invertebrates in summer (Chapter 10). Height of sea level may vary as much as 5 m during a single tidal cycle in the Flatey region. The seas around the island are mostly shallow, dotted with small skerries and submerged reefs, which may become exposed during low tides. Height of the tide level did not however have significant effects per se on attendance by Black Guillemots. The extent of the low-tide period in the afternoon was more important, fewer birds attending nesting area after an extended low-tide period. I suggest this was because low tides impaired feeding, and the birds tried to compensate by staying longer on the feeding grounds before returning to nesting area, if at all. This could be tested by looking at the rates at which adults feed their young.

At first one may perhaps have expected feeding to be easier at low tide, considering the birds' benthic feeding habits. Slater (1976) suggested that food availability would be greatest for Common Guillemots - which live on mid-water fish-around low tide. This is not likely to apply to Black Guillemots in the Flatey region as they are expected to be able to feed on the bottom whether it is low or high tide because of the general shallowness of the sea. My results suggested that

feeding may have been easier at high tide. I believe the answer lies in the activity cycles of their prey, e.g. that of the Butterfish (Pholis gunnellus). This species of fish is an important prey of Black Guillemots (Chapter 10), and is found in the littoral zone, from the shore-line to depths of 10-15 m, less frequently down to 50-60 m (Saemundsson 1927). At low tides, particularly low spring tides, Butterfish are commonly found under rocks above the water-mark on the lower shore (Quasim 1957, pers. obs.). Whether Butterfish, normally living deeper than that exposed during low tides, actually migrate ashore at low tides, appears to be unknown. Whether they do or not, Butterfish probably becomes less available as potential prey for Black Guillemots during low tides. The fish become active again at high tides, hence increased prey availability for the birds, and presumably greater feeding success. This fits in well with data given by Preston (1968: 14) who found that Butterfish were most frequently caught during high tides. This may also apply to some other animals preyed upon by Black Guillemots. In the Double-crested Cormorant, a benthic feeder like the Black Guillemot, Dunn (1975) found a significant tendency for feeding to take place in the first few hours after high tide. This species has a very similar diet to that of Black Guillemots, including Butterfish.

Chapter 5: BREEDING BIOLOGY I: Timing of laying

5.1 Introduction

The present chapter deals with the pattern of laying in Black Guillemots on Flatey. First eggs of individual birds in the population were laid over a relatively extended period of time, 6-6½ weeks. I examine some of the reasons why this may have been so.

In many bird species, it has been demonstrated that individuals which lay early in the season tend to produce more young than those nesting late (e.g., Coulson & White 1956, Perrins 1965, Nelson 1966, Harris 1969). This was also the case in Black Guillemots on Flatey (Chapter 6). Early breeding should therefore have selective advantage, and the birds should try to nest as early as they can.

The timing of breeding in northern regions is relatively fixed in most bird species, mostly taking place in the summer when environmental conditions are on the whole most favourable (see e.g., Thompson 1950). Two kinds of factors affecting the timing of laying, have been proposed, proximate and ultimate factors (Baker 1938). Proximate factors are those which have an effect on the birds' timing, so they may achieve optimum conditions for breeding. The most important of these, is probably increasing day-length as summer approaches (Murton & Westwood 1977: 215 et seq.). In diving birds (such as Black Guillemots), Salomonsen (1943) advanced the theory that water-temperature, more than air temperature, would be important in the timing of breeding.

Ultimate factors are those more concerned with survival value. Lack (1954, 1966, 1968) argued that breeding was timed so as to coincide with the period when food is most plentiful for the young. An important point here is that egg-laying may be started some time before optimum food conditions for the breeding birds are reached. Perrins (1970) argued that in some species laying date was determined by the ability of females to find enough food for egg-formation. In explaining the spread of laying dates in the same population, he suggested

that more and more females are able to find the required amount of food as the season progresses and feeding conditions improve. For the Manx Shearwater, Brooke (1978) extended Perrins' hypothesis, proposing that females not only delay laying until food is sufficient for egg formation, but until there will be enough to allow successful incubation of the egg. I examine the last two hypotheses with regard to Black Guillemots.

This chapter and the next four, all deal with different aspects of the breeding biology of Black Guillemots on Flatey, hence their running title. The data therein are primarily derived from regular inspections of nest-sites. To avoid undue repetition, I outline below how these nest checks were carried out, and the data collected on these occasions, while in Chapter 9 some additional information is given relevent to that chapter alone. This should be kept in mind when reading these five chapters.

5.2 Materials and methods

Nest checks

I kept all the nest-sites on the island under surveillance, so as to obtain precise information on the timing of laying and all subsequent events of the breeding cycle. The sites inspected were those I knew had been occupied in previous years, plus any additional sites discovered in the course of the study. During the 1974 pilot study, 138 nest-sites were numbered sequentially starting with no. 1. Any new sites found in later years were added to the sequence; 189 in 1975, 116 in 1976, and 74 in 1977. Each site kept its number throughout the study, separated only by the year, e.g. 1975.28, 1976.28, etc. Thus by the end of the 1977 field season, I had numbered 517 sites, all of which were under observation, less a small number which had been destroyed by then.

Nest-sites were usually inspected once a day, in the afternoon or early evening. This particular time of day was chosen since it coincided with the absence of majority of the birds, hence hopefully minimizing disturbance. Visits were very rarely prevented by bad weather. Nest-checks were ini-

tiated in the pre-laying period, some days before the first eggs were expected.

Details were noted in field books but transcribed onto individual nest-cards the same day or the morning after. In this way possible errors or anything unusual could be spotted and re-checked if necessary. All known details for particular nest-sites were thus assembled on the appropriate cards.

Usually it was easy to make out in advance where eggs were going to be laid. The birds normally made a simple cup of pebbles or empty shells which had been left over from the time when rats were still on the island. Rats dragged stipes of brown algae with shells attached from the shore into their burrows (H. Gudmundsson, pers. comm.). If the earth was soft a shallow scrape was made. Sometimes the eggs were laid in a different place than anticipated. In these cases the nesting crevice was usually rather complex. As a consequence some eggs were not found until incubation was under way, or it was not known until chicks had hatched that eggs had been laid at all. But these cases were very few. Generally speaking an intimate knowledge was needed for maximum efficiency, first knowing in which general area particular site was located, then knowing which stone to remove to get at the eggs and chicks. Nest checks were especially laborious the first full year (1975), often lasting 7-9 hours a day. With practice this time was cut considerably in later years, in spite of increasing number of sites under surveillance. Nest-sites were identified by painting their number at the entrance, or where the nest was most easily reached.

If the first egg of a clutch (the a-egg) was identified a small dot was painted on its blunt end for later recognition. Similarly the a- and b-chicks were separated by painted or clipped claws.

Nest-sites were generally not checked during most of the incubation and nestling periods. Daily inspections were resumed just before eggs were expected to hatch or chicks to fledge. New sites were more easily spotted during the chick period, because of accumulating excreta or by the piping of newly-hatched young. The location of any likely sites suspected to be occupied, was noted down but not given a number

until, and if, eggs were laid. Frequently it was found that sites which had never been used before were occupied a year before eggs were subsequently deposited there.

Each year I continued to find new nest-sites throughout the whole breeding season. Every new site found in 1976 and 1977 was counted as not having been used the year before. This was not so in 1975, as no attempt had been made to find all sites in 1974. The numbers of sites found in 1975-1977 give, I believe, a very good approximation to the total numbers of sites used for breeding on the island (see also Chapter 2). I did, however, find a few unnumbered sites in 1976 (9), 1977 (2), and 1978 (1) which appeared to have been used the year before. At these sites I found eggs that definitely were not this year's and were judged to be from the year before. If eggs failed for some reason, they were removed.

Practical difficulties associated with nest checks were numerous. Many sites were so situated that inspection was impossible. Also, although eggs could be checked, sometimes chicks could not, as they invariably ran towards the most distant corners of their site. However, the majority of nest-sites were relatively easy to check, and for this a torch was crucial.

If eggs failed they were normally found just outside the nest. Attempts were made to infer the cause of failure. Rejected eggs, in which embryonic development had begun, contained badly smelling reddish fluid, the mixture of the white and yolk. In most cases no sign of embryonic development was evident, indicating that incubation had not proceeded very far when the egg failed. Incubated, rejected eggs in which the white and yolk were separated and looked much like fresh eggs, were considered infertile. Very few eggs vanished without any trace. Some were suspected to have been taken by predators (Ravens, gulls). Some may have been removed by the adult guillemots themselves (vide Preston 1968: 42), or just could not be found. Very few chicks disappeared without any trace. Dead chicks were often found within the confines of the nest-site, in the nest itself if the chicks were newly dead. Later they were removed from the nest by the adults, either pushed aside or thrown outside the site entrance,

occasionally a few metres. The age of chicks and cause of death were inferred, if not known exactly.

Measurements and experiments

The length and breadth of each egg was measured with calipers, to the nearest 0.1 mm. Since nests were inspected once a day, the appearance of an egg was taken as that egg having been laid during the last 24 hours, presumably on average 12 hours previously. Such eggs were designated to day 0 and were weighed to the nearest 1 g with a 100 g Pesola balance. In 1977 fresh-egg weight was also taken even though a few days had passed from laying. By then it was known that no significant changes took place in egg weight during the first few days.

I checked my consistency in weighing and measuring eggs by repeating weighings 2 days later, some of the measurements up to $1\frac{1}{2}$ month later. There was very good constancy; weight ($n=15$, $\bar{x}=50.4$ g, s.d.=4.1; repeat $\bar{x}=50.3$, s.d=4.2), length ($n=18$, $\bar{x}=59.02$ mm, s.d.=2.37; repeat $\bar{x}=59.02$, s.d.=2.35), and breadth ($n=18$, $\bar{x}=39.32$ mm, s.d.=1.01; repeat $\bar{x}=39.29$ mm, s.d. =1.04).

The birds' relaying potential was investigated by a series of egg-removal experiments. All the experimental clutches contained 2 eggs, and the eggs were removed on day 0 of the b-egg. If nests failed, and the day was known, they were also included in the analyses.

As a measure of density of breeding pairs I took the nearest-neighbour distance for all sites used for breeding. The measurement was taken from entrance to entrance.

Analyses

As a result of the nest checks the following information was obtained for a variable number of nest-sites: laying date, clutch size, number of days between laying of the a- and b-eggs, fresh weight and size of eggs, length of the incubation period, causes of egg and chick losses, timing of egg and chick losses, the interval between hatching of siblings, the number of chicks hatching and fledging, among other information more appropriately

dealt with under respective chapters. For a number of reasons, some already described, the whole set of information was not obtained for every nest-site. Care was taken to avoid possible biasses. For example, if a nest was only found when chicks had already hatched, this was not used in productivity calculations. Sample sizes are thus variable as evident later.

The very day on which the first egg of a clutch was discovered (day 0), was used as basis for comparison between nests (vide Swanberg 1950). If not known exactly, the laying date was back-calculated using the mean number of days for the population from other events of the breeding cycle of the nest in question (laying of the b-egg, hatching date, etc.).

When analysing laying dates on a seasonal basis the laying season was divided into "laying periods", each a week in duration. Exceptions to this were the last laying periods of 1976 and 1977, which included several extremely late layings spread over approx. 3 weeks, and the first period of 1977 which was 8 days.

The number of days between eggs (or chicks) was calculated from day 0 of the first egg (or chick) to day 0 of the second. The length of the incubation period was similarly calculated from day 0 of the egg to day 0 of the chick from that egg. Day 0 of a chick was that on which the chick was recorded free from the egg-shell.

In the analyses of breeding performance, all nests that had been experimented with in any way, were excluded: 18(6.0% of all nests) in 1975, 42(11.1%) in 1976, and 20(4.8%) in 1977. Similarly I excluded all nests which were deserted as a direct result of my interference. Most of these were deserted when I surprised a bird on the nest. The numbers thus excluded, were 11(3.7%) in 1975, 20(5.3%) in 1976, and 17(4.1%) in 1977.

Density of breeders was one parameter which was used in analyses of the timing of laying and effect on breeding success. Cases in which nearest neighbour distance was 20 m or more, were excluded, so as to avoid undue weighting of extreme cases. These sites represented only a small fraction of all the sites, 18(6.0%), in 1975, 24(6.3%) in 1976, and 20(4.8%) in 1977. The decision which nests to exclude, was taken by plotting the nearest neighbour distance on a graph. At 20 m the distribution

started becoming discontinuous, hence the division was made there.

5.3 Results

Laying dates for whole island

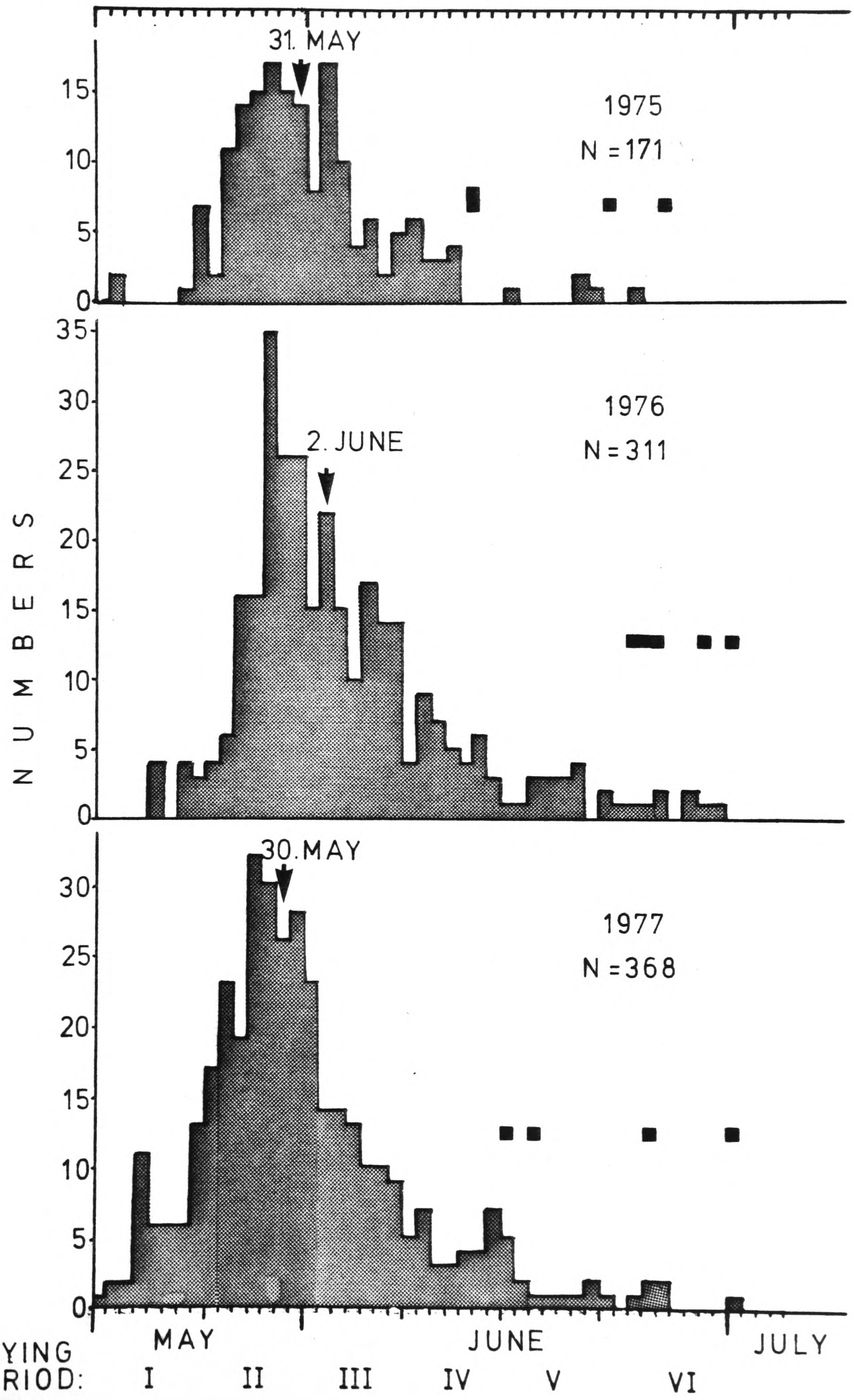
The pattern of laying of first clutches for the whole population, is shown in Fig. 5.1. The overall pattern showed much consistency in all three years, though the beginning of laying and median laying date was somewhat later in 1976 than in 1975 and 1977.

The first eggs in the population were found on 18 May 1975, 21 May 1976, and 17 May 1977. Comparable figures for the end of laying are, 24 June, 30 June, and 1 July, respectively. Thus the spread of laying was 6-6½ weeks (1975:38 days,1976: 41 days,1977: 46 days). The samples on which these determinations were based, are thought to represent the laying pattern of Flatey guillemots very well, being 57% (1975), 82% (1976), and 88% (1977) of the total island population.

All accurately determined instances of natural replacement clutches, were also inserted in Fig. 5.1. Although but few, they did not extend the overall laying season of the population. Yet there was one instance (not shown) which probably was a replacement laying. An estimated 15-day old chick was found in a nest in late August (1976). The egg from which this chick hatched would have been laid around mid-July, by far the latest instance of laying during the study. Replacement layings will be dealt with in more detail in Chapter 7.

The breeding season of Flatey birds appeared more drawn out than that of same species on Kent I., New Brunswick (Preston 1968: 41) or in the St. Lawrence estuary (Cairns 1978: 15), or that of Puffins (Ashcroft 1979) and Razorbills (Lloyd 1976: Fig. 4.2) on Welsh islands. Part of the explanation for this may be the relative sample sizes by which these populations were represented. Asbirk (1978c) recorded an even greater spread of laying dates (44-57 days) for Danish Black Guillemots than was found on Flatey, in spite of his study population being much smaller. This population, as with

Fig. 5.1. Laying dates for the whole island population of Black Guillemots in the 3 study years. Arrows give the median laying date the stippled area first clutches, each black square one natural relaying attempt.



mine, increased rapidly during the 1970's. That is likely to have had an important bearing on the extent of the laying season, as shown later. For a small population of Pigeon Guillemots Drent (1965) recorded 18-42 day spreads of laying dates in different years.

Although the spread of laying was 6-6½ weeks in the Flatey population, the majority of the birds laid within a much shorter time period. By leaving out 10% from each end of the laying-date distribution which, however, was not symmetrical, the remaining 80% of birds laid their first egg over a period of 13 (1975), 17 (1976), and 18 (1977) days. Hence more than 50% of the range extension was due to only 20% of the birds.

Possible effects of snow and ice in 1976

In 1976 when field work commenced in third week of April, snow and ice covered much of the ground, contrary to the situation in 1975 and 1977. This was especially so in concave parts of the island, such as in the nesting areas. This presented the opportunity to study possible effects on laying.

In arctic and subarctic regions snow can inevitably have various effects on breeding schedules of animals (see e.g., Formosov 1946, Bengtson 1963, Pulliainen 1978). In auklets snow melt has been shown to influence the timing of laying (Sealy 1968: 28-34).

Observations were confined to one (out of 15) nesting area on the island. On 23 April, about a month before the commencement of laying, all nest-sites which had been used the year before at nesting area IV, were examined. They were grouped into those obstructed by snow or ice, and those not. These sites were not checked again until just before laying. Then daily visits were made to find out when laying took place, if at all.

The results are given in Tab. 5.I. The same proportion of nests in each group was not used for breeding, and there was no delay of laying at those sites which were full of snow or ice on 23 April. The reasons for these results are probably as follows. During late April-May, the weather was continually improving, and all the snow and ice had vanished by 10-15

Tab. 5.I. Examination of the effect on date of laying at nest-sites filled with snow or ice on 23 April 1976 and those being snow-free. N=95.

Condition on 23 April	Total n	Numbers not laid in (%)	Mean laying date[1]	Range	n
Snow-free	27	4(14.8)	15.5	5-34	23
Snow or ice-bound	68	10(14.7)	15.9	8-32	54[2]

Notes: (1) 1= 17 May, 16= 1 June, 45= 30 June, etc.
(2) Laying date not known for 4 sites.

May. Laying began then about a week later, with the mean laying date at the nesting area about 10 days later still. Snow and ice melt had therefore occurred sufficiently early at the previously obstructed sites to allow undelayed nesting to take place. Possibly if the sites had blocked very much longer, delay may have occurred.

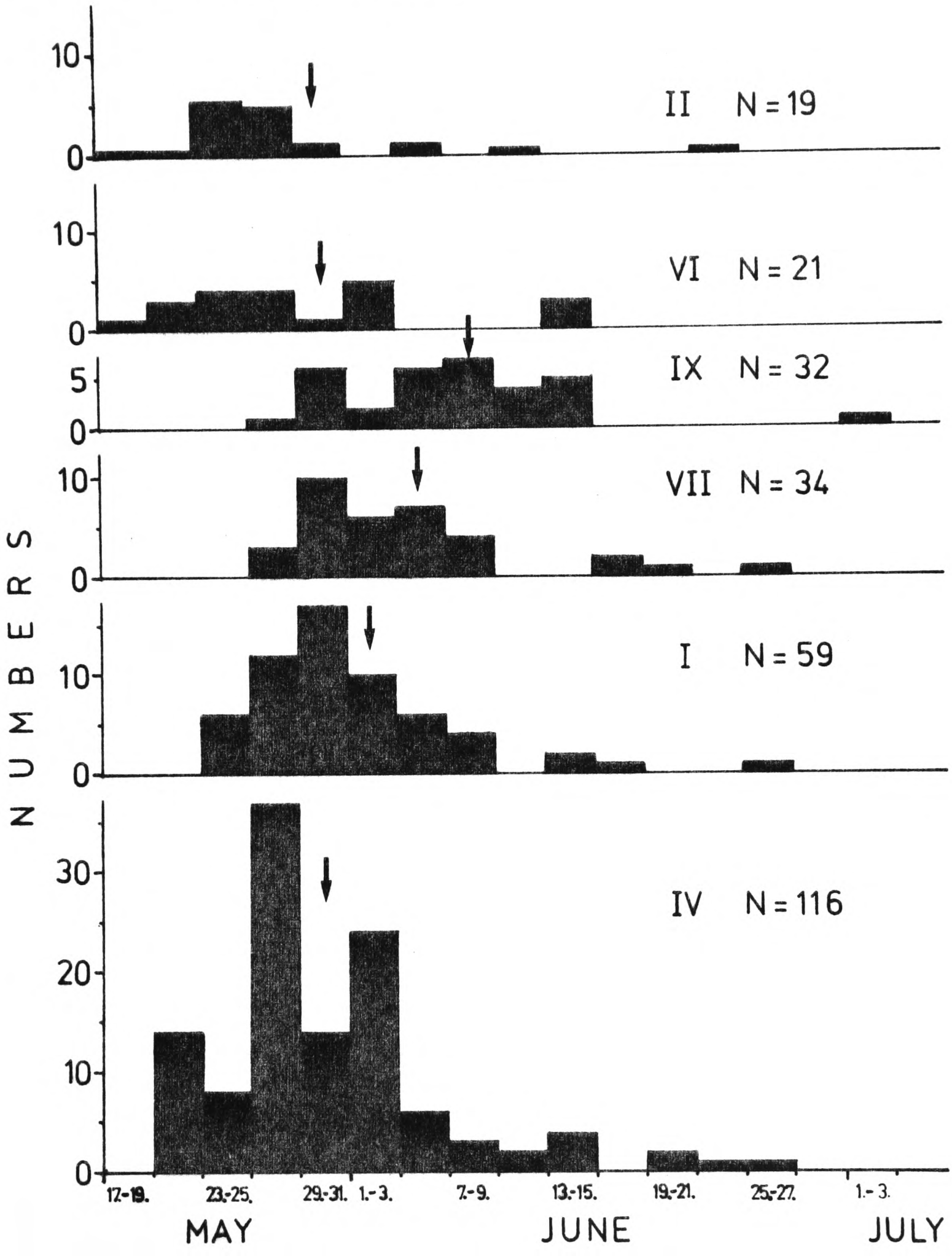
Although the results did not demonstrate what was originally intended, a delay at blocked nest-sites, the fact remains that laying was 2-3 days later in 1976, compared with 1975 and 1977. Snow, ice, and melt water may possibly have delayed laying in other parts of the island, but this is rather unlikely since the area investigated held about a third of the breeding pairs on the island, and piles of snow were most prominent there. It therefore seems likely that some other factor, or a combination of factors, led to a general delay of nesting, affecting those that nested at obstructed nest-sites and those that did not, alike. The delay appeared to be primarily due to delay in the early breeders. As seen in Fig. 5.1 (p.98), the very beginning of laying started later, and there was a less rapid build-up during the first two weeks. It was shown earlier (Chapter 4) that attendance of Black Guillemots in the pre-laying period was affected by wind force and air temperature, besides tides. The first half of May 1976 was unusually cold and windy, compared with 1975 and 1977 (Flatey weather station). This would be the time during which the earliest breeders were developing their eggs, since it takes them about 2 weeks to form the clutch (Chapter 7). Therefore, it seems that these environmental factors may have had a common delaying effect on all early layers, rather than snow delaying those pairs which nested at previously obstructed nest-sites.

Asynchrony between nesting areas

The timing of laying was studied at each of the 15 nesting areas on the island separately. Thirteen of these areas can be said to be "natural groups", i.e. they have well defined natural boundaries and each topograpically uniform.

The pattern of laying is shown in Fig. 5.2 at six of these nesting areas in 1977 which, combined, held 72% of all pairs

Fig. 5.2 Pattern of laying of first clutches at six nesting areas (Roman numerals indicate which). Data from 1977, including areas which held 72% of all breeding pairs on the island. Arrows indicate median laying dates, and observations are grouped in three-day blocks.



Note: (1) t-tests between some of the nesting areas: $t_{II,VI}$ = 0.66, n.s; $t_{II,IX}$ = 2.71, P<0.01; $t_{II,I}$ =1.86,n.s.; $t_{VI,VII}$ = 4.50, P<0.001; $t_{IX,IV}$ = 3.69, P<0.001; $t_{I,IV}$ = 1.76, n.s.

on Flatey. The areas not shown were the two "unnatural" groups, areas with very few pairs, or those that did not show any more variation than those taken as examples.

The greatest difference in median laying dates, was about 11 days. Statistical tests were done using mean laying dates. As seen in the figure some of the differences between areas were statistically significant. Particularly noticeable is the difference between nesting area VI and VII, which are separated only by some 70 m.

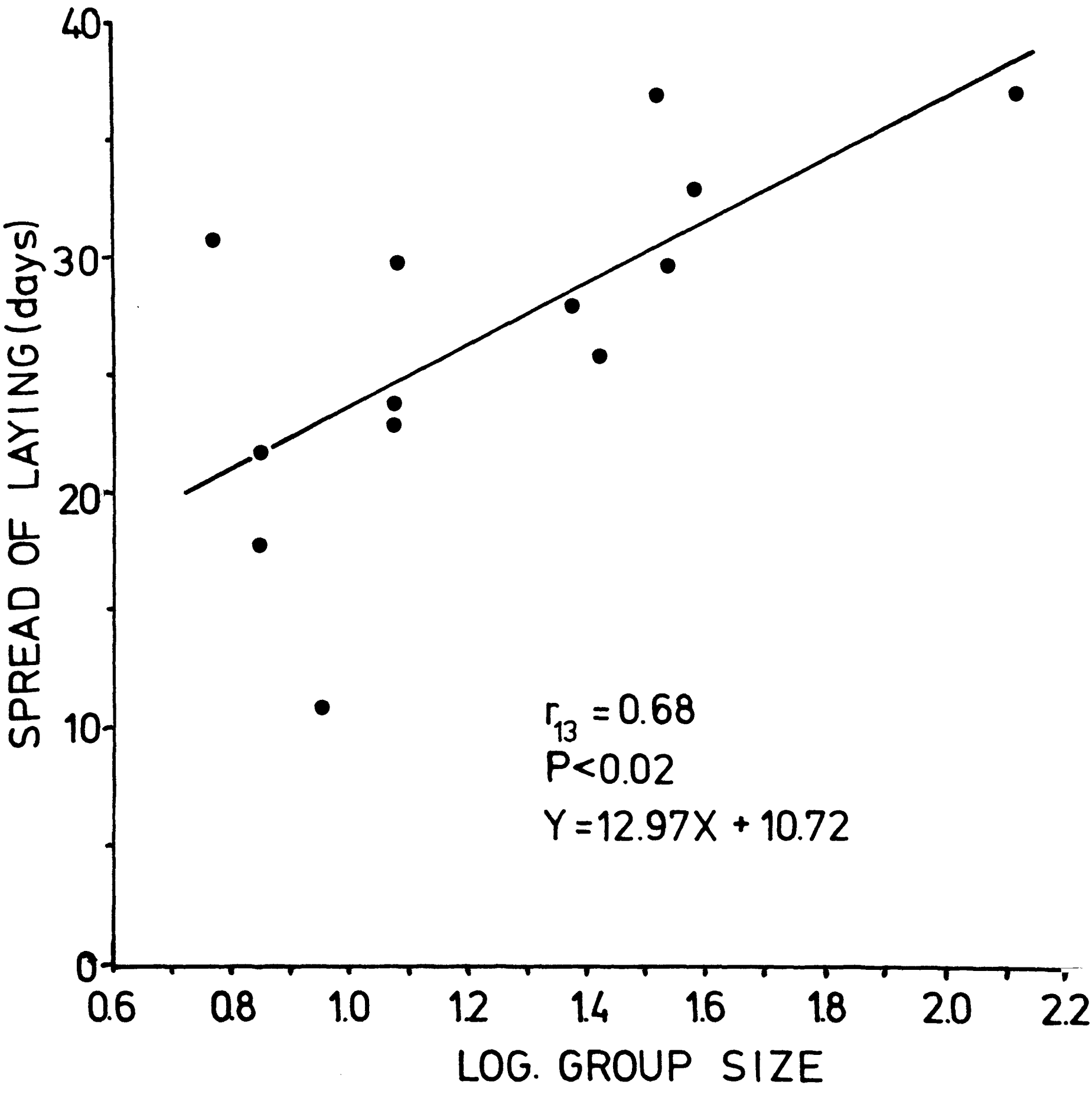
These data are only for one year. There was a tendency for birds to lay at a specific time in the season, relative to other birds in the population. The mean laying date for nesting areas therefore tended to be consistently early or late. The reasons for this, in part at least, were the general area- and nest-fidelity of established breeders (Chapter 3), differential colonization of nesting areas, and differential increases in numbers of breeders between years and nesting areas (see later).

Degree of synchrony within nesting areas

Synchrony in laying is often looked upon as an adaptation by colonial species to avoid predation and thereby enhance their breeding success (e.g., Patterson 1965). The number of days over which laying takes place at different nesting areas, can be taken as a measure of synchrony. One difficulty is that one would expect larger groups to show larger spreads of laying dates by virtue of them having more birds. As Fig. 5.3 shows there was a significant relationship between log group size and the actual spread of laying. Before further analysis was made this "sample-size" effect was removed, by using standard deviation of laying dates as a measure of synchrony (vide Emlen & Demong 1975).

Three factors were thought to be of particular importance to synchrony; (a) density of breeders, (b) size of the breeding group, and (c) the proportional change in group size between years. The rationale behind these ideas is as follows. Denser groups may be more synchronized than less dense ones (e.g., Coulson & White 1960, Birkhead 1977b). Members of a large group may receive greater social stimulus than birds

Fig. 5.3. Correlation between group size and spread of laying within each nesting area in 1977. The original plot was a hyperbola, hence a logarithmic transformation is used for the x-axis.



of a small group, i.e. the "Fraser-Darling effect" (Darling 1938). Lastly, new members of a breeding group may show less synchrony than older and more experienced birds. This was especially pertinent in view of the large increase in the Flatey guillemot population over some 15 years (see Chapter 2). Newcomers would at least have had less experience of Flatey nesting areas than established breeders, if not also, on average, being younger birds.

Analysis was carried out using multiple regression technique, and information for each nesting area formed the basis for comparison. Increase in group size between years, actual group size, and density of occupied nest-sites were included as independent variables. Standard deviation of laying dates was entered as the dependent variable. No significant relationship was found (combined $F\text{-value}_{3,14}=1.04$, 14% of variation explained). The mean "between-group" standard deviation (6.2) was the same as the mean "within-group" standard deviation (6.1). Hence there was no evidence for greater synchrony within each nesting area than in the population as a whole.

Effects of three factors on timing of laying

The difference in timing of laying between nesting areas (cf. Fig. 5.2), prompted me to look more closely for possible reasons for the observed asynchrony within such small area as Flatey.

Three factors were selected; (a) increase in group size between years, (b) actual group size, and (c) density of occupied nest-sites. The rationale is as follows. Lloyd (1976: 49) found a negative relationship between mean laying date and colony size in Razorbills one year although not in others. Denser groups may start breeding earlier than sparse groups. Also newcomers in the breeding population may, on average, be younger and/or less experienced, and may nest later than established breeders (cf. Coulson & White 1960).

The data were analyzed using multiple regression technique and mean laying date for each nesting area was the basic unit of comparison. No significant relationship was revealed

between the variables (combined F-value$_{3,17}$=0.56, 9% of variation explained).

Another analysis was performed, not using the actual figures for each nesting area but changes between years. Thus proportional change in group size, mean change in density, and mean change in group size were regressed against proportional change in mean laying date.

Proportional change in group size did, as shown in Tab. 5.II, have a significant effects on change in mean laying date. Change in density was nearly significant at the 5% level. Changes in group size and density are inevitably negatively correlated (r_{40}=-0.41, P<0.01; y=-0.363x+1.36), since size of the nesting areas did not alter between years. One could therefore question whether density was not contributing towards the significance of change in mean laying date with proportional increase in group size. This is unlikely since there was no relationship between actual, rather than change in, density and laying date. Moreover, increased density is an inevitable result of increase in group size per unit area, not vice versa. One may therefore conclude that the greater the change in group size between years, the greater the effect on the mean laying date of that group.

Most of the changes in pair numbers between years, were increases. Fig. 5.4 shows the relationship was negative. Hence the greater the proportional change in group size, the more retarding effects on the mean laying date. But increase in group size had to be 25% or more if this increase was to have effects on the group's mean laying date. The explanation can only be, that counteracting factors produced the mean laying date; new breeders with retarding effects but former breeders advancing their laying date. If former breeders had not on average advanced their laying date, the population mean laying date would have been retarded even more.

Laying dates at "old" and "new" sites

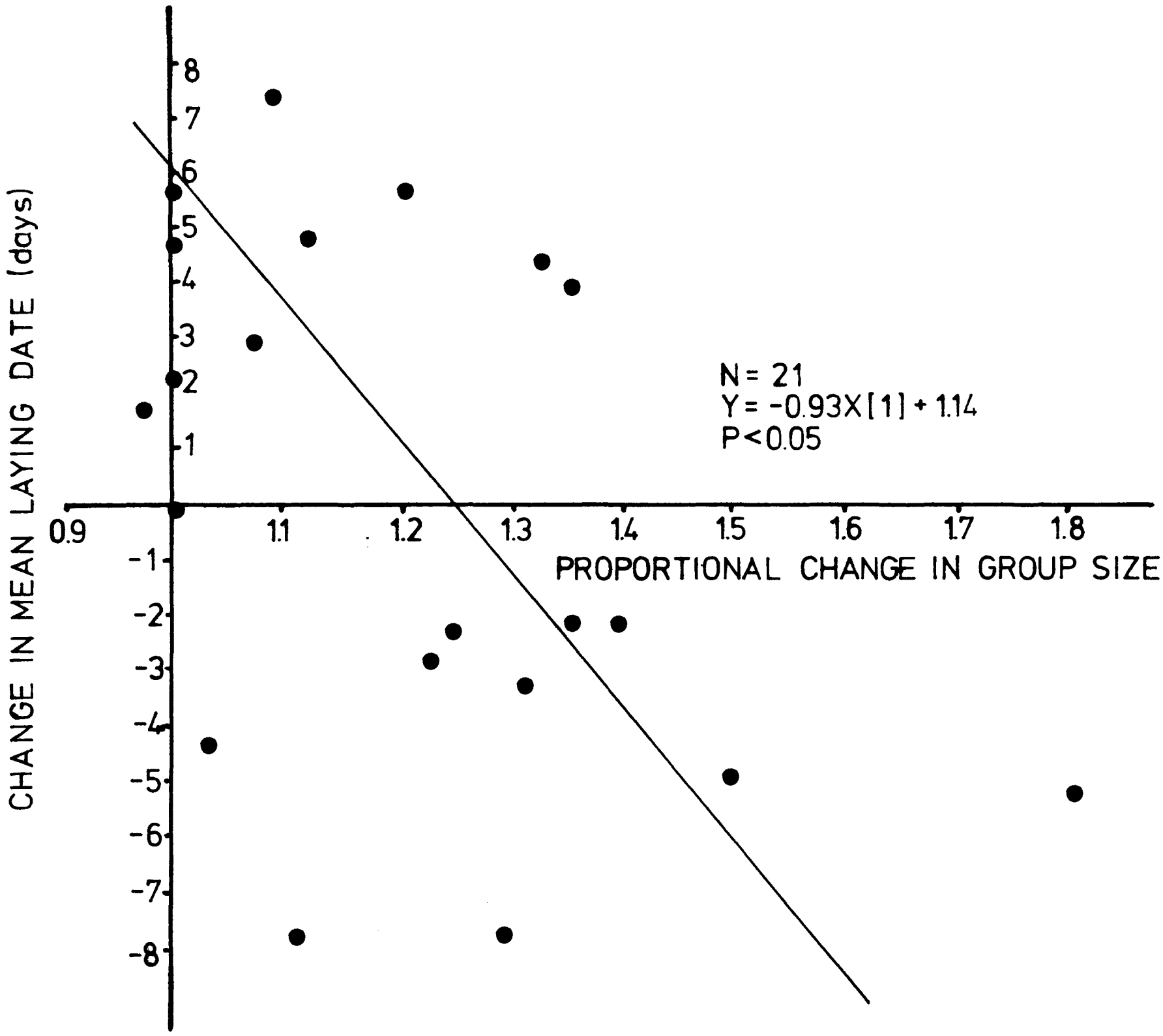
In view of the population expansion which has taken place (Chapter 2) and high degree of mate- and site-fidelity

Tab. 5.II. Calculations of the relationship of change in laying date with 3 variables, using a multiple regression analysis. N=21.

Independant variables	F-value	% explained	Significance
Proportional change in group size [1]	5.98	23.9	<0.05>0.01
Changes in density [2]	4.21	18.1	n.s.
Changes in actual no. of birds [3]	1.43	7.0	n.s.

Regression equation: $y = -0.93x_{[1]} + 1.1435$.

Fig. 5.4. The relationship between change in mean laying date with proportional change in group size [1]. Results from a multiple regression analysis.



(Chapter 3), it is reasonable to assume that sites which had never been used before, were mostly occupied by newly-established breeders. Tab. 5.III shows laying dates at sites which had been used for one or more years ("old") and those never used before during the study ("new"). Eggs were laid, on average, 5 days later at the new sites. It is also noticeable that the difference was almost exactly the same in both years, and when laying was about 2 days earlier in 1977 compared with 1976, this was also so in the "new" category. This result suggests some common influences upon all breeders on the time at which they lay, e.g. climatic factors, as described previously. Although presumably most new sites were occupied by new breeders, some may have had old breeders which had changed sites as recorded once. Also, some new breeders would have bred at old sites, as recorded for one known-aged bird. Hence the real difference in mean laying dates between presumed first-time breeders and those which had bred before, is likely to have been somewhat more than 5 days. Finally, it was often noticed that new sites were occupied the year before without laying. This recalls the situation studied with regard to non-breeders holding sites (Chapter 3) where most appeared to be 2-years old, but the youngest known-aged breeders were 3 years of age (Chapter 11).

Initial colonization and mean laying date

The later average laying date at certain nesting areas, was consistent over several years. Information was available on the initial colonization of some of the Flatey nesting areas, and this was compared with mean laying date at these areas.

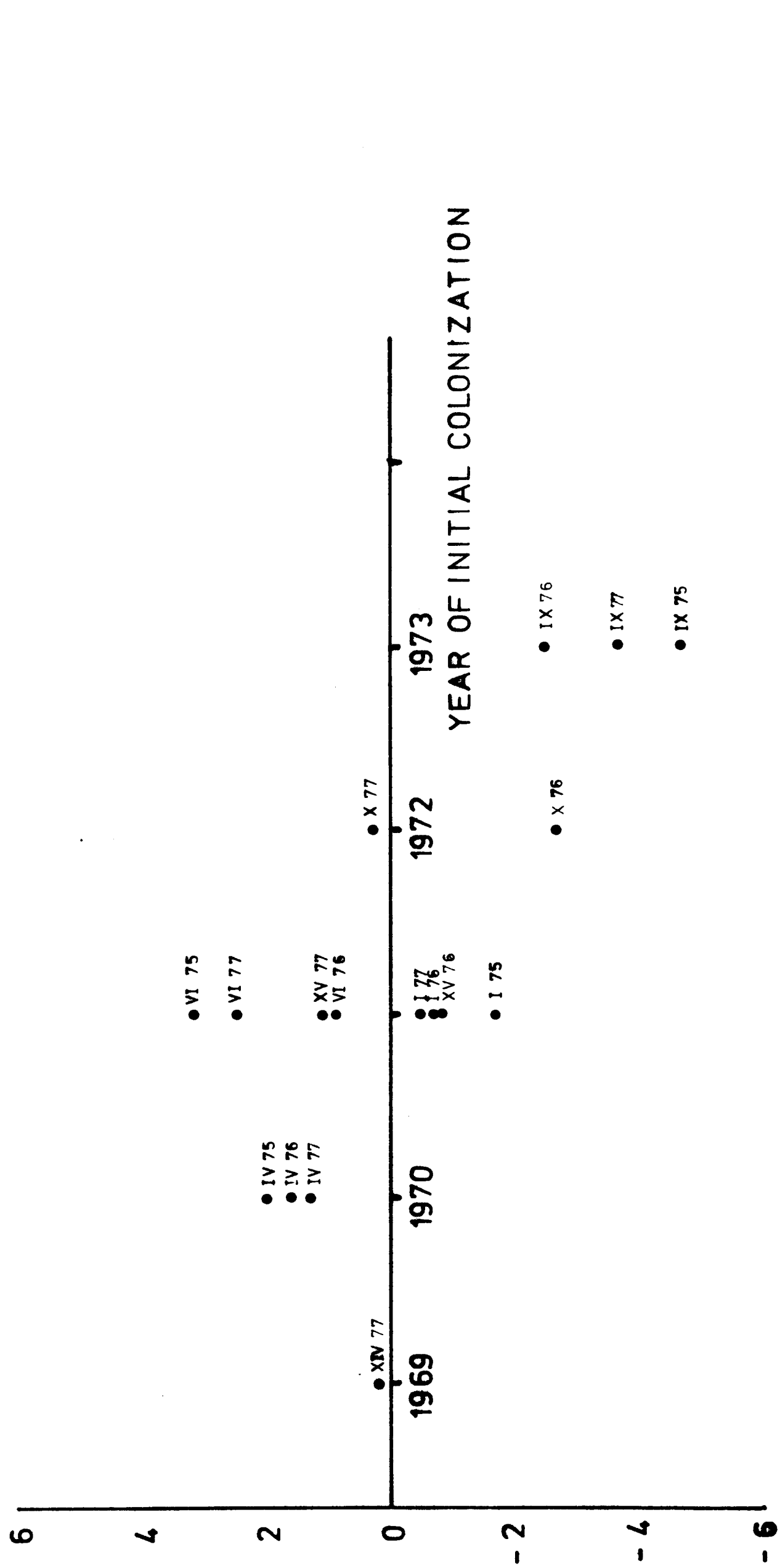
As Fig. 5.5 shows, the later the mean laying date, the shorter the period since the respective areas had been colonized. This held over all the three years of study, but it was also apparent that the mean laying dates at the latest colonized areas were advanced relative to that for the population as a whole. Similarly, the areas that had been longest in use, appeared to have developed a stable average laying date. From these data, it appeared to take the breeders some 4-6 years to reach a stable laying date.

Tab. 5.III. Comparison of mean laying dates at "old" and "new" nest-sites. Old sites were regarded as those that had been used for one or more years, whether breeding was successful or not. New sites were those that had never been laid in during the present study.

Year		Old sites		New sites
1976	n	234		77
	range	5-44 (1)		5-45
	$\bar{x}$	17.0		22.0
	Sd.	6.5		8.7
		t	5.39	
		P	<0.001	
1977	n	319		50
	range	1-45		5-40
	$\bar{x}$	14.8		19.9
	Sd.	6.9		9.1
		t	4.62	
		P	<0.001	

Note: (1) 1= 17 May, 16= 1 June, 45= 30 June, etc.

Fig. 5.5. The mean laying date at some nesting areas on Flatey, in relation to the year at which Black Guillemots were first recorded nesting at the respective areas.



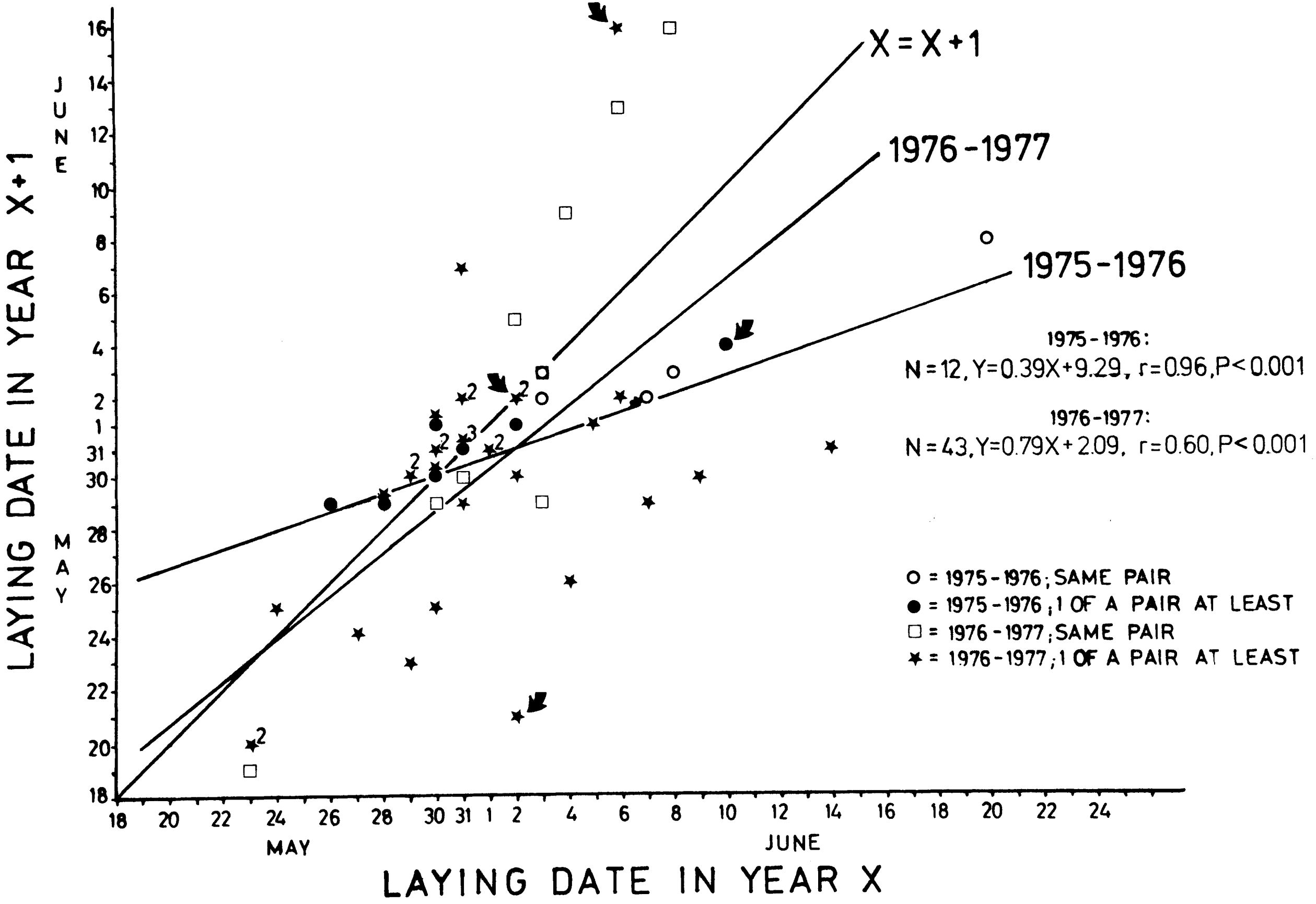
Of course there are many factors which may influence the overall picture of mean laying date at a given nesting area. Therefore, it is perhaps surprising to find that a relationship between year of initial colonization and mean laying date had such a strong effect that it showed through. Factors influencing this relationship, will be discussed further later.

Laying by individual birds and at individual nest-sites

Fig. 5.6 shows laying dates at same nest-sites in subsequent years. These sites were known to be occupied by the same pairs, or at least one member of a pair, in both years. In view of the species' mate and site-fidelity (Chapter 3) and longevity (Chapter 11), one can assume that most pair members in the latter group were the same in both years. However, in that group which included 40 observations, 4 pairs were known to have failed to mate with each other in the second year. Although this small sample size does not say much, apparently failure to mate did not influence the mean laying date at these nest-sites. If anything, failure to mate appeared to bring greater variability between individual birds, as was suggested for Razorbills (Lloyd 1976: 50), but it is clear that many more data are needed.

The main point of Fig. 5.6 is to show that the birds tended to have a specific laying order relative to other birds in the population. If birds nested late one year, they also tended to lay late the year after. Drent (1965) found a similar relationship in Pigeon Guillemots. Specific laying order has been demonstrated in other bird species, e.g. gulls (Harris 1966, Brown 1967, Davis 1975), in Great Tits (Jones 1973[illegible]1) but does not seem to be the case in Puffins (Ashcroft 1976: 64). Yet superimposed on this tendency was another, that of advancing the laying date between years. This was greatest in the very late layers, as shown in Tab. 5.IV. Both these points are especially noteworthy in view of the previous relationship between initial colonization and mean laying date, as well as apparent advance of mean laying date at the youngest nesting areas. Furthermore, what is worth drawing attention to is the variation evident

Fig. 5.6. The relationship between laying date at same nest-sites in two consecutive years. The sample includes nest-sites which were occupied by the same pair, or at least one member of a pair, in both years. Arrows indicate sites at which it was known that both pair members were not involved in both years. The date of laying occurred on the same day if directly on the line X=X + 1.


X = X + 1
1976 - 1977
1975 - 1976
1975 - 1976:
N = 12, Y = 0.39X + 9.29, r = 0.96, P < 0.001
1976 - 1977:
N = 43, Y = 0.79X + 2.09, r = 0.60, P < 0.001
○ = 1975 - 1976; SAME PAIR
● = 1975 - 1976; 1 OF A PAIR AT LEAST
□ = 1976 - 1977; SAME PAIR
★ = 1976 - 1977; 1 OF A PAIR AT LEAST
LAYING DATE IN YEAR X+1
MAY
JUNE
LAYING DATE IN YEAR X

Tab. 5.IV. Changes in laying date in relation to previous year and time of season. Based on data at sites where same pair, or at least one member of previous pair, nested in consecutive years.

Time of season as nos. of days before/ after mean population laying date:(1)	Nos. of days changed: n	range(2)	$\bar{x}$	S.d.	U-test
7-0.1 days before	20	+7.2- -4.5	+1.2	3.5	
0.1-7 days after	29	+12.2- -8.8	+1.6	4.6	z= 0.54 n.s.
8-21 days after	6	+15.2- -6.8	+7.0	7.7	z= 2.14 <0.05

Notes: (1) To eliminate effects of annual variations the laying date was expressed as the difference between mean population laying date and the observed one. 7-0.1 days before the population mean corresponds roughly to laying period II, 0.1-7 days after to laying period III, etc.

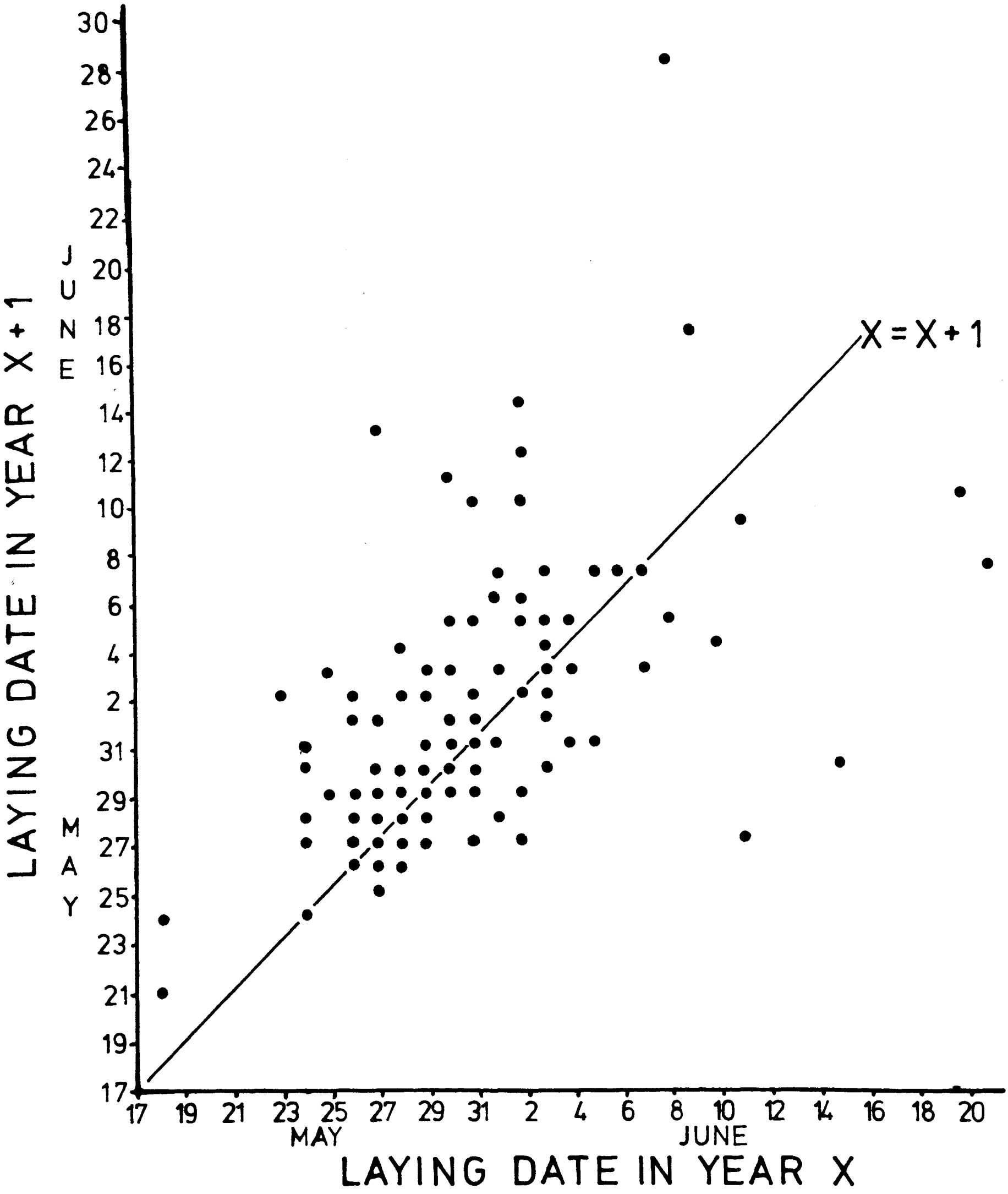
(2) + indicates an advance in laying date, - a delay.

in Tab. 5.IV, occurring between individual pairs, even though the members stayed together and nested at same nest-site in both years.

Regardless of whether the same pairs were involved or not, a similar plot to that in Fig. 5.6 was made for all nest-sites in use in both years 1975 and 1976, and is shown in Fig. 5.7. Since, as mentioned in Chapter 3, about 75% of the nest-sites had the same birds as the year before, Fig. 5.7 shows much the same picture as Fig. 5.6. One point particularly worth stressing here is the greater deviation from expected laying, consedering the former year's, in late-breeding birds. My circumstantial evidence suggests that the late breeders were on average younger birds, and late breeders were also less successful in breeding than early birds (Chapter 6). As shown in Chapter 3, unsuccessful birds were more likely to change sites and possibly also mates. Hence unsuccessful nesting, coupled with site and/or mate changes, appeared to lead to disruption of the pattern of specific laying order. Average laying date at these sites was not necessarily delayed, but many more birds at these sites appeared to greatly advance or greatly delay their laying date. It is suggested that this comes about through re-matings and site-changes, and the governing factors are what kind of mate a bird will re-mate with and what birds will reoccupy sites left vacant.

Two further points are worth raising. Although first-time breeders appeared to lay, on average, later than more experienced birds, there was clearly considerable overlap, as indicated by the data on "old" and "new" nest-sites. Only two breeders were of known age. One nested first when 3 years old, and again when four, and laid on 1 June in both years, at an old-established site. This would be considered relatively early for a first-time breeders, since laying took place around the peak of laying in the population. The other known-age bird nested very late in the season, on 25 June, at a site which had never been used before during the study. If these two birds give an indication about the variability between birds of the same age and breeding experience, one wonders what leads to such a variation. I will be advancing the hypothesis that part of the explanation lies in whether the first-time breeder

Fig. 5.7. A comparison of laying date at same nest-site in two consecutive years, irrespective of same birds being involved or not. The line X=X + 1 indicates laying on same day in both years.



pairs up with an experienced bird or one of similar age, whether nesting takes place at an old or a new site, and which sex is involved. These considerations could equally well fit experienced birds which have failed to pair up with their previous mate. Furthermore, in this context, it is important to note Coulson's (1966) results that of Kittiwakes breeding for the first time, those present at the colony the year before the first time, laid earlier than those which had not been present the previous year.

As a result of young birds laying later than more experienced birds and of being less successful in breeding, several years seem to elapse before they have advanced their laying date to equal that of older birds. Therefore, once more, the earlier relationship between initial colonization and mean laying date will be noted. In this context, it is perhaps worth considering the case of nest-site no. 28, which was the only one used on the island in 1966 (Chapter 2) and was occupied in every year 1974 to 1977. Laying took place among the very earliest in every year, 18 May 1975, 21 May 1976, and 18 May 1977. This site may have been in longest occupancy of all sites on Flatey, and possibly had the most experienced breeders.

5.4 Discussion

Laying date in relation to population expansion

Three factors were considered particularly important in accounting for an extended laying season of Black Guillemots on Flatey: (a) Birds at different nesting areas not laying synchronously, (b) relatively little synchrony within nesting areas, and (c) large sample sizes. The last merely indicates that the sample sizes were thought to be large enough to fully represent the actual spread of laying dates in the population.

The laying dates in different nesting areas, as indicated by median laying dates, differed by as much as 11 days, and this occurred within the island in spite of limited size (0.5 km^2). It was also evident that the spread of laying dates was large within each nesting area, with no tendency towards greater synchrony than in the population as a whole. Hence

relative asynchrony between and within nesting areas were both responsible for the extended laying period observed.

Since the population was rapidly increasing during the study, newcomers made up a sizeable proportion of the total island population (Chapter 2). Although direct evidence is lacking, strong circumstantial evidence indicated newcomers were young birds, breeding for the first time. If nothing else, they were at least less experienced of Flatey nesting areas than birds already established there as breeders.

Increases in numbers of breeders were widely different between nesting areas and between years (Chapter 2). The greater number of newcomers, the later the mean laying date at that area. At the same time, it was known that different nesting areas had been initially colonized in different years, and those years correlated with mean laying dates. Since Black Guillemots are long-lived birds (Chapter 11) and generally site-tenacious (Chapter 3), one would expect many of the original colonizers still to be alive and nesting at the area at which they had bred for the first time, but some of the areas had been used for 2-7 years. Hence if the nesting area had been colonized early the breeders would be, on average, older and laid earlier than still younger birds. Later nesting by young birds has been shown in many bird species (e.g., Coulson & White 1956, Snow 1958, Potts 1966, Haartman 1967). I therefore conclude that asynchrony between nesting areas on the island was primarily the effect of differences in age structure of the breeding groups, due to different times and rates of colonization. Hence, at least in part, the extended laying season observed is likely to have been the result of unusually rapid increase in the population, resulting in a high proportion of young, inexperienced birds, laying later in the season on average than older, more experienced birds.

Although the effect of initial colonization seemed strong, it is obvious that the age structure of a breeding group of birds is influenced by a variety of factors. These include the size of the initial nucleus of birds, recruitment rate of new breeders, mortality of established breeders, and rate of emigration. In this context, one may ask why was the island colonized differentially? Such differences may have arisen

through differences in area or habitat quality, e.g. numbers of potential nest-sites available, or once pairs started to breed in a particular area they may have served as attractants to other birds, e.g. as that place is likely to be free of predators and they are more likely to find mates there.

Why an extended period of laying?

It was shown that the overall laying period of Flatey Black Guillemots was extended by the unusually high number of new recruits laying later than the more experienced birds. Circumstantial evidence suggests that late breeders are on average younger than early layers. Why then did young birds lay later than older birds? Perrins' (1970) hypothesis is that young birds needed longer time to collect the reserves necessary for egg formation. Brooke (1978) could not reconcile this with observed information for Manx Shearwaters. He extended the hypothesis, suggesting birds not only delayed laying until they were able to form eggs, but also to incubate those eggs successfully.

Inherent in both hypotheses is the average leaner condition of young birds necessitating longer time to gather enough reserves to form the eggs. Two main points are important in this context. Young birds may be less efficient in gathering food, or young birds may arrive later on the breeding grounds. The latter may in fact be the result of the former.

In many seabirds, including Black Guillemots, pre-breeding birds may arrive at breeding stations later than do the breeders (e.g., Nelson 1966, Fisher & Fisher 1969, Ashcroft 1979, Chapter 3). Whether Black Guillemots which are starting to breed for the first time arrive later, is questionable. This is not necessarily to be expected, since even some yearlings are found at nesting areas long before laying starts. However in Kittiwakes, Coulson (1966) found the most experienced breeders laid earlier, than the less experienced ones, and the first time breeders are the last to lay.

If birds differ in their food-gathering ability, it is contended that as they grow older, they become better at finding food, are able to advance their laying date, increase

their egg size, and consequently their breeding success. It is possible to distinguish two aspects of feeding efficiency; young birds may take longer time locating and handling prey in a given area, or they may be less efficient in locating good feeding grounds. Although no one has demonstrated that feeding efficiency increases over 3-5 years (which are the ages at which Black Guillemots become mature), Orians (1969) and Dunn (1972) showed this was carried over 1-2 years in Brown Pelicans and Sandwich terns, respectively, comparing hunting success of young and old birds in same area. Norton-Griffiths (1968) found that Oystercatchers developed their skill of handling mussels over 3 years. These birds are all rather specialized in their feeding techniques and may be expected to take long to develop the technique. Perhaps one would not expect the same to happen in the surface-diving Black Guillemots.

Nelson (1966) and Ashcroft (1976: 151) found it difficult to believe that differences in feeding efficiency could persist for 4-5 years. Yet Brooke (1978) found that Manx Shearwaters increased in weight up to age 8-10, and suggested increased feeding efficiency was responsible up to 5-6 years. Also, in many species which do not get mature until several years old, young birds have been shown to be less able at feeding chicks than older birds (e.g. Coulson & White 1960, Ainley & Schlatter 1972). Hence there are obviously some factors associated with feeding which differ among young and old breeders.

The absolute amount of food available may be the determining factor. In Black Guillemots, the highest numbers of non-breeders seems to be in the pre-laying period (Chapter 3). If food was in short supply this is not to be expected. Also, 2-egg clutches were more common early in the laying season, there were no seasonal differences in fledging success, and no starvation evident (Chapter 6). Hence there is nothing which points to insufficient food being available early in the season.

None of these arguments mean that Perrins' and Brooke's hypotheses do not apply. Young birds may still find it more difficult to reach a required level of reserves, leading to their later laying. There is another aspect which may turn

out to be important, namely greater energy expenditure in young birds, perhaps by having to spend more time localizing good feeding areas; but also, I believe more importantly, in getting a suitable nest-site and mate. It is this latter point which I want to expand on.

In Razorbills, which show a specific laying order like Black Guillemots, the pattern of laying-date advance was disrupted if the pair-bond was not maintained, although apparently no delay of laying ensued (Lloyd 1976: 50). In Manx Shearwaters Brooke (1978) found a slight delay in laying following new pairing in established breeders. He also suggested that the pair-bond had a greater influence on the timing of laying than age or breeding experience.

In Black Guillemots it appeared that greater variability was introduced in the pattern of laying in the population late in the season (Fig. 5.7). This is to be expected since late layers were on average less successful, and if so, more likely to change sites and possibly mates (Chapter 3).

When individual birds start to breed may depend on several conditions, other than their fitness, e.g. which sex is involved, if the inexperienced bird mates with an established breeder or an equally inexperienced bird, and if the mate is already attached to a suitable nest-site or if the new pair has to find a vacant site. This will of course also apply to experienced birds whose pair-bond has previously broken up.

Even if no variability is introduced due to pair-bond breakages, site-changes, etc., birds laying at same time of season still showed much variation with respect to each other. Some birds advanced their laying date, while others retarded it, yet there was a net advance of laying date in those birds which kept same site and mate. These individual differences were probably associated with varying fitness of this category of birds, coupled with age and breeding experience.

From these, I conclude that greater failure in breeding by late-layers, leading to more site- and mate-changes, will delay their advance of laying date within their first few years of breeding; it may therefore take several years for these birds on average to reach an "optimum" laying date.

Chapter 6: Breeding biology II: Reproductive parameters, and factors affecting breeding success.

6.1 Introduction

The total number of eggs laid is the maximum reproductive potential of a population. Numerous factors are important in affecting the final outcome of breeding, which in the present context was the number of young fledging from the island.

This chapter is divided into two sections. The first deals with the main breeding parameters, clutch size, egg size, and reproductive output, the last represented by the number of eggs hatching of those laid (=hatching success), the number of chicks fledging from those hatched (=fledging success), and, finally, the number of chicks fledging from those eggs laid (=breeding success). The latter section deals with factors associated with the breeding performance of the birds, particularly concentrating on the significance of egg size.

6.2 Results

I. Breeding parameters

Clutch size

Unlike all other N. Atlantic alcid species, Black Guillemots normally lay 2 eggs in a clutch. So do their two N. Pacific congeners, the Pigeon Guillemot (Winkler 1947, Thoresen & Booth 1958, Drent et al. 1964) and the Spectacled Guillemot (Austin & Kuroda 1953), although Kozlova (1957:79) claims the last species only has one egg. Of the 22 extant species of alcids, the other species which normally lay 2 eggs are the two species in each of the genera Endomychura and Synthliboramphus (Dawson 1920, Storer 1945, Austin & Kuroda 1953, DeWeese & Anderson 1976). The two Brachyramphus species most likely only lay a single egg in a clutch (Kuzyakin 1963, Kishchinskii 1965, 1968, Sealy 1972, Bailey 1973, Binford, Elliot & Singer 1975, Simons 1980), although Dawson (1920) claims they normally lay two eggs. The frequency of 1-egg clutches within the Alcidae, is oftern over-emphasized.

As seen from above, about one-third of the family normally lays 2 eggs in a clutch.

The mean clutch size for Black Guillemots on Flatey was 1.93 eggs (1975, n= 189), 1.88 (1976, n= 346), and 1.90 (1977, n= 400). These give a weighted mean clutch size of 1.90 eggs, all years combined.

Two eggs was by far the most common clutch size (1975: 91.0% of the sample clutches; 1976: 87.9%; 1977: 85.5%). This is well-known for Black Guillemots (e.g., Hyde 1937, Winn 1950, Dennis 1966, Preston 1968: 28, Asbirk 1979b). Every year a sizeable proportion of the population of Flatey laid only one egg in a clutch (1975: 7.9%; 1976: 12.1%; 1977: 12.5%). A one-egg clutch is also a typical feature of the species' breeding phenology, although the proportions reported for different populations vary from 0 to 23% of the sample clutches (Hyde 1937 and Preston 1968:28 on Kent I. (New Brunswick), Bergman 1971 in Finland, Divoky, Watson & Bartonek 1974 in Alaska, Asbirk 1979b in Denmark, M. Norderhaug, pers. comm. in Spitsbergen). In Pigeon Guillemots the recorded frequency of 1-egg clutches is 7-21% for different populations (Thoresen & Booth 1958, Drent et al. 1964, Aitchison 1972: 6). I believe the methods and date of these observations have contributed at least as much to this variability as any actual, regional variations.

Clutches of 3 eggs were also recorded on Flatey; at 2 nests in 1975 (1.1% of the sample clutches), none in 1976, but 8(2.0%) in 1977. Three-egg clutches have been reported several times for Black and Pigeon Guillemots (e.g., Bianki 1967:187), constituting 0.5-3.5% of the sample clutches (Hyde 1937, Winn 1950, Drent et al. 1964, Preston 1968: 28, Aitchison 1972: 5). Most authors have regarded 3-egg clutches to be due to more than one female. Cairns (1978: 70) showed this in Black Guillemots through ringing, as did Drent (1965) in Pigeon Guillemots.

Of the 10 clutches of 3 eggs in the present study, 6 had one egg which differed from the others in size, shape, and colour, perhaps meaning that 2 females were involved. It is worth noting here that eggs in the usual 2-egg clutches rarely differed from each other in these respects. Of the four remaining clutches, each contained 3 eggs of similar appearence, so only

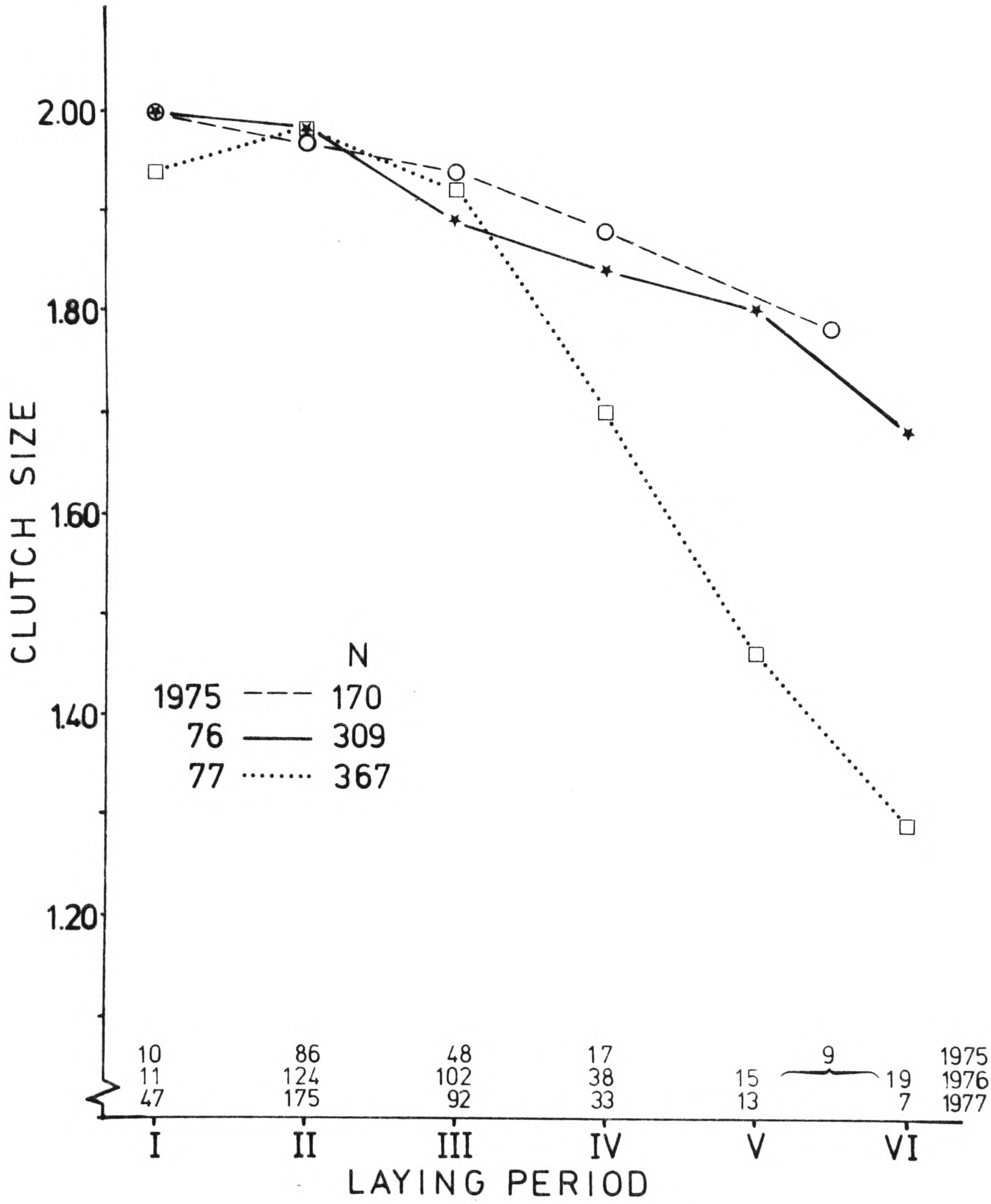
one female may have been involved. Three of these 4 clutches appeared to have been formed when one egg cracked, yet remained in the nest when a replacement clutch of 2 eggs was laid. Usually when eggs got broken or otherwise failed, they were removed from the nest, although frequently retained within the confines of the nest-site. Hence there was only one clutch of 3 eggs in which all the eggs may have been laid with the "intention" of forming a 3-egg clutch.

One nest (in 1977) contained 4 eggs. This was probably formed when the two eggs of a first clutch became cracked, two more being added later while the first set of eggs was retained in nest. Judging from size and colour all four eggs were laid by the same female. I have once before (on Hrisey I., N. Iceland) found 4 eggs at the same nest-site. The eggs were arranged in pairs but only one set was incubated. Colour of each set was similar but differed between sets, probably meaning two females were involved. "Clutches" of 4 eggs have rarely been reported in the literature for Black Guillemots (Bianki 1967: 187, Cairns 1978: 70, Asbirk 1979b).

Mean clutch size was analyzed by seven-day laying periods. As shown in Fig. 6.1 there was a decline in clutch size as the season progressed, as a larger and larger proportion of the clutches laid were 1-egg clutches. The more complete data for 1976 and 1977, adequately covering the whole of the laying season, showed a 16% decline in clutch size in 1976 between the first and the last laying period, but a 33.5% decline in 1977. Most of the changes between subsequent laying periods were not statistically significant but the total decline was (1976, $t_{28}=2.18$, $P<0.05$; 1977, $t_{52}=5.62$, $P<0.001$).

The pattern of decline in clutch size differed considerably in the latter half of 1977 from those in 1975 and 1976. The reason for this is not clear. Possibly preferred food species may have been less available in 1977, hence affecting egg production. Since this proportionally greater decrease in 1977 only took place late in the season, the mean clutch size for that year was not affected as only a small proportion of the total population was involved.

Fig. 6.1 The seasonal pattern in clutch size. Sample sizes are also given for each year and each laying period.



Egg size

Data for egg size, including fresh weight, length, breadth, and a volume index ($l \times br^2$), are given in Tab.6.I. There was a large range of egg sizes, in 1975 the lightest egg (32 g) was only 52% of the weight of the heaviest egg (62 g). The light egg was abnormally small, so a comparison between egg weights at the normal ends of the population distribution, is more appropriate. These were 39 and 61 g, the lightest egg being 63% of the weight of the heaviest egg. The extreme of intra-specific variation so far recorded among birds are, 58% in the Emperor and King Penguins (Lack 1968: 255), 59% in the Lesser Snow Goose (Ankney & Bisset 1976), and 58% in the Swift (O'Connor 1979). Such variation could be usual for many other bird species (C.M. Perrins, pers. comm.).

The size of eggs can have a profound influence on their success as demonstrated by Parsons (1970) in the Herring Gull. He also showed there were size differences between eggs of the same clutch according to laying order. The third egg in a clutch was the smallest and at a clear disadvantage to the other two eggs. Similar differences according to laying order, have been shown in many other species of gulls (see references in Mills 1979) and Woodpigeons (Murton, Westwood & Isaacson 1974), among others.

In Black Guillemots on Flatey the a-egg in a clutch tended to be bigger than the b-egg in 2-egg clutches, as shown in Tab. 6.II. The a-eggs were on average, 2.2% heavier than the b-eggs in the population. There was a good correlation between eggs of same clutch; if the a-egg was big, the b-egg also tended to be big (r_{91}=0.75, $P<0.001$; $y= 0.77x + 10.26$; data for 1975 only). But interestingly, the difference between the two eggs was not equal over the whole size range of eggs. If eggs in a clutch were small, there was tendency for the b-egg to be the larger of the two, but the reverse if the eggs in a clutch were large, as seen in Fig. 6.2. It is not quite known why this was the case, but this variation according to egg size may have survival value, as discussed more fully later (Chapter 8).

As with clutch size there was a progressive decline in mean egg size with season. This is illustrated using data on egg volume, for which sample sizes were greater than for fresh weight. Being indicators of the egg's biomass, volume is biologically the

Tab. 6.I. Fresh egg weight, length, breadth, and volume of Black Guillemot eggs from Flatey. Combined data for whole island.

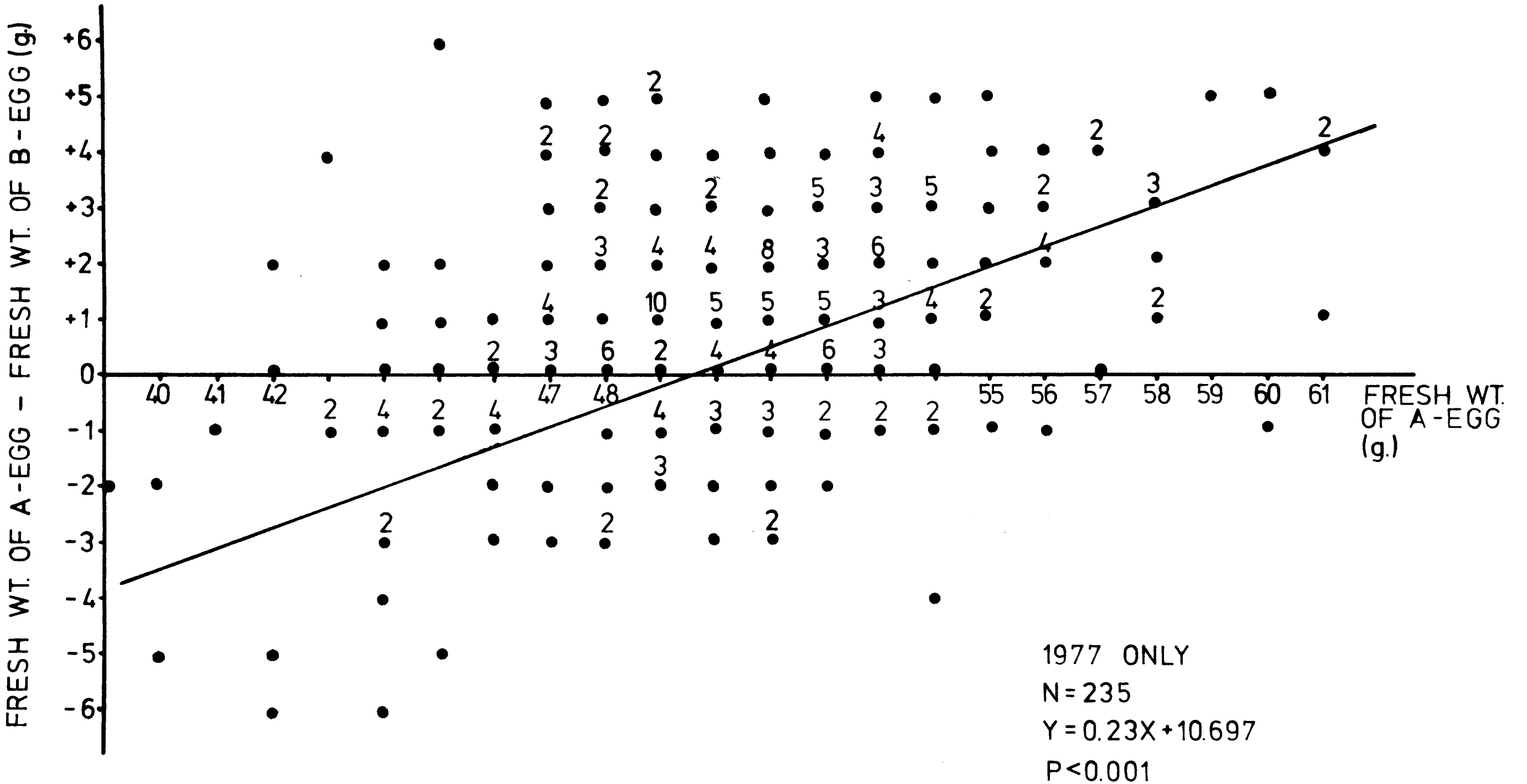
	Year	n	Range	Mean	S.d.
Fresh weight	1975	220	32 - 62	49.4	4.1
	1976	392	35 - 61	49.8	3.9
	1977	607	39 - 61	49.7	3.9
Length	1975	306	49.7x33.7 - 64.9x39.0	58.36	2.26
	1976	595	52.3x34.6 - 67.7x36.8	58.36	2.19
	1977	685	50.4x37.6 - 64.4x38.9	58.16	2.18
Breadth	1975	306	49.7x33.7 - 61.6x42.4	39.37	1.24
	1976	595	52.3x34.6 - 60.4x42.6	39.31	1.18
	1977	685	54.6x35.7 - 59.5x42.5	39.23	1.12
Volume($l \times br^2$)	1975	306	57.1 -110.8	90.61	7.37
	1976	595	62.6 -110.1	90.44	7.11
	1977	685	69.3 -109.9	89.62	6.90

Tab. 6.II. Comparison of fresh weight of the a- and b-eggs of same 2-egg clutch.

	Year: 1975	1976	1977	All years
Total no. of sets	91 .	163	235	489
No. of sets where:				
-a-egg=b-egg	10(11%)	28(17%)	34(14%)	72(15%)
-a-egg>b-egg	62(68%)	104(64%)	143(61%)	309(63%)
-a-egg<b-egg	19(21%)	31(19%)	58(25%)	108(22%)
a-egg:				
-Range	42 - 62	40 - 61	40 - 61	
-Mean	50.1	50.5	50.3	50.3
-S.d.	4.0	3.7	4.1	
b-egg:				
-Range	32 - 59	39 - 60	39 - 61	
-Mean	48.8	49.4	49.4	49.3
-S.d.	4.1	3.8	2.2	
Mean difference (%) (1)	2.7	2.2	1.8	2.0
t	2.14	2.67	2.56	
P	<0.05	<0.01	<0.02	

Note: (1) $\frac{\text{a-egg - b-egg}}{\text{b-egg}} \times 100$

Fig. 6.2. The difference in fresh weight of the eggs in 2-egg clutches according to the fresh weight of the a-egg in the respective clutch.


FRESH WT. OF A-EGG - FRESH WT. OF B-EGG (g.)
+6
+5
+4
+3
+2
+1
0
-1
-2
-3
-4
-5
-6
40
41
42
47
48
55
56
57
58
59
60
61
FRESH WT. OF A-EGG (g.)
1977 ONLY
N = 235
Y = 0.23X + 10.697
P<0.001

best to represent egg size but it should not matter whichever is used, as they were highly correlated (r_{219}=0.92, P<0.001; data for 1975 only).

Fig. 6.3 shows the seasonal decline in egg size. Most of the differences between subsequent laying periods were not statistically significant, but those between laying period I and laying periods V + VI were, as shown in the figure.

Consequently, not only did early nesters lay, on average, more eggs in their clutch, but their eggs were bigger. The same appears to be the case in Black Guillemots in Denmark, as 1-egg clutches were laid late in the season, and these eggs were smaller than those of 2-egg clutches (Asbirk 1978a: 24, 26-27).

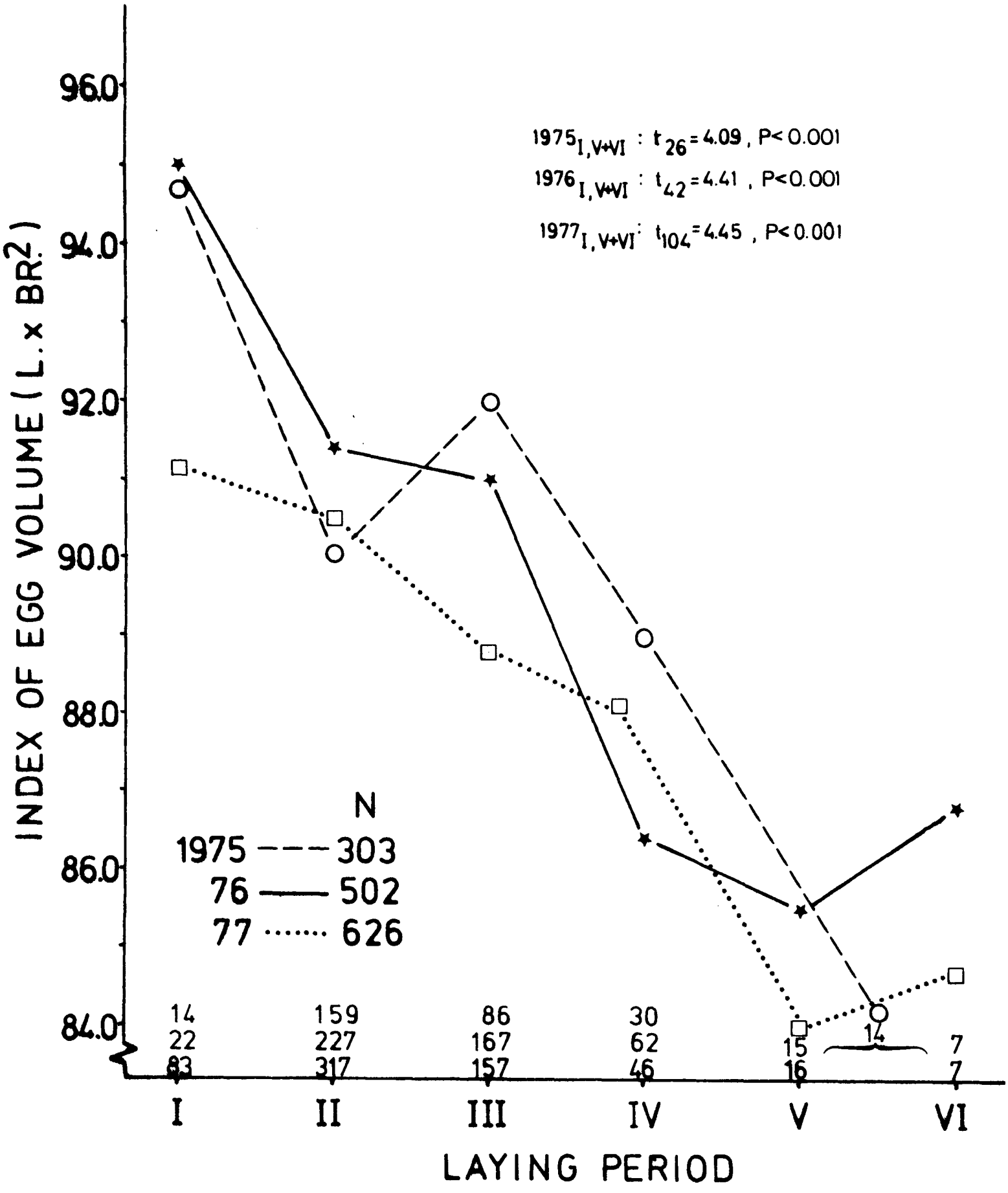
Reproductive output

Tab. 6.III summarizes the breeding performance of the Flatey Black Guillemot population in all three study years. The mean number of chicks fledging from the island, was 1.29 per nest, giving an overall breeding success of 67.9%. All the figures are calculated for the whole population, including unsuccessful nests. The losses of eggs were decidedly higher than losses of chicks, comparing those at risk. Breeding success was lowest in 1977. That year many eggs and chicks were lost during periods of heavy winds combined with high tides. This happened in early June at the beginning of the incubation period for most birds, and again in early July at the peak of hatching in the population (see Tab. 2.I, p.22).

As shown earlier (Fig. 6.1, p.126) there was a seasonal decline in clutch size. Given equal egg and chick mortality over the season, there would inevitably be a similar decline in the numbers of chicks fledging per nest. Instead this decline was more abrupt than that in clutch size, meaning losses were not equal over the laying season. They became progressively greater as the season progressed, as shown in Fig. 6.4. This means that deleterious factors associated with egg and/or chick quality became more and more prominent as the season progressed. This will be examined in more detail in section II.

II. Some factors associated with breeding performance

Fig. 6.3 Seasonal changes in egg size, as presented by egg volume (length x breadth^2).



Tab. 6.III. Reproductive performance of Flatey Black Guillemots 1975 - 1977.

	1975		1976		1977		Overall	
	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$
Clutch size	189	1.93	346	1.88	400	1.90	935	1.90
Nos. hatch.	164	1.56	296	1.60	354	1.41	814	1.51
Hatch. succ. (%)		80.8		85.1		74.2		79.5
Nos. fledg.	139	1.32	263	1.42	324	1.17	726	1.29
Fledg. succ. (%)		84.6		88.8		83.0		85.4
Breed. succ. (%)		68.4		75.5		61.6		67.9

Notes: (1) Clutch size: Mean no. of eggs laid at nests where eggs were laid at all.

Nos. hatching: Mean no. of chicks hatched per nest.

Hatching success: % of eggs laid which hatched.

Nos. fledging: Mean no. of chicks fledged per nest.

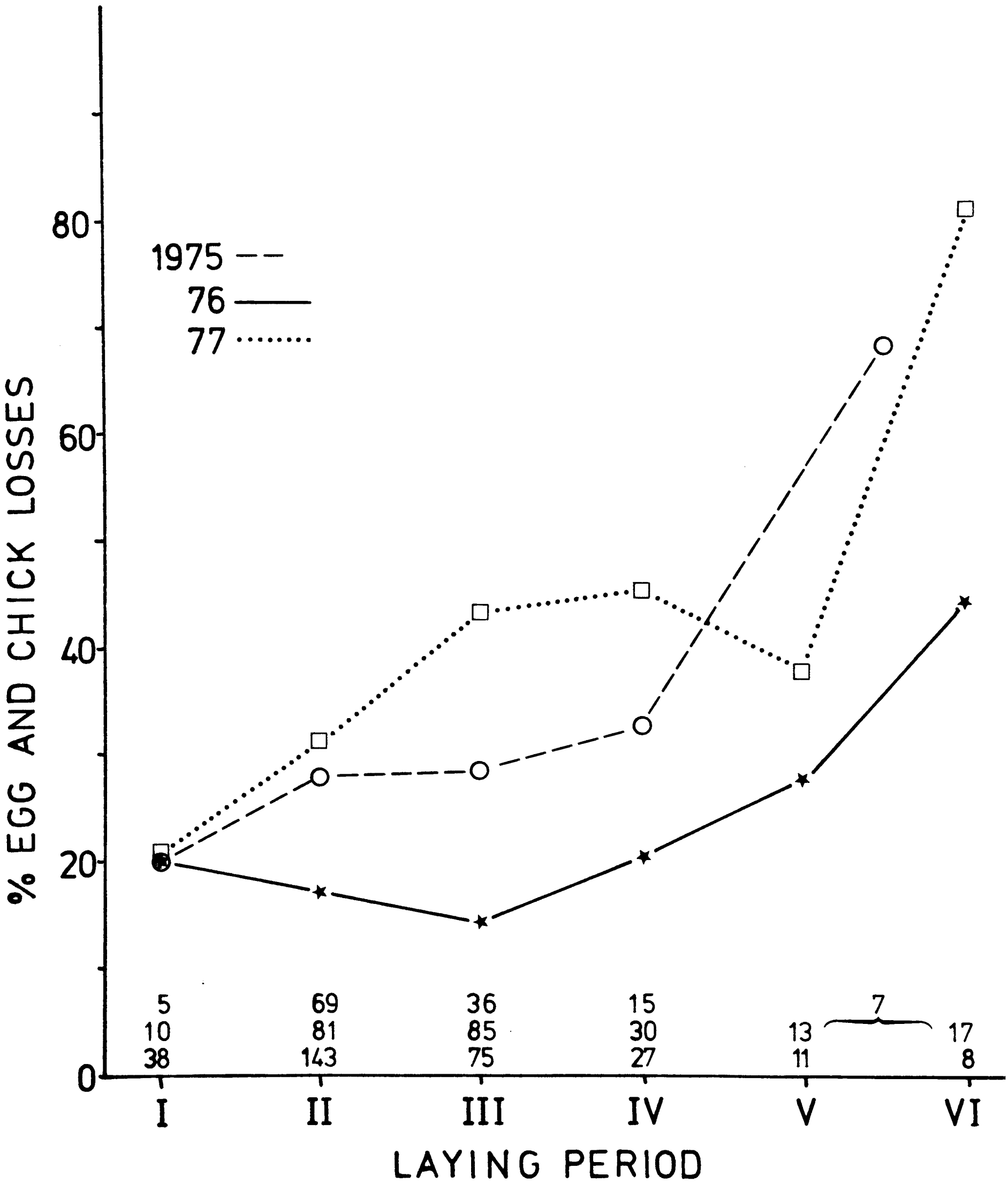
Fledging success: % of chicks which fledged per egg hatched.

Breeding success: % of chicks which fledged per egg laid.

(2) If clutch failed and was replaced, the success of the replacement clutch was included in the calculations.

(3) No experimental broods or those that failed as a direct result of my interference, are included.

Fig. 6.4. Seasonal changes in combined egg and chick losses.



Note: (1) The numbers in the figure represent the sample sizes; upper line for 1975, middle for 1976, lower for 1977.

Many factors have been shown or suggested to be associated with breeding performance in birds. These include, for instance, age and experience of breeders, time of season, position in colony, density of breeders, predation, dominance, nest-site and habitat quality, clutch size, and food availability. The study of each of these is greatly complicated by the inter-relations with each other. For example, nest-site quality may affect the breeding performance, but the choice of nest-site may be further influenced by age and/or experience of the breeders, which may independently affect the timing of laying. This may in turn be crucial for the outcome of breeding. Furthermore, the reproductive success can be influenced by the age or experience of the breeders directly, by them being good or bad incubators or feeders of chicks, or indirectly through choosing a good or bad nest-site.

In the earlier section it was shown that the quality of the eggs and/or chicks which hatched from them, was strongly associated with breeding success. In the present section I want to look more closely at this relationship, and try to identify some factors which may have influenced this result. The key questions I am asking are:(a) since low breeding success was associated with small egg size, was it because the eggs were small or because they were laid late in the season? (b) since clutch size declined with season, what influence did this have independent of egg size and season? (c) although having no effects on the laying date, did density and group size of the breeders have any effects on breeding success? (d) increase of new breeders affected mean laying date, which in turn was associated with breeding success; which of these had greater influence, if indeed there were independent effects of each on breeding success? and (e) was the lower success of small eggs associated with lower hatchability of the eggs or survival of the chicks which hatched from them?

Egg size and breeding performance

It may be inferred from the results of progressively lower breeding success as the season proceeded and the relationship between egg size and time of laying, that there was a strong relationship between egg size and breeding success. Egg size, presented by volume and given in steps of 5 cm^3, was plotted

against the proportion of eggs of each size class, giving rise to fledged chicks, and shown in Fig. 6.5. The results show the larger the eggs the proportionally greater was the breeding success. A similar relationship was shown by Parsons (1970) between egg size and chick survival in Herring Gulls, the first demonstration of such a relationship under field conditions, as pointed out by Davis (1975). Such a relationship has been repeatedly shown in chickens (see review by Landauer 1951). A positive correlation between egg size and hatchability was also shown in Quail (Insko et al. 1971). Yet, many studies have failed to show such relationships (see references in Parsons 1970).

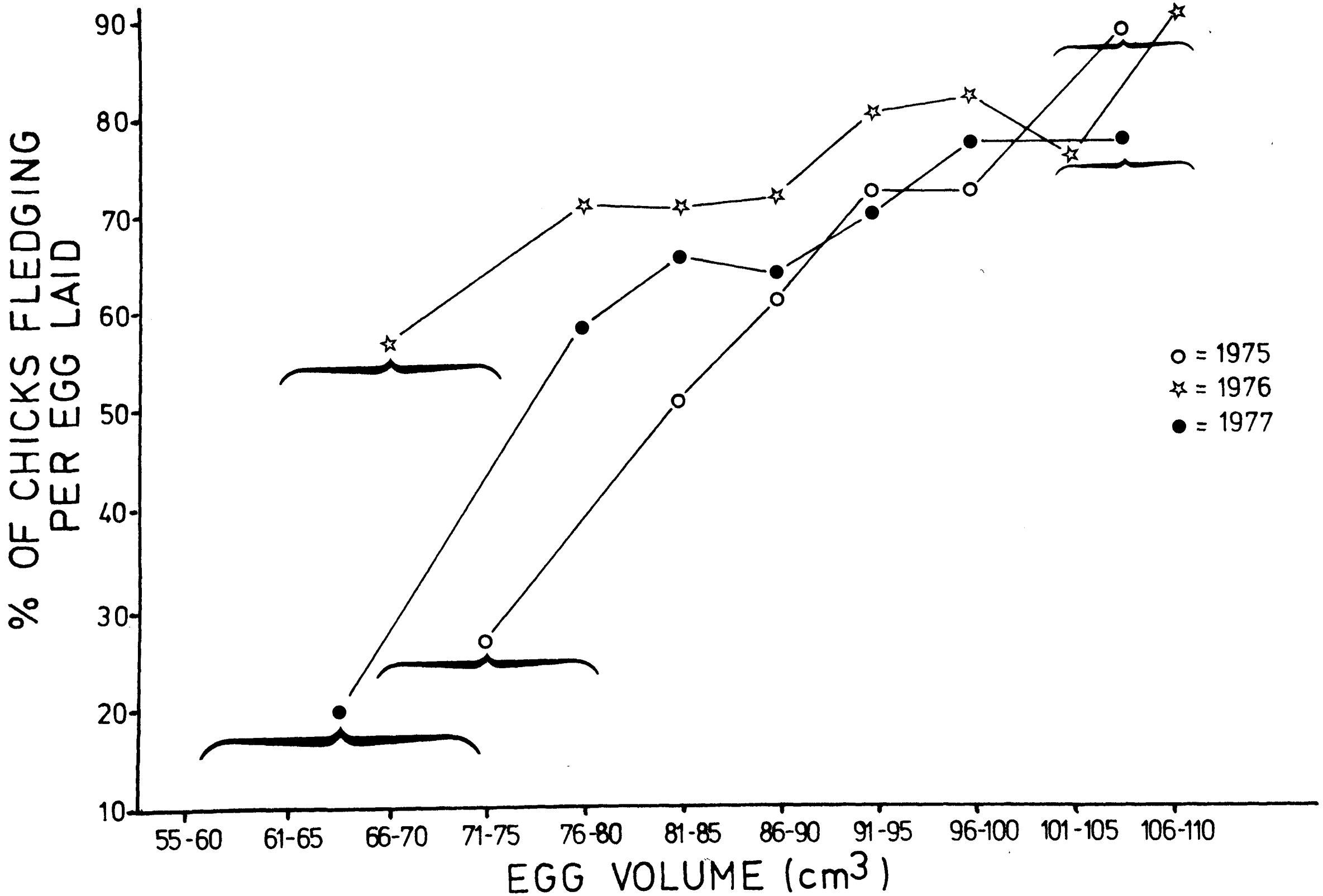
A relationship such as that in Fig. 6.5, may have arisen because of egg size directly, time of laying per se, or both. To distinguish between these effects, I analyzed the data according to egg size and time of season simultaneously. This is presented in Tab. 6.IV, which shows that breeding success was strongly correlated with both time of season and egg size. These results open up three basic questions: (a) what features of lateness of season lead to greater mortality of eggs and/or chicks?, (b) why were small eggs less successful than large eggs, and (c) why were eggs of same size but laid late in the season less successful than those laid early? These questions will be discussed later, the latter two in Chapter 8 in particular.

Clutch size and breeding performance

There was a seasonal decline in mean clutch size, as found for mean egg size. Hence small eggs were associated with small clutches. This means that since 1-egg clutches were laid, on average, later in the season than 2-egg ones, smaller eggs were found in 1-egg clutches. This is shown in Tab. 6.V.

It is possible that any potential effects of clutch size on breeding performance is direct or indirect, the latter by having effect through egg size. This was not expected a priori, since there was very little variation in clutch size, practically only one and two eggs.In a partial regression analysis, both clutch size and laying date were significantly correlated with egg size, as expected and shown in Tab. 6.VI. Decidedly

Fig. 6.5. The relationship between the size of eggs (volume) and the breeding success of those eggs, i.e. the % of chicks fledging per egg laid.



Tab. 6.IV. Changes in breeding success (%) with season, independently of egg size, and with egg size, independently from time of season. Sample size in parentheses. The means are unweighted. All years combined.

	Egg size ($l \times br^2$):				
Laying period	110-96	95-91	90-86	85-55	Means
I	100.0(14)	70.0(20)	77.8(18)	81.8(11)	82.4
II	82.6(46)	75.0(76)	76.5(68)	44.0(50)	69.5
III	72.2(18)	67.6(34)	50.0(34)	37.1(35)	56.7
IV,V,VI	62.5(8)	57.1(7)	46.2(13)	37.0(27)	50.7
Means	79.3	67.4	62.6	50.0	

Tab. 6.V . Differences in egg size (fresh weight) according to clutch size.

Year:	1975	1976	1977	All combined
1-egg clutches:				
n	8	21	32	61
range	43 - 56	39 - 52	39 - 58	39 - 58
$\bar{x}$	47.3	47.3	48.7	48.0
s.d.	3.8	3.6	4.0	
2-egg clutches:				
n	197	311	469	977
range	32 - 62	39 - 61	39 - 61	32 - 62
$\bar{x}$	49.5	50.1	49.8	49.9
s.d.	4.0	3.8	3.8	

Tab. 6.VI . Partial regression correlation, showing effects of clutch size and laying date, independently, on egg size. N= 17.

Independent variables	F-value	% explained	Significance
Mean clutch size [1]	22.84	60.4	P<0.001
Mean laying date [2]	68.12	82.0	P<0.001

Significance of mean clutch size added to mean laying date:

$$\frac{1.247}{2.28523} = 0.5457 \quad \text{n.s.} \quad df = 1, 16$$

more of the variation in egg size was explained by laying date than by clutch size (82%) and clutch size did not explain significantly more of the variation. Therefore clutch size can be ruled out as having an independent effect on egg size.

As expected, breeding output was strikingly related to clutch size, as shown in Tab. 6.VII. Not only did fewer chicks fledge from 1-egg clutches in actual but also in relative terms. Birds laying 2 eggs fledged about 3 times as many chicks as birds laying 1 egg. Since 1-egg clutches were laid, on average, later in the season, this difference may have been entirely due to timing of laying. A comparison was therefore made between breeding success of 1- and 2-egg clutches from same time of season, and is shown in Tab. 6.VIII. On the whole, 1-egg clutches did less well than 2-egg clutches laid at same time. But in two out of the seven laying periods compared, one-egg clutches did better in relative terms. Yet 2-egg clutches always fledged more chicks in actual numbers.

Effect of density, group size, laying date, and increase in group size on breeding output.

The above four independent variables were regressed against the number of chicks fledging as the dependent variable in a multiple regression analysis. Averages for nesting areas for which sufficient data were available, were used as basic units in the analysis.

The results are given in Tab. 6.IX, showing that an increase in breeders was the only significant variable. The greater the increase in new members of the breeding group, the less the breeding output per pair. This was not unexpected since this variable affected the timing of laying which in turn was correlated with breeding performance. It is worth mentioning also, that only 21% of the variation was explained, meaning that other factors are also very important. What was unexpected perhaps, was that laying date was not significant on its own, since there was a seasonal effect on breeding success independent of a egg-size effect. But as laying date was influenced by the proportional number of new breeders (p. 106) this can only mean that laying date per se is not important, rather something to do with the breeding birds

Tab. 6.VII . Breeding performance of Flatey Black Guillemots 1975 - 1977, analyzed according to clutch size. Natural first clutches only. Sample sizes in brackets. Only the "normal" clutch sizes of 1 and 2 eggs.

Cl. size	Year	Nos. hatch.	% H.S.	Nos. fledg.	% F.S.	% B.S.
1	1975	0.71 (14)	71.0	0.57 (14)	80.3	57.0
	1976	0.59 (39)	59.0	0.55 (38)	93.2	55.0
	1977	0.55 (47)	55.0	0.43 (47)	78.2	43.0
	All years	0.59 (100)	59.0	0.50 (99)	84.7	50.0
2	1975	1.65 (148)	82.5	1.42 (123)	86.1	71.0
	1976	1.75 (257)	87.5	1.56 (225)	89.1	78.0
	1977	1.56 (298)	78.0	1.32 (268)	84.6	66.0
	All years	1.65 (703)	82.5	1.43 (616)	86.7	71.5

Tab. 6.VIII.Breeding success (%) of Black Guillemots according to clutch size and time of season (in weekly laying periods).

Clutch size	Laying period	% Breeding success 1975	1976	1977
2	I	80.0	80.0	81.5
	II	76.0	81.5	71.0
	III	72.0	88.0	59.0
	IV	60.5	80.0	53.0
	V + VI	33.5	64.5	50.0
1	I	-	-	-
	II	-	-	50.0
	III	-	64.0	43.0
	IV	-	57.0	73.0
	V + VI	-	67.0	42.0

Unweighted means of figures in the boxes:	2-egg clutches:	77.5	58.3
	1-egg clutches:	62.7	52.0

Tab. 6.IX. Multiple regression analysis regressing numbers of chicks fledging (as the dependent variable) against % increase in breeders (x1), group size (x2), density (x3), and laying date (x4)(as the independent variables). N= 28.

Independent variable	F-value	% explained	Significance
% increase (x1)	6.79	21	<0.05
Group size (x2)	1.40	5	n.s.
Density (x3)	2.61	9	n.s.
Laying date (x4)	1.89	7	n.s.

themselves. As shown later, this is consistent with no effect of season on chick survival, hence presumably no effect of food availability throughout the season.

Analyses of egg and chick losses

An effort was made to identify the reasons for egg and chick losses during the study. The data were derived from examination of lost eggs and chicks, and an assessment made of the circumstances involved with mortality. In some cases the causes of mortality were known, in others these were assumed. It is realized that some of the causes may have been indirect only, and some other factor (or a combination of factors) may have been the ultimate cause. Some of the mortality categories to which losses were assigned, may therefore have been interrelated to some extent. The losses were categorized according to what was known or assumed to have happened.

Data for egg losses are given in Tab. 6.X, for chick losses in Tab. 6.XI. I divided the mortality categories into losses due to "independent" and "dependent" factors. Independent factors were regarded as those not related to the breeding birds themselves, rather they were environmental factors (rain, tides, rock fall, etc.). Dependent factors were those directly attributable to behaviour of the birds (egg breakage, desertions, etc.). Obviously these arbitrary groups are inter-related to a degree, e.g. adverse weather may have influenced parental behaviour, subsequently leading to losses. But below I present a synthesis of these data.

High tides: An appreciable part of all losses was attributed directly to high tides, as nest-sites were full of sea-water or fresh sea weed brought by high tides. This factor caused greatest losses in 1977, when during days of extreme high tides, amplified by heavy winds, many eggs and chicks were swept away. Many chicks also appeared to have died through chilling. These sites were situated low on the shore and if not actually flooded, received heavy sea spray. This happened in the beginning of June, when most birds were starting incubation and later in early July, when there was peak of hatching in the population.

Tab. 6.X . Analysis of egg losses.

Year:	1975	1976	1977	All yrs.
Total eggs lost	67	92	192	351
% losses associated with "independent" factors:				
-High tides	12	22	26	22
-Heavy rain	4	9	4	5
-Heavy winds	0	1	0	0
-Rock fall	3	0	0	1
-Death of parent	0	0	3	1
-Raven predation(?)	6	0	1	1
% losses associated with "dependent" factors:				
-Infertility	4	6	4	5
-Fell from site	0	0	1	1
-Exposure: died 1st week	15	9	12	12
- " : died mid incb.per.	1 } 20	2 } 19	0 } 19	1 } 20
- " : died last week	4	8	7	7
-Difficulty in incubating	7	0	10	7
-Cracked in nest	1	17	6	8
-Clutch deserted:never incub.	27 } 36	6 } 14	8 } 10	11 } 16
-Clutch deserted:incubated	9	8	2	5
% other losses:				
-Vanished from site	1	3	4	3
-Cause (and time) unknown	3	9	11	9
Egg losses as % of all losses:	74	79	77	77

Tab. 6.XI . Analysis of chick losses.

Year:	1975	1976	1977	All yrs.
Total chicks lost:	24	24	58	106
% losses associated with "independent" factors:				
-High tides	13	13	10	11
-Heavy rain	4	4	2	3
-Rock fall	0	0	2	1
-Death of parent	0	0	9	5
-Raven predation(?)	4	4	0	2
-Disease	8	8	0	4
-Stuck between rocks	4	4	0	2
% losses associated with "dependent" factors:				
-Fell from site	8	8	2	5
-Exposure: died first days	17	17	52	36
- " : died mid incub.per.	8 } 25	8 } 25	10 } 64	9 } 46
- " : died last nestl.per.	0	0	2	1
-Vanished from site	21	21	9	14
-Choked	4	4	3	4
% other losses:				
-Cause (and time) unknown	8	8	0	4
Chick losses as % of all losses:	26	21	23	23

Heavy rain: Several nest-sites, usually the same ones in different years, became flooded during torrential rains, when run-off filled sites as water could not filter away fast enough. These were primarily sites at which eggs were deposited on bare earth or solid rock.

Death of parents: This was only evident in 1977, although in most cases this could not be proven. Fishing for Lumpsucker (Cyclopterus lumpus) was started in 1975 in the Flatey region, but pursued especially intensively in 1977. This fishery was a cause of mortality of adults, as well as immature birds (Chapter 11). In 1977 it was calculated that 11 Flatey breeders had drowned during the breeding season (see p.294). In one case only could egg losses be traced directly to the death of an adult. The surviving mate did not manage to incubate the eggs to hatching.

Infertility: About 5% of all eggs which did not hatch were judged to be infertile. This constituted 0.9% (1975), 1.0% (1976), and 1.2% (1977) of the total eggs at risk (= eggs in nests where hatching success was known). Although the numbers were generally small, interestingly the greatest proportion of infertile eggs occurred either very early or very late in the breeding season, as shown in Tab. 6.XII. Most often only one of the eggs in 2-egg clutches was infertile. Of 8 eggs of known hatching order, 4 were a-eggs, and 4 b-eggs. Hence there was no difference in which egg was more often infertile.

Difficulty in incubating: This refers to eggs in 3-egg clutches. Black Guillemots only have two brood patches, and it was obvious that incubating birds were not able to cover 3 eggs adequately (see Chapter 12).

Exposure: This seemed one of the most important causes for egg and chick losses. This was most marked the first few days of the incubation and nestling periods, but also in eggs in the pipping stage.

Egg-breakage: Eggs apparently got cracked when accidentally knocked about by the adults. This is more likely to have happened at sites which had a rough nest substrate, most frequently seen in new sites. Old sites had normally been improved by accumulation of nest material. Cairns (1978: 67-70) found a significant relationship between particle size in nests'

Tab. 6.XII . Seasonal changes in the frequency of eggs judged to be infertile. Data for 1975, 1976, and 1977 combined.

Laying period	Nos. of eggs at risk	Nos. infertile	% infertile
I	133	4	3.0
II	761	5	0.7
III	463	3	0.7
IV	158	1	0.6
V	58	1	1.7
VI	45	2	4.4

substrates and hatching success in Black Guillemots; the coarser particles, the greater chance of egg damage.

Desertion: If clutches were deserted, and this was an important cause of loss, this most commonly took place before incubation had started. The reasons for desertion were unknown. Chicks were never deserted.

Vanished from site; Cause unknown: These categories probably included eggs and chicks which had died of exposure, and eggs which were cracked. Included were eggs and chicks which were never found or those pushed out of the nest even though the other egg/chick remained.

Heavy wind, Rock fall, Fell from site, Disease, Choked, Predation, Stuck between rocks: These were all very minor causes of loss. It is particularly interesting to note that predation was virtually non-existent. Ground predators no longer existed on the island (cf. Chapter 2), avian predators comprised almost exclusively Glaucous and Great Black-backed Gulls, and Ravens, but these normally had no chance to get at eggs and chicks. The low frequency of predation is especially pertinent in light of Asbirk's (1979b) results for same species. He found that predation by Herring Gulls, (and probably Great Black-backed Gulls and Hooded Crows) was the major cause of egg and chick losses. The majority of his Black Guillemot nest-sites were rather open and shallow, especially those among boulders. This is contrary to the situation on Flatey.

Seasonal changes in egg and chick losses

It was shown earlier (Fig. 6.5, p.138) that there was a relationship between egg size and breeding success, smaller eggs giving rise to relatively fewer chicks. Thus the question is raised; did small eggs show less hatchability, the chicks from these survive less well, or both?

In order to answer this question, I analyzed the egg and chick losses separately, and the results are shown in Figs 6.6 and 6.7. The pattern of egg losses followed closely the trend in overall losses, while chick mortality was much the same throughout the season. Therefore, birds which laid small eggs had lower breeding success because of lower hatchability of their eggs. Since small eggs were laid, on average, later in the season, late breeders not only laid fewer eggs but showed less overall

Fig.6.6. The seasonal changes in hatching success, i.e. the % numbers of chicks hatching per egg laid.

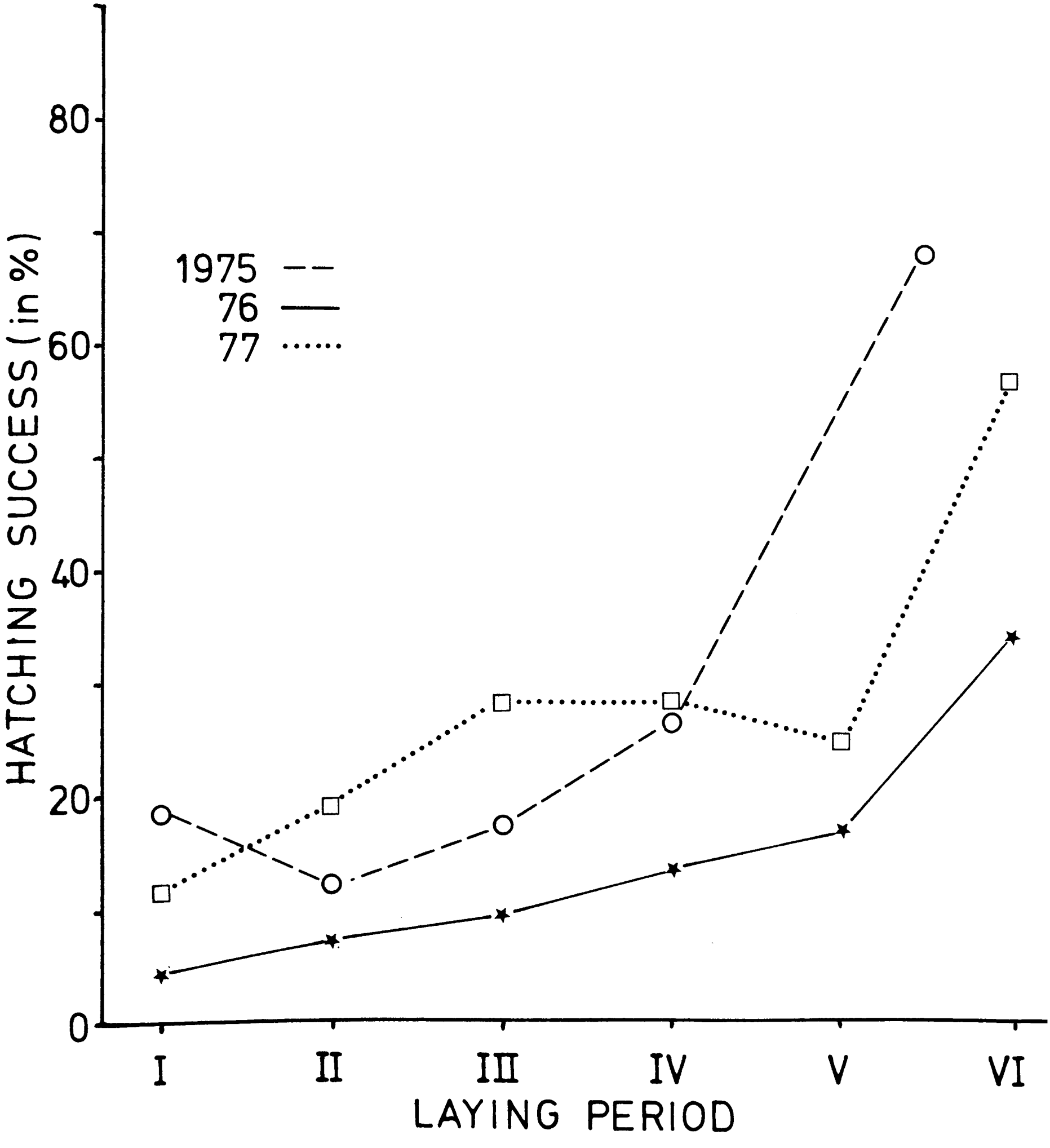
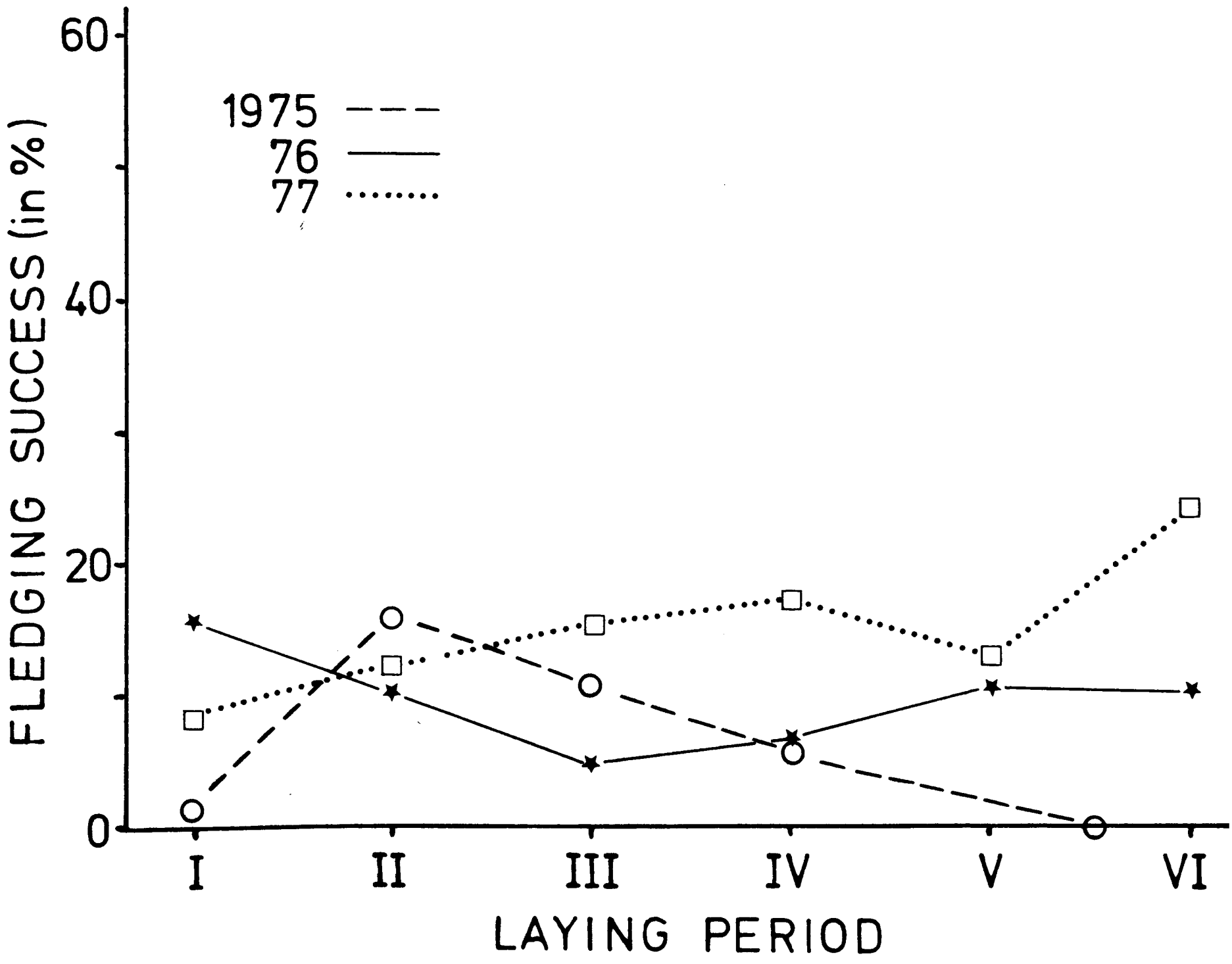


Fig. 6.7. The seasonal changes in fledging success, i.e. the numbers of chicks fledging per egg hatched.



breeding success. But as long as birds laying small eggs managed to hatch their eggs, they showed just as good fledging success as those laying large eggs.

Egg-component analysis

One reason why small eggs may have been less successful than large eggs, is if they had relatively fewer reserves for the developing embryo. In an analysis of egg components the yolk and white were separated and weighted, the remainder being shell and membranes.

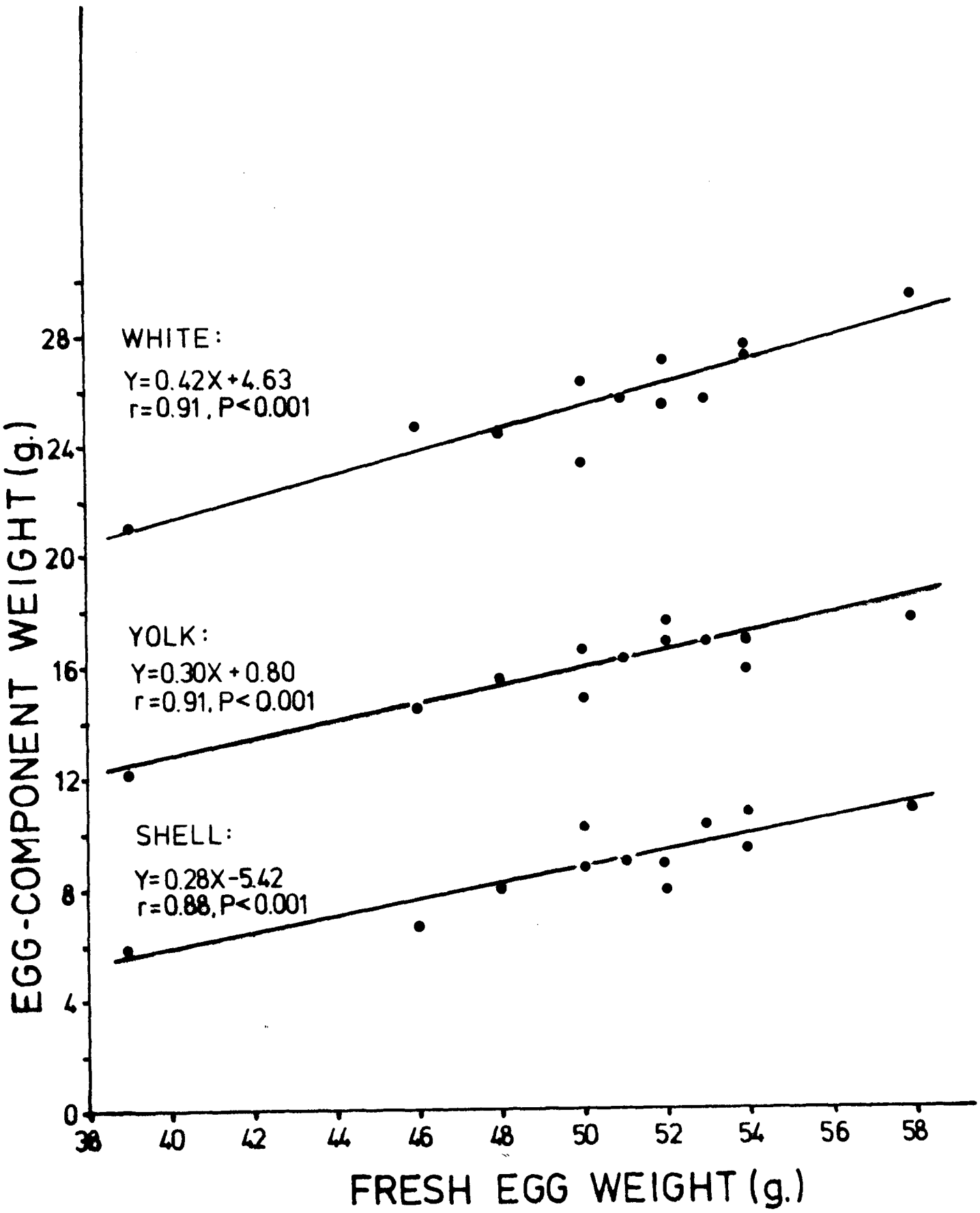
Fig. 6.8 shows there was a linear relationship between fresh egg weight and all the egg components, which were present in the same proportions whether eggs were large or small.

Possible effects of disturbance on breeding success

Cairns (1978, 1980), studying Black Guillemots on islands in the St. Lawrence estuary, concluded that poor breeding success was mainly due to observer disturbance and dismissed that density, habitat characteristics, or other features were more important. Robert & Ralph (1975), studying Western Gulls, also found that with increasing levels of disturbance, an increasing proportion of the eggs at risk was lost as the season progressed, while chick survival tended to increase at the same time. These results reflect very much the findings on Flatey, proportional egg losses increasing with season, while chick mortality stayed similar. My data from Flatey therefore need to be examined in light of these findings, although disturbance effects were not anticipated at the start of the study.

Potential levels of disturbance were undeniably present on Flatey. All the nesting areas were walked through daily to quantify the basic breeding parameters and this may have had adverse effects at critical stages in the birds' breeding cycle. Adults were captured on nests and it was known that nests were deserted as a direct result of my interference, on average 4.4% of the sample nests every year (see p. 96). It is much more difficult to quantify possible indirect effects. Even

Fig. 6.8 The relationship between fresh weight of Black Guillemot eggs and three components of those eggs, yolk, white, and shell.



though Black Guillemot nests were not being examined, walking in the neighbourhood of their nesting areas caused some of the breeders to leave their eggs and fly down to the water. This occurred when tourists, for instance, walked over the island, although not necessarily in the immediate vicinity of the Black Guillemot nesting areas. Alarm calls from Redshanks, Arctic Terns and Oystercatchers, the first two very common breeders (Petersen 1979), readily elicited escape responses in Black Guillemots nearby.

These are then the main arguments for observer disturbance on Black Guillemot breeding success, but below I argue against this effect being important.

In general, Black Guillemots appear to be very tolerant of humans, and nest in close vicinity to them, underneath occupied houses, in piers, etc. where there is constant traffic by people every day. I have hypothesized elsewhere (Petersen 1979) that Black Guillemots have evidently been able to colonize Flatey in such large numbers because the island was inhabited. This comes about through possible competition with Puffins, which tend to be more reluctant to nest close to human quarters than Black Guillemots.

Cairns (1978: 68) found average breeding success 19.4-50.0% on different study islands. On Flatey, this was 61.6-75.5% in different years. Even when all nests which failed due to direct interferences are included, the breeding success was still 58.4-70.2% on Flatey, or much higher than Cairns' 19.4% for heavily disturbed area and somewhat higher than the 50.0% for his lightly disturbed areas. Hence breeding success was much better on Flatey, even though the birds were subjected to daily visits as was Cairns' heavily disturbed area.

I divided the island into two areas of "lightly disturbed" and "heavily disturbed" zones. This was based on the location of the settlement area where traffic was constant every day and within which most tourists confined themselves during their visits to the island. The lightly disturbed area was not much visited by people other than the observer. The results, found in Tab. 6.XIII, indicate that if anything breeding success was higher in the heavily disturbed zone. Yet the results are not conclusive. It is possible that those birds which were more susceptible to human disturbance tended to colonize the eastern

Tab. 6.XIII. Breeding success (%) of Black Guillemots nesting in "lightly disturbed" and "heavily disturbed" areas on Flatey.

	1975	1976	1977
Lightly disturbed	62.7%	74.2%	63.2%
Heavily disturbed (1)	69.4%	76.2%	65.6%

Notes: (1) Includes the western half of the island where the settlement was located and the north side of the island towards the observation hut on that side (see Fig. 1.4, p. 13). This includes nesting areas XIII, XIV, XV, I, II, III, IV, and V, see Fig. 2.3, p. 25.

half of the island rather than the part where the settlement is located. Also, levels of disturbance, due to my nest inspections every day, may have been above a certain critical limit anyway, so disturbance due to other people may not have had additive effects.

Another analysis was made, comparing chick productivity on Flatey as a whole with the uninhabited, very much undisturbed, islands within about 1 km radius of Flatey. The data are presented in Tab. 6. XIV. The mean number of fledged chicks was the same comparing the two time series, but that on the uninhabited islands a little higher, which seems trivial for the purpose of the present analysis. This is especially so by noting the variations between years; sometimes the Flatey estimate was higher in a given year, sometimes that from the other islands. I conclude that no observer, or disturbance, bias could be detected in the Flatey data.

6.3 Discussion

Productivity estimates in other populations

In Tab. 6.XV I collected all the available information from the literature and other sources on reproductive performance of Black Guillemots in other parts of the species' breeding range. As far as was possible, these were standardized so as to be directly comparable with Flatey data. The different ways in which the authors presented or gathered their data made this difficult. In some cases it was known (nos. 4,15) or suspected (8,9) that figures included only successful nests, and in most studies the data were not collected over the whole laying season. One (11) was known to be from only the latter part of the season. There may be seasonal changes in breeding success as seen on Flatey. Therefore if breeding data were collected only in certain parts of the laying season, some variability may have resulted, when comparing studies.

The figures used for direct comparison with my results, the percentage breeding success, were all calculated in same way. Much variation was evident between populations, ranging from 82.0% (Russia) to 26.1% (Canada). Ten studies, other than mine, gave an unweighted mean breeding success of 47.1%, compared with my 67.9%.

Tab. 6.XIV. A comparison of chick productivity (=the mean number of chicks fledging per nest) between Flatey and the surrounding islands. The sample sizes (numbers of nests in calculation) are given in parentheses. The information available is divided into two periods of time (see below).

	Flatey:	Other islands:
The years 1975-1977:(1)		
1975	1.32 (139)	1.51 (100)
1976	1.42 (263)	1.17 (35)
1977	1.17 (233)	1.38 (93)
Mean	1.30	1.35
The years 1978-1980:		
1978	1.22 (362)	1.17 (116)
1979	1.23 (334)	- -
1980	1.43 (346)	1.53 (68)
Mean	1.29	1.35

Note: (1) The reason for dividing the data into 2 time periods is as follows: During 1975-1977 the effort on Flatey was extensive, while productivity estimates in other islands were based on single visits. Hence these were not comparable in accuracy. In 1978-1980 on the other hand, estimates were made in the same way, on Flatey and in the surrounding islands.

Tab. 6.XV . Reproductive performance in various Black Guillemot populations.

Authority	Study yr(s)	Country	Clutch size		Nos.hatch.		% H.S.	Nos.fledg.		% F.S.	% B.S
			n	$\bar{x}$	n	$\bar{x}$		n	$\bar{x}$		
Bergman (1971)	1963 - 1970	Finland	31	1.91	31	1.91	100.0	31	0.90	47.1	47.1
Nordberg (1950)	1945	Åland	9	(1.56)(1)	9	(1.56)(1)	(100.0)(1)	9	1.33	85.3	<85.3
Anderson & Rosenlund (1973)	1963 - 1972	Sweden	-	-	79	1.46	-	65	1.2	82.2	>60.0
Olsson (1974)	1954 - 1973(?)	Sweden	-	-	-	-	-	105	1.62	-	-
Asbirk (pers.comm.)	1975 - 1976	Denmark	244	1.82	244	1.04	57.1	244	0.52	50.0	28.6
Barrett(" ")	1973 - 1975	Norway	140	1.94	68	1.62	83.5	68	1.36	84.0	70.1
Norderhaug (pers.comm.)	1970	Spitsbergen	10	2.00	10	1.70	85.0	-	-	-	-
Bianki (1967: 196)	1957 - 1958	Russia	194	2.00	-	-	-	194	1.64	-	82.0
Rabodzei (in Bianki 1967: 195)	1958 & 1960	Russia	29	2.00	29	1.5	75.0	29	1.4	93.3	70.0
Petersen(pres. study)	1975 - 1977	Iceland	935	1.90	814	1.51	79.5	726	1.29	85.4	67.9
Broad (pers.comm.)	1973 - 1977	Britain	104	1.43	104	0.56	39.2	46	0.41	73.2	28.7
Winn (1950)	1947	Kent Island U.S.A.	49	1.84	46	0.96	52.4	46	0.48	50.0	26.1
Preston (1968: 28)	1962, 1964 - 1967	Kent Island U.S.A.	189	1.78	189	0.96	53.9	189	0.85	88.5	47.8
Hyde (1937)	1936 - 1937	Kent Island U.S.A.	92	1.95	-	-	-	-	-	-	-
Gaston (pers.comm.)	1976	Pr.Leopold Is.,Canada	-	-	-	-	-	25	1.25	-	-
Cairns (1978:68)	1976	St. Lawrence estuary, Can.	212	1.88	212	1.07	56.9	212	0.69	64.5	36.7
Divoky, Watson & Bartonek (1974)	1972	Alaska, U.S.A.	17	1.76	-	-	67	-	-	50	33.5

Notes: (1) Some egg losses have probably incurred.

There appear to be differences between birds nesting towards the middle of the overall range of the species and those nesting more peripherally. This is shown in Fig. 6.9. One may perhaps expect fringe areas to be in some way less suited for living than more central ones. A species' distribution is of course determined by an array of factors (cf. MacArthur 1972:127 et seq.) but the ultimate balance lies with recruitment and losses. In Black Guillemots as in other species of birds, too little is known about emigration, age of first breeding, adult survival, and other factors influencing population dynamics, to allow any meaningful comparison between areas. If breeding success is generally low in fringe areas, the population may not be able to maintain themselves without immigration unless the age of first breeding is lower.

Productivity estimates and disturbance

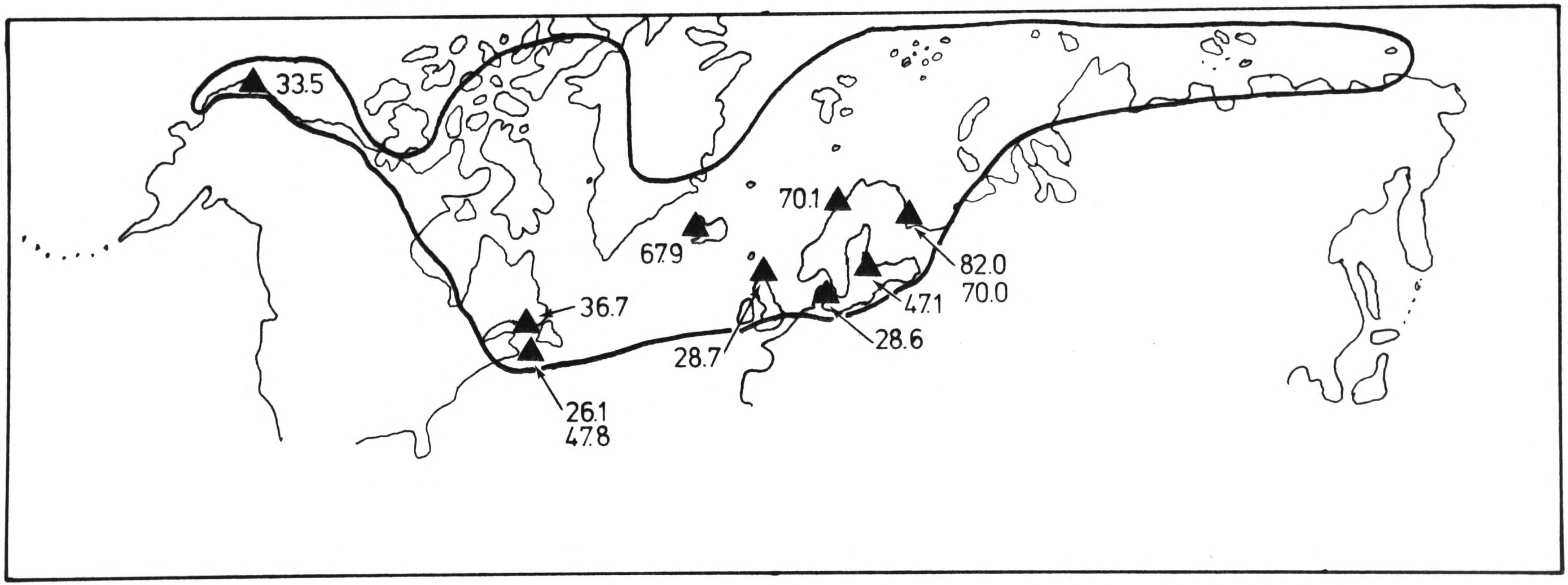
Studying productivity in birds can run the risk of the researcher causing undue disturbance. Cairns (1978, 1980) showed this in Black Guillemots, results which could not be ignored in the present study, although no special study of this was included when the field work was planned.

Ashcroft (1976: 74) noted in Puffins that productivity estimates were mostly unsatisfactory due to human disturbance. Such effects have long been known in open-nesting birds, where the researchers have increased the inter-specific or intra-specific rate of predation (e.g., Hunt 1972, MacInnes & Misra 1972, Gillet, Hayward & Stout 1975, Ellison & Cleary 1978). Often no account has been taken of such effects, although recognized as relevent.

In the present study it could neither be satisfactorily proved nor disproved that no harmful effects resulted from the nest inspections. This was nonetheless greatly suspected, in light of rather unusual patterns of egg and chick losses observed, which were similar to those found in Western Gulls by Robert & Ralph (1975) who experimented with different levels of disturbance.

If there was a real disturbance effect on Flatey the

Fig. 6.9. The breeding success (in %) for various Black Guillemot populations which have been studied. The figures are found in Tab. 6.XV. The thick, continuous line represents the boundaries of the world breeding distribution of Black Guillemots.



Note: (1) Adapted from Voous (1960: 171), with additional information from Dementiev et al. (1951: 232), Swatrz (1966: 655-656), MacLean & Verbeek (1968), Divoky et al. (1974), Brown et al. (1975: 192), Kuyt et al. (1976), and Sowls, Hatch & Lensink (1978: 20).

observed seasonal patterns of egg and chick losses may have come about as follows. As the season progressed, more and more of the breeders would be young, inexperienced birds, presumably more susceptable to disturbance than more experienced birds. Hence more and more eggs were lost, or to put it the other way round, a selection was made for the most competent birds, i.e. those able to hatch their eggs. Therefore, as the season progressed, the average "standard" increased from what it was at the time of egg laying. This may have resulted in the observation that mean fledging success did not change with season. However there are other interpretations of those results as mentioned later.

Given there was an observer effect, one may ask if the results would not be of greatly less use. To some degree this will be so, e.g. if one wants to discuss the evolutionary significance of Black Guillemot breeding strategy. But for many other aspects the data should be perfectly valid.

The ecological significance of egg size

Seasonal effects dominated in every aspect of Black Guillemot breeding. Laying dates spread over 6-6½ weeks (Chapter 5), mean clutch size, mean egg size, and average breeding success declined with season. It is particularly noteworthy that breeding success declined more rapidly than expected from the seasonal changes in mean clutch size.

Numerous studies have shown that early breeders rear greater number of young to fledging than late layers, that young birds lay on average later than older birds, and young birds lay smaller eggs than older birds. Some studies of these aspects, include: Yellow-eyed Penguin (Richdale 1955), Kittiwake (Coulson & White 1956, Coulson 1963), Great Tit (Perrins 1965), Short-tailed Shearwater (Serventy 1966), Oystercatchers (Harris 1969), Shag (Coulson, Potts & Horobin 1969), Red-billed Gulls (Mills 1973), Herring Gulls (Parsons 1975), Arctic Tern (Coulson & Horobin 1976), Puffins (Ashcroft 1976),Razorbills (Lloyd 1976). My circumstantial evidence for Black Guillemots indicate that young birds laid on average later than old birds, hence laid smaller eggs and did worse in terms of numbers of chicks fledged.

It has been debated what characteristics of late breeding

lead to greater losses. Perrins (1965, 1970) argued that late breeders were unable to feed as efficiently as early breeders. Late breeders may be in poorer condition, in turn an effect of their feeding efficiency. If this was so, it would be expected that late breeders were not as able to feed their young as early layers, other factors, such as food supply, being equal. Since chick losses were proportionally the same over the whole season, late layers may have been just as efficient food-providers as early birds. However, there are other explanations as mentioned earlier and later. In Chapter 5 I suggested that late breeders may not necessarily be any less efficient in finding food, but may have to procure greater amount of food, partly because they may spend more energy on site-and mate--finding, perhaps coupled with lower social status, or because of these activities have less time to spend on feeding.

In Black Guillemots there was a clear relationship between egg size and breeding success, the bigger the eggs the greater their success. It has been long known in poultry that chicks hatching from large eggs have a better chance of surviving than those from small eggs (Upp 1928, Wiley 1950). Parsons (1970) was the first to show such relationship in wild birds, the Herring Gull. Schifferli (1973) showed similar relationship in late-nesting Great Tits, not apparent in early nesters. Parsons suggested this relationship resulted from small chicks having less lipid reserves, but Davis (1975), working on same species, contested that idea and suggested the difference was due to the age structure of the population, younger birds laying smaller eggs. This certainly appeared to be so in the present study, but Parsons' argument is by no means ruled out. Nisbet (1978) did some egg-change experiments to look at the role of these factors in Common and Roseate Terns. He concluded that lipid content did not seem important, nor did he consider the observed differences in breeding success between two study colonies to be explicable in terms of differences in age structure. It was suggested that differences in chick survival were mainly due to the amount of protein available.

Unlike the above studies, differences in egg size and breeding success between Black Guillemot pairs, were emphasized

at the egg stage rather than the chick stage. As argued earlier, this may have come about through observer interference, but even if that was true, the relationship between egg size and breeding success will be valid, reflecting individual differences. The seasonal decline in egg size was most likely associated with on average increasingly younger birds as the season progressed. This relationship may have come out particularly strong because of unusually high numbers of birds with little or no breeding experience.

Since egg size was highly correlated with time of laying, the greater success of large eggs may have been associated with laying date (which, in effect, means the birds themselves) or egg size per se. Both effects were prevailing, which brings out two questions; why did late-nesting birds which laid large eggs do worse than early layers which laid same size of eggs, and what characteristics of small eggs made them less successful than large eggs laid at same time?

I suggest the answer to both questions, is the same. Birds which lay late and those which lay small eggs, are less attentive, because they are poorer "quality" birds. Admittedly it can be argued that they are less attentive merely because they are younger and less experienced breeders. I believe condition is the underlaying factor, and in this context, the results in Shag by Coulson, Potts and Horobin (1969) are of interest. They showed that late layers of same age as some early layers, laid smaller eggs. They attributed this to decreased "reproductive drive" but did not define that further, although saying, as did Parsons (1975) for Herring Gulls, that late layers may have shorter periods for egg development. If this was right, this would show up in the length of the laying interval between eggs. No regular relationship was revealed in the case of Black Guillemots, although large eggs tended to be formed after either a long or a short laying interval than the usual 2-3 days (Chapter 8).

If birds which lay later in the season are less attentive, because their body condition is worse, small eggs are at an added disadvantage compared with large eggs, as they loose heat faster. Drent (1970) showed that parental attendance in Herring Gulls was low in the very beginning of incubation but increased gradually, with similar pattern of decline at the end

of the incubation period. If this applies to Black Guillemots, egg losses would be expected to be greatest exactly during these periods, which was observed (Tab. 6. X, p.147). Drent (loc.cit.) demonstrated that small eggs loose heat faster than large ones. As a result small eggs would be exposed to a potentially lethal temperature regime for longer time than large eggs, hence be more liable to failure. At the end of the incubation period, it may be expected that embryos have started to generate some heat, so their survival will be to some extent dependent on the reserves available. Since there was a linear relationship between egg size and the egg components, and there is a linear relationship between existence metabolism and body weight (Kendeigh 1970), large embryos should be able to last longer on their reserves than small ones. So in conclusion, if late nesting birds are both less attentive and have smaller eggs, the egg losses will be expected to show an exponential relationship with season, what was observed (Fig. 6.6, p.152).

One question remains to be answered; why should late layers be expected to be less attentive? To some extent this may also apply to early birds laying small eggs. I suggest the answer may be along the following lines. Large eggs are clearly at a selective advantage since more chicks survive from these. If to be modified by natural selection, egg size needs to be partly genetically determined. Jones (1973:57-58) found that 22% of the variability in egg weight was associated with differences in body weight. If same applies to Black Guillemots, a greater share of egg weight variation is due to some other factor than body size. This may be the birds' overall condition or fitness. Possibly some late nesters try to form large eggs, as this is selectively better, but their condition does not allow them to sustain incubation as effectively as early layers which have laid same sized eggs. Other late layers may only be able to lay small eggs because their condition is so bad that laying early or late and large eggs is not feasible. Important here is the suggestion by Murton, Westwood & Isaacson (1974) that Woodpigeons laying small eggs were probably low in weight and needed longer time to feed. From Tab. 6.IV(p.139) it appears that laying early and smaller eggs is better than laying late and large eggs.

This may possibly be because small birds of similar fitness as some large birds, are able to improve their condition upon laying eggs faster than large birds since they need smaller absolute amount of food. These interpretations are therefore in line with Brooke's (1978) hypothesis that Manx Shearwaters not only delay their laying date in order to improve their condition sufficiently to be able to lay an egg, but also to allow successful incubation. However, there is likely to be an important difference between Manx Shearwaters and Black Guillemots, since the latter presumably are much quicker to improve their condition because of easier access to feeding areas.

My general conclusion from the observation of seasonal trends in breeding success, is that much of the losses resulted from "inadequate" behaviour of the parent birds, although environmental factors, such as tides, winds, and temperature, may have modified their behaviour. Ashcroft (1976: 77) attributed lower success of late breeding Puffins to the birds themselves, rather than any environmental factors associated with season, such as food availability. In the Black Guillemots, inadequate behaviour of adults may have accounted for approximately 2/3rds of the egg losses and 4/5ths of the chick losses. These were the so-called "dependent" factors, of which exposure and desertations were the most important. Preston (1968: 33-35) also noted chilling a major source of mortality of Black Guillemot chicks on Kent I. The rest of the mortality of eggs and chicks on Flatey was due to "independent" factors, flooding by tides being the most important.

So far, little has been said about the observation that early and late breeders fledged proportionally same number of chicks. Since late nesters laid fewer eggs, of course they fledged actually fewer chicks.

There are several possible explanations of these results: (a) fewer birds around feeding chicks late in the season, (b) young breeders just as good in feeding chicks as early, on average older, breeders, (c) greater food availability later in the season, (d) the "bad" breeders "selected" out at the egg stage, through observer disturbance, and (e) late nesters had fewer chicks to begin with, therefore fledged these at same success as early breeders.

Given no changes in food supply with season, fewer birds were left late in the season. More food could be around per bird, esp. since post-breeding adults and fledged chicks disperse quickly away from the breeding area (Chapter 3).

If young, late-nesting adults are just as good feeding chicks, this would contradict Lack's (1954, 1968) thesis that clutch size is geared towards the number of chicks parents are able to fledge. Neither does that tally with Perrins' (1970) hypothesis that late breeders are less efficient foragers. This would be consistent with my arguments that young birds may have to spend more energy and cannot compensate for weight losses by spending more time feeding.

Whether food was more available late, is totally a matter of conjecture. At least the time available for feeding is less since effective night has already started, whereas in the height of summer there is continuous light (Chapter 10). If there is a decline in food late, there may still be enough to rear chicks efficiently.

If more "bad" layers are found late in the season and their eggs become lost, so do their chances of rearing chicks that season since late breeders do not normally replace a lost clutch (Chapter 7). Therefore of all birds laying at a given time, only the most efficient managed to hatch their eggs. So as the season goes, more and more bad birds were weeded out, with subsequent rise in average "quality" of the breeders still left with eggs or chicks. Late breeders may therefore be capable of raising proportionally as many chicks as early nesters, other factors being equal.

Lastly, it can be argued that late breeders were as successful raising chicks to fledging as early birds, because they had fewer chicks per nest. This being so, Lacks (1954, 1968) hypothesis would not be contradicted. This could be tested with chick-swopping experiments.

Chapter 7: BREEDING BIOLOGY III: Replacement laying

7.1 Introduction

The capacity to replace a clutch if lost, differs considerably among seabird species. In some, clutch replacement seems to be very rare, as e.g. in the Procellariformes (Marshall & Serventy 1956, Harris 1966). In others, gulls for instance, it is possible to induce protracted laying (Parsons 1976).

To some degree, at least, replacement appears to be related to the probability of the birds losing their clutch, e.g. how exposed birds are to predation. Yet the ultimate control of whether replacement takes place or not, may be whether sufficient reserves exist for further egg production (cf. Perrins 1970) or whether it is feasible to raise a chick late in the season (cf. Lack 1954: 53-66).

In this chapter I examine some factors affecting replacement of lost clutches in Black Guillemots, the time needed for replacement to take place, and compare the success of replacement clutches with that of first clutches from the same nest-sites and first clutches of different nest-sites in same time of season.

7.2 Results

The frequency of replacement

As long as one egg remained in the nest incubation proceeded as normal. Replacement only occurred if the whole clutch was lost and even then rarely. The frequency of replacement clutches is given in Tab. 7.I. Of those that failed completely before hatching there was a replacement frequency of 9.1-16.0%. The differences between years were apparently associated with the timing of losses relative to other events of the breeding cycle.

Factors affecting replacement

Two factors influencing the replacement of lost clutches were examined: (a) the time of season at which the loss occurred, and (b) the state of incubation at the time of loss.

There was a significant difference ($t_{46}=2.77$, $P<0.01$)

Tab. 7.I. Replacement frequency of lost clutches.

Year	Nos. of first clutches which failed to hatch	Nos. of these that were replaced (%)
1975	25	4(16.0)
1976	40	6(15.0)
1977	77	7(9.1)

between the mean laying dates of a-eggs of lost clutches which were replaced (n=11, $\bar{x}$=14.9, s.d.=2.8) and those not replaced (n=37, $\bar{x}$=23.5, s.d.=10.1). The mean for clutches which were replaced was around the peak of laying in the population (15=31 May). The mean for birds which did not replace lost clutches, was about 9 days later, in the 4th week after the start of laying in the population. Consequently, the later clutches were laid in the season the less likely was their replacment if lost. Similar results were obtained by Birkhead (1976a: 15-16) for Common Guillemots and Lloyd (1976: 70) for Razorbills. Winn (1950) stated that late-nesting Black Guillemots would not lay again.

Similarly there was a significant difference (t_{40}=2.88, P<0.01) between the numbers of days for which clutches had been incubated, comparing those subsequently replaced (n=12, $\bar{x}$=4.7, s.d.=7.5) and those not replaced (n=30, $\bar{x}$=16.7, s.d.=13.6). No seasonal effect was involved here since there was no difference (t_{40}=0.73) between mean laying dates of those that had been incubated 0-19 days (n=28, $\bar{x}$=21.3, s.d.=10.1) and those that had been incubated 23-39 days (n=14, $\bar{x}$=18.9, s.d.=9.8). Therefore the longer eggs had been incubated before (and if) failing, the less the probability of a replacement clutch being formed.

The replacement potential of Black Guillemots was investigated in order to see how this changed with stage of season, independently from the state of incubation. This was done by using data for nest-sites where the first clutch had failed before any incubation had occurred, plus data for sites from which first clutch was experimentally removed on day 0 of the b-egg. The sample thus included clutches where continuous incubation had not started, and only 2-egg clutches.

Tab. 7.II gives the results. Numbers of clutches that were replaced fell sharply with progressing season. Replacement rate was 100% in laying period I but 0 after laying period III. Hence if a clutch failed later than a week after the peak of laying in the population, a replacement clutch was not formed.

Although no similar approach was attempted to study the effect of number of days incubated on replacement rate it is clear from earlier results that the further incubation was advanced when the clutch was lost the less likely was its

Tab. 7.II. Changes in number of clutches replaced with season. Based on clutches never incubated after laying of the b-egg, or clutches experimentally removed on laying of the b-egg. Combined data for 1975, 1976, and 1977.

Laying period (of 1st clutch)	Total n	Nos. replaced	(%)	Nos. not replaced	(%)
I	5	5	(100)	0	(0)
II	23	19	(83)	4	(17)
III	14	7	(50)	7	(50)
IV-VI	5	0	(0)	5	(100)

replacement. The three longest incubation periods recorded before the clutch was lost and subsequently replaced, were 23, 13, and 12 days. These are probably rather exceptional as most of the 12 clutches which had been incubated when lost and subsequently replaced, failed in the very first days of incubation.

No attempt was made to investigate whether there was a difference in replacement rate between birds laying one egg or two eggs in their first clutch. Firstly, 1-egg clutches were rather few in the population as a whole (7.5-12.7% of the sample clutches in different years). Secondly, 1-egg clutches could have been incubated for some days before it was clear that no b-egg was to appear. Hence the results would not have been directly comparable with the data for 2-egg clutches. Thirdly, one would expect relatively fewer 1-egg clutches to be replaced compared with 2-egg ones, as these were proportionally more common in the latter half of the laying season (about 4 times, Chapter 6) compared with the first half. As seen above replacement took place only in the first half of the laying season.

Length of replacement period

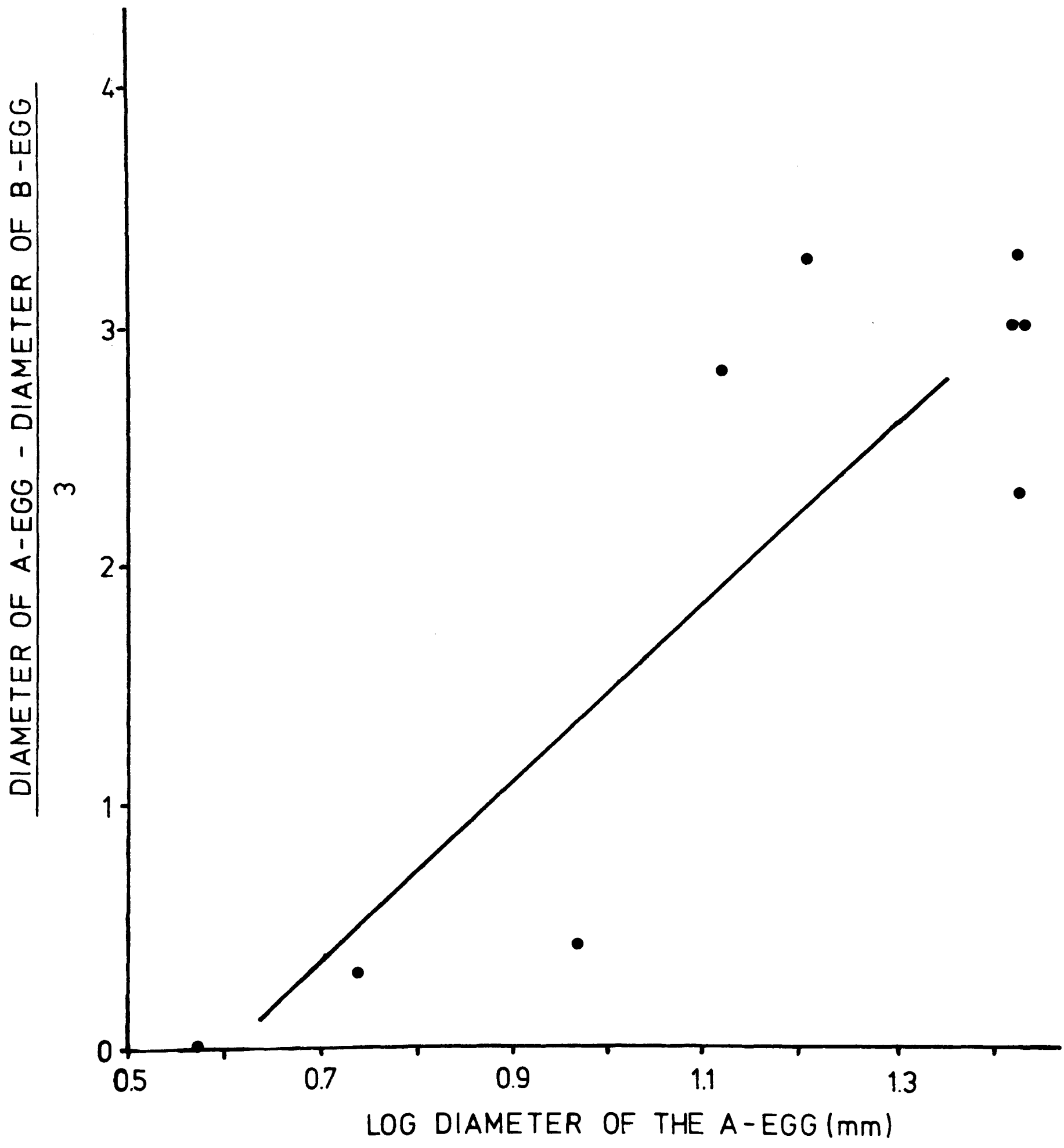
If lost clutches were replaced at all, approximately 2 weeks passed before the replacement clutch was laid. This was calculated from the day the first clutch was lost until the a-egg of the replacement clutch was laid. The mean interval was 14.7 days (n=28, range=9-32, s.d.=4.4). The total range was great but 82% of the birds relaid after an interval of 12-16 days. Asbirk (1979b), studying Black Guillemots in Denmark, found a similar replacement period, of 15 days (n=8, range=12-23). Ashcroft (1976: 66) found that Puffins needed on average 12 days to replace a lost clutch. Birkhead (1976a: 16) obtained 14.8 days for Common Guillemots, Lloyd (1976: 70) 14.14 days for Razorbills, and Manuwal (1972: 150) 14.8 days for Cassin's Auklets. A replacement period of about two weeks thus appears to be very constant and a general rule among alcids.

Although the sample size was small the length of the replacement period did not seem to depend on how many days

incubation had proceeded. Four clutches, incubated on average 8 days (range=2-13) before they were lost, were replaced after a mean of 14.8 days (range=13-17), or the same period as clutches which had not been incubated when lost and later replaced. Thus if birds were going to replace a lost clutch any incubating of their previous one did not seem to lengthen the period needed to form the replacement clutch as might have been expected. Wooller (1980) found Kittiwakes took shorter time to replace a lost clutch the more recent the clutch was when removed. My small sample size may have been the reason why no similar results were obtained in Black Guillemots.

An attempt was made to calculate the rate of egg formation (=replacement rate) by another method, using measurements of developing ovarian follicles. The diameter of the two largest follicles was measured in ovaries of females collected in May and June. As long as no ovulation had taken place the two follicles were considered the yolks of a- and b-eggs in 2-egg clutches. Rate of yolk formation was calculated as the difference between the a- and b-follicles, dividing by 3 since a- and b-eggs were normally laid 3 days apart (Chapter 8). The sample size is small, but Fig. 7.1 shows the log diameter of the a-follicle plotted against the rate of yolk formation. The rate follows an asymptotic curve (Anthony 1970) so a log transformation was made of the x-axis. Yolk diameter in freshly laid eggs is approximately 30 mm. To obtain the mean rate the middle value between the x-intercept (antilog 0.605=4.03) and 30 was read off the figure. This was log 1.1139, i.e. 13.0, giving the average rate per day as 1.86 mm. Dividing 26(30-4.03) by 1.86 gives 14 days. In Domestic chickens it has been found that an egg is laid about 24 hours after ovulation (Romanoff & Romanoff 1949: 230). Using this figure the calculated rate of egg formation in Black Guillemots by this method, was 15 days, comparing well with the mean observed replacement rate of 14.7 days. Recently Roudybush et al. (1979), using a new technique of measuring the rate of yolk formation in birds, developed by Grau (1976), obtained the time for rapid yolk formation in Black and Pigeon Guillemots as 8 and 10 days, respectively. The authors claim that only

Fig. 7.1. Relationship between the rate of yolk formation and diameter of the a-follicle in Black Guillemot ovaries.



the "bulk" of the yolk is deposited in this time. Allowing for some time at the beginning and end of rapid yolk deposition, plus albumen and shell formation, estimate of egg formation using their results approaches those from the present study, perhaps a little lower.

Comparison between first and replacement clutches

A strict comparison of the size of first and replacement clutches, laid by different birds but at same time of season, was not possible because of the unequal ratios of 1- and 2-egg clutches in the samples. The birds laying a replacement clutch, had all laid 2 eggs in their first clutch, whereas the first clutch layers used for comparison had laid either 1 or 2 eggs. The main point is, however, that the decline in clutch size with progressing season tended to be more rapid in replacement clutches compared with first clutches compared with first clutches (Tab. 7.III), although the difference was not significant ($\chi^2_3=0.013$).

The time interval between laying of eggs in 2-egg replacement clutches was a little shorter (n=7, range=2-3, $\bar{x}$=2.71 days) than in first clutches (n=245, range=1-10, $\bar{x}$=2.94) but the former sample was small and the difference not significant ($t_{250}=0.76$).

Eggs in replacement clutches were, on average, smaller than those replaced. The difference was not significant ($t_{54}=1.52$), comparing fresh weight of a-eggs in the first clutches (n=28, $\bar{x}$=51.7 g., s.d.=4.9) with those in the replacement clutches (n=28, $\bar{x}$=49.7., s.d.=2.2). In a regression analysis, a significant relationship was found ($r_{27}=0.40$, $P<0.05$) between the same variables, indicating that birds which laid large eggs in their first clutch, replaced them with large eggs if the first clutch was lost.

A comparison was made between size of replacement eggs and that of first clutch eggs laid in same laying periods (by different birds). The results are found in Tab. 7.IV, indicating that replacement eggs were, on average, larger, but the difference was small. This was to be expected, since the replacement eggs were laid by birds which had laid large

Tab. 7.III. Comparison between clutch size of birds laying first clutch and those laying replacement clutch during same laying periods. Data from all years combined.

Laying period	First clutches		Replacement clutches	
	n	$\bar{x}$	n	$\bar{x}$
III	242	1.91	4	2.00
IV	88	1.80	10	2.00
V	34	1.71	13	1.85
VI	29	1.55	13	1.46
Average decline (%)		18.8		27.0

Tab. 7.IV. Comparison of egg volume (l. x br.^{2}) between replacement eggs and eggs of first clutches laid at same time. All years combined.

Laying period	First clutches		Replacement clutches	
	n	$\bar{x}$	n	$\bar{x}$
III + IV	548	89.65	12	92.39
V	41	84.73	10	89.91
VI	18	85.02	10	86.34
Means:		86.47		89.55
Av. decline(%):		5.2		6.5

eggs in their first clutch earlier in the season.

There was an average decline in size of replacement eggs with progressing season just as found for eggs in first clutches (see Tab. 7.IV). As with size of replacement clutches earlier, there was a greater decline in size of replacement eggs than those of first clutches laid at same time of season, but this effect was small.

The main conclusion from the points raised above is that there were "intra-bird" declines in egg and clutch sizes with progressing season, just as there were "inter-bird" declines. Also, the declines for replacement clutches tended to be a little more than those for first clutches laid at the same time of season by different birds, but differences were not statistically significant.

There was a considerable difference in the length of replacement time between birds which were to lay 1 or 2 eggs in their replacement clutch. It may have been expected that birds laying 2 eggs would need longer time to form the eggs than birds forming only one egg. The reverse was the case, formation of 2-egg clutches took shorter time (n=23, range= 9-23, $\bar{x}$=13.4 days) than 1-egg clutches (n=6, range=14-32, $\bar{x}$= 19.8), the difference being significant (t_{27}=3.97, P<0.001). This was not a "date-effect" since there was no difference in the time of season when the first clutches were lost before their subsequent replacement (t_{27}=1.24).

Lastly, breeding performance differed between birds laying the first clutch in the last laying period (VI) of the laying season and those laying replacement clutch in the same laying period. In Tab. 7.V it is shown that replacement clutches did worse although the samples were not statistically significant (X^2_1=0.028). The differential losses took place at the egg stage but once young hatched the fledging success was the same.

7.3 Discussion

There were two important factors which were associated with whether replacement of lost clutch took place or not; the time of season and the length of incubation prior to loss.

Tab. 7.V. Breeding performance of Black Guillemots laying eggs for first time in the season and those that laid replacement clutch upon loss of first clutch. Data for laying period VI, i.e. eggs laid 22.6.-1.7., all years combined.

	First clutch		Replacement clutch	
	n	$\bar{x}$	n	$\bar{x}$
Clutch size	29	1.55	10	1.60
Nos. hatching	30	0.83	9	0.56
% hatching success		53.5		35.0
Nos. fledging	28	0.64	9	0.44
% fledging success		77.1		78.6
% breeding success		41.3		27.5

The reproductive organs start regressing once incubation is under way (Anthony 1970), presumably making it increasingly difficult for females to start egg production again. However, there is great variation between individuals; some may not replace a lost clutch even though it was fresh, others may lay a replacement clutch in spite of the lost first clutch having been incubated for much of a normal incubation period. Eisner (1958) suggested that the onset of incubation led to increased prolactin production which terminated laying. This may apply to the Black Guillemot, whose a-egg may receive some intermittent incubation before laying of the b-egg, as has been well documented in the Pigeon Guillemot (Drent 1965).

Seasonality effects were striking in all aspects of breeding of Flatey Black Guillemots (Chapter 6), and were also prominent among replacement layers. No replacement clutches were laid in the latter half of the laying season, and in most respects replacement layers did worse than birds laying their first clutch at the same time of season. Although replacement clutch and egg sizes declined more rapidly with season than was the case in first clutches, egg size declined very much less than clutch size. Hence it would seem that it was more important to have bigger eggs than more eggs. Some birds which had 2 eggs in their first clutch replaced it with only one egg. These birds took longer to produce one egg than other birds took to produce 2-egg replacement clutches and perhaps were less fit (cf. Perrins 1970) than birds which laid replacement clutches of 2 eggs. Differing fitness, e.g. in terms of reserves, may also explain why clutch size in replacement clutches declined more with season than first clutches, and why hatching success of replacement layers was lower than that of first-clutch breeders. Yet as long as chicks hatched, first-clutch and replacement layers did equally well, presumably because only the "top-quality" replacement layers were involved. I suggest that lowered hatching success of replacement clutches was due to the birds being less attentive with their eggs, because the birds needed to spend greater time feeding to improve their condition (cf. Chapter 8).

Food availability in itself cannot have been the cause of the observed changes with progressing season. Chicks were hatching from about 20 June well into July (Chapter 9), and there was sufficient food for a very high fledging success (which did not differ with progressing season, Chapter 6), and apparently for subsistence of the food-bearing adults as well.

From data on seasonal spread of laying dates (Fig. 5.1, p. 98) and replacement rate (Tab. 7.II, p. 182) I have calculated that 61% of all breeders in the Black Guillemot population on Flatey ought to have had the potential to replace a lost first clutch if this was fresh when lost. All the replacement layings fell in the first half of the laying season, none in the second half when hatching success was much lower (69.1% vs. 85.5%).

Similar replacement potentials seem to prevail in other seabird species which have been studied by removal experiments. Manuwal (1972: 151) studying Cassin's Auklets, found that 54% of the experimental birds laid a replacement clutch. In Kittiwakes, Wooller (1980) induced re-laying in 60% of the birds. Replacement potentials of this degree may be widespread in many seabirds. Yet Sealy (1972: 77) doubted if replacement ever took place in Ancient Murrelets. But here a distinction has to be made between what the population is capable of doing if eggs are experimentally removed and what normally happens. For example, even though 61% of the Black Guillemots may potentially re-lay upon loss of first clutch, only 9.1-16.0% of them actually replaced their lost clutch. This was primarily because lost clutches had been formed late in the season or had been incubated for some time. Belopol'skii (1957: 144), quoting Kaftanovskii's (1951) results, claimed that higher replacement potentials could be induced in populations which were exploited for their eggs, such as those of Brünnich's Guillemots, even up to 100%. I believe, however, that the experiments on which this claim is based were not controlled carefully enough to take account of variations in stage of season and length of incubation of the first clutch.

It appears from data on alcids that a certain relationship exists between replacement rate and nesting habitat.

Species which nest in the open appear to have higher frequencies of replacement than those nesting in more sheltered places. This has been suggested earlier by Sleptsov (1948, in Belopol'skii 1957: 145). This may possibly be related to the probability of losing the clutch, e.g. through predation. Thus, replacement frequencies of 21% (Gaston 1975: 36) and 45% (Sleptsov 1948 in Belopol'skii 1957: 143) have been found in Brünnich's Guillemots, 52.2% (Birkhead 1976a: 16) and 64.3% (Sleptsov 1948 in Belopol'skii 1957: 143) in Common Guillemots, and 20-34% (Lloyd 1976: 70) and 36% (Sleptsov 1948 in Belopol'skii 1957: 145) in Razorbills. Similarly, 32% of Kittiwakes relay (Maunder & Threlfall 1972) and Black-headed Gulls (Weidmann 1956). These species usually nest in rather open situations. Black Guillemots, on the other hand, had a replacement frequency of 9.1-16.0%, Puffins 4-14% (Ashcroft 1979), and Cassin's Auklet 10% (Manuwal 1979). These 3 species are burrow-nesters, which are more or less free from avian predators, and like many seabirds, nest in places free from terrestial predators. The greater replacement frequency of the former group of birds may not necessarily mean that their capacity to replace lost clutch was any higher, although this is likely. For the time being, it appears that the main difference between the groups are; those having higher replacement frequency, are capable of relaying because egg losses take place earlier in the season and higher proportion of early layers are capable of producing another clutch. The capacity to replace a lost clutch, would be intimately linked with the birds' capacity to provide the extra reserves needed for replacement of lost clutch. For example, Laysan Albatrosses, which nest in the open, will not replace a clutch if it is lost (Fisher 1968). The same appears to be the case in Fulmars (Ollason & Dunnet 1978), and Manx Shearwaters very rarely replace a lost clutch (Harris 1966). In this respect there seem to be fundamental differences between Procellariformes and the charadriiform seabirds, examples of which were mentioned above.

Chapter 8: THE BREEDING BIOLOGY IV: The incubation period

8.1 Introduction

In Chapter 6 it was suggested that parental behaviour, combined with effects of differential egg size, were the most important factors influencing seasonal differences in breeding success. In light of this it seemed pertinent to look closely at the incubation period to try and discover the key to some of the relevent questions, of how losses occurred.

The biological function of egg size differences has only recently been tackled in wild birds. In poultry it has been long known that chicks from large eggs grow faster and survive better than those from small eggs (e.g., Wiley 1950, Skoglund, Seegar & Ringrose 1952). Parsons (1970) was the first to show a relationship between egg size and chick survival in a wild bird, the Herring Gull. Several studies have followed since then, showing correlations between egg size and chick survival (e.g., Nisbet 1973, O'Connor 1975, Lundberg & Väisänen 1979). The present study was unusual in the respect that differential losses were emphasized at the egg stage, rather than the chick stage.

The chances of survival of the younger chick in 2-chick broods depend much on how well synchrony at hatching is achieved. Since eggs of the normal 2-egg clutches were usually laid several days apart, it may be expected a priori that hatching synchrony was difficult to attain, especially in light of the dissimilar size of eggs of the same clutch. There is a general relationship among birds that large eggs need longer incubation than small ones (Lack 1968: 189-193). Parsons (1972) has also shown this to hold intra-specifically.

In this chapter I look at various aspects of incubation in order to elucidate some of the factors which may have caused variability in breeding success between birds on Flatey. I examine: (a) the length of the incubation period, (b) the pattern of weight decline during incubation, (c) the laying interval between eggs, (d) factors affecting the length of the incubation period, (e) hatching synchrony and how this is

achieved.

8.2 Results

Length of the incubation period

Tab. 8.I gives the length of the incubation period for eggs in the most common clutch size of 2 eggs. The incubation period was calculated individually for each egg, from the day an egg appeared in the nest until the chick from that egg had freed itself. The average incubation period of a-eggs was 31.1 days, 28.8 days for b-eggs. These are the same as found by Asbirk (1979b) in Danish Black Guillemots, of 31.1 and 28.5 days, respectively. Much the same has been recorded for Pigeon Guillemots, 32.0 and 29.5 days, respectively (Drent et al. 1964).

Comparing a-eggs of 2-egg clutches and eggs of 1-egg clutches, Tab. 8.II shows that there as no difference in the length of their incubation periods in 1975 but there was in 1976. This difference may not be very meaningful since the samples were drawn from different times of the season. This can be crucial as shown later. For all years combined no difference was apparent between 1-egg and a-eggs of 2-egg clutches.

The range of incubation periods, was considerable in the population. Some birds needed up to 12 more days, or 46% longer time, to complete incubation of their eggs (of same laying order) than the quickest birds. Even greater spread was recorded in Danish Black Guillemots, some of which took up to 70% longer time to hatch their eggs than others (Asbirk 1979b).

This difference between birds could be shown in another way. In 2-egg clutches the embryonic development in eggs of same clutch proceeded at similar rate; if the a-egg of a clutch took long time to hatch, so did the b-egg of same clutch (r_{112}= 0.87, $P<0.001$; $Y=0.746x + 5.324$).

Differences in incubation period could potentially be exercised at two stages; at the laying interval (in 2-egg clutches only) or during incubation itself. As shown later, variation existed at both stages between individual clutches, although there was no simple relationship, e.g. with time of season.

Tab. 8.I. Length of the incubation period in Black Guillemots. Data for all eggs for which the incubation period was accurately determined.

Year	Laying order	n	Range	Mean	Sd.
1975	a-egg	45	28-37	31.7	2.2
	b-egg	61	26-38	29.2	2.3
1976	a-egg	79	27-37	30.6	1.6
	b-egg	73	26-33	28.1	1.3
1977	a-egg	23	28-36	31.7	1.8
	b-egg	32	27-38	29.6	2.4
All combined	a-egg	147	27-37	31.1	1.9
	b-egg	166	26-38	28.8	2.0

Tab. 8.II. Length of the incubation period in Black Guillemots according to clutch size. Comparison is made between 1-egg clutches and a-eggs of 2-egg clutches.

	1975	1976	1977	All combined
1-egg clutches:				
n	7	8	2	17
Range	28-36	28-37	(30)	28-37
$\bar{x}$	30.7	32.0	(30.0)	31.2
S.d.	2.7	2.8	-	2.6
2-egg clutches:				
n	45	79	23	147
Range	28-37	27-37	28-36	27-37
$\bar{x}$	31.7	30.7	31.7	31.1
S.d.	2.2	1.6	1.8	1.9
t	1.11	2.06	-	
P	n.s.	<0.025	-	

Egg weight decline during incubation

Fig. 8.1 shows the pattern of weight changes in eggs weighed at weekly intervals throughout the incubation period. Many of the eggs used, and these were a- and b-eggs of 13 clutches, had hatched by day 28, hence the low sample size that day.

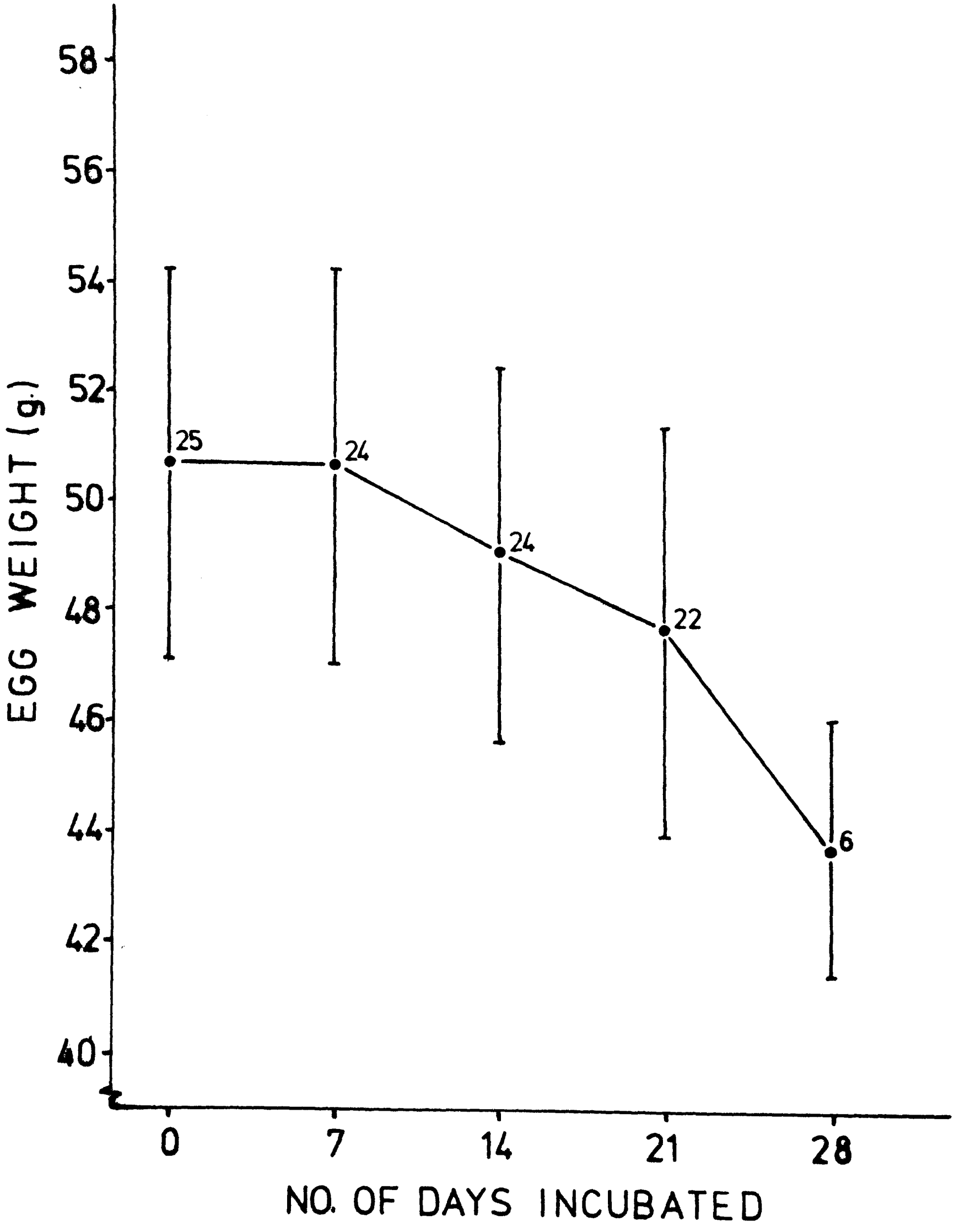
No measurable weight changes took place during the first week, but thereafter there was a decline which was most rapid during the last few days before hatching. In Herring Gulls, Drent (1970) found a steady daily weight loss from about 2 days after clutch completion, rapidly increasing towards the end of the incubation period, as in Black Guillemots. The rapid increase occurs after the star fracture has developed and the eggs pip, as rate of water loss is greatly increased due to the piercing of the egg shell (Rahn et al. 1976).

In the Black Guillemot egg weight loss up to day 28 in the above sample averaged 13.6% of the mean initial weight. A much greater sample of eggs (n=98) was weighed when fresh ($\bar{x}$=59.6 g, range=42-60, s.d.=3.8) and again when the star fracture had formed at hatching ($\bar{x}$=43.4 g, range=33-54, s.d.= 4.3), giving an average weight decline of 6.2 g, or 12.5% similar to that in the other sample. Belopol'skii (1957: 202) gives an average weight loss of 17.9% for Black Guillemot eggs, which is much higher than my results. In his sample a hole may have been formed, resulting in greater water loss, and possibly some pieces of egg shell falling off.

Weight loss up to star fracture was analyzed according to egg size. The results, given in Tab. 8.III, show weight loss was proportionally greater the smaller the eggs, with the exception of the largest eggs which lost as much weight relatively as the smallest eggs.

Two factors were considered, which may have been important in affecting the rate of weight loss, namely egg size and date. To distinguish their independent effects, a multiple regression analysis was carried out, with decline in egg weight as the dependent variable, and egg weight and date as the two independent variables Since there was not a full linear relationship between egg size and weight loss, as shown above, squared

Fig. 8.1. The pattern of weight changes of eggs during incubation. One standard deviation is given. The numbers indicate the sample sizes.



Tab. 8.III. Decline in weight during incubation according to fresh egg weight.

n	13	27	28	21	9
Fresh egg wt. range (g)	42-45	46-48	49-51	52-54	55-60
Average fresh wt. (g)	43.9	47.0	49.9	52.9	57.1
Average wt. decline (g)	6.9	6.1	5.5	5.5	8.7
% wt. decline	15.7	13.0	11.0	10.4	15.2
Z (1)	1.49	3.10	1.33	7.01	
P	n.s.	<0.001	n.s.	<0.001	

Note: (1) Mann-Whitney U-test.

transformations of egg size and date were also incorporated into the program. The results are given in Tab. 8.IV. Although egg size squared explained almost twice as much as the untransformed figure, egg size effects were not significant. Date was highly significant, but the squared variable not more so. Yet this explained only 14% of the variation in weight loss, other important factor or factors clearly being missing. I suggest the relationship with date has come about through the behaviour of the birds.

Laying interval and breeding success

Eggs of the most common clutch size of 2 eggs, were normally laid several days apart. The information concerning this is compiled in Tab. 8.V. In over two-thirds of the clutches laying interval was 3 days, the overall mean being 2.94 days. This is in accordance with published records (Hyde 1937, Winn 1950, Bianki 1967: 187, Asbirk 1979b), also with those for Pigeon Guillemots (Thoresen & Booth 1958, Drent 1965). The total range for Flatey birds was large, or 1-10 days. Presumably some of the variation may have been due to the recording system of single daily visits. The mean, however, should not be affected, as long as the birds laid at random times during the nest-inspection period; the diurnal rhythm of egg-laying in Black Guillemots - if any - appears to be unknown.

The length of the laying interval could potentially have decisive effects on breeding success, e.g. through hatching asynchrony.

Tab. 8.VI shows that hatching success varied according to length of the laying interval, being highest in the most common intervals of 2 and 3 days. If the interval was greater or less than 2 or 3 days, hatching success was significantly lowered.

To further interpret these results it is appropriate to ask, what factors could be affecting, or be related to, length of the laying interval? Two such factors could be egg size and laying date. There was a tendency for the longer laying intervals to be associated with smaller eggs and later laying date, but the results were not significant, perhaps mainly

Tab. 8.IV. The effect of egg size, egg size^2, date, and date^2 on decline in egg weight during incubation. Multiple regression analysis. N=98.

Independent variable	F-value	% explained	Significance
Fresh egg weight (x1)	0.16	0.17	n.s.
Fresh egg weight^2 (x2)	0.29	0.31	n.s.
Date (x3)	15.70	14.06	<0.001
Date^2(x4)	15.77	14.11	<0.001

Tab. 8.y. Laying interval (in days) between eggs in 2-egg clutches.

Laying interval (in days):	1975 n	1975 %	1976 n	1976 %	1977 n	1977 %	All years combined n	All years combined %
1	3	4	-	-	2	5	5	2.0
2	13	16	21	17	6	14	40	16.3
3	53	67	93	76	28	64	174	71.0
4	10	13	6	5	7	16	23	9.4
5	-	-	1	1	-	-	1	0.4
6	-	-	-	-	1	2	1	0.4
10	-	-	1	1	-	-	1	0.4
Total n=	79		122		44		245	
Mean (in days)=	2.89		2.95		3.00		2.94	

Tab. 8.VI. Hatching success of Black Guillemots on Flatey in relation to the length of the interval between laying of the a- and b-eggs of 2-egg clutches. Data pooled for all years.

Laying interval	1	2	3	4-10
n	4	38	146	23
Nos. hatching/nest	1.00	1.79	1.66	1.30
% hatching success	50.0	89.5	83.0	65.0
		2.35	1.13	2.25
t				
P		≤ 0.025	n.s	<0.025

because of great variance in sample.

Characteristic of clutches in which there was a short (1 day) or long (4-10 days) laying interval, was a greater dimorphism in size of the two eggs. This is shown in Tab. 8.VII. As outlined earlier (Chapter 6) the a-egg was usually the bigger of the two in 2-egg clutches, but the difference was not the same over the whole range of egg sizes. If the eggs were large, the a-egg was usually the bigger of the two, and vice versa if the eggs were small. Intra-clutch deviations in size were more and more, the further from the average population egg size. In clutches with long or short laying intervals, the difference in egg size relative to the mean was most marked in the a-egg; hence these clutches tended to be the ones with the largest eggs in the population. These also had the greatest hatching success although this declined with season (Chapter 6). Relatively few birds were recorded with a long or short laying interval (12.6%, Tab. 8.V), hence only a small number of birds suffered reduced hatching success in association with laying interval. Nonetheless, here is a relationship which could, in conjunction with others, set an upper limit to the size of the egg which it is profitable to lay. How the increased losses came about, is a matter of speculation, but probably this had to do with different length of time needed by each egg in a clutch to be incubated to hatching.

Factors affecting length of the incubation period

Studies have shown a seasonal decline in the length of the incubation period (e.g., Parsons 1972). Since seasonal effects were very prominent in most aspects of Black Guillemot breeding biology, an analysis was carried out to see whether the incubation period in Black Guillemots on Flatey decreased with progressing season. This analysis showed no statistically significant relationship (r_{174}=-0.021), all years combined, nor when each year was analyzed separately. Since there was little variation in mean laying interval with date as shown in some species (e.g., Nisbet & Cohen 1975), this had no effects on the relationship.

It is a general rule among birds that those with big eggs

Tab. 8.VII. Difference in egg size (volume) according to the length of the interval between laying of a- and b-eggs in 2-egg clutches.

Length of the laying interval (in days)	Volume of a-egg - volume of b-egg: n	range	$\bar{x}$	s.d.	t	P
1	5	-3.2 - +12.7	+5.7	4.0	2.19	<0.025
2	39	-6.9 - +10.9	+1.6	3.9	0.14	n.s
3	165	-10.4 - +17.3	+1.5	4.1	1.99	<0.025
4-10	25	-4.8 - +24.8	+3.4	6.2		

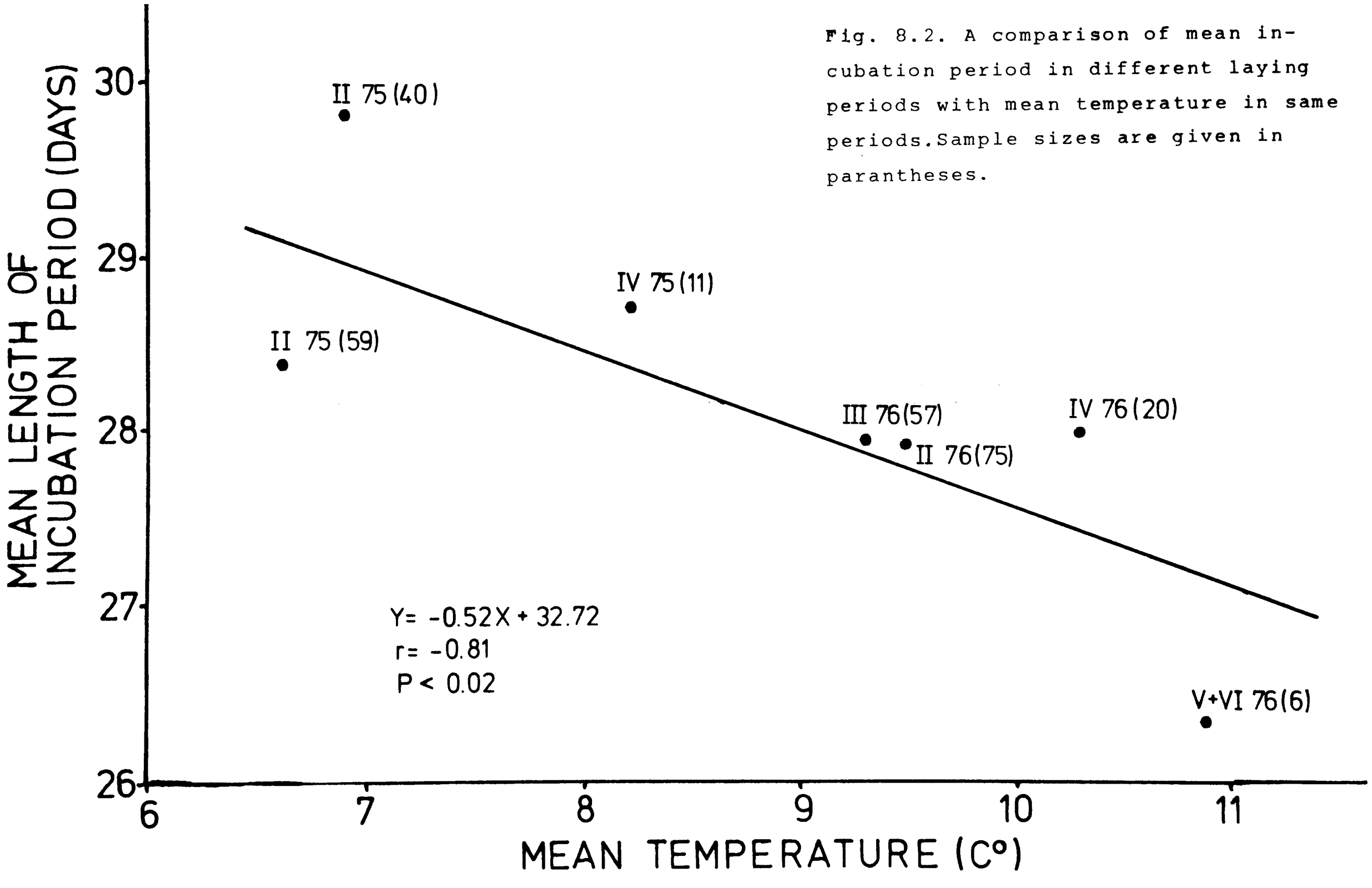


Fig. 8.2. A comparison of mean incubation period in different laying periods with mean temperature in same periods. Sample sizes are given in parantheses.

take longer to hatch them than those with small ones, but only in broad terms (Lack 1968: 189-193, Nisbet & Cohen 1975). If this holds inter-specifically, it may also be expected intra--specificially, as Parsons (1972) has shown. This being true, small eggs are expected to have a shorter incubation period than large eggs.

Ambient temperature is one factor which has been shown to be correlated with incubation period (Drent 1970, Mac-Roberts & MacRoberts 1972). Air temperature can possibly have direct effects during incubation, but this is unlikely unless fluctuations are rather great. Temperature can also affect the behaviour of the incubating birds (see Davis & Dunn 1976), but again this is less likely in a hole-nesting species like Black Guillemots, where temperature fluctuations are less variable (see Manuwal 1973:49-54) In Black Guillemots the most likely effect of temperature is that of cooling the eggs when the incubating birds are away. Hence any correlation between temperature and incubation period is most probably a reflection of the attentiveness of the birds. The rate of cooling would depend on how long the eggs were uncovered and the temperature gradient. Thus the warmer it is, the slower rate of cooling. This was shown to be true, by comparing mean incubation periods in different laying periods and in different years (see Fig. 8.2).

Other factors being equal, one would expect smaller eggs to need less incubation, and a shorter incubation period with increased temperature. A comparison was made between small and large eggs laid at similar time of season and in the same year to rule out any temperature effect, but no significant results emerged. A similar analysis of incubation periods, comparing eggs of similar size early and late in the season, again produced non-significant results.

Since it is unlikely that there are no effects of temperature (cf. Fig. 8.2) and of egg size under controlled conditions, these results indicate that there are likely to be some factor(s) counteracting their effects. This factor would then increase as the season progressed. I suggest this factor was parental attendance.

Hatching synchrony and the consequences of asynchrony

Particularly heavy losses of eggs occurred early in the incubation period, as was shown earlier (Chapter 6). Other difficult periods were when young were about to hatch and the first days after hatching.

If food was plentiful, the birds would be expected to aim for hatching synchrony. The chicks would therefore be at a similar stage of development and there would be less likelihood of sibling competition which could lead to death of the younger chick. On the other hand, it may be expected a priori that hatching synchrony was difficult to achieve since eggs were usually laid several days apart and perhaps because the eggs differed somewhat in size, needing different lengths of time to be incubated to hatching.

As shown earlier (Tab. 8.V, p.193) the overall mean between laying in 2-egg clutches, was 2.94 days, with a range of 1-10 days. The length of the incubation period was calculated from day 0 to day 0 of the chick from the respective egg for each of the two eggs in the clutch independently. Therefore the calculated length of the incubation period was longer in the a-egg. Other factors being equal, and the a-egg receiving full incubation from the time of laying, the a-egg would have hatched 2.94 days earlier than the b-egg. However, at the time of hatching, the lengths of the incubation periods in eggs of same clutch, differed by 2.63 days, as shown in Tab. 8.VIII. Hence, the difference at the time of hatching was on average 0.31 days less than at the time of laying. This may have been brought about by two means; the bigger embryo - more often that of the a-egg - growing a little faster than the smaller embryo, and/or intermittent incubation of the a-egg before laying of the b-egg. Big chicks grew faster after hatching than small ones (Chapter 9), so big embryos may possibly have grown faster than small ones.

Although this mechanism of synchronization could possibly be present in many bird species, such as waders, gulls, anatids, and passerines, which lay more than one egg in a clutch, hatching synchrony is more effectively brought about by other means,

Tab. 8.VIII. Difference in length of the incubation period of a-eggs and b-eggs as calculated from day of laying (day 0) to day of hatching (day 0). Comparison only between eggs of same clutch.

Year	n	$\bar{x}$ a-egg	$\bar{x}$ b-egg	a-egg - b-egg
1975	43	31.63	29.19	2.44
1976	58	30.81	28.07	2.74
1977	11	32.00	29.18	2.82
All	112	31.24	28.61	2.63

namely little or no incubation of eggs in an uncompleted clutch. From Tab.8.IX it is evident that Black Guillemot chicks hatched on average 0.52 days apart. In 54% of the cases perfect synchrony was attained; siblings hatching the same day. In 46% of the cases, however, siblings hatched 1-3 days apart, as expected the a-chick usually first, but the b-chick first in 9% of the cases.

If only minor adjustment to bridge the gap between eggs at laying took place during incubation, apparently little or no "social facilitation" (vide Vince 1964, 1969) occurred. Further hatching synchrony must have been brought about by little or no incubation of the a-egg before laying of the b-egg. On most occasions during nest inspections, the a-egg was cold before the b-egg was laid, but not always, meaning some intermittent incubation may have occurred in Black Guillemots as Drent (1965) showed in Pigeon Guillemots. In this context it is of interest that eggs in 1-egg clutches were cold for several days after laying (see also Preston 1968: 113). Hence there was an effective "laying interval" also in 1-egg clutches, perhaps in anticipation for a second egg which never materialized.

On the whole chick mortality was less than egg losses, even taking into consideration the numbers at risk; 21.5% (= the reverse of hatching success) of eggs at risk failed, 14.6% (=the reverse of fledging success) of the chicks (see Tab. 6.III, p.134). Most of the chick mortality occurred during the few first days of the nestling period (see Tab. 6.XI , p.148), asynchrony at hatching being one factor associated with failure. In broods in which both chicks hatched there was a greater probability that one chick died if they hatched 1-3 days apart (15/86) than if they hatched on the same day (6/82) (P=0.027; Fisher Exact test). As expected, more often the younger failed (34/427) than the older (25/427) (P=0.052; Fisher Exact test). Asynchronous hatching therefore led to greater chick mortality than if the chicks hatched synchronously. Despite asynchronous hatching in 46% of the 2-egg clutches, fledging success was high, and in 87% of the broods in which the chicks hatched asynchronously both chicks fledged successfully.

Tab. 8.IX. Hatching interval between a- and b-chicks in same clutch.

	1975	1976	1977	All yrs.
b-chick 1 day before a-chick	7(12%)	5(6%)	4(12%)	16(9%)
chicks hatched on same day	27(47%)	46(55%)	22(65%)	95(54%)
a-chick 1 day before b-chick	20(34%)	28(33%)	8(23%)	56(32%)
a-chick 2 days before b-chick	3(5%)	4(5%)	0(0%)	7(4%)
a-chick 3 days before b-chick	1(2%)	1(1%)	0(0%)	2(1%)
Sample sizes	58	84	34	176
$\bar{x}$ no. of days between chicks	0.62	0.52	0.35	0.52

8.3 Discussion

Factors affecting incubation period

Several studies of birds have shown that the length of the incubation period decreases as the season progresses (MacRoberts & MacRoberts 1972, Parsons 1972, Courtney 1979). No similar significant relationship was found in Black Guillemots, although there was a slightly negative trend.

Of factors which have been shown or suggested to be associated with seasonal differences in incubation period, the main ones have been egg size, ambient temperature, and parental behaviour, although other ecological factors have not been ruled out (e.g., Parsons 1972).

There is a general relationship among birds that those with large eggs take longer to incubate their eggs than those with small ones (Drent 1975: 338). Such correlation has also been shown to hold intra-specifically (Isenmann 1970, Parsons 1972), as would be expected since the incubation period is basically the amount of heat applied to the egg and greater amounts are needed for larger egg masses. Yet there are various other factors which may affect the incubation period, which is only the net result of the incubation process as long as this is successful.

Air temperature is one such factor. Since this increases as the season progresses, temperature may be correlated with shortening of the incubation period (e.g., MacRoberts & MacRoberts 1972). Temperature may influence in various ways. Drent (1970) showed how Herring Gulls were able to maintain a stable incubation temperature over the range 12-28° C. Whether Black Guillemots are able to do likewise at lower temperatures is unknown. Temperatures down to -6°C occurred on Flatey in the beginning of the breeding season, at the time when the largest eggs in the population were being laid. Therefore possibly birds incubating at that time may not have been able to maintain normal incubation temperature, with the result that the eggs lost undue weight (Tab. 8.III, p. 189). There is also the other explanation that these eggs were too big to be adequately covered.

On the whole, temperature is more likely to have greater effects in other ways. Behaviour of the birds may be affected, influencing them to stay longer or shorter on their eggs. In open-nesting birds, such as gulls, the danger of overheating is imminent, even at higher latitudes, so their behaviour has been geared towards shading the eggs (see MacRoberts & MacRoberts 1972). The situation of burrow-nesters, such as Black Guillemots, is different, at least at higher latitudes. The burrow has stabilizing effects on temperature fluctuations (see Manuwal 1972: 49-54), and a cooling effect more imminent than overheating when birds leave the eggs uncovered.

It was evident that the incubation period differed by as much as about 50% between clutches. Nice (1954) concluded that the rate of embryonic development was the crucial factor determining the length of the incubation period in birds. During incubation the embryo metabolizes energy from the egg reserves (Drent 1975: 339), and energy transfer is a function of the heat applied to the egg. During this process the egg loses weight, of which 75% is water vapour (Simkiss 1974), and this weight loss is inversely related to the length of the incubation period (Rahn et al. 1976). It was shown that the smaller the egg the proportionally more of the initial weight was lost during the incubation (Tab. 8.III, p. 190). Once eggs are exposed to air temperatures, as long as this is lower than incubation temperature, small eggs will lose heat faster than large eggs (Drent 1973: 399-400) and presumably use up greater energy to counteract the heat loss. However, small eggs are at an advantage once incubation has been resumed in that they take less time to warm up again (Drent 1973: 384-385). Large eggs may therefore be exposed to sub-incubation temperatures just as long as small eggs. The crucial point is though that small eggs could be exposed to potentially lethal temperatures for longer periods than large eggs. This was most likely one factor leading to lower hatching success of small eggs (Chapter 6). An unexpected deviation from the above pattern of weight loss was shown by the very largest eggs, for which explanations have already been offered.

Drent (1970) showed that 15% of Herring Gulls eggs studied were addled or died in pipping, due to what he called "faulty

incubation technique". This took place during periods when parental attentiveness was at its lowest, at the beginning and in the end of the incubation period. These were also the periods during which heaviest losses occurred in Black Guillemots, if not directly through environmental agencies (Tab. 6.X , p.147). There is strong reason to believe that in Black Guillemots smaller eggs needed less incubating, amplified by a rise in ambient temperature as the season progressed, although this could not be shown directly. At the same time there was no decline in incubation period with season. I suggest this came about through gradually lowered attentiveness in birds as the season progressed, coupled with age or experience. Age has been shown to have profound effect on breeding behaviour in Ring Doves (Lehrman & Wortis 1967). Hence longer and longer absences would have lengthened the period needed to incubate the eggs to hatching, at the same time putting the eggs at greater risk of failing. The results of Boersma & Wheelwright (1979) are of particular interest to these points. They found a direct relationship between the incubation period and egg neglect in Fork-tailed Storm Petrels such that the longer eggs were neglected the longer the incubation period. Greater egg neglect was moreover correlated with greater egg weight loss and increased chick mortality.

Why differences in egg size within clutch?

It was shown (Tab. 8.VII, p.196) that long or short laying intervals were associated with greater differences in egg size than found in the more common laying intervals of 2 or 3 days. This was further correlated with decreased hatching success and therefore was clearly of importance. I want to try to develop the argument that differences in size of eggs within a clutch may have come about through some eco-physiological factors involving the overall condition (or fitness) of the birds. In particular, an attempt is made to explain the curious relationship presented earlier between a- and b-eggs of the same clutch (Fig. 6.2, p.130).

If birds are in good condition, they are likely to stay longer at the nest. For instance Drent (1970) showed there

was a good correlation between length of incubation stints and foraging time in Herring Gulls. Parsons' (1976) results imply that incubation behaviour may have a depressing effect on egg size, thus accounting for the smaller c-egg in larids (see also Lundberg & Väisänen 1979). Since intermittent incubation has been found in Pigeon Guillemots (Drent 1965) this probably also occurs in Black Guillemots. Eisner (1958, 1960) suggested that the onset of incubation led to increased prolactin secretion which terminated laying. This hormonal activity may therefore serve to reduce the size of the b-egg in Black Guillemots which lay large eggs.

If birds lay small eggs on the other hand they may be in lean condition. The same could apply to birds laying large eggs late. They would therefore have to spend more time away from the nest feeding to improve their condition and get the necessary reserves for formation of a b-egg. Hence there would be little or no intermittent incubation with no suppressing effects on the b-egg during its formation. Since food is ample and near at hand in summer, the birds may be quick in improving their condition and hence be able to lay a larger b-egg than earlier in the season.

Chapter 9: BREEDING BIOLOGY V: The nestling period.

9.1 Introduction

Intraspecific differences in egg size can basically have effects at two stages in the breeding cycle; the incubation period, discussed in the last chapter, and the nestling period. It was shown in the preceding chapter that smaller eggs did worse in terms of numbers of fledged chicks. This was not only because smaller eggs were laid later in the season; also those laid at the same time as big eggs did worse (Chapter 6).

In poultry it has been shown that chicks hatching from large eggs grow faster and survive better than small chicks (Skoglund, Seagar, & Ringrose 1952, Godfrey, Williams & Marshall 1953, Gardiner 1973). In wild birds, such a relationship was first shown by Parsons (1970) in Herring Gulls, but has been shown subsequently in other species as well (Schifferli 1973, Davis 1975, Howe 1976, 1978, Nisbet 1978).

In Manx Shearwaters, Perrins (1966) found a negative relationship between fledging date and percentage of birds recovered in later years. Later, Perrins, Harris & Britton (1973) showed a similar relationship between fledging weight and the percentage of birds recovered, and suggested that the greater fat reserves of heavy chicks allowed them to survive better in the immediate post-fledging period, while deteriorating feeding conditions were responsible for the average decline in fledging weight observed as the season progressed.

In the present chapter I examine various data relating to these aspects of the breeding biology of Black Guillemots.

9.2 Materials and methods

Size was measured for as many chicks as possible on the day of hatching (= day 0). This information formed the basis for intra-specific comparisons of size and growth. Growth was examined for samples of chicks from both 1-and 2-chick broods. In 1975 measurements were taken every fifth day until the approach of fledging, then the chicks were measured every day so

as to obtain their "fledging measurements" on the last day of their nestling period. Measuring every fifth day was considered too long an interval. Hence, in 1976, the chicks were measured every third day for most of the nestling period, then daily towards the end as in 1975.

Besides weighin the chicks, measurements were taken of tarsus, culmen, and wing. These were taken as follows: Weight was taken using 50, 100, and 500 g Pesolas (accuracy 0.5, 1, and 5 g, respectively). Tarsal length was measured from the inter-tarsal joint to the tarso-phalangial joint of the middle toe of the right leg. Culmen was measured from the growth line at the top of the upper mandible to the tip of the bill. Wing length was taken on the right wing, according to the maximum chord method.

Samples of full-grown Black Guillemots were also measured, and in the same way as for chicks. These samples included: (a) Live adults from Flatey in the breeding season (May-August), (b) study skins of adults from Flatey, collected in the breeding season, and (c) immature birds from outside the breeding season (September-April), from Flatey and other parts of Iceland. These skins are deposited in the collections of the Museum of Natural History, Reykjavik.

The length of the nestling period was calculated from day 0 to the day the respective chicks had vanished from their nest-sites, these having been checked daily prior to the chicks' departure.

Chicks ringed on Flatey during 1975-1977 and recovered up till 31.12.1980, formed the basis of analysis of post-fledging survival according to the time of fledging. Of 958 chicks (89% of those ringed 1975-1977) 28 recoveries were reported, having been ringed 1 or more year before recovery.

9.3 Results

Size of chicks at hatching

The process of hatching, from its first signs till the chick was free, extended over three days. On the first day a star fracture formed in the egg shell. The following day a hole was pierced, later developing into a slit. The third day the chick freed itself. Chicks normally hatched through the

blunt end of the egg, but on one occasion a chick was recorded emerging from the pointed end.

Tab. 9.I gives the size of chicks on the day of hatching (= day 0), represented by weight, and lengths of culmen, tarsus and wing. The average size was practically identical in all three years. However, individual chicks varied considerably, expecially in weight; some chicks were twice as heavy as others. This variation is a potential for differential mortality between chicks.

Egg size had profound effects on size of the chicks hatching from these eggs. As shown by a regression analysis, there was a good correlation between egg volume ($l \times br^2$) and day 0 weight ($r_{85}=0.79$, $P<0.001$, $y=0.72x - 0.40$; data from 1975 only). Some variation is likely to have been introduced by the fact that these chicks may have hatched at any time during a 24-hour period; thus they may have been at slightly different developmental stage and some received food from their parents.

Heavier chicks may also have been heavier because (a) they were structurally larger, or (b) they had proportionally more yolk reserves. It was shown earlier (Chapter 6) that yolk in freshly laid eggs increased linearly with increase in egg size, and was proportionally the same irrespective of the egg size, about 32% of the egg weight. Chicks showed similar proportional increase in weight of the yolk sac with increase in chick weight, but this was more pronounced than in the eggs (differences in regression slopes, $t=_{16}2.24$, $P<0.05$). This means that embryos in small eggs lost relatively more of their yolk reserves during incubation than those in large eggs. Hence upon hatching large chicks had proportionally more yolk than small ones. A partial regression was also run between four size variables of chicks, weight, and lengths of culmen, tarsus, and wing. The results are shown in Tab. 9.II which indicate that weight and tarsus were the best indications of size and that heavier chicks were structurally bigger.

Length of the nestling period

Tab. 9.III gives the length of the nestling period for 1-and 2-chick broods combined, being on average 34.4 days

Tab. 9.I. Size of chicks on the day of hatching (=day 0).

	Year:		
Size parameters	1975	1976	1977
Weight (g):			
n	218	137	53
range	23 - 44	22 - 43	27 - 43
$\bar{x}$	35.0	35.1	35.4
s.d.	3.7	3.8	3.2
Culmen (mm):			
n	218	135	31
range	10.0 - 14.8	11.9 - 15.0	12.6 - 14.0
$\bar{x}$	13.0	13.3	13.4
s.d.	0.6	0.5	0.4
Tarsus (mm):			
n	218	135	52
range	16.1 - 20.9	16.8 - 21.2	16.6 - 20.5
$\bar{x}$	18.8	18.8	18.4
s.d.	0.8	0.8	2.1
Wing (mm):			
n	-(1)	135	53
range	-	17 - 24	18 - 23
$\bar{x}$	-	19.9	19.9
s.d.	-	1.2	1.2

Note: (1) Not measured in 1975.

Tab. 9.II. Partial regressions between size parameters (weight, and lengths of tarsus, wing, and culmen) in chicks on day of hatching. Number of observations= 133.

Relationship	Correlation coefficient (r)	P
Weight(wt): cul,tars,wg.	0.60	<0.001
Culmen(cul):tars,wg,wt.	0.29	<0.05
Tarsus(tars): wg,wt,cul.	0.58	<0.001
Wing(wg): wt,cul,tars.	0.49	<0.001

Tab. 9.III. Lengths of the nestling period in 1975 and 1976. No data available for 1977.

Year	n	Range (days)	$\bar{x}$	s.d.	t	P
1975	105	30 - 40	34.4	1.7	5.09	<0.001
1976	108	27 - 38	33.1	2.0		

(1975) and 33.1 days (1976). The 1.3 day average shorter nestling period in 1976, may have resulted from the higher average ambient temperature that year; +5.7 C° in June 1975 compared with +8.7 C° in 1976 (Vedurstofa Islands 1975, 1976). This may have resulted in less expenditure of energy for thermo-regulation in chicks.

The average nestling period of Flatey Black Guillemots was substantially shorter than reported by Preston (1968: 43) from Kent I. of 35-40 days, by Asbirk (1979b) of 39.5 days in Denmark, and Cairns (1978: 16) of 37.3 and 36.1 days at two study islands in the St. Lawrence estuary. Other authors have reported a nestling period of between 30 and 40 days (Hyde 1937, Winn 1950,Uspenski 1956: 83, Belopol'skii 1957: 219). In Pigeon Guillemots, Drent et al. (1964) found nestling periods of 29-39 days, with a mean of 35 days.

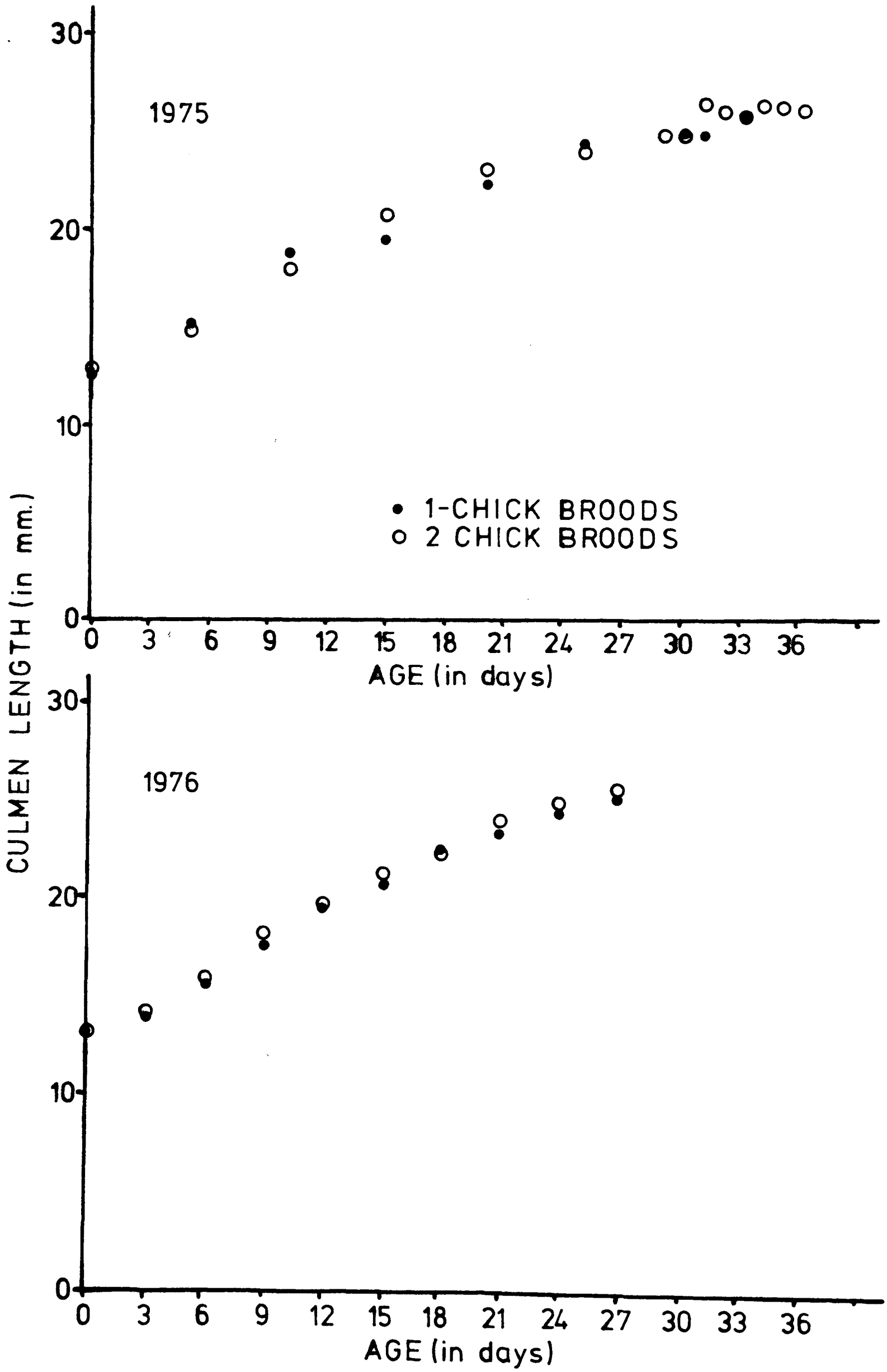
Some of the variation in length of nestling periods between studies may be due to differences in feeding conditions for the young. Cairns and Asbirk for example, reported low breeding success and long nestling periods, compared with my data. If feeding conditions were poor the nestling period may be lengthened.

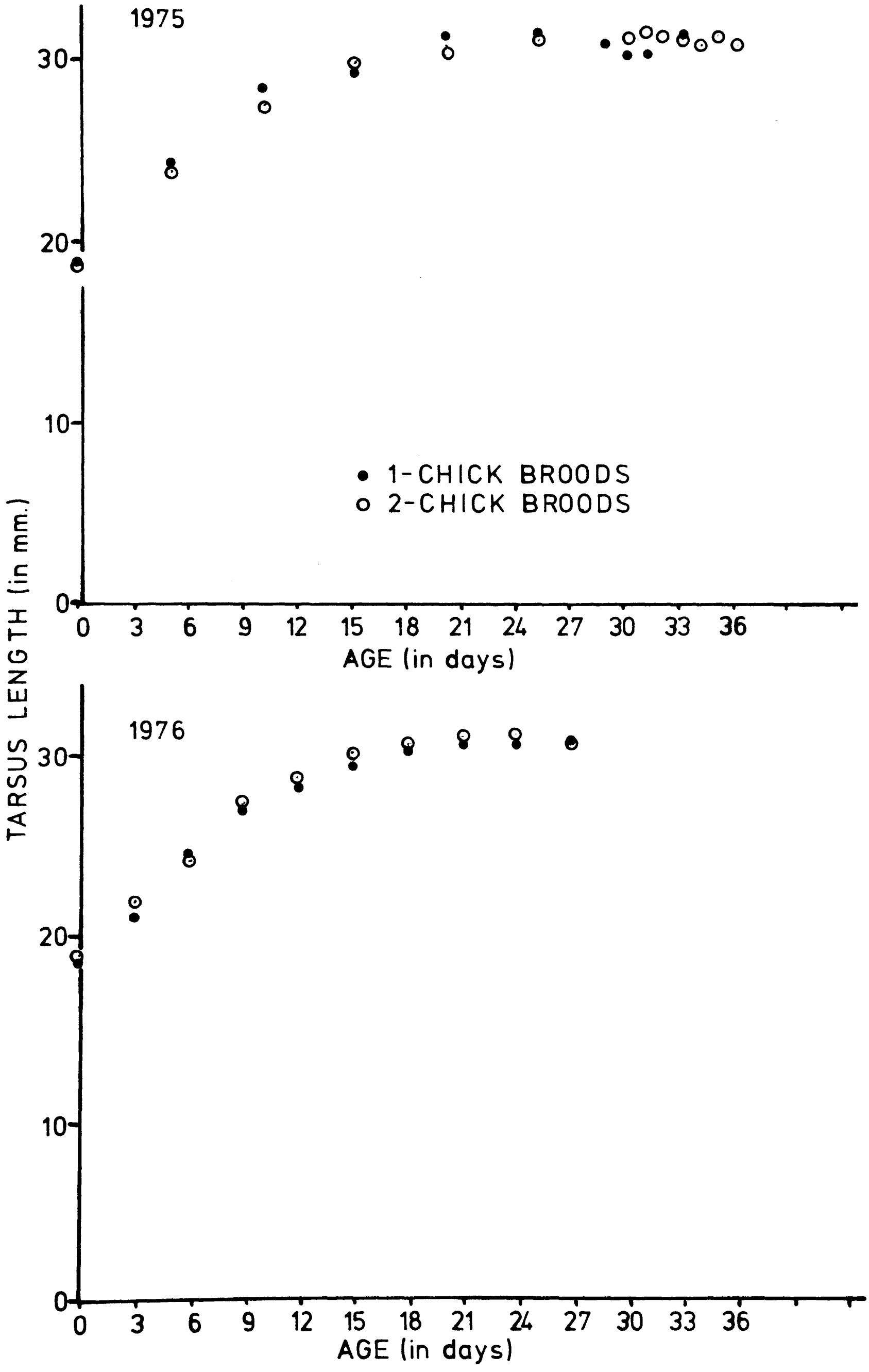
Growth rate

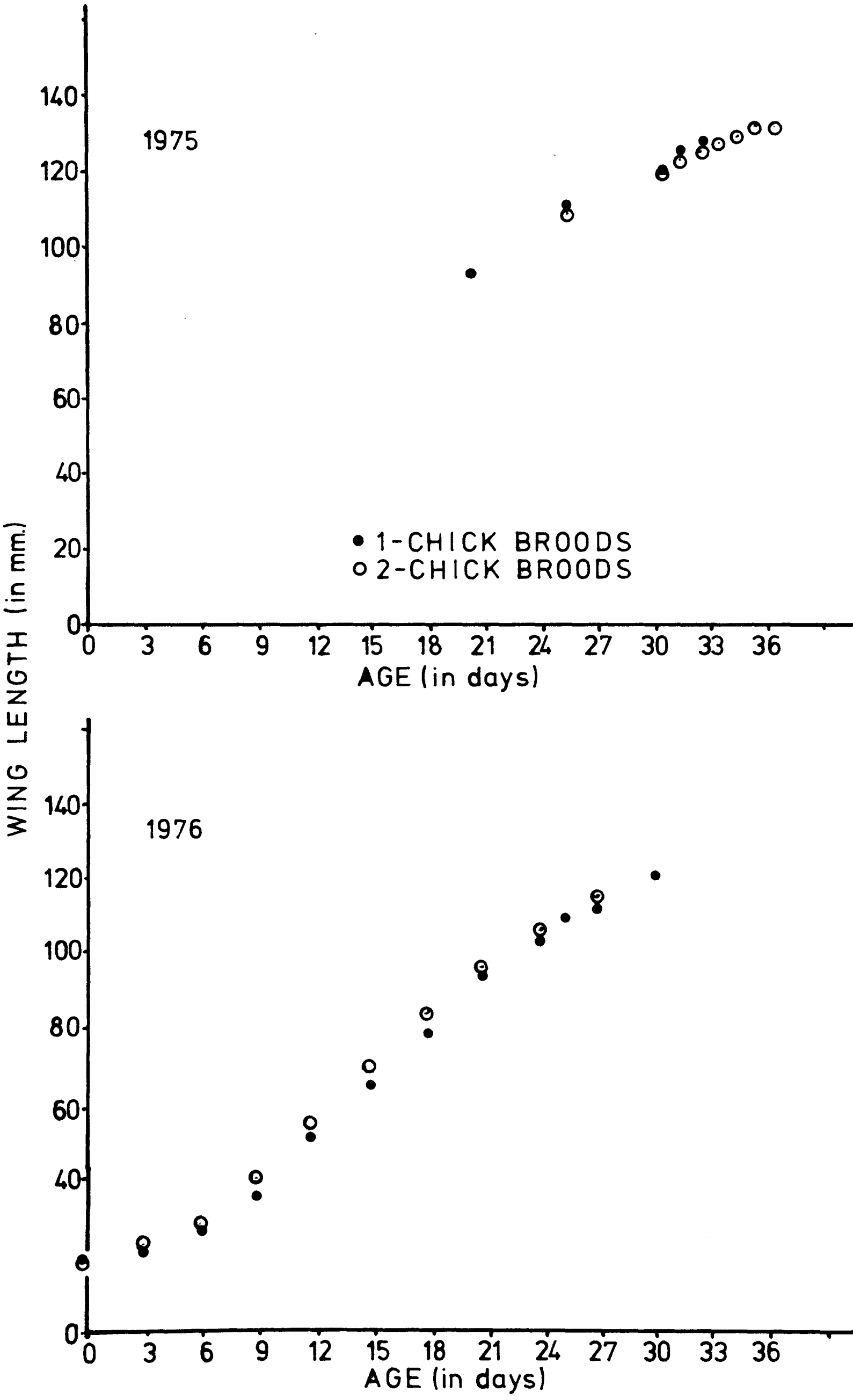
In Figs 9.1 - 9.4 growth curves are presented for weight, and three linear body measurements, lengths of wing, tarsus, and culmen. Growth was practically identical in chicks from 1-and 2-chick broods. Also, there was no difference between the two years. It is noticeable how different the curves were for the different characters, in form, magnitude, and shape.

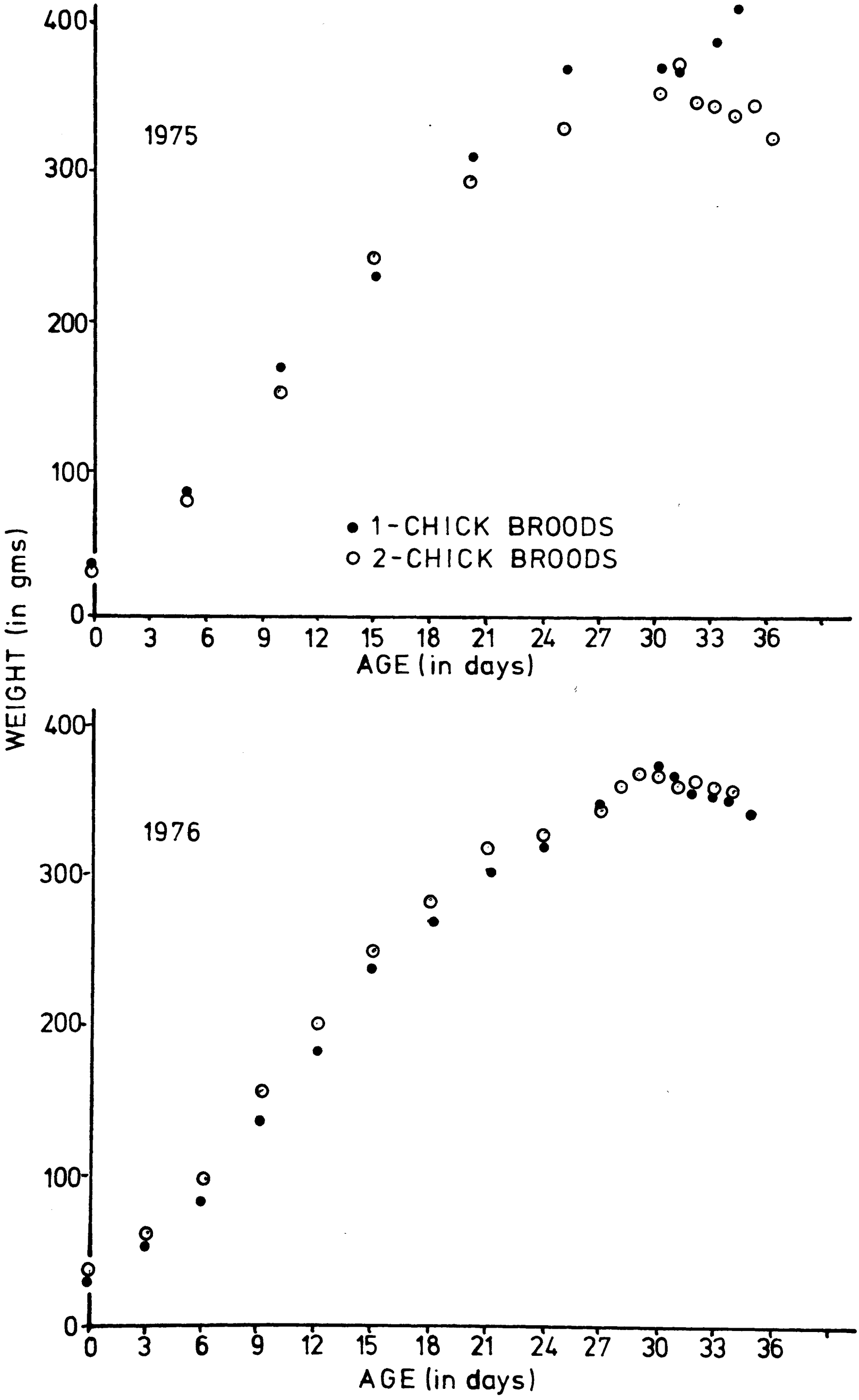
The culmen grew continuously during the nestling period and appeared to be reaching a near asymptotic level by the end of the nestling period. This level (ca 26mm) was much below the average culmen length of adults (n= 215, range= 26.4- 34.6, $\bar{x}$= 30.5 mm, s.d.= 1.5). The form of the growth curve indicates that the remaining growth takes place over a long time and that indeed appears to be the case. Black Guillemots in their first year, collected in various parts of

Figs 9.1 - 9.4. Growth curves for Black Guillemot chicks. Linear measurements of three characters were taken, culmen, tarsus, and wing, as well as weight. The data are given for chicks of 1- and 2-chick broods and for two years, 1975 and 1976. The sample sizes at given chick ages varied considerably; in 1975 2-20 for 1-chick broods, but 7-14 in 1976, for 2-chick broods 3-70 in 1975 and 13-73 in 1976.


1975
1976
• 1-CHICK BROODS
o 2 CHICK BROODS
CULMEN LENGTH (in mm.)
AGE (in days)
0
10
20
30
0 3 6 9 12 15 18 21 24 27 30 33 36


1975
30
20
10
0
0 3 6 9 12 15 18 21 24 27 30 33 36
AGE (in days)
• 1-CHICK BROODS
o 2-CHICK BROODS
TARSUS LENG
1976
30
20
10
0
0 3 6 9 12 15 18 21 24 27 30 33 36
AGE (in days)


1975
1976
• 1-CHICK BROODS
o 2-CHICK BROODS
WING LENGTH (in mm.)
AGE (in days)
0
20
40
60
80
100
120
140
0 3 6 9 12 15 18 21 24 27 30 33 36


1975
1976
• 1-CHICK BROODS
o 2-CHICK BROODS
WEIGHT (in gms)
AGE (in days)
0
100
200
300
400
0 3 6 9 12 15 18 21 24 27 30 33 36

Iceland and prepared as study skins, were measured and compared with adult-plumaged birds, also prepared as skins. First-year birds from September-October (n= 9) had a mean culmen length of 27.6 mm (s.d.= 1.5), birds from November-December (n= 20) had 28.1 mm (s.d.= 1.2), while birds from May-June (n= 8) had 29.5 mm (s.d.= 1.2). Adult-plumaged birds from May-August (n= 26) had a culmen length of 30.0 mm (s.d.= 1.3). Hence the bill appears to be growing the whole first winter, and by the end of the first year has still not reached adult size. Therefore it appears that the culmen may take 1-2 years to develop fully.

Growth of the tarsus was quite different. Live adults had a mean tarsus length of 31.0 mm (n= 210, range= 27.5-34.7, s.d. = 1.1) This length was attained by chicks about 20 days after hatching, about two weeks before fledging. From this rapid development of tarsal length, one may assume it is rather important for the guillemots to attain full growth of the legs very early. As pointed out by Asbirk (1979b) the chicks run towards the adults when they bring food to the nest. It may be important for the adults to dispose of the food as quickly as possible, and that is what normally happens. Otherwise the food may be lost to kleptoparasitic robbers. Moreover, the chicks may possibly be liable to predation if the nest cavity is shallow or the chicks near the entrance, e.g. when they are exercising their wings just before fledging. Thus it may pay the chicks to have well developed legs to seek shelter quickly. Lastly, and perhaps most importantly, Black Guillemot chicks walk to the sea on fledging, at least where the nests are not in cliffs, and they are fully independent after that (see Chapter 3). Fledging normally takes place around midnight, presumably to avoid predation as far as possible. The chicks would need well developed legs to be able to walk the distance to the sea, often over rough terrain, for making an escape if needed, and for swimming when on the sea.

Wing growth makes a slow start in Black Guillemots, but by about the 10th day, the development of the wings is fully under way and continues up to fledging. By that time the wing length has only reached about three-quarters (ca 130 mm)

of its full length; live adults (from May-August) have a mean wing length of 163.2 mm (n= 219, range= 154-174, s.d.= 3.5). By extrapolating from the pre-fledging growth rate and assuming this is similar after fledging, full adult wing length would be gained about 10 days after fledging, at the age of about 44 days. This estimate fits in with observational data of when first chicks have been seen in flight (Chapter 3).

The increase in weight during the nestling period was typically sigmoid in form. The weight increased to a peak level, with subsequent weight recession in the end. This is more clearly shown by the more extensive data from 1976, and given in Fig. 9.5. The peak value was reached four days prior to fledging. At that point, the chicks averaged 95.1% of the mean adult weight during May to August (n= 252, range= 340-520, $\bar{x}$= 400.1 g, s.d.= 26.9). After reaching peak weight, weight declined steadily and at fledging the chicks averaged 89.0% (1976) of the mean adult weight, a decline of 6.5% from peak weight, which matches Asbirk's (1979b) 6% for the species in Denmark.

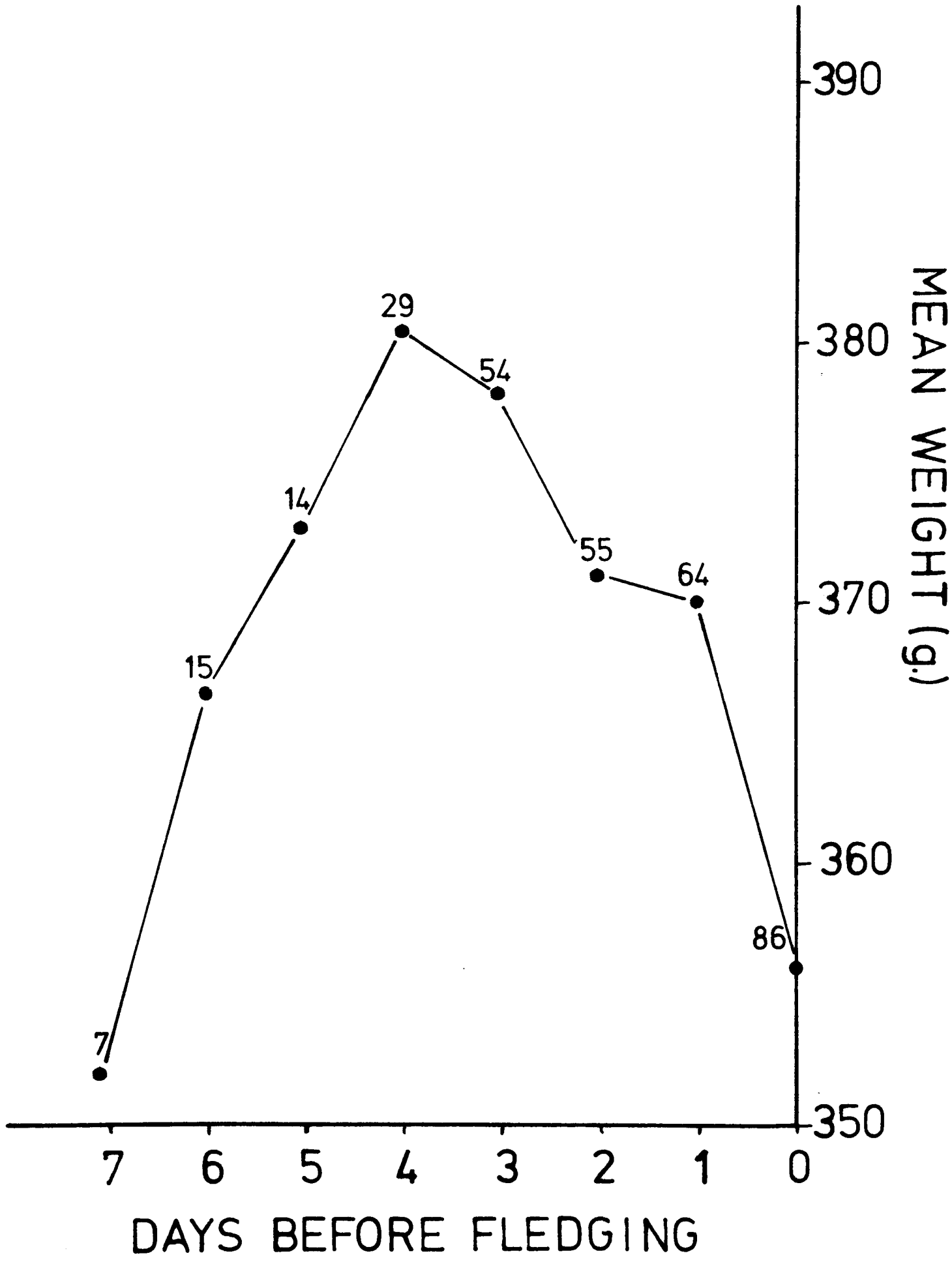
Nestling mortality

In Chapter 6 the known (or assumed) causes of chick mortality were given, and it was pointed out that this was much less than that of eggs, even taking into consideration the numbers at risk.

Tab. 9.IV shows the distribution of chick mortality over the nestling period. By far the greatest mortality (78% of the total) took place in the first week after hatching. Once chicks reached the age of about two weeks, which was about half the nestling period, they were almost certain to fledge successfully.

Since most of the mortality took place in the very first days after hatching, one may ask what caused or what factors were associated with this mortality? In Tab. 6. XI. (p.148) it was shown that about a third of the mortality may have resulted from "independent" factors most of which are unpredictable and related to the environment. On the other hand over two-thirds may have been associated with the birds

Fig.9.5. The variation in weight of Black Guillemot chicks during the last week of their nestling period. Sample sizes are shown in the figure.



Tab. 9.IV. The estimated (or known) age of chicks at time of death.

Year	Age at time of death: 0 - 6	7 - 15	16 or more	Unknown
1975	11	2	1	4
1976	25	4	0	9
1977	37	12	2	7
	73	18	3	20
% of those known	78	19	3	

themselves and their pattern of breeding. One such factor is the failure to achieve hatching synchrony, as shown in Chapter 8.

Factors affecting the length of the nesting period and fledging condition

The condition of the chicks upon fledging may be crucial to their subsequent survival. What happens to the chicks during the nestling period is therefore of utmost importance. Various factors, such as brood size, hatching order, timing of fledging of the chicks in 2-chick broods, and environmental (sea condition, tides, etc.), can have effects on this.

As perhaps expected, the younger of the chicks in 2-chick broods more often failed to fledge, as seen earlier (p.201). Also those chicks which failed to fledge (n= 19, range= 30-40 days, $\bar{x}$= 33.5) were on average lighter that those which fledged successfully (n= 116, range= 28-43, $\bar{x}$= 35.2) although the difference was not statistically significant (t= 1.94, n.s.; P= 0.05 = 1.98).

Daily weight increments were compared with six factors in a multiple regression analysis; date, chick age, sea condition, hatching order, tidal cycle, and brood size. None were significant ($F_{6,73}$= 1.06). In the case of the environmental factors, conditions which may have had effects, may not have been recorded in the program.

The length of stay in the nest was analyzed according to the number of chicks in the nest. Tab. 9.V shows that the young stayed on average the same number of days whether from 1-or 2-chick broods.

In 2-chick broods an analysis was made comparing how long siblings remained in the nest. Tab. 9. VI shows that the later-hatching chick (the younger) stayed on average half a day less than its elder sibling. One reason for this may be that fledging of the elder chick influenced the other to leave earlier than it otherwise would have done. But this was not the reason in all cases, since only 50% of the chicks in 2-chick broods fledged on the same day and not always did the elder chick leave first. In some cases on which the chicks hatched

Tab. 9. V. The lengths of the nestling period by chicks in 1- and 2- chick broods separately.

Year	Brood size	n	range	$\bar{x}$	s.d.
1975:	1	16	32 - 37	34.0	1.6
	2	89	30 - 40	34.5	1.8
1976:	1	16	27 - 38	33.4	2.7
	2	92	29 - 38	33.1	1.8

Tab. 9.VI. The fledging age (=the length of the nestling period) of sibling chicks.

Year	n	range	$\bar{x}$	s.d.	t	P
1975						
Older	26	31 - 37	34.7	1.6	1.05	n.s.
Younger	26	30 - 37	34.2	1.8		
1976						
Older	22	30 - 36	33.0	1.6	1.13	n.s.
Younger	22	30 - 35	32.5	1.6		

the same day the siblings fledged as much as 3 days apart. If the chicks hatched one or more days apart the elder chick fledged one or more days before the younger one twice as often than vice versa. These data are shown in Tab. 9.VII. Two cases (not in the table) were known in which the chicks fledged at least 6 days apart.

Tab. 9.VIII gives the weight and measurements of chicks on the last day in the nest, on average 12 hours before fledging. Only small differences were in linear size measurements between individuals, with about a 4% standard deviation. The variation in weight was more than twice that; the heaviest chicks were about 40% heavier than the lightest ones. This could lead to differential mortality in the post-fledging period.

Tab. 9.IX shows that there was no difference in the weight at fledging between chicks from 1- and 2-chick broods, despite the smaller average quantities of food received per chick by those in 2-chick broods (cf.p.267). One possible explanation is that two chicks saved heat by staying in the same nest, hence needed less food for similar rate of growth to take place as that of singletons.

The weight at hatching did not influence the fledging weight. However, hatching weight was correlated with subsequent weight for about half of the nestling period. Tab. 9.X gives correlations between hatching weight and weight at different intervals during the nestling period, including the fledging weight.

A comparison was made between fledging age (= the length of the nestling period) and the fledging weight. The data are found in Tab. 9.XI. The results were significant in 1975; the longer the nestling period, the less the fledging weight. However, no similar relationship was found in 1976. My interpretation of the 1975 results is that chicks fledge because they are heavy, but not because they stay long in the nest. Chicks which are low in weight may try to compensate for its low weight by staying longer in the nest.

Post-fledging survival

Perrins (1966) found a negative relationship between

Tab. 9.VII. A comparison of when chicks in 2- chick broods fledged relative to each other. Data from 1975 and 1976 only.

	Number of nests		
Fledged on same day		40	(50%)
Hatched one or more days apart, and:			
-Older fledged:			
-1 day earlier	7		
-2 days -	4		
-3 - -	1		
-4 - -	1		
-5 - -	1	14	(17%)
-Younger fledged:			
-1 day earlier	4		
-2 days -	1		
-3 - -	1		
-4 - -	1	7	(9%)
Hatched on same day, but fledged:			
-1 day apart	15		
-2 days -	3		
-3 - -	1	19	(24%)

Tab. 9.VIII. The size of Black Guillemot chicks on the last day before fledging.

Year	Weight(g.)	Culmen(mm.)	Tarsus(mm.)	Wing(mm.)
1975:				
n	33	33	33	33
Range	295-415	23.8-28.1	28.4-33.2	122-139
$\bar{x}$	346.8	26.4	31.0	129.5
S.d.	30.2	1.2	1.3	4.3
1976:				
n	86			
Range	290-415			
$\bar{x}$	355.9	-(1)	-	-
S.d.	25.1			
% of mean adult size(2)	86.7 (1975) 89.0 (1976)	86.7	100.2	79.4

Notes: (1) No observations available

(2) See pp. 213-220.

Tab. 9.IX. Fledging weight and fledging age of Black Guillemot chicks in relation to brood size and year.

	1-chick broods:				2-chick broods:					
	n	Range	$\bar{x}$	s.d.	n	Range	$\bar{x}$	s.d.	t	P
1975:										
-Age	8	30- 39	33.5	3.3	25	30- 36	33.4	1.7	0.16	n.s.
-Weight	8	325-415	360.0	32.3	25	295-415	342.6	28.8	1.45	n.s.
1976:										
-Age	16	30- 37	32.7	1.7	70	29- 37	32.1	1.7	1.28	n.s.
-Weight	17	290-400	356.8	36.1	74	300-415	355.5	22.1	0.18	n.s.

Tab. 9.X. Regression correlations between hatching weight and subsequent weight at different stages of the nestling period.

Year	Age (days)	r	d.f.	P
1975	5	0.58	33	<0.001
	10	0.63	18	<0.01
	15	0.76	15	<0.001
	20	0.36	10	n.s.
	25	0.57	33	<0.001
	30	0.17	31	n.s.
	Fledging	0.17	29	n.s.
1976	3	0.78	26	<0.001
	6	0.66	21	<0.001
	9	0.64	25	<0.001
	12	0.70	29	<0.001
	15	0.41	25	<0.05
	18	0.42	28	<0.02
	21	0.34	31	n.s.
	24	0.35	23	n.s.
	27	0.23	30	n.s.
	30	0.21	35	n.s.
	33	0.30	19	n.s.
	Fledging	0.14	37	n.s.

Tab. 9.XI. A comparison of fledging age (= length of the nestling period) and the fledging weight.

Year	r	d.f.	P
1975	- 0.51	24	<0.01
1976	0.12	85	n.s.

fledging date and the percentage of birds recovered in later years in the Manx Shearwater. A similar analysis was carried out for Black Guillemots. It was not expected a priori that similar relationship would be found, e.g. because no differential nestling mortality was recorded depending on the time of season (see Fig. 6.7, p.153).

Although sample size was low, Fig. 9.6 shows that there appeared to be no differential mortality in chicks which fledged, according to the time of season the eggs were laid from which these chicks hatched. The number of chicks which fledged in the last laying period (VI) were but few, and the high recovery rate of these presumably was a sample-size effect rather than a real one of a high post-fledging survival in the immediate period after fledging.

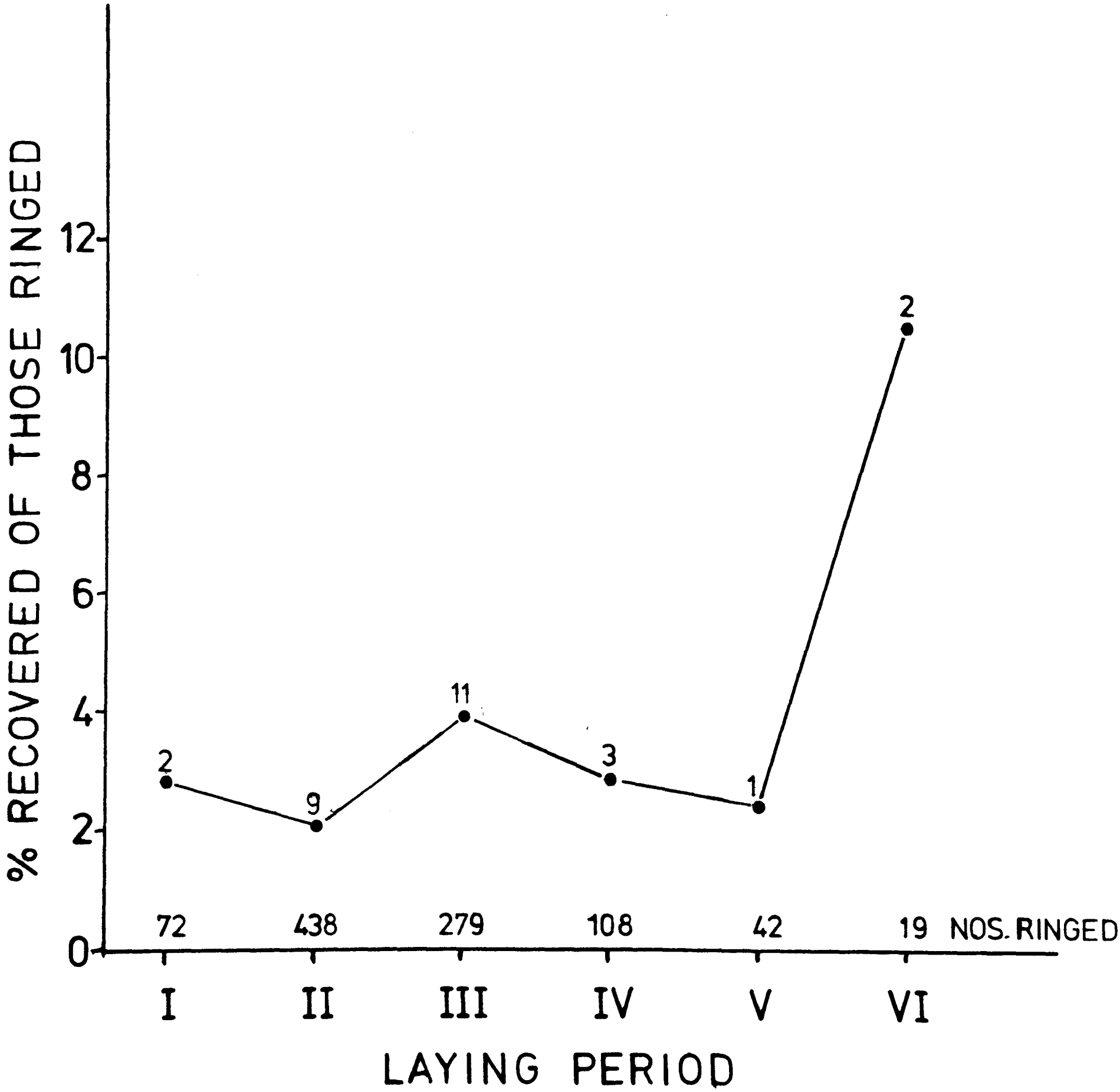
9.4 Discussion

Fledging condition and weight recession

Sealy (1973) maintained that Pigeon Guillemots showed little or no weight loss just prior to fledging. This species is likely to exhibit similar nestling growth as Black Guillemots which have a clear weight recession; peak weight is reached 4 days prior to departure (cf. Fig. 9.5, p.221). The weight loss was about 6% of adult weight, or more than documentated for some other auk species by Sealy (1973: Tab. V).

Ricklefs'(1968) review of the literature on weight recession indicated this was mainly found in oceanic birds as well as swifts and swallows. The reason for a weight recession in birds has been debated. Earlier it was thought the young would fast since they were deserted by their parents, e.g. in the Puffin (Myrberget 1962). In Puffins Harris (1976c) found that the young were not deserted despite a weight recession. He suggested that extra fat could be disadvantageous to the birds for diving. Ricklefs (1968) suggested that water loss from the maturing tissues may be the reason for weight loss, perhaps due to increased activity (Sealy 1968:113). Hudson(1979a:73 et seq.) thought Puffins had to reach a critical wing-loading before fledging. Although these may be the reasons for a weight recession, it is not

Fig. 9.6. The percentage of Black Guillemots, ringed as chicks and recovered one or more years later, according to the time of laying of the egg from which these chicks hatched. The chicks were ringed 1975-1977; the numbers are given in the figure. The numbers recovered are also given. The recoveries included those reported up till 31.12.1980.



clear why chicks have to reach peak weight, later to decline in weight.

In Black Guillemots the chicks are fed by their parents right up to fledging. But the frequency declines the last days, and this may result in a decline in weight since the birds are actively growing at the time of departure. In those cases when one chick left one or more days before the other chick, the parents continued feeding the remaining chick. Drent (1965) observed adult Pigeon Guillemots returning with food after the chicks had left. I observed the same in Black Guillemots, e.g. the case when an adult entered the nest with a fish, departed again and ate the fish itself.

Black Guillemot chicks are completely independent from their parents upon fledging (Chapter 3). In fact the parents do not recognize their young as shown by experiments where additional chicks were introduced in nests (cf. Chapter 12). There is no need for a parent-chick bond to develop, as in Common Guillemots for instance (Tschanz 1968) since the chicks fledge alone and are independent upon fledging.

The fledging of a chick may not be determined by its age as such, rather its condition, e.g. partly by the amount of food received from its parents. Fig. 10.4 (p.265) showed that the rate of feeding declines from chick age 25-29 days until fledging. This was reflected in the loss of weight of the chicks the last days before fledging (see Fig. 9.5, p.221).

Puffins, similar to Black Guillemots, show a decline in feeding rate towards the end of the nestling period. Hudson's (1979b) results implied that this was controlled by the parents rather than the chick, while the reverse may be the case for duration of the nestling period. Black Guillemot data rather suggested same took place as in the Puffin; that chicks fledge because they are heavy and they fledge totally alone. Drent (in Sealy 1973) had evidence that Pigeon Guillemot chicks refused food just prior to fledging. I never witnessed this in Black Guillemot, nor that chicks were enticed by the parents as suggested by Winn (1950) and I consider unlikely to take place.

Post-fledging survival

Perrins (1966) found that the earliest fledging chicks of the Manx Shearwater, had the highest survival and there was a seasonal decline. He hypothesized that heavier chicks may have had more fat and thus survived better. Nisbet & Drury (1972) also found same results in Herring Gulls. Later, Perrins, Harris & Britton (1973) found that heavier chicks had higher survival than light ones.

It was not necessarily expected in Black Guillemots, that a difference in post-fledging survival would be found, according to the time of season these chicks were raised. Late-nesting breeders appeared to be just as good raising chicks as early ones, as long as they managed to hatch their eggs. But these results may have been an artifact since late-nesting birds had fewer chicks per nest. Hence the average brood each late-nesting pair had to feed, was smaller than that of early-nesting pairs. Whatever the answer, no seasonal trend was detected in the post-fledging survival of Black Guillemot chicks, although undenibly the information available was minimal.

In spite of this, heavier chicks may still survive better than light ones. This has still to be investigated. The weight at fledging may turn out to be more critical in Black Guillemots than Common Guillemots, Brünnich's Guillemots, and Razorbills for instance. In these species, the chicks are dependent upon their parents for weeks after fledging. Black Guillemot chicks however, fledged independent from their parents, and appear to lead a principally solitary existence until the next breeding season.

Chapter 10: The food of Black Guillemots, and aspects of their feeding and prey selection

10.1 Introduction

The Black Guillemot has been considered one of the most typical inshore-feeding members (vide Lack 1967: 3-4) of the auk family, Alcidae (Lack 1968: 264, Bédard 1969, Sealy 1972: 200, Cody 1973). The same applies to its congener, the Pigeon Guillemot, and probably Spectacled Guillemot, all of which appear to have remarkably similar feeding habits, indeed similar life histories (Austin & Kuroda 1953: 454-456, Kozlova 1957: 58-60, Drent 1965), although there is very little information for the latter species.

Several accounts exist on the food of Black Guillemots but none from Iceland. Food studies have covered only either full-grown birds or chicks, but in the present study it was possible to compare both at same time in same area.

The main aims of this study, were to: (a) analyze and compare the diet of full-grown birds and chicks, (b) identify feeding areas, and (c) quantify and discuss some factors influencing the amount and types of prey brought to young. Two further points were also dealt with but mainly qualitatively; the behaviour of adults bringing food to chicks and kleptoparasitic attacks on Black Guillemots.

10.2 Materials and methods

Feeding observations

Observations on food carried to chicks by adults were made from hides at two nesting areas (IV and IX). The observation bouts varied from 2-13 hours, and were made at all hours of the 24 hour cycle. On each occasion a number of nests was kept under surveillance, and the following details were known for each nest: (a) the location of the nest as seen from the hide, (b) the number of chicks, (c) the age of the chicks, and where possible (d) the identity of at least one member of the adult pair. Throughout the summer efforts were made to colour-

ring as many adults as possible at nests visible from the hides, as well as to identify the nest-sites of birds which had been ringed earlier years. This work was also part of that on annual adult survival (Chapter 11) and mate- and nest-site fidelity (Chapter 3). As part of routine nest checks (Chapter 5) all sites used for feeding observations were inspected to see when chicks hatched so their age would be known exactly, and later if any chicks had fledged or not.

Chick food and feeding

During feeding observations the following details were noted whenever possible: (a) time of arrival of adult with food in the neighbourhood of the nesting area, (b) time at which feeding took place, (c) nest number, (d) identity of the food-bearing adult, (e) prey species, and (f) prey size. Later, age of the respective chick(s) was added to the data base. An effort was made to collect the smallest and largest food items in order to obtain the range of prey sizes taken. Collecting all food items would have been impractical since this would have led to too much disturbance and loss of food to young. Especially in the first year of study many food items were collected to confirm species identification. These were sampled from birds which were carrying food to young. In areas other than those used for feeding observations I also put collars round the necks of chicks to prevent them from swallowing prey which I later collected. Prey not measured directly, were estimated against the adult's bill (ca 30 mm). Length was estimated in steps of half a bill length. The weight of these items was estimated from length/weight curves, worked out using collected food items or individuals of same prey species secured in other ways. The length-weight relationships for the four most important prey groups, are given in Tab. 10.I. Some food items which were not secured involved species which had not been identified previously. Hence they remained unidentified and their size not measured directly. These constituted a very minor proportion of the chick diet. On a few occasions prey species could be identified but their length not estimated. This accounts for the slight discrepancy in Tab.

Tab. 10.I. Length (L.)/ weight (Wt.) relationship for some fish species taken as prey by Black Guillemots.

	n	r	Regression curve
Butterfish (Pholis gunnellus)	29	0.992	$Wt=0.00105 \cdot L^{3.3440}$
Sandeels (Ammodytidae)	41	0.975	$Wt=0.00240 \cdot L^{3.0856}$
Redfish (Sebastes sp.)	5	0.991	$Wt=0.00802 \cdot L^{3.2142}$
Bullrout (Myoxocephalus scorpius)	40	0.990	$Wt=0.01078 \cdot L^{3.0824}$

10.II, shown later. Some taxonomically difficult species were not identified to the species level (sandeels, Redfish).

Adult food

In 1975 full-grown Black Guillemots were collected by shooting for food analysis, 3-6 km away from Flatey, once a month from May to August. In 1976 this was not necessary as I received birds drowned in fishing nets. The main advantage of the latter sampling method was that the birds were on the feeding grounds actively feeding when drowned. Therefore none of the birds had an empty stomach contrary to some in the shot samples, which also had fewer food items per stomach (on average 7.8 vs 11.5).

Adult food was analyzed by counting the numbers of different food items in the stomachs. Whole prey items or characteristic parts of prey, were counted, and the maximum number of any prey species counted was used. The prey items which were intact could be used for comparison with partially digested items. Prey species identification was made using the following guides: Polychaeta- Gardarsson (n.d.); Mollusca- Oskarsson (1962, 1964), and with the help of Mr. J. Bogason, the Marine Research Institute, Reykjavik; Malacostraca- Saemundsson (1936b), Ingolfsson (n.d.), and identified specimens at the Museum of Natural History, Reykjavík; Fish- Muus & Dahlstrøm (1964), Jonsson (1975). Nomenclature follows same works.

Observations on behaviour

Behavioural observations (of adults feeding young) mainly qualitative but based on detailed notes of individual sequences. These were made primarily in 1975. Since behaviour analyses were not the primary goal, on later occasions notes were not kept of behaviour sequences unless they had not been observed and noted before.

Feeding area observations

In 1975 observations were made of the direction taken by adult birds which, having fed chicks, left the island. This was done in order to obtain information on where adult Black

Guillemots from Flatey were feeding. Further information was gained from birds ringed as adults on the island and later found drowned in fishing nets in surrounding waters (cf. Chapter 3). Some information was also obtained from local people and on many excursions at sea.

10.3 Results

The food of chicks

At least 12 species of fish and 2 species of invertebrates were taken to young by their parents. Adult birds were never seen carrying more than one prey item in their bill at a time to their young. Chicks were fed almost exclusively fish, on average 94% of the numbers of prey items recorded. Three prey groups predominated, Butterfish (Pholis gunnellus), Bullrout (Myoxocephalus scorpius), and sandeels (Ammodytidae), as shown in Tab. 10.II. Other prey groups were mostly of minor importance, although some formed important parts in the diet of individual nests, as shown later. There was a striking similarity in the diet composition in the three years, presumably reflecting the relative stability of benthic communities around Flatey. The major differences were: (a) greater numbers of Butterfish in 1975 compared with 1976 and 1977 ($P=0.001$; Fisher Exact Test), (b) greater occurrence of Bullrout in 1977 ($P=8^{-5}$), and (c) greater occurrence of Ammodytidae in 1977 than 1975 and 1976 ($P=0.05$).

Butterfish was by far the most common prey species, representing 49-61% of the diet by numbers. It's proportion was slightly higher by weight (52-64%) with the importance of Bullrout, but especially sandeels, correspondingly less. This means that for an average length unit Butterfish were slightly heavier than the other two species. Butterfish also has high calorific value (5.9 kJ/g, Dunn 1975; converted to SI units, cf. Baron 1977: 33), but not as high as sandeels (6.5 kJ/g, Harris & Hislop 1978). Myoxocephalus aenaeus, a congeneric of Bullrout and presumably of similar calorific value, had the lowest calorific value of these species (5.1 kJ/g, Dunn 1975).

Butterfish is well-known as a major prey of Black Guillemots in Iceland (Saemundsson 1926: 171, 1936a: 647, Gudmundsson

Tab. 10.II. Food brought to Black Guillemot chicks during their nestling period. The data cover most of the nestling period in the population (1975: 28.6.-18.8.; 1976: 21.6.-17.8.; 1977: 19.6.-10.8.).

Prey species	Year 1975 %nos.	1975 %wt.(1)	1976 %nos.	1976 %wt.	1977 %nos.	1977 %wt.
Hermit Crabs (*Eupagurus* sp.)(2)	5	6	8	9	1	2
"Shrimp"(3)	0	0	3	1	2	1
Cod (*Gadus morhua*)	1	1	0	0	0	0
Unident. gadid(4)	1	1	0	0	2	2
Butterfish (*Pholis gunnellus*)	61	64	50	60	49	52
Snake Blenny (*Lumpenus lampretaeformis*)	1	1	0	0	0	0
Spotted Snake Blenny (*Leptoclinus maculatus*)	0	0	0	0	1	3
Unident. blennies(5)	0	0	0	0	2	3
Sandeels (Ammodytidae)(6)	15	10	19	10	12	9
Greater Sandeel (*Hyperoplus lanceolatus*)	1	2	4	5	1	2
Redfish (*Sebastes* sp.)(7)	5	5	2	2	1	2
Moustache Sculpin (*Triglops murrayi*)	0	0	0	0	1	1
Bullrout (*Myoxocephalus scorpius*)	13	10	14	13	26	24
Unident. cottid(8)	1	1	0	0	0	0
Lumpsucker (*Cyclopterus lumpus*)	1	1	3	1	4	1
Unident. flatfish	1	1	0	0	0	0
Total prey numbers	358		80		171	
Total prey numbers on which weight was based(1)		349		75		169
Total prey weight (g)		2754		590		1074.5

Notes:
(1) Percentage weight is the % of total estimated prey weight.
(2) *E. bernhardus* and *E. pubescens* are both present in Flatey waters, and probably both represented in food samples.
(3) Most likely *Pandulus* sp.
(4) Most likely *Melanogrammus aeglefinus* (Haddock), *Boreogadus saida* (Polar cod), *Merlangius merlangius* (Whiting), and/or *Pollachius virens* (Saithe).
(5) Most likely either *Lumpenus lampretaeformis* or *Leptoclinus maculatus*.
(6) Probably both *Ammodytes tobianus* and *A. marinus*. The taxonomy of this group has caused confusion, e.g. Richards et al. 1963. Difference between 1976 and 1977 marginally significant; Fisher Exact Test, P=0.05.
(7) Both Icelandic species, *S. marinus* and *S. viviparus* present in Flatey waters. Probably both included in food samples.
(8) Probably *Triglops murrayi* (Moustache Sculpin)

1953, Bardarsson 1975), where it is sometimes called "Tystie-fish" as in Sweden (Lönnberg 1937). Similarly, Butterfish has been found to be of overriding importance in the food of Black Guillemot chicks in other parts of the N. Atlantic; Kent I., New Brunswick (68% of items brought to young, Preston 1968: 13), Greenland (ca 45%, P.G.H. Evans, pers. comm.), Norway (41%, R.T. Barrett, in litt.), Denmark (67%, Asbirk 1979b), and Shetland (46.9 and 70.7%, Slater & Slater 1972a; 79%, P.G.H. Evans, pers. comm.). Butterfish does not occur in the eastern Baltic but is replaced there by a related species, the Eelpout (Zoarces viviparus), which has similar habits (Wheeler 1969: 447-448) and which is the almost exclusive prey of Black Guillemots in Finland (Bergman 1971, 1978).

Prey size was similar in all three years, and the data therefore combined in Tab. 10.III. Of note in the table, is that maximum length of different prey species varied considerably. Longer individuals were taken of thin and not so deep-bodied species (Butterfish, sandeels, blennies) as of species with much lower length: breadth (Bullrout) or length: depth (Redfish) ratio. Secondly, there were great differences in the weight of meals (which would not be exactly the same if expressed in calorific or protein terms). These differences were prominent both within and between prey species. Blennies gave, on average, the highest return, while shrimps and Lumpsucker fry were rather insignificant prey.

The food of full-grown birds.

The diversity of prey eaten by full-grown Black Guillemots, was much greater than that given to chicks. At least 9 species of fish and 27 species of invertebrates were taken. Many prey items were not identified to species because they were partly digested, thus may have included species otherwise not detected.

Data are given for 1975 and 1976, and found in Tabs 10.IV and 10.V, analyzed by number of items and proportion of birds containing particular food group compared with the total number of stomachs in the sample. Invertebrates formed much greater part of the food than in that of chicks, 80% (1975) and 88% (1976) by numbers of prey items. There were some differences between years in the diet composition. There were fewer fish

Tab. 10.III. Length and weight ranges, estimated mean length and weight (=meal weight) of main prey species brought to young. Data combined for 1975, 1976, and 1977.

Prey species	n	Length ranges (cm)	Mean length (± s.e.)	Weight ranges (g)	Mean meal weight (± s.e.)
Butterfish	334	7.5-23	14.0(0.16)	1 -37	8.0(0.13)
Sandeels	88	9 -19	12.9(0.27)	1.5-28	6.3(0.46)
Bullrout	100	5 -12.5	7.6(0.17)	2.5-24	6.0(0.37)
Redfish	18	4 -12	8.4(0.53)	2 -26	10.0(1.51)
Lumpsucker	8	2 - 4	3.0(0.19)	1 - 3	2.0(0.18)
Blennies	6	12 -29	18.8(2.74)	5 -31	13.2(3.95)
Hermit crabs	24	-(1)		5.5-13.5	10.0(0.24)
Unident. shrimp	5	-		0.5	0.5(0.00)

Note: (1) Length not measured.

Tab. 10.IV. Food of full-grown Black Guillemots from the Flatey area. Birds shot on feeding grounds or at nesting areas during 17.5.-23.8. 1975. No. of birds= 38. Total no. of food items= 296.

	Nos.	%	% occurrence (1)
Polychaeta:			
Nereis sp.	57		39
Harmothoë sp.	3		8
	60	20	
Mollusca:			
Spirorbis planorbis	1		3
Lacuna divaricata	1		3
Lunatia pallida	1		3
Natica clausa	2		3
Modiolus modiolus	1		3
Nucula tenuis	8		3
Onoba striata	10		8
Indet. squid	1		3
	25	8	
Malacostraca:			
Hyas sp.	10		21
Eupagurus bernhardus	2		5
E. pubescens	2		5
E. spp.	1		3
Pandulus montagui	96		42
P. borealis	3		8
P. spp.	4		8
Spirontocaris gaimardi	4		8
S. pusiola	13		16
S. polaris	7		11
S. spinus	4		11
S. spp.	8		11
Crangon allmani (?)	1		3
	155	52	
Fishes:			
Clupea harengus	1		3
Unident. gadid	1		3
Ammodytidae	9		8
Pholis gunnellus	22		37
Lumpenus or *Leptoclinus* sp.	8		11
Sebastes sp. (?)	1		3
Myoxocephalus scorpius	2		5
Unident. fish	12		32
	56	19	
Miscellaneous:			
Protozoa	+		3
Hydrozoa	+		5
Bryozoa	+		5
Cirripedia	+		5
Copepoda	+		3
Unident. mass	+		3

Note: (1) Percentage occurrence is the proportional number of stomachs containing the respective food item.

Tab. 10.V. Food of full-grown Black Guillemots from the Flatey area. Birds drowned in Lumpsucker (Cyclopterus lumpus) fishing nets 19.5.-12.7. 1976. No. of birds= 31. Total no. of food items= 355.

	Nos.	%	% occurrence (1)
Polychaeta:			
Nereis sp.	183		68
	183	52	
Mollusca:			
Margarites groenlandicus	2		3
M. helicinus	1		3
Onoba aculeus	12		7
Lacuna divaricata	4		7
	19	5	
Malacostraca:			
Hyas sp.	5		13
Eupagurus sp.	2		7
Spirontocaris pusiola	2		7
Pandulus borealis	3		7
P. montagui	3		7
P. spp.	30		29
Gammarellus homari	1		3
Themisto sp.	1		3
Caprella sp.	1		3
Jassa sp.	4		3
Anonyx nugax	43		10
Amphipoda indet.	4		7
Decapoda indet.	12		13
	111	31	
Fishes:			
Gadus morhua	1		3
Pholis gunnellus	7		19
Ammodytidae	27		39
Myoxocephalus scorpius	4		13
Agonus cataphractus (?)	1		3
Cyclopterus lumpus	1		3
Unident. fish	1		3
	42	12	

Note: (1) Percentage occurrence is the proportional number of stomachs containing the respective food item.

in 1976 (12%) than in 1975 (19%) (X_1^2=6.34, P<0.02). No amphipods were represented in 1975 against 15% in 1976. Similarly, polychaetes were much scarcer in 1975 (20%) than in 1976 (52%) (X_1^2=67.51, P<0.001). Shrimps (Pandulus, Spirontocaris) formed 47% of the food items in 1975 against only 11% on 1976 (X_1^2= 107.17, P<0.001). Most food items occurred in stomachs more or less in proportion to their numbers as a whole, i.e. if many items were recorded, these were found in many stomachs. The main exceptions were the shrimp, Pandulus montagui (in 1975), and the amphipod, Anonyx nugax (in 1976) which occurred in relatively few stomachs but in abundance when they did. The crab, Hyas (both years) tended to occur in small numbers but in many stomachs.

The importance of polychaetes in both years deserves mentioning, since these were never seen to be carried to the young for which a polychaete could presumably constitute a substantial meal. The fish species in stomachs were much the same ones as given to young.

Some of the food items found in Black Guillemots stomachs are likely to have originated from stomachs of their prey. This is particularly applicable to molluscs and amphipods which form important parts of the diet of Butterfish in the Flatey area (Vikingsson et al. 1978). The food of other fish in the Flatey area, e.g. Bullrout, is unknown.

In contrast to fish prey, most of the invertebrates were small, the main exceptions being polychaetes and hermit crabs. The food value of individual invertebrate item was therefore considerably less by weight than by numbers. This would be even more so considering the indigestible chitinous exoskeleton of the many invertebrates and its substantial part of the weight of individual prey items. Since the food in the stomachs was partly digested, it was difficult to quantify accurately the relative importance of food items. According to data for young, and assuming the same applied to full-grown birds, the average weight of a fish was 7.4 g. I estimated the average weight of an invertebrate prey item was 1.5 g in 1975 but 2 g in 1976. Therefore, taking account of the different proportions of fish and invertebrate prey in the 2 years, fish formed about half of the diet of full-grown birds in 1975 but only

about one-third in 1976. This is strikingly less than the average of 94% in the chick diet.

Behaviour of adults feeding chicks

Black Guillemot chicks were fed in the nest from the very day of hatching until the day they fledged. On eight occasions I recorded chicks receiving food during the first 24 hours after hatching. Information in Thoresen & Booth (1958), Kartaschew (1960: 72), and Drent (1965) indicates that Black and Pigeon Guillemot chicks do not receive food until the second day after hatching.

The pattern of behaviour of adults returning with food from the feeding grounds was typically as follows. Food-bearing adults came flying in and landed on the water in front of the nesting area. They tended to keep to themselves, further away from the shore than other guillemots attending the nesting area. Sometimes adults flew straight to their nest-site, as long as there was no disturbance in the area, and it tended to be the same individuals which repeatedly did this. Still others waited on the water just in front of the shoreline among the other guillemots, or came ashore at communal roosts (which shifted with the tide), especially if the waiting period was prolonged. In both the latter cases the food-bearing adults were harassed frequently by other guillemots. Having decided to feed the chicks, the adult, whether ashore or on the water, took off, flew in a big circle out to sea, this often being repeated several times, and then landed beside the nest-site. There they might hesitate before entering the site. The chicks, hearing a bird approach, started squeaking and so did other chicks in the immediate vicinity. The food-bearers were sometimes joined by their mate which tried to seize the food, and this hastened the feeding of the chicks. The delivery itself was quick, esp. after the chicks had grown large enough to meet the adults at the nest-site entrance. Afterwards, the adult flew straight to sea, some directly on another foraging trip, while others waited on the water for some time, perhaps settling among the other birds at communal roosts, often preening, before flying off again. Slater & Slater (1972b) described two behaviour sequences in

Black Guillemots approaching nesting area with food: (a) flying directly in to site, and (b) splashing down on the water and walking up the shore. This latter behaviour was never witnessed on Flatey.

On receiving a prey item, the chicks swallowed it head first. This normally happened in seconds, especially in the older chicks. The correct positioning of fish prey was particularly important for Black Guillemot chicks since some of their prey were heavily armoured with sharp spines, notably two of the major prey species, Butterfish (in the dorsal fin) and Bullrout (on the gill covers). If swallowed tail-first these spines would stick out and could harm the birds. On a few occasions small chicks were found dead with a big fish in the oesophagus. Some may have choked, others had the fish's spines sticking through the gullet. Gochfeld (1975) describes the danger to terns of swallowing tail-first, and Hunt & Smith (1964) describe possible adaptive values of this behaviour in Herring Gulls.

While waiting on the water adults were frequently seen dropping the prey and grabbing it again, repeatedly squeezing it. This was also seen on the feeding grounds when adults surfaced with a prey (see also Kozlova 1957: 64-65). Presumably this was meant to kill the prey, the squeeze usually directed at the most sensitive parts of the fish, the head and gill regions, where fish were also normally held in flight. In spite of this, Butterfish were commonly brought to chicks alive (see also Winn 1950). Butterfish, in contrast to other prey species, are very resistant to desiccation. They live in an environment,the lower shore, which partially dries out, although they tend to stay in moist places under stones (Quasim 1957, pers. obs.). Hermit crabs were always removed from their shell before being taken to the chicks. The chelae were also removed, presumably since these could potentially harm young and adult birds. Both these happened before the adult reached the nesting area, and presumably took place upon capture of the crabs.

Kleptoparasitism

If adult Black Guillemots with food in their bill, were

sitting on the rocks below, or swimming on the water in front of the nesting area, other Black Guillemots, even the other member of the pair, frequently tried to seize their food (see also Slater & Slater 1972b). It is unknown if they meant to steal the prey for their own offspring, or eat it themselves as has been observed by Thoresen & Booth (1958) in Pigeon Guillemots. Reaction of other guillemots usually induced the food-bearing bird to give its prey to the young more quickly. Once I recorded another Black Guillemot - surprisingly a yearling - successfully stealing prey from an incoming adult. The adult had driven the yearling away when another adult-plumaged Black Guillemot approached, whereupon the food-bearer attacked, dropping its prey; at the same time, the yearling sneaked in again and ate the prey. Adults with food normally waited alone, as described earlier, and interference from the other members of the nesting area assembly may account for this behaviour.

Three other seabird species were recorded robbing Black Guillemots of their food; Arctic Skua, Kittiwake, and Arctic Tern. Elsewhere, various gulls (Great Black-backed, Herring, Common) have been reported stealing food from Black Guillemots (Winn 1950, Bergman 1971, Cairns 1978: 23-24), and skuas (Montague 1926).

Arctic Terns were the most common robbers of Black Guillemot food on Flatey. They nested in large numbers close to the guillemots' nesting areas (Petersen 1979). In spite of this, kleptoparasitism was rather infrequent, and terns were only seen singly at nesting areas at any one time. The terns flew around or sat waiting at the nesting area until a guillemot with food approached, then a chase was given. If over the sea, the guillemot quickly splashed onto the water and dived. The tern attempted to follow the bird by hovering just above the water surface. When the diving guillemot had to surface, and the tern managed to follow it, the tern grabbed the prey as the bird surfaced. Such behaviour sequences were well documented by Bardarson (1975) at another Icelandic Black Guillemot breeding station, where the terns could easily see the guillemots underwater because of the shallowness of the water. If already overland when a tern gave chase guillemots either tried to reach their nest-site or, failing that, rapidly turned towards

the sea and the same behaviour pattern described above, was repeated.

Kittiwakes, the next most frequent robbers, behaved in a similar way to the terns, but were less successful in following the movements of the guillemots underwater, and most often turned away when the guillemots dived. Kittiwakes seemed, on the whole, less successful than the terns in obtaining a meal by kleptoparasitic attacks. Few Kittiwakes nested on Flatey itself (Petersen 1979) although they were very common in nearby islands (pers. obs.).

Arctic Skuas did not nest regularly in the islands (Tab. 1.I, p. 14), and they were only once seen robbing a guillemot.

There was a clear selectivity in what Arctic Terns tried to steal from the guillemots. Terns were frequently seen taking dives at guillemots bringing in fish, but if these were not silvery (practically all sandeels), e.g. Butterfish or Bullrout, the terns invariably turned away and did not molest the guillemot any further on that occasion. Sandeels were almost the sole food of young Arctic Terns on Flatey. Although Kittiwakes also fed their young almost exclusively on sandeels, adult Kittiwakes took whatever they could form the guillemots.

Nervousness played a dominating role in the behaviour of adults approaching the nesting area to feed chicks. Bill-dipping was frequent during waiting on the water, during which the bill and prey were emerged in the water at frequent intervals. This behaviour had a clear association with alarm situations (see also Drent 1965, Preston 1968: 66, Asbirk 1979b), Bill--dipping may also function to keep the prey wet and slippery, if the adults have a long wait, and to aid ingestion of the prey (see also Thoresen & Booth 1958).

Food-bearing adult Black Guillemots were more reluctant to go ashore to feed their chicks when no other guillemots were present at the nesting area, as also commented on by Bergman (1971) and Slater & Slater (1972b). If alarm call (Preston 1968: 63; also termed the Scream, Drent 1965, Asbirk 1979c) was given by another bird when adults were flying in to deliver food or when they were perched, escape was easily made towards the sea. Even if gulls were just flying past and happened to be in the flight course, the guillemots would

hastily splash down on the water, or fly another circle out over the sea. The time spent waiting before flying in, appeared to be highly individualistic. The longest time recorded of a bird waiting, was 65 minutes, which was exceptional. On several occasions the wait ended by the adult itself ate the prey. This general nervousness among food-bearing Black Guillemots, may stem from an innate fear of kleptoparasitic attacks, and also perhaps the danger of giving away the whereabouts of the young to potential predators.

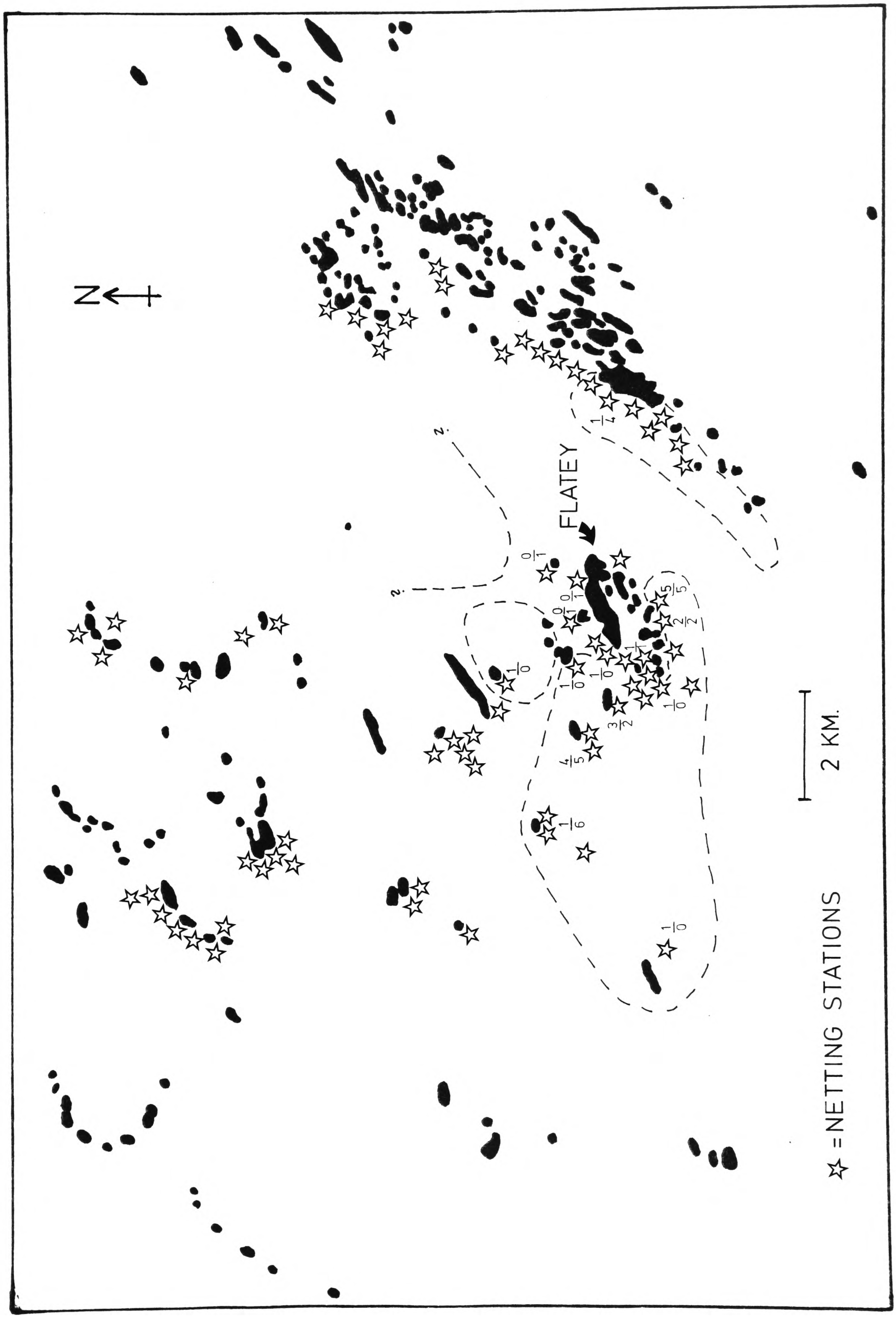
Feeding areas

Only a general idea was obtained of the location of the feeding areas used by Black Guillemots from Flatey. The picture was complicated by the numerous islands, nearly all of which had nesting Black Guillemots. Hence birds seen feeding could have come from various islands.

Information on location of feeding areas of Flatey Black Guillemots came primarily from two sources: (a) birds ringed on Flatey and recovered drowned in fishing gear, and (b) records of flight directions taken by adults upon leaving nesting areas. The findings are summarized in Fig. 10.1, giving approximate boundaries of feeding areas. The birds were recovered in fishing nets and were actively feeding when drowned. Their recovery position therefore showed where they were fishing. Most of the birds were found on the "west" fishing grounds, although commercial fishing effort was also greatest there. The importance of this foraging area for Black Guillemots in the Flatey region, was also evident on many excursions I made at sea, and from information by local fishermen. It is worth noting that no Black Guillemots nesting on Flatey were recovered at the many netting stations towards the northwest or northeast of the island.

It was rare to see birds leave Flatey nesting areas and splash down on the water within a kilometer or so of the island and start feeding. It was correspondingly rare to see birds come flying from somewhere else and start feeding in the vicinity of Flatey. On many occasions I followed birds with a telescope but usually they went too far out of sight or behind other islands. On those occasions when I saw them land and begin feeding

Fig. 10.1. Approximate boundaries of feeding areas used by Black Guillemots from Flatey. Based on observations where adult birds (upper figure) and immatures (lower figure) were drowned in Lumpsucker (Cyclopterus lumpus) nets, and direct observations (see later in Fig. 10.2). Adults were considered those ringed as fullgrowns on nest, and birds ringed as chicks, recovered 4 or more years later (cf. age of first breeding in Chapter 11). Stars indicate the stations at which Lumpsucker nets were placed. Data from 1975-1980.


N
FLATEY
2 KM.
☆ = NETTING STATIONS

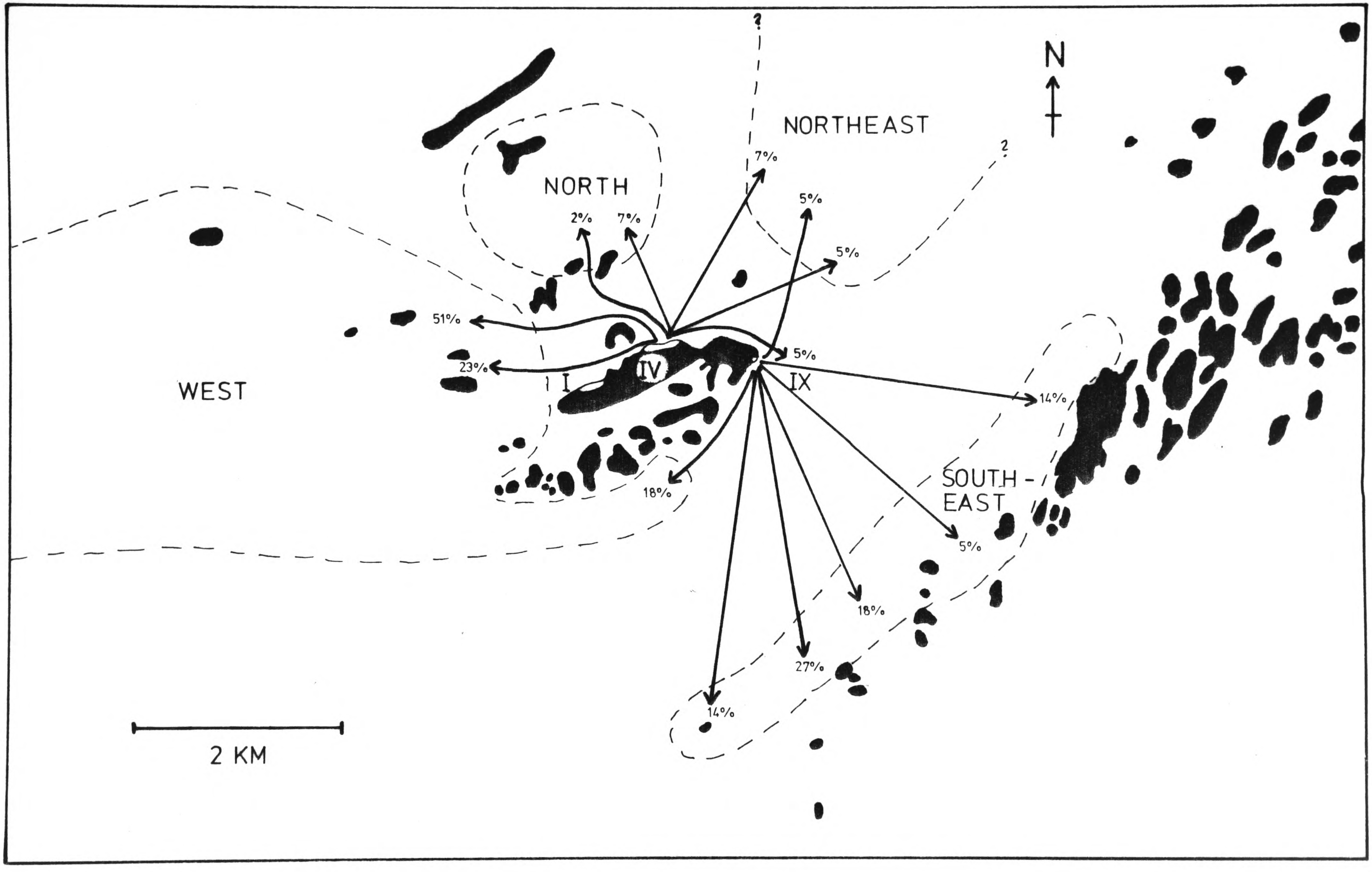
they took a direct course to the feeding area, although sometimes deflected by islands. Hence I am satisfied that flight direction gave a good indication of where birds were heading.

The flight direction of Flatey breeders, actively feeding young, was observed from two nesting areas (IV and IX). Preliminary observations indicated that the routes taken by birds upon leaving the nesting areas, were relatively fixed. At nesting area IV the detailed course of the route taken depended on the location of islands but the general direction was already fixed upon leaving the nesting area. At nesting area IX, on the other hand, there are no islands in the immediate vicinity to deflect the birds. But again the birds' course was fixed immediately on leaving the nesting area for particular islands or skerries which I later used for ascertaining any particular bird's flight direction. Fig. 10.2 shows the flight directions taken by birds from the two nesting areas. Birds from the island's north side mainly flew west upon leaving the nesting area. Birds from the east end flew south or southeast. Unquantified observations during attendance studies in the pre-laying period (Chapter 4), indicated that birds from the northwest side of the island (nesting area I, Fig. 10.2) nearly always left towards and arrived from the west.

Besides preferences for different feeding areas by birds these two nesting areas, the scanty data available appear to indicate preferences by individual members of the same nesting area, even members of the same pair, for individual feeding areas. Five (marked) birds, each of which were followed on 3-6 successive occasions, left on 17 out of 19 occasions in the same direction as first observed. Also, in the case of one colour-ringed pair, one member consistently left towards the northeast while the other went southeast.

Individual preferences for foraging area, may also manifest themselves in the types of prey brought to young. Such differences were most obvious when uncommon prey species were brought to nest. Frequency of prey species at individual nests varied significantly from random in three out of 4 observation periods (see Tab. 10.VI). Such difference were also noted by Slater & Slater (1972b) and Cairns (1978: 23) in Black Guillemots, and in Pigeon Guillemots by Drent (1965). This may mean that the birds

Fig. 10.2. Flight directions taken by adult Black Guillemots upon leaving Flatey nesting area IV (n=43) and IX (n=22) to obtain food for their you-g. Another area, nesting area I, mentioned in text, is also shown.


N
NORTHEAST
NORTH
WEST
SOUTH - EAST
I
IV
IX
2%
7%
7%
5%
5%
51%
23%
5%
14%
18%
5%
18%
27%
14%
2 KM

Tab. 10.VI. Tests for significant differences in frequencies of prey species fed to young per same unit time.

Nesting area[1]	Year	Nos. of nests	No. of prey species	Nos. of deliveries	D.f.[2]	X^2	P
IX	1975	12	8	256	77	207.45	<0.001
IX	1976	9	6	36	40	56.05	<0.05
IX	1977	14	8	73	91	56.74	n.s.
IV	1977	6	8	53	35	68.42	<0.001

Notes: (1) Only parts of the nesting areas were under observation

(2) Degrees of freedom

(3) A worked example of how calculations were done: In 1977 73 meals, comprising 8 different prey species, were brought to 14 nests under observation. Not all prey species were brought to all nests in the sample.

from different nests foraged on different feeding grounds, at least in the short term.

Sharing between the sexes in feeding of chicks

There was a significant correlation between numbers of feeds brought to the nest in a unit time by each of the pair members (r_{40}=0.64, P<0.001; y=0.85x + 0.59). This was recorded at sites where one or both members of the pair were colour-ringed. Hence if one parent brought many items per unit time the other did also. Because of the difficulties of sexing live Black Guillemots it was nearly always unknown which was the male and which the female. The numbers of food items brought to nest were not exactly equal between the two pair members, as shown by the correlation coefficient of 0.64. Therefore it is unknown if one sex consistently brought more items, or if individuals varied only temporarily in their feeding rate and the sexes brought equally many items to the nest over longer periods. In Chapter 3 it was suggested that one of the sexes did much of the feeding for the young during the brooding period.

I made an analysis of the frequency of feeding the young by each pair member. Since the sex was mostly unknown, birds which brought the greater number of items, were grouped together, those bringing less forming the other category. The data, given in Tab. 10.VII,gave significantly different results for one sample, indicating that each pair member brought prey species in different proportions and frequencies. But the other sample was not significant, and although more data are needed on this aspect, the latter sample may have included too few deliveries for any significant difference to emerge. If one of the sexes consistently brings more food, significant results would mean that the sexes could either be obtaining or delivering prey at different frequencies. Still, if food provisioning was shared in a 1:1 ratio, such results would reflect differences in prey selection between pair members.

The literature on the role of the sexes in feeding is conflicting. Drent (1965) concluded for Pigeon Guillemots, that the sexes took an equal part in feeding. The more intensive data for Black Guillemots by Preston (1968: 16) and Asbirk (1979b)

Tab. 10.VII. Selectivity of food for young by each adult member of Black Guillemot pairs. See text for further explanation.

Nesting area	Year	Nos. of nests	No. of prey species	Nos. of deliveries	D.f.(1)	χ^2	P
IX	1975	7	7	143	6	19.41	<0.005
IX	1977	10	8	59	7	7.07	n.s.

Note: (1) Degrees of freedom

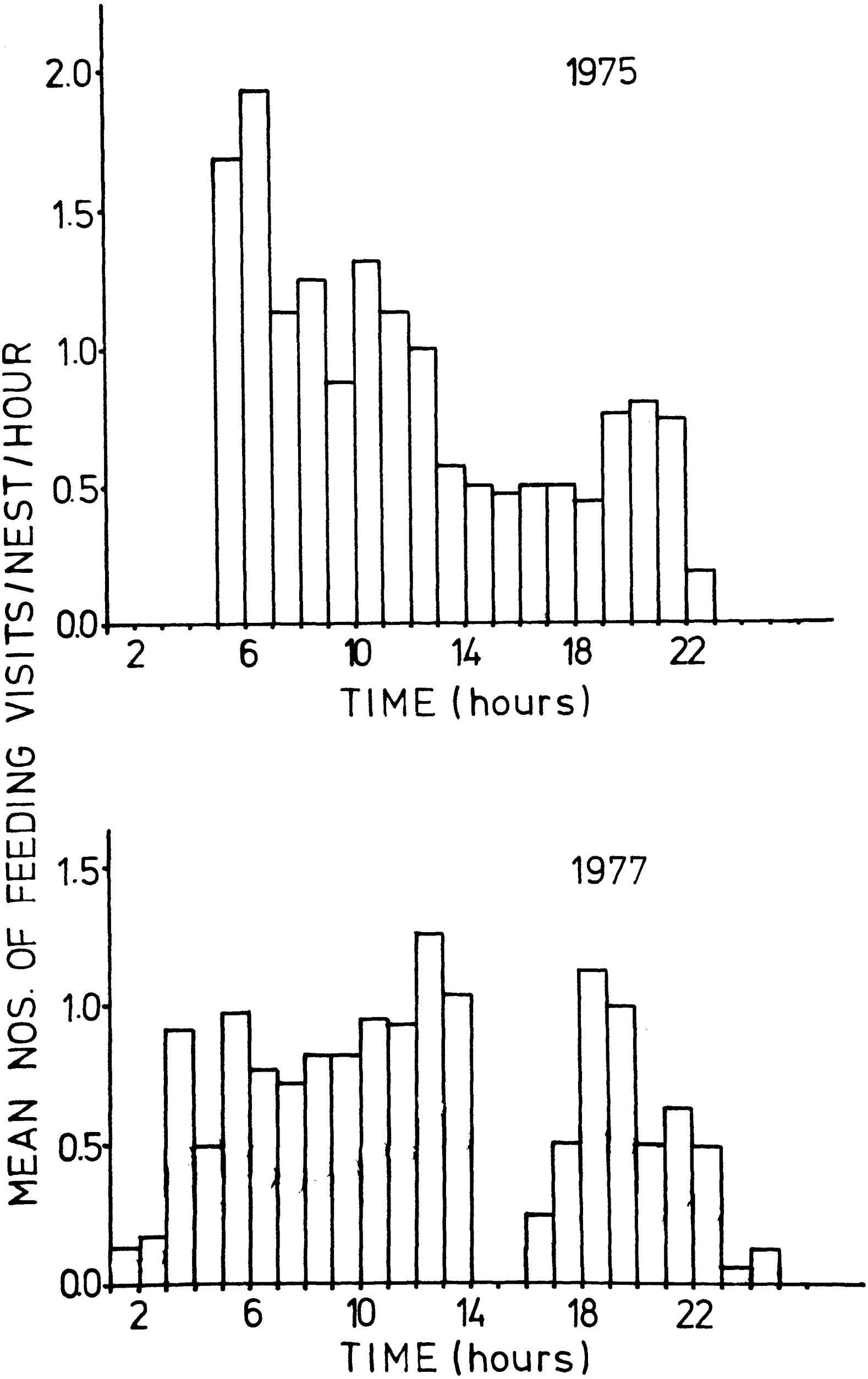
indicate that males took a greater share. Preston found males brought 134 items while females brought only 31, a ratio of 4.3:1.Asbirk found males brought 75 items while females brought 55, a much lower ratio of 1.4:1. One possible explanation for these different ratios, is that the role of the sexes changes with the age of the chicks. On Flatey, in one pair in which the sexes were known, the male brought 16 prey items while the female brought twelve, a ratio of 1.3:1, or similar to Asbirk's results. The few data there are on this subject, indicate that male Black Guillemots bring more food to the chicks than the female.

The diurnal rhythm of feeding of chicks

The pattern of chick-feeding was studied in 1975 and 1977. The data, given in Fig. 10.3, indicate a bimodality in feeding over the 24 hours, with, in 1975, peaks in the morning (0500-0600 hrs) and evening (1900-2200 hrs). These peaks coincided with the pattern of attendance at the nesting area in the pre--laying period (Chapter 4). Most of the feeding took place in the morning, analogous to the longer periods of attendance in the pre-laying period. The pattern was not as clear in 1977 as in 1975. Variation was introduced mainly by the differing age of chicks and time of year, also possibly by the number of chicks per nest. There were important differences between the years, feeding taking place at all of the 24 hours in 1977 but not in 1975. This relates to the time of year the data were collected. The 1977 data were mainly from the first week of July but from the second week of August in 1975. In midsummer there is continous light over the whole 24 hours in Iceland. By August it has started to become too dark for feeding to take place in the middle of the night. Nonetheless there was a clear drop in feeding rate at that time of day in July. In Pigeon Guillemots, Koelink (1972: 21) found a direct relationship between the start of feeding and sunrise, and between cessation and sunset in the evening.

Similar diurnal variation in feeding has been reported for Black Guillemots in Finland (Bergman 1971), in Canada (Cairns 1978: 25), and for 2-chick broods of Pigeon Guillemots (Koelink 1972: 19), also implicit in Aitchison's (1972: 15)

Fig. 10.3. The diurnal rhythm of feeding of chicks by adult Black Guillemots over the 24 hours. The histograms are based on 473 (1975) and 410 (1977) "nest-hours" of observations.



data for the same brood size. Storteir (in Bergman 1971) and Asbirk (1979b) did not find such a rhythm for Black Guillemots in Finland and Denmark respectively, nor did Drent (1965), Aitchison (1972: 15) and Koelink (1972: 19) in Pigeon Guillemots, the latter two in artificial 3-chick broods. Other studies have shown a morning peak with a decline in feeding rate as the day progressed (Bianki 1976: 195 for Black Guillemots, Koelink 1972: 19 for 1-chick broods of Pigeon Guillemots). The differences in feeding rates appear to relate to the food requirements of the broods; with one chick a high feeding rate in the morning is all that is needed, whereas 2 chicks need extra food in the evening. In the artificial 3-chick broods, the parents apparently had to feed their young also in the afternoon to fulfil their requirements, resulting in a high feeding rate for most of the daylight hours (see Aitchison 1972: 15, Koelink 1972: 19).

On Flatey the number of feeds per nest per 24 hours, were 15.8 (1975) and 14.7 (1977), giving average hourly rates of 0.66 and 0.61, respectively. These feeding rates are a mixture of 1- and 2-chick broods. If only the length of the feeding period was taken into account in 1975 (19 hrs) the hourly feeding rate was 0.83 feeds per nest. These feeding rates were similar to those reported from Finland, of 10-20 feeds per nest per 24 hours, recorded by means of radioactive marking of adults (Storteir & Palmgren 1971, Storteir in Bergman 1971) and 14 found by Bergman (1971) in 1970, although in most years he obtained very much lower rates, or average of 5.3 in 1963-1968. The low feeding rates were attributed to scarcity of food in these years, and the high 1970 due to greater abundance of food that year (Bergman 1971, 1978).

Some factors affecting feeding rate and prey selection

The amount of food received by chicks from their parents, centered around three variables: (a) the number of feeds, (b) prey species, and (c) prey size. In Tab. 10.VIII I have listed some factors which could potentially affect these variables. The list is not meant to be exhaustive, although I believe the more important direct factors have been included. Of course, that some of the factors are inter-related, and others not mentioned may have an important bearing on these.

Tab. 10.VIII. A list of some factors which potentially may affect prey species, prey size, and numbers of feeds brought to young Black Guillemots by their parents.

	Prey species	Prey size	Number of feeds
Chick age	x	x	x
Number of chicks	(x)?	(x)?	x
Time of day	x		x
Time of season (=food availability)	x	x	x
Tides	x		x
Weather factors	x		x
Location of feeding area (=food availability)	x	x	x
Distance to feeding area			x
"Parental efficiency"			x

I will deal here primarily with the first two on the list, while the diurnal rhythm of feeding has already been outlined. Others are mentioned in discussion.

Chick age

Winn (1950) and Radozei (in Bianki 1967: 197) stated that feeding rate increased with age in Black Guillemot chicks, and so did Drent (1965) for Pigeon Guillemots. Aitchison (1972: 16-17) found a gradual decline in feeding rate with age of Pigeon Guillemot chicks in 2-chick broods, but an increase until day 20-23 with a subsequent decline in 3-chick broods. Asbirk (1979b) found no correlation between chick age and feeding rate in Black Guillemots.

Hence the literature is conflicting. My data, in Fig. 10.4, show an increase in feeding rate with age up to day 25-29, then a decline. It seems to me that this pattern is the most logical one, considering the changing energy demands of the growing chicks. Not only are the chicks growing rapidly but their plumage is developing. The pattern of feeding with chick age, correlated well with the pattern of weight increase of chicks on Flatey (Chapter 9).

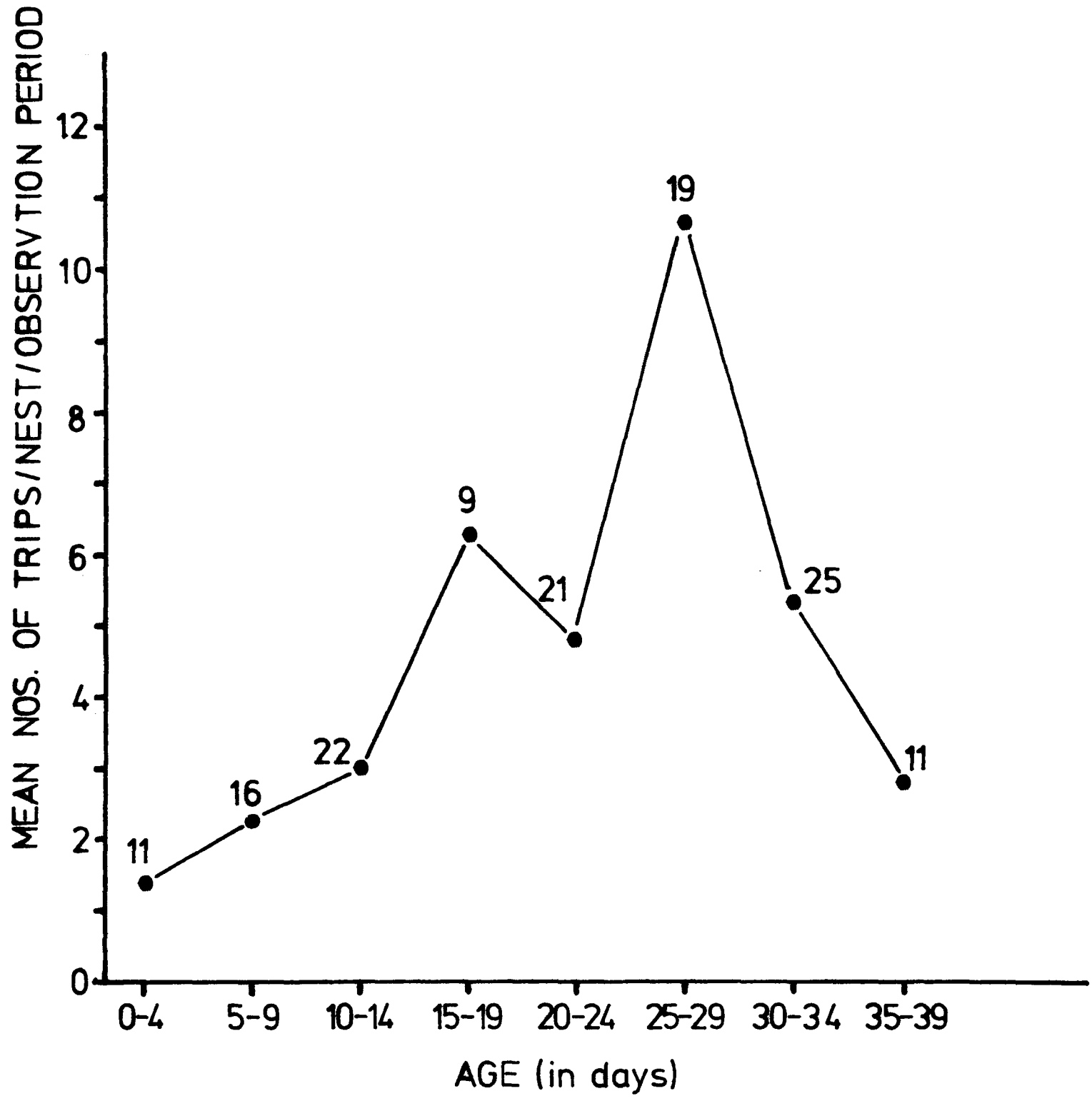
The size of prey received by the chicks was not constant throughout the nestling period but increased as the chicks grew older. This was more striking in 1975 than in 1977, as shown in Fig. 10.5. This also appeared to be the case in Black Guillemots in Denmark (see Asbirk 1979b: Fig. 5).

There were some differences in types of prey given to the young according to its age. This was especially prominent with sandeels. Significantly more sandeels were brought to young chicks (0-19 days) than to old ones (20-39 days) (1975: $P=0.0004$. 1976: $P=0.0007$; Fisher Exact Test).

Number of chicks

Aitchison (1972: 16-17), working with Pigeon Guillemots, obtained a feeding rate of 25.7 feeds/24 hrs at 2-chick broods but 45.8 at 3-chick broods. These figures are higher than my averages for combined broods of 1 and 2 chicks of 15.8 (1975) and 14.7 (1977), presented earlier. Some of this difference may be linked with the larger average size of Pigeon Guillemots

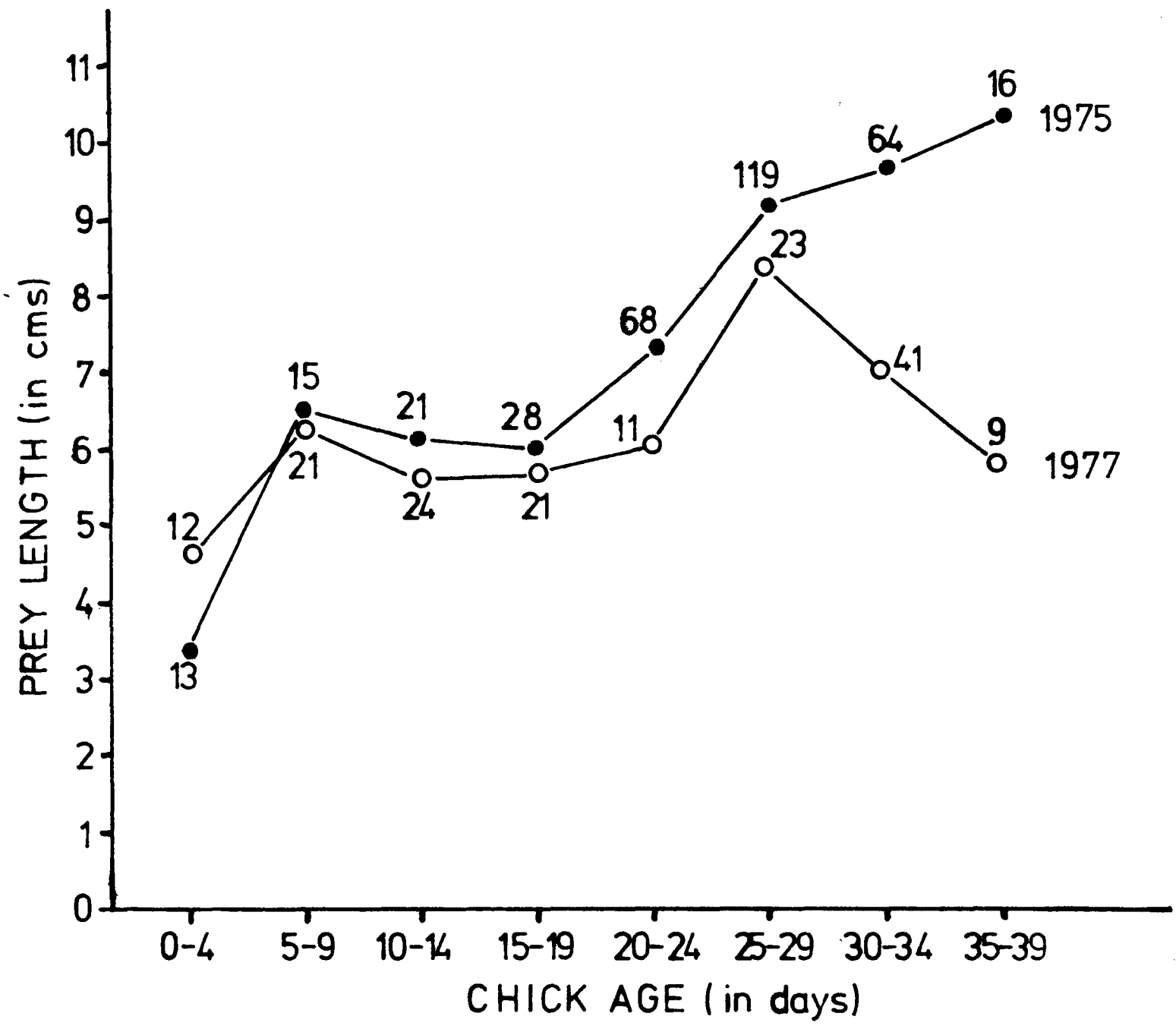
Fig. 10.4. The variation in the rate of feeding Black Guillemot chicks by their parents according to the chicks age. Data from 1975 and 1977 combined.



Notes: (1) The observation periods varied in length from 2-13 hours.

(2) The numbers show how many nests were under observation with chicks of given age.

Fig. 10.5. Changes in prey size with age of chicks. Data from 1975 and 1977 shown separately.



Note: (1) The figures show sample sizes of prey given to chicks of given ages.

(cf. Sealy 1972: 282), other factors being equal. Yet it appears that Pigeon Guillemots take smaller fish items than Black Guillemots (pres. study and Follett & Ainley 1976).

The number of chicks clearly affected the rate of food provisioning by adults. On Flatey, single-chick broods received 13.9 feeds/24 hrs.but 2-chick broods 18.8, or 9.4 feeds per chick, which is about 30% less per chick than for singletons. Average number of feeds per chick per 24 hrs was 12.8 in 2-chick broods of Pigeon Guillemots but 15.3 in the artificial 3-chick broods (Aitchison 1972: 16-17). Asbirk (1979b) got 0.57, 0.87, and 1.38 feeds per brood per hr in respective 1-, 2-, and 3-chick broods of Black Guillemots, or 13.7, 10.4, and 11.0 per chick per 24 hrs. These figures compare well with my data, yet it is not certain if Asbirk's figures were averages for 24 hours (cf. pp. 53-54, 75). Preston (1968: 42-43), who got 1.2 feeds per hr (which would give 28.8 per 24 hrs), appears to have studied feeding rate only during periods of high feeding intensity.

10.4 Discussion

Food and feeding

The diet of Black Guillemots has been described by various authors. The most comprehensive study for full-grown birds, is that by Belopol'skii (1957: 28 et seq.). Others include Hartley & Fisher (1936), Madsen (1957), Uspenski (1958: 86), and Kartaschew (1960: 76), but see also references in Storer (1952). My results for full-grown birds are in general agreement with these studies, showing great diversity of prey in full-grown birds.

Diet of chicks has received greater attention than of full-grown birds, especially by Winn (1950), Kozlova (1957: 64), Preston (1968: 11), Bergman (1971), Slater & Slater (1972b), Cairns (1978: 19 et seq.), and Asbirk (1979b). Compared with full-grown birds, all these studies showed more specilization on fish for the chicks, as did mine. The overriding importance of Butterfish has already been mentioned, while blennies, gadoids, sandeels, and cottids were also important. High numbers of prawns (ca 28% by number) in the chick diet in Greenland (P.G.H. Evans, pers. comm.) is exceptional.

Less in known about the diet of the congeneric Pigeon Guillemot, especially that of full-grown birds. Being a N. Pacific species, it's diet consists of species different from those taken by the Black Guillemot, yet the diet of both consists of closely related species, drawn from benthic communities (Legg 1954, Thoresen & Booth 1958, Drent 1965, Aitchison 1972: 19, Koelink 1972: 25, Scott 1973: 69, Follett & Ainley 1976, references in Storer 1952).

The diet of Black Guillemots differs markedly from that of other Atlantic auk species. Little Auks are plankton feeders (Norderhaug 1970: 558-559, Evans 1981), Common Guillemots, Brünnich's Guillemots, Razorbills, and Puffins feed their young mainly on mid-water, schooling fish, primarily the Herring family (Clupeidae), gadoids, sandeels, anchovies, Capelin, and smelts (Tuck 1960: 166-177, Pearson 1968, Harris 1970a, Birkhead 1976: 84, Harris & Hislop 1978, Nettleship & Gaston 1978: 28-30). The full-grown birds of these species take, like Black Guillemots, a different selection of prey, consisting of greater proportion of invertebrates (references in Storer 1952, Belopol'skii 1957: 28 et seq., Kartaschew 1960: 76, Ogi & Tsujita 1973, 1977). Of the two Uria species, the more northerly Brünnich's Guillemot takes, as pointed out by Bédard (1969), a greater proportion of invertebrates (Swartz 1966: 667). They have even been reported bringing invertebrates (about 6% by numbers) to chicks (Tuck & Squires 1955).

The comparison of full-grown and chick diets of Black Guillemots on Flatey has clearly shown the difference in these two age groups in the same area and season. It is obviously advantageous for the birds to maximize the return per trip to and from the feeding grounds. The bigger the prey the fewer the trips needed to satisfy the chicks' needs. Preston (1968: 13) stated that Black Guillemots tended to take whatever was locally abundant. I believe this applies well to the adults' diet, while fish was selected for the young. These observations are consistent with central-place foraging theory (cf. Orians & Pearson 1978).

Feeding areas

Black Guillemots on Flatey appeared to feed at similar

distances from their nesting areas as found for same species elsewhere, perhaps a little further afield. Preston (1968: 5) noted that Black Guillemots on Kent I. fed from the shoreline up to 1.5 km from the island. Bergman (1971) reported Finnish birds feeding 1.5-4 km away. Asbirk (1979b) found that Danish birds fished 0.5-4 km from nesting areas. Flatey birds fed primarily 2-4 km away, although some flew as far as 7 km, some perhaps further. There were differences in feeding areas of birds from different nesting areas, as also suggested by Eldridge & Kuletz (1979).

It is not certain why the birds flew that far from the island to obtain food. Presumably this had mainly to do with the distribution of available prey in the vicinity of the island. Shoals of sandeels, for instance, were especially plentiful all summer in the waters west of Flatey, with many bird species taking advantage of these. Sandeels were seldom seen in the immediate vicinity of Flatey, or in the large stretch of water east-northeast of the island. If seen, the surfacing shoals were found in the sounds north or south--southeast of the island (cf. Fig.10.2, p.256), and were followed by great numbers of Arctic Terns, Kittiwakes, Puffins,and gulls (Great Black-backed, Glaucous), in particular. These shoals came from the west, and I think it is safe to conclude that this food source was much more abundant west of the island than at any other feeding areas used by Black Guillemots from Flatey. Yet, at the same time, Butterfish, one of the most important prey species, were very abundant on the shores of Flatey. In standardized collections in late June 1975, 86 individual Butterfish were picked up by two persons in 10 minutes on a 50 m coastline (unpubl. and Vikingsson et al. 1978). Furthermore, Shags and Cormorants were often seen surfacing with Butterfish or Bullrout in the island's vicinity.

Slater & Slater (1972b),noting differences in prey selection by individual Black Guillemots, proposed two explanations; that fishing was done in same area on successive occasions, or the birds had a search image for certain prey types. My scanty data indicate that Flatey Black Guillemots went to the same fishing area on successive occasions, and that they tended to bring the same food species on subsequent occasions,

(see also Eldridge & Kuletz 1979). It is difficult to tell whether this was because the birds had specific search image, were responding to local abundance of prey, or both. The last is most likely. Local abundance may be the ultimate decisive factor but it was also apparent that certain prey types and sizes were selected for young and in accordance with the age of chicks. It is possible to argue in this context that changes in diet with age of chicks, and therefore with season, were due to food availability, but this is unlikely (see also later).

It seems beneficial to the birds to utilize the same feeding area on consecutive occasions, as long as they had been fishing there successfully before. They would then "know" that food was to be found in the area, and would not have to spend time locating new fishing grounds. Although travelling time to and from the nest may be somewhat longer, it may still be more profitable to utilize the same feeding area. Distance to feeding grounds is, however, one factor which may influence the rate of provisioning chicks, and subsequently their growth rate and survival.

Other factors affecting feeding and prey selection

There are many factors which may influence what is taken to the young, and at what rate. One major difficulty in studying food of seabirds, is that any measure of availability of potential foods is usually impossible to obtain.

It was shown that the return per feeding trip was highly variable, from the small Lumpsucker fry or shrimps of about ½ g in weight to the largest meal, a 37 g Butterfish. The profitability of small prey presumably varies, e.g. according to availability in relation to large prey and travelling distance. Invertebrates were generally smaller than fish prey, hence would more often be less economical. However, if invertebrates were much more abundant their capture time would be decreased and hence they may become profitable to exploit. This may have been the case with Black Guillemots in Greenland where shrimps formed a greater part of the chick diet than reported elsewhere. In general, this may also be a difference between high and low latitudes. But even if profitable in size or quantities, invertebrates may be unsuitable as bulk food for growing chicks,

as indicated by Tuck & Squires' (1955) observations on a Brünnich's Guillemot chick fed solely on gammarids. The excreta became a solid mass of chitin and the bird died. Four other chicks were fed on fish and fledged successfully.

When actively diving, an adult Black Guillemot may be expected to ingest whatever prey it encounters, however small. Since energy has already been spent on the dive, small items may be better than nothing, especially if present in large numbers. Many small items can presumably be swallowed in the course of a dive, whereas the bird would do best to surface with large prey, as shown experimentally in captive auks (Swennen & Duiven 1977).

There are obviously limits to what an adult Black Guillemot can carry in the bill. The heaviest fish recorded (37 g) was about 9% of the average adult weight. Gape width of chicks is a further influencing factor on the size of prey which can be accepted, as prey is swallowed whole. The prey size received varied with chick age, although (as mentioned before) it could be argued that this was a date effect, i.e. food availability. This is unlikely, however, since sampling of Butterfish at several times between April and July (unpubl.) showed no differences in average fish length; important differences in size of other prey species are unlikely over the nestling period of ca 34 days (Chapter 7), and there were no differences in chick mortality (Chapter 6), and presumably fledging weight,over the season.

It is clear from Tab. 10.III(p.243) that girth dimension of prey was important. Of the fish species taken to chicks, those which were relatively deep-bodied (Redfish) or broad (Bullrout) in comparison with their length, were much shorter than long and thin species. It is to be expected that adults sometimes make mistakes and bring fish that are too deep-bodied or broad for the chicks to swallow. These are probably the so-called "rejects" which are often found at Black Guillemot nest-sites. No special notes were taken of rejects in my study but Drent (1965), working on Pigeon Guillemots, noted that rejects tended to be heavily armoured fish or of awkward form. This also seemed to be so in Asbirk's (1979b) study on Black Guillemots (see his Tab. 5: 52).

Length of prey per se obviously did not matter to the chicks, which were often found with the tail end of a fish sticking out of their bill. As digestion proceeded at the front end the fish gradually passed down the chick. The longest fish recorded during the study (29 cm) was far longer than the chick which had partially swallowed it. Similar conclusions were reached by Swennen & Duiven (1977) in their experimental study on captive auks.

It was especially noticeable that sandeels were given to young chicks. This probably related to their physical ability to swallow prey, but sandeels are very smooth and thin compared with their length, and presumably easiest of all to swallow. Although a Butterfish, Bullrout, or Redfish gave, on average, higher return than sandeels per weight, this would be compensated for by sandeels' higher calorific value. The spines on Butterfish, Redfish and Bullrout, and the form of the latter two, may have been unsuitable for very young chicks, even potentially dangerous for them. Small chicks with a big fish stuck in the oesophagus, were found dead on several occasions. Some may have choked, others had spines sticking through the oesophagus. But here again, it is possible to argue that sandeels were less common late in the season when chicks had grown larger. Again, this is unlikely since sandeel shoals were seen off Flatey all summer through. As late as 21 August (when most chicks had fledged, see p. 58), nine such shoals were located in an area of about 12 km^2 west of Flatey. The four most common seabird species in the Flatey general region, Shag, Kittiwake, Arctic Tern, and Puffin, had chicks in the nest during July and August, at the same time and longer than Black Guillemots, and almost their sole diet was sandeels (pers. obs.).

Another factor which seemed to vary with the age of chicks, was the role of the sexes in feeding (Chapter 3). While the chicks are very young, they have to be brooded. Meanwhile one of the sexes appeared to do most of the feeding. But the thermoregulatory mechanism takes only 3-6 days to develop in Black Guillemot chicks (Rol'nik 1948, Kartaschew 1960: 73, Rol'nik & Kaftanovskii in Shilov 1968: 141). This is much faster than in Common Guillemot chicks, which do not reach full homeothermy until they are 9-10 days old (Johnson & West 1975). The

quicker onset of thermoregulation in Black Guillemots may be an adaptation to allow both parents to start feeding the chicks, which often number two, in contrast to the Common Guillemot's one. Because of increasing demands of the chicks as they grow, and the need of the brooding adult to feed, I suggest early homothermy is advantageous. In Common Guillemots which nest in the open, one parent always guards and broods the chick, presumably, among others, as insurance against predation (Birkhead 1977a). If Black Guillemot chicks need to develop homeothermy early for energetic reasons, such demands in Common Guillemots have probably been solved by fledging early (Birkhead 1977a). Sealy (1973) developed a similar argument for the precocial murrelets, Endomychura and Synthliboramphus. They fledge after only 2-4 days (Sealy 1972: 282-283), with presumably early development of homeothermy. In Black Guillemots there is no need to guard the chicks against predators since they nest in burrows. The microclimate of a burrow is also much less variable than in the open, presumably to the chick's benefit (see Manuwal 1972: 49-54).

Kleptoparasitism could potentially affect the growth of chicks and their subsequent survival. Nettleship (1972) demonstrated the lowered survival of Puffin chicks due to robbing of food by gulls. Although no analysis was made of such effects on Black Guillemots on Flatey, I consider them unlikely. Kleptoparasitic attacks were relatively infrequent, and since feeding rate of the guillemots was high, at least compared with other auks, occasionally losing a meal is not likely to have had detrimental effects. Chick starvation was also non-existent in the three years of study (Chapter 6). The most common robber, the Arctic Tern, also tried to take sandeels only.

Various environmental factors can affect Black Guillemot foraging. Dunn (1975) demonstrated the effect of high winds and seas on feeding in terns. Although terns are "surface plungers" and not "pursuit divers" (sensu Ashmole 1971: 227) like Black Guillemots, such weather conditions can still have important effects, directly or indirectly, in the shallow waters around Flatey. Birkhead (1976b) demonstrated effects of sea condition on feeding in Common Guillemots. Fewer Black

Guillemots attended the nesting area when wind was strong or temperature low in the pre-laying period. It was suggested (Chapter 4) that feeding was impaired. Tides had also effects; Slater (1976) showed a tidal effect on Common Guillemots, while Preston (1968: 13-14) suggested a tidal influence on Black Guillemots.

One further factor which may affect feeding, deserves mentioning. Parents can differ in their overall efficiency in providing for their young (Coulson, Potts & Horobin 1969). Such differences could manifest themselves in how many chicks are raised to fledging and their condition upon fledging (cf. Chapter 9). This may in turn depend on the bird's responses to some of the factors mentioned above.

Having outlined some of the many factors which may act upon the rate at which feeding takes place in Black Guillemots, one may speculate what adaptations such diversity of factors may have imposed upon the birds. In general benthic communities supposedly offer a more varied and static source of food than pelagic ones, i.e. they show greater resilience in time (vide Holling 1973). Benthic communities can be temporarily unstable, due to many perturbations, yet have high resilience (Gray 1977). Pelagic communities show great patchiness in time and space, presumably more so than benthic communities. This leads to predators in such an environment, as e.g. offshore alcids, having to follow their prey around. Benthic communities also show patchiness in time and space due to variation in the physical character of the sea-bed (Steele 1976: 98). But while various components of the benthic systems may undergo oscillations at times, there is less likelihood of local extinctions than in pelagic communities. In this sense I think it is fair to say that benthic communities are more dependable as a food source. For a benthic predator like the Black Guillemot, I suggest it is good to be a diverse, generalized feeder which can switch from one prey species to another if one is temporarily in short supply. This does not mean that pelagic or offshore habits are evolutionary unstable. MacArthur (1955) established theoretically that a given stability may be achieved by a small number of predator species eating a variety of prey (the Black Guillemot case) or by many species each of which has

a restricted diet (in the manner of offshore auks). Although patchiness of food in a pelagic environment may perhaps be greater than inshore, the amount of food per unit area may be, on average, just as great if not even greater. The main point is, however, that the inshore environment is much smaller in extent, being essentially linear, compared with the offshore environment . Hence one would expect less numerous populations utilizing the inshore environment than the offshore one, as demonstrated for tropical seabirds by Diamond (1978).

Chapter 11: Population dynamics of Black Guillemots

11.1 Introduction

In seabird studies, four basic parameters are usually considered the most important in population dynamics: (a) reproductive output, (b) age of first breeding, (c) pre-breeding survival, and (d) annual adult survival. The first of these was dealt with in Chapter 6, the remaining three are discussed below.

Three further parameters can be considered: (e) emigration, (f) immigration, and (g) degree of non-breeding among established breeders. These are often disregarded when dealing with population dynamics. Usually they are much less important than the four parameters mentioned above, but they are very difficult to quantify.

In stable populations emigration and immigration are usually presumed to be equal, thus cancelling each other out. In the present study immigration could not be disregarded, but emigration of adults was thought to be unimportant since the Flatey Black Guillemot population was increasing and there was a surplus of nest-sites on the island (Chapter 2). For the same reason non-breeding among adults was thought to be rare and unimportant. This could not be quantified, but as described earlier (Chapter 3), there was one record of an established breeder (ringed as an adult on nest) pairing with a 2-year old bird without eggs being laid by the pair that season. Thus, non-breeding did occur but was unknown among pairs which were known to have bred before.

The present study had three main objectives: (a) to quantify various population parameters, (b) compare these with information for other N. Atlantic alcids studied in sufficient detail; Common Guillemots (Birkhead 1976a,Birkhead & Hudson 1977), Razorbills (Lloyd 1976, Lloyd & Perrins 1977), and Puffins (Ashcroft 1976, 1979), and (c) use population parameters to construct a model of the Flatey Black Guillemot population, especially to show that only a massive immigration could account for the rapid increase that took place during the 1970's in numbers of breeders on the island.

11.2 Materials and methods

Age of first breeding

Ringing of Black Guillemots on Flatey was first carried out in 1973 (by T. Tryggvason). Only a few birds were ringed, and none of them were colour-ringed. Tab. 11.I gives the number of chicks that have been ringed on the island 1973-1980, and 1974-1980 in neighbouring islands, altogether 3042 chicks. As the table shows, a very high proportion of all chicks fledging from Flatey were ringed. Ringing in neighbouring islands was done at the same time as the size of the island populations was estimated (Chapter 2).

Constant watches were kept the entire breeding season for birds colour-ringed as chicks but the methods were not standardized in any way. Because the main study only covered three years, only a limited amount of data could be collected on the age of first breeding of Flatey-reared Black Guillemots. Therefore, I also collected information from other countries on this subject.

Pre-breeding survival

Two methods can be useful for studying pre-breeding survival. The first considers birds that have died, using recoveries of birds ringed as chicks. This method has the difficulty that seabirds are seldom found dead, and if recovered through activities of man there are dangers of biasses in the samples.

The alternative method is to count the numbers of surviving birds, colour-ringed as chicks, at natal areas in different years after ringing. Neither of these methods proved satisfactory in the present study, as explained more fully later.

To get some idea of pre-breeding survival, I resorted to using recoveries of birds ringed as chicks under various ringing schemes. Very few Black Guillemots had been ringed in Iceland prior to the present study, so the Icelandic Bird--Ringing Scheme did not provide information other than that from Flatey. Sufficient numbers of recoveries were available for birds ringed in Greenland, Norway, Sweden, Denmark, and

Tab. 11.I. The number of chicks ringed on Flatey since 1973, and since 1974 in neighbouring islands and at sea.

	Year:								
	1973	1974	1975	1976	1977	1978	1979	1980	Total
Flatey:									
Nos. ringed	12	52	308	385	378	433	390	464	2422
Nos. colour-ringed of those ringed	0	50	307	385	378	0	0	0	
% of chicks ringed of the total numbers fledging[1]	-	-	77.2	79.2	84.4	85.4	75.9	77.9	
Neighbouring islands[2] and at sea:									
Nos. ringed	0	6	139	38[3]	126[4]	123	63	125	620
Nos. colour-ringed of those ringed	0	4	139	38	126	0	0	0	
Total numbers ringed 1973-1980									3042

Notes: (1) Based on information in Tab. 11.X. (p. 298).

(2) This is the area shown in Fig. 1.4 (p. 17).

(3) 1 of these ringed at sea.

(4) 2 of these ringed at sea.

Finland to warrent analysis. This material was put at my disposal by the corresponding ringing centres. The material and sources are given in Appendix V . Subsequent analyses included all recoveries, irrespective of cause of death.

So that these recoveries could be used, an assumption had to be made regarding the age of first breeding. On average, Black Guillemots were considered to commence breeding when 4 years old, in light of information presented later. The recoveries were analyzed using Lack's survival estimate (Lack 1951: 431 et seq.). All the birds must therefore have had the same likelihood of becoming 4 years old (cf. Haldane 1955). To comply with that requirement, the numbers of recoveries used in the analyses were sometimes less than those available from the sources.

Annual adult survival

A total of 322 adult breeders were ringed during 1973-1980. Most adults caught in 1974 and 1975 were colour-ringed in addition to the numbered stainless steel ring. During 1976-1979 only those caught in the vicinity of the two observation huts were colour-ringed.

Most of the birds were caught by hand at nest-sites, a few by placing a coarse fishing net over the nest-site entrance when adults were feeding young. All colour-ringed adults had an individual combination of colour- and steel rings. Tab. 11.II gives the number of adults that were ringed and the numbers of these that were colour-ringed.

As with pre-breeders, no standardized methods were employed when searching for colour-ringed adults. The principal methods whereby ringed adults were sighted are better explained in the appropriate section.

Mortality factors

Mortality of recovered Black Guillemots ringed on Flatey and under various ringing schemes is discussed.

Population model

Most of the methods used for this are better explained

Tab. 11.II. Number of adult Black Guillemots ringed on Flatey since 1973, and in neighbouring islands since 1974.

	Year:								
	1973	1974	1975	1976	1977	1978	1979	1980	Total
Flatey:									
Nos. ringed	1	30	15	89	108	62	8	3	316
Nos. colour-ringed of those ringed	0	27 (1)	15	34	24	11	3	0	
Neighbouring islands:									
Nos. ringed	0	3	4	2	0	0	0	0	9
Nos. colour-ringed of those ringed	0	3	0	0	0	0	0	0	
Total numbers ringed 1973-1980									325

Notes: (1) One of these birds was the one steel-ringed in 1973, but colour-ringed when re-caught in 1974.

(2) These are the islands depicted in Fig. 1.4 (p. 17).

in the Results section. However, the calculations were based on information about the number of pairs breeding each year (Chapter 2), chick productivity (Chapter 6), as well as age of first breeding, pre-breeding survival, and adult survival, presented in this chapter.

11.3 Results

Age of first breeding

Only two birds of known age were recorded as definite breeders during the years of intensive study (1975-1977). One of them was ringed in 1973 and repeatedly seen carrying food to young in 1976, at the age of three. This bird nested at the same nest-site in 1977. This bird was ringed with steel ring only, but the number could be read through telescope.

The other bird was colour-ringed in 1974 and re-trapped on eggs in 1977, then 3 years old. This was presumably the same bird as seen in 1976, attending the same sub-section of the nesting area at which it nested in 1977. The bird was unpaired in 1976, and the only one of those ringed in 1974 seen at this particular nesting area.

In 1977 a special effort was made to discover breeding birds of known age. Checks were made of as many breeders as possible whether they were ringed or not. At 62 nest-sites (15% of all on island) both members of a pair were checked, and one of each pair at 130 sites. This involved 260 birds, or 31% of the 834 breeders on Flatey in 1977. None of these were of known age except the two already mentioned.

The number of chicks ringed in 1974 was small (58), of which only 10-15 could be expected to have reached the age of three in 1977. Besides the 1974 chick mentioned above, only one other bird of the same cohort was seen in 1977. That bird, possibly paired to a 2-year old, was definitely not breeding. The rest of the presumed survivors of the 1974 cohort may have bred on the island without being noticed, but probably most did not breed at all. It is possible that some bred on other islands. It is known that Black Guillemots may settle to breed away from their natal area. A Danish bird, ringed as chick, was retrapped on a nest 50 km from where it

had been raised (Andersen-Harild 1969). The possibility of this as far as Flatey birds goes was presumably lessened when the population was expanding and there was a surplus of nest-sites on the island.

If Black Guillemots on Flatey started breeding at the age of two, many more such birds would have been found breeding than 3-year old birds. This was especially applicable in 1977. Then the 1975 cohort was 2 years old, and 447 chicks were ringed that year. As the Flatey population was increasing, young birds were expected to start breeding earlier than normal in stable populations. The reasoning for this is as follows. If stable populations included non-breeding birds which are prevented from laying by the lack of nest-sites, this constraint would not exist on Flatey. Yet two-year old birds did not seem to breed, let alone one-year old birds. Two-year old birds did pair and occupy nest-sites but the production of eggs was not confirmed (see Chapter 3). (Since then one 2-year old bird has been found breeding, in 1980).

Information in the literature on the age of first breeding in Black Guillemots, is very limited and somewhat confusing. The Russian literature is the principal source, although concrete evidence is usually not presented and Russian authors tend to quote each other without critical examination of the data.

I have collected from the literature information on the age of first breeding in Tab. 11.III. The Russian references do not state categorically whether the birds were recorded at nest-sites containing eggs or chicks, or merely among birds attending nesting areas. I suspect the latter, because of Bianki's (1967) statement that Black Guillemots nest in large numbers when two and occasionally when one (p. 181). For the relative numbers of birds of these age-classes attending nesting areas, see Chapter 3. If merely attending, these birds cannot be regarded as breeders with certainty.

Asbirk (1979b) recorded one ringed 2-year old breeder. Another breeder was judged to be 2 years of age on the basis of remaining brown juvenile feathers in the wing patch. This is not an unequivocal character, however, since one of my known 3-year olds had brown irregular spots in the wing patch, still

Tab. 11.III. A summary of the existing data on the age of first breeding in Black Guillemots.

Source	
Kaftanovskii 1951: 73	Mature in 3rd year
Belopol'skii 1957: 147	Mature at end of 2nd and 3rd year
Kartaschew 1960: 77	Mature at end of 2nd year
Bianki 1967: 181	Large proportion when 2 years, occasionally when 1 years of age
Preston 1968: 26	One 4 year old breeding, one 3 year old not breeding
Andersen-Harild 1969	Recorded one 5 year old breeding
Asbirk 1979b	One 2 year old breeding, one thought to be 2 years on plumage characteristics
U. Unger, pers. comm.	One 2 year old breeding
R. Broad, pers. comm.	Four years: 2 individuals Five years: 1 indiv. Six years: 3 indiv. Seven years: 3 indiv. Eight years: 1 indiv.

persisting when the bird was 4 years old.

The best documentation of age of first breeding in Black Guillemots, is that by R. Broad on Fair Isle (Shetland). Some of his older birds may have bred prior to being re-discovered, but more importantly no birds were recorded at an earlier age than four. (Since 1977, I have also discovered on Flatey that most birds start breeding when four years old.).

To summarize, the present evidence suggests that most Black Guillemots start breeding when 4 years old, although some may start when 3 or even two. The average age at which Black Guillemots start breeding may change according to the state of the population, thus with time within same population (cf. Petersen 1976a). There are great difficulties in determining age of first breeding on the population level.

Conclusive evidence for age of first breeding in other alcids, is largely lacking. The small N. Pacific Cassin's Auklet start to breed when 2 or 3 years old (Manuwal 1972: 197). Some Puffins, Razorbills, and Common Guillemots first breed when 4 years old, but most probably not until 5-6 years old (Ashcroft 1976: 143-144, Lloyd 1976, Petersen 1976a, Birkhead & Hudson 1977, Lloyd & Perrins 1977).

Pre-breeding survival

Estimating survival of pre-breeders using sightings of surviving birds, depended on a high degree of philopatry, and on spotting birds attending the nesting areas.

Of those ringed in 1973 and 1974 only a few birds could be expected to be alive after 3-4 years (besides the 1973 cohort was not colour-ringed). Of the 1973 cohort, one bird was seen in 1976 (8.3%) when 3 years old, and again in 1977. Only two (3.4%) of the 1974 cohort were seen in 1977, when 3 years old. These survival figures are clearly unsatisfactory, and there are possibly four main reasons for this: (a) pre-breeding Black Guillemots are not as philopatric as some other auk species, e.g. Common Guillemots (Birkhead 1976a) and Puffins (Ashcroft 1976), thus emigrate more than expected, (b) difficulties in spotting colour-ringed pre-breeders which spend less time on land than adults, (c) age of first breeding generally later than 2-3 years, and (d) attendance at nesting areas

by pre-breeders less regular than that of adults.

Pre-breeding Black Guillemots were widely distributed when attending nesting areas. They were seen at various other nesting areas than where ringed and mixed freely with the breeders (Chapter 3). This differs from pre-breeding Common Guillemots, for instance, which gather in distinct "clubs" at the natal areas (Birkhead & Hudson 1977). Pre-breeding Black Guillemots were also frequently seen visiting islands other than those where they were raised. Moreover, one to three year old birds, ringed on Flatey, have been recovered in the breeding season hundreds of kilometers away from the natal area (Chapter 3). These were most likely non-breeders as it appears that most Black Guillemots started nesting when 4 years of age. Hence all the above factors may contribute to the difficulty of using sightings of pre-breeders at natal area for estimating pre-breeding survival.

Another method was tried; that of using birds ringed as chicks and later recovered 1-4 years later. These birds were all drowned in fishing nets in summer (May-July). The data were analyzed using Lack's (1951: 433) survival estimate, and included only birds ringed in 1973-1976, allowing every bird the same probability of having reached age four. The data are shown in Tab. 11.IV. Estimated pre-breeding survival was 46%, which is about twice that expected. One may expect mortality to be greatest the first year and then decline. This figure was a measure of the overall (composite) survival until age four. This method was clearly unsatisfactory, the reason being that birds of different ages, differed greatly in their likelihood of staying in the natal area in summer. This was seen earlier in Fig. 3.2 (p. 40). Since older birds were more likely to be near Flatey in summer than younger birds, they were more likely to be recovered, hence boosting the survival estimate.

Using data from ringing schemes, Tab. 11.V gives the composite survival up to the age of four. The difference between countries was great, or from 16% (Norway) to 32% (Finland). The Norway figure may be abnormally low because of a sample size effect. The mean survival, all populations included, was 24%.

Tab. 11.IV. Estimate of pre-breeding survival of Black Guillemots. Birds recovered drowned in fishing nets during May-July.

		Age at recovery:			
Ringed in:	Nos. ringed:	1	2	3	4
1973	12	0	0	0	1
1974	58	1	1	0	0
1975	445	7	5	2	2
1976	423	6	1	2	0
	938	14	7	4	3

Lack's survival estimate=46% $\pm$ 7

Notes: (1) Average age of first breeding assumed to be four years.

(2) Birds of all cohorts had same likelihood of becoming four years old.

Table 11.V. Estimated post-fledging survival of pre-breeding Black Guillemots. Sources given in Appendix V

	Nos. recorded each yr. interval[2]				Composite survival (%)[3]	SE[1]
Country	n	0-1	1-2	2-3	3-4	
Greenland	657	509	81	42	25	27	1
Norway	53	45	6	2	0	16	5
Sweden	111	88	18	3	2	21	3
Denmark	141	107	23	10	1	25	3
Finland	174	124	28	11	11	32	3
					Mean:	24	

Notes: (1) SE= Standard error

(2) 1st July taken as dividing line between years

(3) Ring loss due to wear was considered unimportant in these first years after ringing.

Looking at other alcid species, pre-breeding survival has been estimated somewhat higher, in spite of the age of first breeding being assumed to be 5 years instead of four. Using data in Lloyd (1974) the estimated pre-breeding survival of Razorbills was 42%, of Puffins 28% using data in Mead (1974). For different Common Guillemot populations Birkhead (1976a: Tab. 2.12) estimated 27.0-41.1% survival, and 19.0-52.9% for various Brünnich's Guillemot populations.

Annual adult survival

Four years data were available on annual adult survival. These are summarized in Tab. 11.VI. The mean survival rate was 87%, which obviously is a minimum figure since several factors, other than mortality, may have affected the estimates, namely ring loss, search effort, and emigration.

Ring loss: Of the birds colour-ringed in 1974, one was known to lose a colour-ring shortly after ringing. The bird became entangled in a net, and probably lost the ring because of its poor design and fitting. Colour-rings used in later years were better made. This bird excluded, only 2 birds in 129 "bird-years" (0.9%) were known to lose a colour-ring in an interval between years. These two birds were both ringed in 1974 (as the bird above) and lost one ring each between their 2nd and 3rd summer after ringing. These birds had an additional colour-ring (besides the numbered steel ring) which was not lost. Most colour-ringed adults had two colour-rings. Since it is not likely that birds would lose both colour-rings in the same year interval, birds which had lost a colour-ring are likely to have been spotted despite the ring loss, as was the case with the two birds above.

Of course the longer birds carried the colour-rings, the greater the probability of losing them. Many birds were handled after having worn rings for 3-4 years. In all cases wear had not proceeded to the point where loss of the ring was imminent. Sometimes the ends of the 1974 colour-rings had become separated, overlapping only a little. When birds were recaptured later, many rings were replaced by new ones.

Tab. 11.VI. Annual adult survival of Black Guillemots on Flatey. Data for colour-ringed birds.

Year interval	Nos. known to be alive in yr. x	Nos. recorded in yr. x + 1		Additional birds not seen in yr. x + 1 but later		% annual survival
		n	%	n	%	
1974-75	29	23	79	2	7	86
1975-76	40	30	75	3	7.5	82.5
1976-77	65	52	80	8	12	92
1977-78	85	69	81	5	6	87

Mean annual adult survival 1974-78: 87%

The steel rings were extremely durable and as good as new after 3-4 years wear. This ring type has already proven its extreme usefulness on Puffins which in Iceland have been ringed with steel rings since 1959 (Petersen 1976a). I conclude that loss of steel rings was non-existent, while that of colour-rings was negligible and not likely to affect survival estimates.

Search effort: Three main methods were employed when searching for colour-ringed adults; re-trapping at nest-sites, observing birds on communal roosts or on the sea, and observing birds carrying food to young (sight records). The last method was the most successful one. Searches for colour-ringed adults were concentrated in those areas where the birds had been ringed. If not found there, the search area was widened to both sides.

Searching for colour-ringed birds was very time-consuming, and colour-ringing the legs of the birds rather an inadequate method, since Black Guillemots are easiest to observe when on the water at times of high nesting-area attendance. Then they are calm and it is easy to check one bird after the other, but leg rings are very difficult to see through the water unless it is absolutely calm. When on land at communal roosts, there was difficulty in that the birds usually rested on the belly, making the legs invisable. Some other method of marking individual Black Guillemots would thus be highly desirable for increased efficiency in spotting marked birds.

Tab. 11.VI shows clearly that birds were missed in yr. x + 1 but spotted in later years, and without these, survival estimates would be considerably lower. This reflects the difficulties of searching for the colour-ringed birds.

Emigration: This factor is not thought to have affected survival figures. Only once was an established breeder seen attending a nesting area other than where it nested. This was in the post-fledging period and the area attended next to the bird's own nesting area. Established breeders from Flatey were never encountered on islands in the neighbourhood (Chapter 3). Emigration was not likely since the Flatey population was increasing and there was a surplus of nest-sites on the island (Chapter 2).

Since adult Black Guillemots are not easily caught in large numbers, survival data are not available for this age

category from ringing schemes. Most ringing of Black Guillemots has involved chicks, but relatively few birds have been recovered after reaching breeding age. There are probably 2 main reasons for this. Mortality of pre-breeding (particularly 1st year) Black Guillemots is heavy compared to other auk species, and secondly, ring loss affects numbers recovered. Ring loss does not start to have an effect until several years after ringing (Andersen-Harild 1969, Lloyd 1974). Too few recoveries are thus available from ringing in countries where Black Guillemot chicks have been ringed in any numbers, except Greenland (Salomonsen 1967: 282) but no analysis has been published using that material. Anyway, the results are bound to be biassed because of uneven ring loss with age, since all ringing has been carried out using aluminium rings (S. Asbirk, pers. comm.).

The only information in the literature on adult survival of Black Guillemots is that by Preston (1968: 26) on Kent I. (New Brunswick) and by Asbirk (1979b) in Denmark. Both used birds colour-ringed as adults, as I did. Preston found an annual survival rate of 80.4%, but Asbirk 82-89%, an average of 85% comparing well with my estimates of 82.5-92% with an average of 87%.

The survival of some of the other N. Atlantic alcids, is higher than that of Black Guillemots. Lloyd & Perrins (1977) found 89.0% and 92.1% survival for Razorbills on Skokholm and Skomer Islands (Wales), respectively. Ashcroft (1976: 46, 1979) estimated adult Puffin survival as 94-96%, and Birkhead & Hudson (1977) found 91.5-94% survival rate for Common Guillemots, both studies from Skomer. All these studies were done using colour-ringed birds.

Survival estimates using ringing recoveries tend to give lower figures than those obtained through colour-ringed birds, because of ring losses (Grosskopf 1964, Birkhead 1974), unless only that part of the material before ring losses become important is used, e.g. Mead (1974).

Mortality factors

Two aspects of Black Guillemot mortality seem especially worth examining; mortality due to man's activities and predation.

Various activities of man appear by far the most important mortality factors at the present time. There are certain difficulties concerned with using such recoveries, because of potential of biasses. If ringed, birds killed by man are more likely to be reported than birds killed by natural causes. Also, man's various activities tend to be seasonal rather than of the same intensity throughout the year.

Table 11.VII shows the causes of recovery of Black Guillemots ringed as chicks in various countries. The percentage "shot" and "caught in fishing gear" far exceeds that for Common Guillemots (Birkhead 1974) and Razorbills (Lloyd 1974) in Britain. It is possible however that shooting of Common Guillemots, Razorbills and other alcids in Norway could prove a very important cause of recovery (cf. Birkhead 1974, Lloyd 1974, Mead 1974, Reinert 1976). Other recovery categories for Black Guillemots are unimportant except the "found dead" one, which undoubedly includes some birds found dead in fishing gear.

In Iceland, a fishery for Lumpsucker (Cyclopterus lumpus) takes place from April to July (May-July in the Flatey region). This was the cause of all the mortality in fishing gear. The importance of this mortality factor varies in different parts of the country. This is perhaps particularly heavy in the Flatey region since the birds' fishing grounds overlapped extensively with the Lumpsucker fishing grounds (Fig. 10.1, p. 252).

I estimated the scale of this mortality in 1977 in terms of the Flatey breeding population. This was done by comparing the proportion of the 1977 Flatey breeding population estimated to be ringed, with the numbers of ringed birds recovered in nets. The calculations are shown in Tab. 11.VIII. In total, 11 breeders from Flatey were estimated to have been killed by this fishery in 1977, or 1.3% of the breeding population. Of course many other guillemots, drowned in nets, were immature, but the impact of this mortality factor on future breeding population size could not be assessed.

If this mortality varies between different regions, there could also be variations between years in the same region. The intensity with which the Lumpsucker fishery has been carried out in Iceland, has been extremely variable. This has depended

Tab. 11.VII. Causes of recovery of Black Guillemots ringed as chicks in different countries

	Iceland		Norway		Sweden		Denmark		Finland		Greenland		Russia	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Fishing gear	54	71	25	42	7	12	40	34	105	40			-	22
Shot	15	20	17	28	22	37	58	49	69	26	-	12		
Found dead	3	4	13	22	23	39	14	12	67	26				
Oiled	-	-	-	-	2	3	5	4	-	-				
Oiled-mink (?)	-	-	1	2	-	-	-	-	-	-				
Controlled	3	4	-	-	4	7	1	1	6	2				
Found injured and killed	1	1	-	-	1	1	-	-	2	1				
Unknown	-	-	4	7	-	-	-	-	13	5				
Total in sample	76		60		59		118		262		-		-	
Sources	(1)		(2)		(3)		(4)		(2)		(5)		(6)	

Notes: (1) Present study: Birds ringed as chicks 1973-1979
(2) From sources in Appendix V
(3) Andersson & Rosenlund (1973)
(4) Andersen-Harild (1969)
(5) Salomonsen (1967: 282)
(6) Bianki (1967: 196)

Tab. 11.VIII. Estimated number of Flatey breeders killed in Lumpsucker nets during May-July 1977, based on ringing recoveries, known size of the breeding population, and estimation of ringed breeders alive.

The calculations were done according to the following equation:

$$X = \frac{\text{Nos. of breeders on Flatey } 1977^{(1)} \times \text{Nos. killed in nets of those ringed as breeders 1973-1977.}}{\text{Nos. of breeders ringed 1973-1977 estimated to be alive}^{(2)}}$$

or

$$X = \frac{834 \times 3}{224} = 11 \text{ (or 1.3\% of the 1977 population).}$$

Notes: (1) See Chapter 2

(2) Using a survival estimate of 0.87 per year, the estimated number of surviving, ringed breeders was calculated from data in Tab. 11.VI (p. 289).

much on the market price of "pseudo-kaviar", the sought-after roes of the Lumpsucker.

It is worth commenting on the seasonal differences of various mortality factors. As already mentioned the Lumpsucker fishery takes place from April till July in Iceland, and is by far the biggest source of mortality according to reported recoveries. Most of the shooting takes place outside the breeding season, since Black Guillemots are protected during the breeding season from 20 May to 31 August (Stjornartidindi A 1966).

Some predators on Black Guillemots recorded in the literature are listed in Table 11.IX. Black Guillemots appear to be only a minor prey species of these predators. They represented only 3.6% of food items of White-tailed Eagles in Norway (Willgohs 1961: 82),0.9% in the food of Eagle Owls in Norway (Willgohs 1974), and 1.7% in the food of Great Skuas on Foula (Furness 1974).

In Iceland Black Guillemots are predated by Gyrfalcons (Buxton 1933, Lewis 1938: 235) but is an unimportant source of food (1% in food remains at 7 seaside eyries, O.K. Nielsen, pers. comm.). Other predators are White-tailed Eagles (1.7%; Ingolfsson 1961: Tab. 3), feral Mink (Chapter 2), and possibly Arctic Foxes (see Saemundsson 1939: 4), large gulls (Larus spp.), and Great Skuas.

These figures do not say anything about the impact of the predators on Black Guillemot populations, rather they appear to reflect prey availability. Predation pressure on Black Guillemots is presumably greater in winter when far fewer numbers of other seabirds are present along the coasts of Iceland than in summer (pers. obs., unpubl. Christmas counts at Mus. Nat. Hist.).

Population model

The stability of animal populations depends on how well the basic equation: recruitment=losses, can be balanced. This equation can be broken into different parameters, as follows:

Recruitment from natal population + immigration=
adult mortality + % adults breeding + emigration.

Tab. 11.IX. A list of some bird and mammalian species which have been recorded as prdeators on Black Guillemots.

Birds:	Sources:
Gyrfalcon	Kartaschew (1960: 77)
Peregrine	Bianki (1967: 196)
Goshawk	Kartaschew (1960: 77)
White-tailed Eagle	Kartaschew (1960: 77); Willgohs (1961: 82); Kampp & Wille (1979)
Great Skua	Furness (1974, 1979)
Eagle Owl	Willgohs (1974)
Snowy Owl	Økland (1928: 36); Uspenski (1958: 86) Kartaschew (1960: 77)
Mammals:	
Mink (*Mustela vison*)	Gerell (1972); Olsson (1974); Folkestad (1978); pres. study
Stoat (*Mustela erminea*)	Kartaschew (1960: 77); Bianki (1967: 196)
Arctic Fox (*Alopex lagopus*)	Uspenski (1958: 87); Kartaschew (1960: 77)

The Flatey population increased from 1966 till 1977 (Chapter 2), resulting in values on the left-hand side of the equation exceeding those on the right-hand side.

The percentage of adults which did not breed and emigration of former established adults were not thought to be important, as already mentioned. Immigration was believed to be very important in accounting for the population increase which took place on Flatey. This was particularly obvious if one keeps in mind the lag of 3-4 years from rearing of the young to their eventual recruitment into the breeding population. To show this, I calculated the expected rate of immigration, as shown in Tab. 11.X.

This can only be treated as a model since the underlying assumptions are numerous. Yet, it is clear that the increase in the Flatey population (up to 1977) has almost exclusively been the result of immigration, although its importance may have declined as an increasing number of natal Flatey birds reach maturity.

For the population to maintain itself in a state of balance, given no immigration, adult survival of 87%, and reproductive output of 1.29 chicks/nest (Chapter 6), the survival of pre-breeders has to be 20-21%, up to the age of four. This is not very different from the average obtained from ringing analyses of 24%, which means that adult survival could be 85% instead of 87%. Given the variation observed in adult survival from ringing data, 92% survival only needed 12% of pre-breeders to survive to breeding age, but 27% if the adult survival was only 82.5%.

11.4 Discussion

Whereas Common Guillemots, Brünnich's Guillemots, Puffins, and Razorbills all appear to have similar life history strategies (Birkhead & Hudson 1977, Lloyd & Perrins 1977, Ashcroft 1979), Black Guillemot population dynamics shows different features. In contrast to the other alcids, Black Guillemots most often lay two eggs in their clutch. Since breeding success per egg is proportionally similar to the other species (Birkhead & Hudson 1977, Lloyd & Perrins 1977, Ashcroft 1979,Chapter 6), the breeding output of Black Guillemots is nearly twice that of the other

Tab. 11.X. Calculations relating to detecting the levels of immigration of new breeders into the Flatey Black Guillemot population, and expected numbers of recruits natal to Flatey.

Year	Nos. of breeders (Nos. of prs x 2)	Nos. breed. indiv. in yr. x, dead by yr. x + 1	Total new indiv. n	%	Chick prod.	Nos. of pre-breed. recr., natal to Fl.	Nos. of immigr.	% of imm. birds	% of natal birds
1966	1(2)	0	-	-	1	-	-	-	-
1967	6(12)	0	10	83	8	-	-	-	-
1968	15(30)	4	22	73	19	-	-	-	-
1969	31(62)	8	40	65	40	-	-	-	-
1970	53(106)	14	58	55	68	0	58	100	0
1971	83(166)	22	82	49	107	2	80	98	2
1972	121(242)	32	108	45	156	5	103	95	5
1973	168(336)	44	138	41	217	10	128	93	7
1974	224(448)	58	170	38	289	16	154	91	9
1975	299(598)	78	228	38	390	26	202	89	11
1976	380(760)	99	261	34	486	37	224	86	14
1977	417(834)	108	182	22	448	52	130	71	29
1978	417(834)	108	108	13	507	69	39	36	64
1979	419(838)	109	113	13	514	96	17	15	85
1980	419(838)	109	109	13	599	117	- 8	0	100
Notes:	1	2	3		4	5	6	7	8

Notes: (1) 1966, 1967, 1975 - 1980 are observed values. Other values calculated by the regression log. year (x)/ log. nos. (y) using the observed values for 1966-67, and 1975-77 (r_4 = 0.998, $P<0.001$). A log. transformation was used since the increase is likely to have followed an exponential curve rather than a linear one.

(2) Nos. of individuals breeding in year x (nos. of pairs x 2) x 0.13 (the annual adult mortality rate).

(3) Nos. of individuals breeding in year x - Nos. of individuals breeding in year x-1 + Nos. that had died.

(4) 1.29 (mean no. of chicks fledging/pair 1975-1977) x calculated nos. of pairs breeding except where observed (1975, 1976, 1977, 1978, 1979, 1980).

(5) Average age of first breeding assumed 4 years. Chick productivity in year x-4 x 0.24 (composite prebreeding survival up to age of 4). No emigration of first breeders from Flatey assumed.

(6) Column 3 - column 5.

(7) Nos. in column 6 as % of column 3.

(8) Nos. in column 5 as % of column 3.

auks. This greater breeding output goes to balance the lower survival of Black Guillemots, both that of pre-breeders and breeders. Furthermore, Black Guillemots appear to become mature about one year earlier than other auks.

It was shown that the Black Guillemot population on Flatey increased rapidly during the 1970's, and this can only be accounted for by massive immigration from somewhere else. I have speculated earlier (Chapter 2) where these birds may have come from.

In the past, data for pre-breeding and adult survival, have been used to calculate the state of balance in seabird populations (Perrins, Harris & Britton 1973, Birkhead & Hudson 1977, Lloyd & Perrins 1977). Because of various difficulties, pre-breeding survival could not be estimated with any degree of accuracy for the Flatey population. However, from data from various ringing schemes, an average pre-breeding survival of 24% was obtained, and this did not differ greatly from that needed to balance the annual adult mortality observed in Flatey birds. The main difficulties in estimating pre-breeding survival in Black Guillemots appear to be spotting the pre-breeders which freely mingled with breeders, but also attended natal nesting areas less regularly and seemed less philopatric than some other alcids. Furthermore, most Black Guillemots seem to start breeding when 4 years old, and very few had reached that age by the end of the main study in 1977. The vast majority of first-time breeders on Flatey during 1975-1977 were immigrant birds (see Tab. 11.X, p.298). However, the proportion of new recruits, natal to Flatey, was potentially increasing. The breeding population has been stable since 1977 the most likely limiting factor being availability of nest-sites on the island (see Chapter 2).

When the population was increasing rapidly, it was expected that the birds started breeding at an earlier age than in stable populations e.g. because of no nest-site limitations. Data from Russia, Denmark and Sweden (see Tab. 11.III, p.283) had suggested that Black Guillemots could start breeding when 2 years old, some even as yearlings. Thus it was surprising to find that most Flatey Black Guillemots did not start until they were four. One possible reason is that birds may still

compete though nest-sites were plentiful, as they may compete for the "best" nest-sites. In this context it is pertinent to mention that even though about 650 nest-sites have been used on Flatey one year or more up till 1980, the breeding population has been stable at about 420 pairs 1977-1980. Although a few sites have become unsuitable for nesting, most have not changed. One reason why a particular nest-site is not used, is that another site is in use nearby and within that pair's "home range", thus preventing potential breeders from nesting.

There are several possible dangers inherent in the analyses of ringing recoveries. The age composition of recovery samples may be biassed by factors which give undue weight to certain age classes over others. Ring wear leading to ring loss is one factor, but should not be serious in the present material. A very high proportion of the material involved birds recovered through activities of man, mainly fishing and shooting (see Tab. 11.VII, p.293). It is possible that younger birds are more liable to get caught in fishing nets, or are less wary of hunters. Yet, hunters are not able to select by sight the birds they shot, in spite of the differences in wing patch pattern between first winter and older birds. Such selection does occur, however, in some other seabird species in Iceland, e.g. Shag and Cormorant. A difference in the distribution of young and old birds is possible and may bias the age distribution of the recoveries. If this is for the better or worse as far as young birds are concerned, is not immediately clear.

The Lumpsucker fishery in Iceland produced most of the recoveries of Black Guillemots ringed on Flatey. In spite of this it was calculated that adult mortality due to this agency was 1.3% which is only 10.2% of the total annual adult mortality (13%). Hence other factors are clearly more important.

One reason why Black Guillemots show higher mortality than other alcids may be their preference for inshore waters (cf. Willgohs 1961: 115). Although Puffins, Common Guillemots, Brünnich's Guillemots, and Razorbills necessarily find themselves inshore in summer, much of their feeding takes place offshore (e.g., Pearson 1968, Cody 1973, Scott 1973: 28 et seq.),

where predation is presumably less. In winter these species are pelagic (e.g., Witherby et al. 1941: 142 et seq., Brown et al. 1975: 154 et seq.), whereas Black Guillemots are inshore, where predatory birds are likely to be more common. But conversely, adult Black Guillemots may show higher mortality because of raising more young than the other auks (cf. Chapter 12).

Chapter 12: Clutch size in Black Guillemots: Results of experiments with supernormal clutch and brood sizes.

12.1 Introduction

Black Guillemots most commonly lay 2 eggs in their clutch, but some have a 1-egg clutch, the proportion of which becomes more and more common as the laying season progresses. Those birds which lay 2 eggs are more successful, not only because they lay 2 eggs instead of 1, but also proportionally (Chapter 6).

Since the two-egg clutch is the more productive of the normal clutch ranges of Black Guillemots, greater selection for that clutch size is to be expected. Yet it is of interest that the 1-egg clutch is a general feature of Black Guillemot's breeding phenology.

One may look at clutch size in Black Guillemots from two viewpoints: (a) why has 1-egg clutch been retained in the species, and (b) why do Black Guillemots not lay more than 2 eggs? The first question is, in the present context, basically equivalent to asking, why is there a seasonal decline in clutch size?

12.2 Materials and methods

In part this chapter is a discussion of results and points raised in the preceding chapters. It is with intention that I have refrained from discussing the evolutionary side of clutch and brood sizes up till now in this thesis. The other part of this chapter contains the results from experimenting with supernormal clutches and broods.

Nests with 3 eggs were followed until chicks fledged; these were both "natural" 3-egg clutches and experimental, the latter being 2-egg clutches to which one egg was added. All egg transfers were made on day 0 of the b-egg of the 2-egg clutch. The eggs which were added to 2-egg clutches, were also at their day 0 stage.

Three-chick broods were established by introducing a third chick to a brood of 2 chicks. Transfer was made on day 0 of all the chicks.

12.3 Results

The frequency of naturally occurring supernormal clutches

The occurrence of clutches of more than 2 eggs, are generally very rare in Black and Pigeon Guillemot populations. A 4-egg "clutch" was only recorded once in the present study, and 3-egg clutches ten times. This was only 1-2 % of the sample clutches each year. The occurrence of supernormal clutches was most often suspected to be due to two females laying in the same nest. See further details on the frequency of 3-and 4-egg clutches in Chapter 6 (pp. 124-125).

Length of the incubation period

Very scanty information is available for the length of the incubation period in clutches of 3 eggs, since most of them did not hatch anyway. Those that did, had an average incubation period of 34.3 days (n=7, range= 29-42, s.d.=4.1) which is significantly longer (t_{335}=4.74, P<0.001) than that for eggs in 1- and 2-egg clutches (n= 330, range= 26-38, $\bar{x}$= 30.0, s.d.=3.0).

Some of the eggs in 3-egg clutches hatched after a normal period of incubation. One way in which this seemed to have been achieved was when one egg failed in course of the incubation period and was pushed out of the nest, hence leaving a 2-egg clutch to be incubated. Normally when sites with 3 eggs were checked, one of the eggs was decidedly cooler than the other two. This is hardly surprising considering Black Guillemots only have 2 brood patches.

It was therefore obvious that the birds could not cope with incubating 3 eggs at the same time. I conclude that eggs of 3-egg clutches took on average longer, because they received less heat for embryonic development. They were also more liable to failure, as shown below.

Breeding success of 3-egg clutches

Tab. 12.I shows the breeding success of 3-egg clutches, natural and experimental combined. The hatching success of 25% was greatly lower than that of 79.5% overall for the population (see Tab. 6.III, p.134). Fledging success was

Tab. 12.I The breeding success of 3-egg clutches (n=16) compared with 1- and 2-egg clutches.

Clutch size	Numbers hatching	% H.S.(1)	Numbers fledging	% F.S.(1)	% B.S.(1)
3	0.75	25.0	0.44	58.7	14.7
1(2)	0.59	59.0	0.50	84.7	50.0
2(2)	1.65	82.5	1.43	86.7	71.5

Notes: (1) % H.S. = % hatching success
% F.S. = % fledging success
% B.S. = % overall breeding success
(2) Data from Tab. 6.VII, p. 143.

also lowered, 58.7% compared with 85.4% for the population. The overall breeding success of birds with 3-egg clutches was thus a mere 14.7%, giving 0.44 fledged chicks per nest, about a third of that for the population as a whole, even though the start was made from 3 eggs rather than 1 or 2 eggs.

Fledging success of 3-chick broods

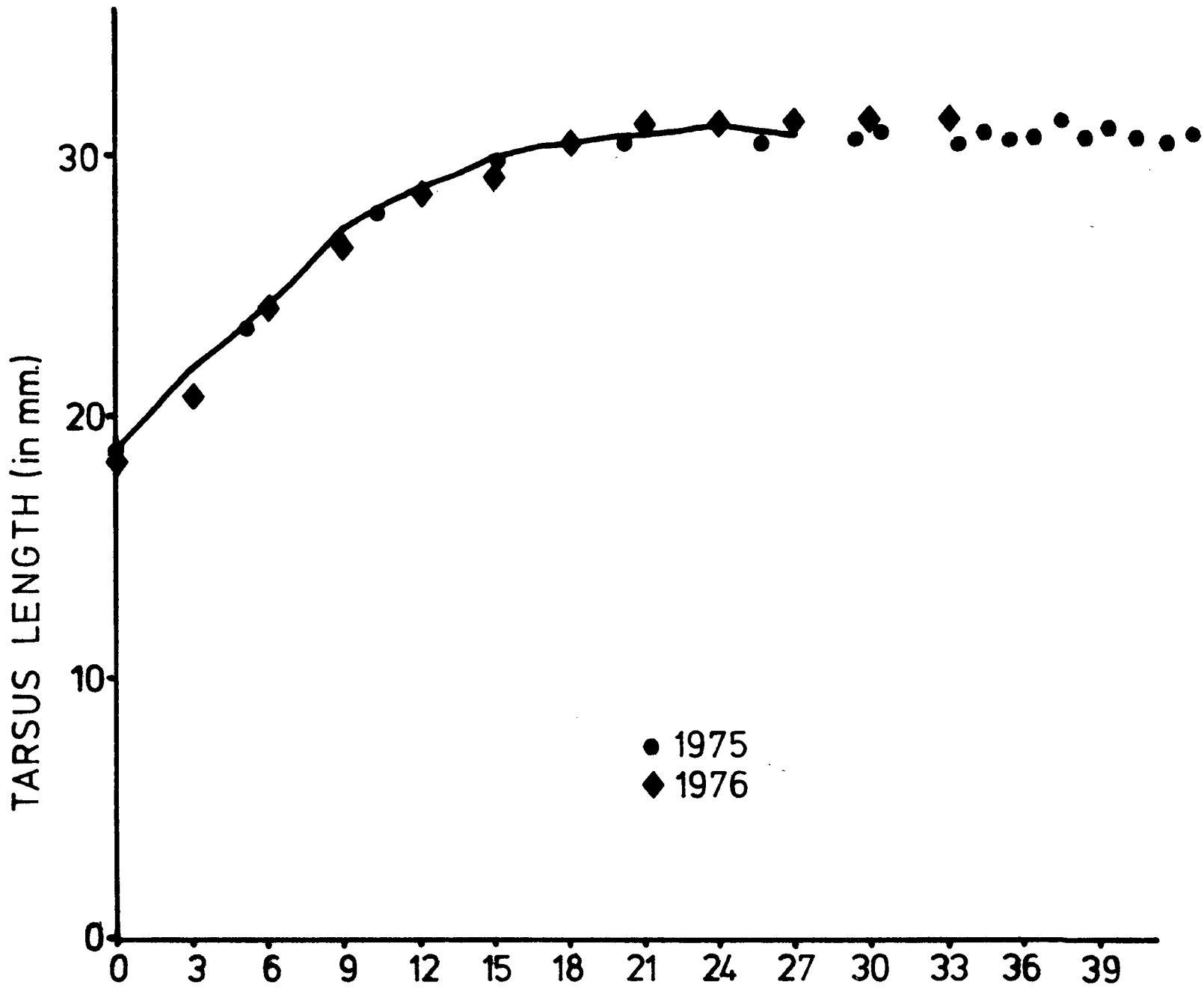
Artificial broods of 3 chicks were created to look at their success in relation to the natural brood sizes of 1 and 2-chicks. Fledging success was high in 3-chick broods, on average 78.8% with 2.36 chicks fledging per nest (n= 14, range= 0-3). Proportionally, this was a little lower than that for normal brood sizes; 1-chick broods: 84.0%, 0.84 chicks fledging per nest (n=146), 2-chick broods: 89.5%, 1.79 chicks fledged per nest (n=448). In these figures all years were combined. For 1-chick broods no distinction was made between real 1-chick broods and those formed when one of the eggs in 2-egg clutches failed. In this context it is possible that birds which "intended" to raise two chicks would do better than those laying only one egg.

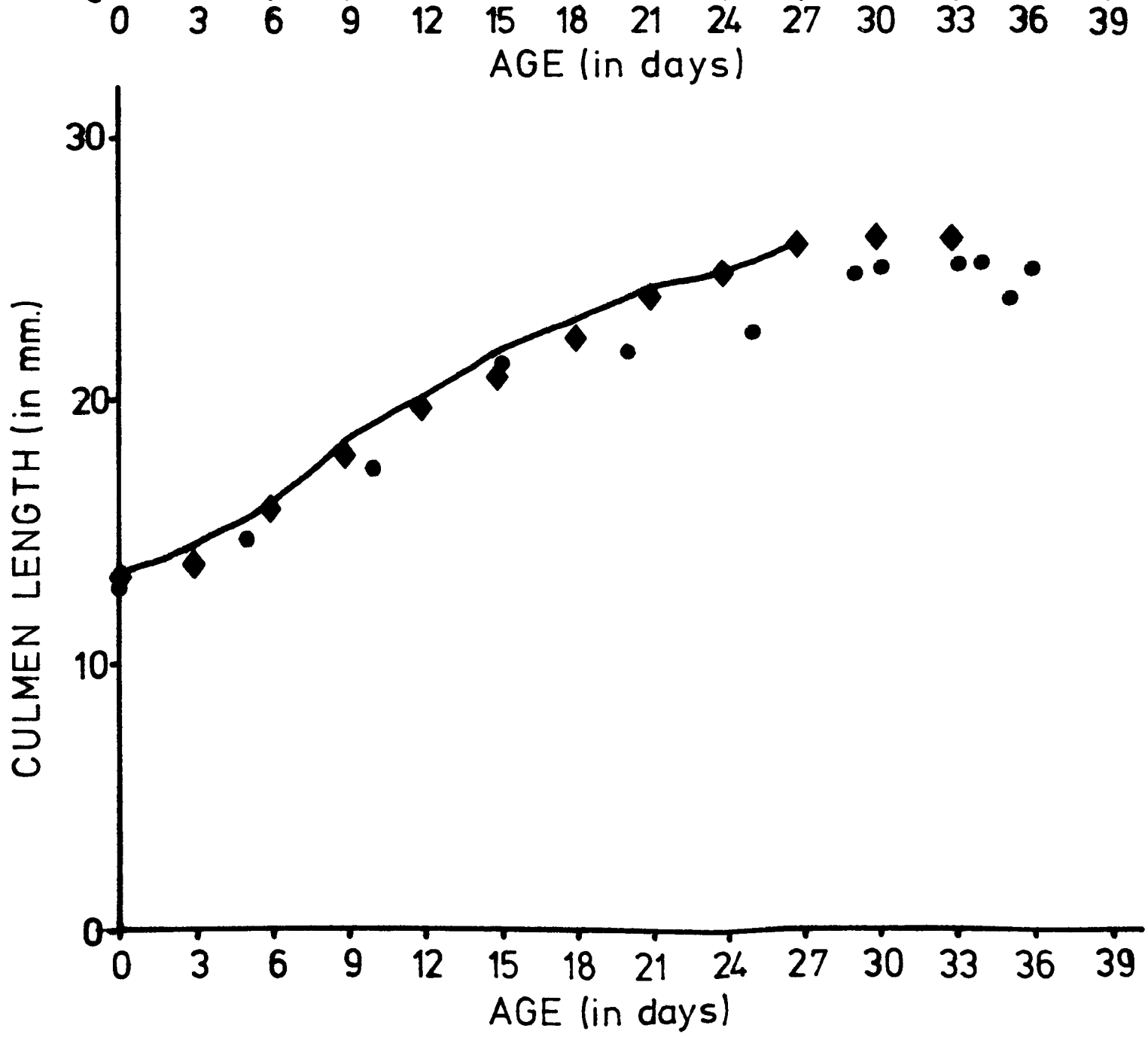
Hence birds with artificial 3-chick broods produced 32% more fledged chicks than those with 2-chick broods, but about 3 times as many as birds which hatched only one chick. These results indicate that food was not a limiting factor, and was plentiful for the birds of the area, a conclusion reached earlier when dealing with food (Chapter 10).

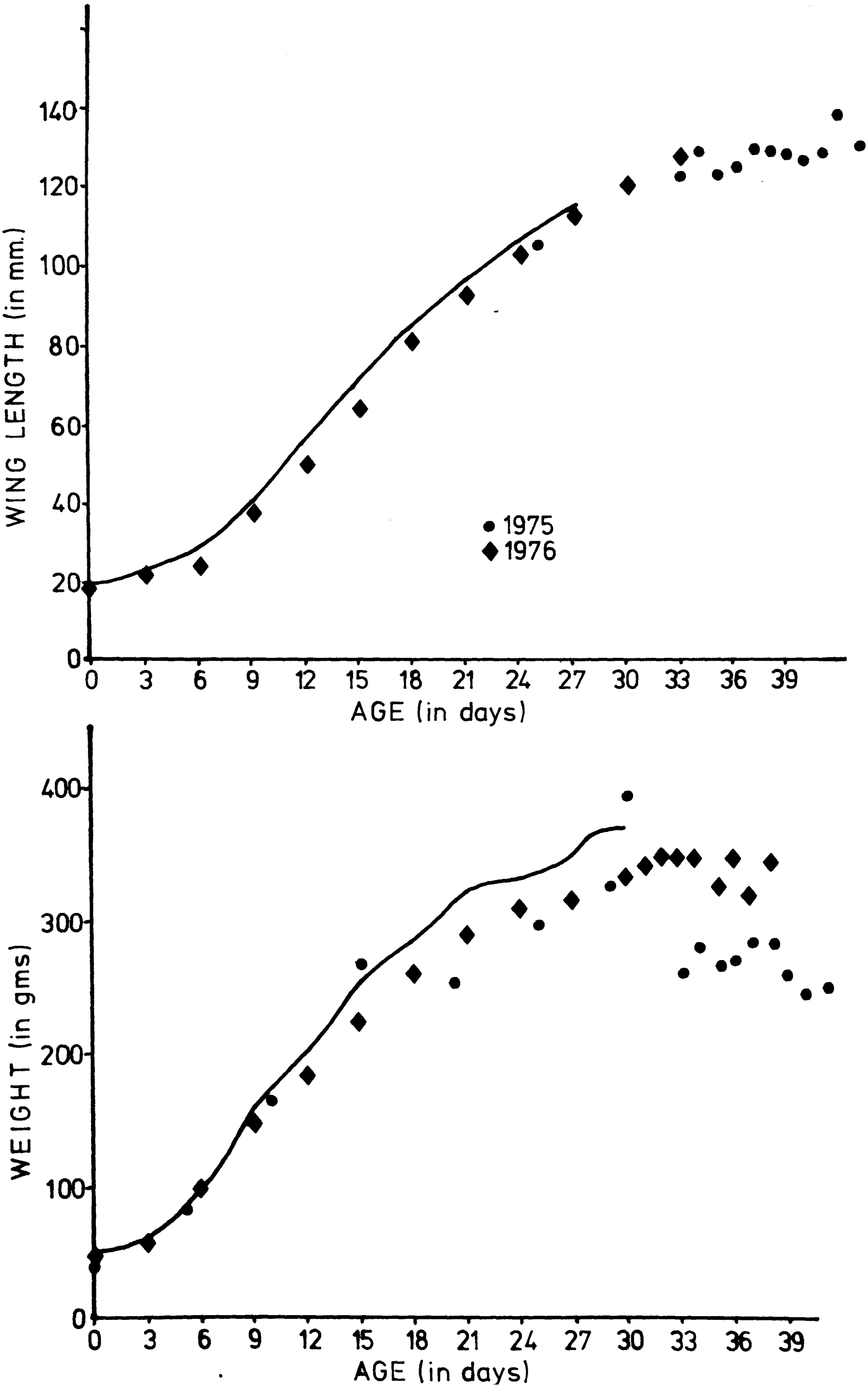
The growth of 3-chick broods

Growth curves for weight, wing, culmen, and tarsus of triplets, are given in Figs 12. 1-2. These are shown in comparison with same for chicks in 2-chick broods (cf. Figs. 9. 1-4, pp. 215-218). The growth of the tarsus proceeded at similar rate to that for chicks in the normal brood sizes, over the whole nestling period. There were differences in the growth rate of culmen and wing length according to year. In 1976 the growth proceeded very similar to that in 2-chick broods, but in 1975 both were a little retarded. Weight on the other hand proceeded at a similar rate to that for chicks in 2-chick broods

Fig. 12.1-2. Growth curves for chicks in 3-chick broods, compared with the growth of chicks in 2-chick broods (unbroken line). Data are given for tarsus, culmen, and wing lengths, as well as weight. Information from two years, 1975 and 1976.


TARSUS LENGTH (in mm.)
30
20
10
0
0 3 6 9 12 15 18 21 24 27 30 33 36 39
AGE (in days)
● 1975
◆ 1976


CULMEN LENGTH (in mm.)
30
20
10
0
0 3 6 9 12 15 18 21 24 27 30 33 36 39
AGE (in days)
AGE (in days)


WING LENGTH (in mm.)
0
20
40
60
80
100
120
140
0 3 6 9 12 15 18 21 24 27 30 33 36 39
AGE (in days)
1975
1976
WEIGHT (in gms)
0
100
200
300
400
0 3 6 9 12 15 18 21 24 27 30 33 36 39
AGE (in days)

for the first 3 weeks but lagged behind over the latter part of the nestling period. Energy demands of the super-normal broods were presumably too much in that period to allow normal weight increase to take place. Asbirk (1979b) obtained essentially similar results for Black Guillemots in Denmark (although chicks that fledged from supernormal broods did so at normal weight), and so did Kœlink (1972: 61-62) for Pigeon Guillemots.

Length of the nestling period

Tab. 12.II gives the information for length of the nestling period of chicks in 3-chick broods, compared with those in the normal 1-and2-chick broods. It is obvious that chicks in the supernormal broods spent considerably longer time in the nest than the comparative chicks, especially in 1975. That year did chicks not do as well as in 1976; although tarsus and wing showed normal growth, culmen but weight in particular did not. The chicks fledged at a lower weight than the chicks from same brood size in 1976 (see later). For chicks from the normal brood sizes, in 1975 it was found that the longer the nestling period, the lower the chicks' weight upon fledging (Tab. 9.XI, p. 231). No similar relationship was revealed in 1976.

Fledging condition

The chick's condition upon fledging can be all important for its survival in the immediate post-fledging period. This is especially so in Black Guillemots since the chicks are entirely independent from their parents after fledging.

In Tab. 12.III measurements are given for chicks in 3--chick broods on their last day before fledging. These are compared with chicks from 1- and 2-chick broods.

What is especially noteworthy in the table, is the lesser weight of chicks from the supernormal broods, in particular in 1975. In that year, there was also a greater difference between chicks from the 1-and 2-chick broods than in 1976, indicating perhaps that feeding conditions may have been worse in 1975. It is also of interest that growth of culmen was retarded in 1975. The growth of tarsus and wing were normal, however, indicating the importance for the chicks to maintain normal growth of these for as long as possible.

Tab. 12.II. A comparison of the length of the nestling period between chicks from 3-chick broods and the normal 1-and 2-chick broods.

Year	Brood size	n	Range	$\bar{x}$	s.d.
1975	3	7	37 - 46	40.9	3.5
	2	25	30 - 36	33.4	1.7
	1	8	30 - 39	33.5	3.3
1976	3	13	32 - 45	36.7	3.9
	2	74	29 - 37	32.1	1.7
	1	17	30 - 37	32.7	1.7

Tab. 12.III. The fledging condition of chicks from 3-chick broods compared with chicks from the normal brood sizes.

	Brood size	n	Range	$\bar{x}$	s.d.
Fledging weight (g):					
1975	3	7	200-330	297.1	44.2
	2	25	295-415	342.6	28.8
	1	8	325-415	360.0	32.3
1976	3	13	300-400	344.2	30.9
	2	74	300-415	355.5	22.1
	1	17	290-400	356.8	36.1
Fledging culmen (mm):					
1975	3	7	24.0-27.5	25.53	1.39
	2	25	23.8-28.1	26.54	1.21
	1	8	24.5-27.6	26.06	0.91
Fledging tarsus (mm):					
1975	3	7	29.8-31.4	30.77	0.68
	2	25	29.8-33.1	31.23	1.05
	1	8	28.4-33.2	30.38	1.89
Fledging wing (mm):					
1975	3	7	121-139	133.6	6.3
	2	25	122-137	129.9	4.0
	1	8	123-139	128.3	5.3

Note: (1) No measurements of culmen, tarsus, and wing of chicks of 3-chick broods, available in 1976.

12.4 Discussion

Various factors have been suggested or found to be associated with the size of the clutch in birds. In the Great Tit, Perrins (1965) showed that habitat, age of the female, laying date, and density of breeders accounted for some 70% of the variability in clutch size. Much of the remaining variation was found to be of genetic origin (Perrins & Jones 1974). It is generally accepted that natural selection influences the number of eggs birds lay. For that to take place, although shaped by environmental factors, clutch size has to be genetic, at least in part.

Lack (1954: 21-31) advanced the hypothesis that clutch size was limited by the number of chicks the parents were able to feed. Theoretically, this could be tested by adding chicks to broods to produce larger-than-normal broods and observe how well parents coped with raising them. Harris (1970) summarized many of the "twinning" experiments which have been conducted and found them inconclusive. It has been unfortunate that great many of these experiments have been done on species which are undergoing dramaticincreases in numbers, possibly because of favourable feeding conditions at present. Williams (1966) produced a refinement of Lack's principle, by calling attention to the connection between clutch size and adult survival. This was further advanced by Charnov & Krebs (1974), who introduced the "optimal clutch-size" concept, being "that which maximizes an individual fitness" (p. 217). They showed that the optimal clutch size would be smaller than the most productive one, if in raising that number of chicks,adult mortality was unduly increased.

Black Gullemots are unusual among alcids in having most often 2 eggs in a clutch while a sizeable proportion of the birds lay only a single egg. They could therefore be better than most other auks for studying the factors influencing clutch size.

About 2/3rds of the alcid species lay only a single egg in a clutch, but most have two brood patches (Sealy 1972: Tab. 27), being possible relics from evolutionary earlier times (Fisher & Lockley 1954: 272). The genera Uria and Alca are generally

considered the most specialized alcids (e.g. Hudson et al. 1969). Uria are considered nearer the ancestral stock than Cepphus, and Uria (and Alca) have only one brood patch (Storer 1952: 192). The 2-egg clutch in the Cepphus species may therefore be looked upon as primitive. However, this need not necessarily be so. The brood patches are located on either side of the sternum, and developing a patch on one side only, may be physiologically impossible.

The reason why Black Guillemots have retained a 2-egg clutch, is most likely a stable, favourable food situation for the birds. Their feeding areas are accessible, being inshore and close at hand. The food supply is probably relatively stable but also diverse, so for successful exploitation of this, the birds need to be rather generalized. It is argued that this applies well to Black Guillemots (Chapter 10).

Thus because of favourable feeding conditions, Black Guillemots are able to feed 2 chicks in the nest, contrary to most auks. The closeness of the feeding grounds allows them to make many trips a day to and fro the nest; this also promotes rapid growth of chicks and they can be fed to near adult size in the nest. This is advantageous, since the chicks are well developed at fledging and have no need for parental care after fledging. The adults are therefore relieved from their parental duties upon fledging of their chicks and can start moulting without being involved with other, presumably energy-demanding, processes.

Other auk species which also usually lay 2 eggs in a clutch, are the Black Guillemot's congeners, the Spectacled and Pigeon Guillemots, as well as the genera Synthliboramphus and Endomychura. The two guillemots are ecologically similar to the Black Guillemot. The other genera have evolved an extremely short nestling period of only 2-4 days (Sealy 1972: Appendix V), and unusually large eggs, which undoubtedly are related to their extreme precociality (Sealy 1972). In these species the adults take their young to sea and stay with them for many weeks. This is likely because of energetic reasons, as in Uria and Alca where the young only stay in nest for about 3 weeks and follows the parents out to sea (Sealy 1972).

Having two chicks in the nest, presumably makes heavy

demand on the parents. Black Gullemots are burrow-nesters and this is a prerequiste if both parents are to leave the chicks at the same time. In Common Guillemots one parent has to guard the chick at all times and this imposes a limit to the feeding frequency of the pair (Birkhead 1977a).

Although the Black Guillemot chicks are guarded by their nest-site, predation pressure has been proposed as having influenced the evolution of clutch size in Black Guillemots (see e.g. Asbirk 1979b). Same could be argued for kleptoparasitism although this appeared to be negligable under present conditions (see Chapter 10). Both these could increase out of proportion if the adults have to increase the number of feeding trips to and fro the nest. At a point predation and kleptoparasitism may have so much influence that any gain from increasing the number of feeding trips may be counteracted.

There was a clear seasonal decline in clutch size in Flatey Black Guillemots, as 1-egg clutches became increasingly more and more common as the season proceeded (Chapter 6). One-egg clutches are a constant feature of Black Gullemot breeding phenology,and the question is, why this is retained in the species. Preston (1968: 30) attributed 1-egg clutches to younger birds, and my circumstantial evidence supports that. Density of the breeders was not found to have any effects on clutch size, which was, however, highly correlated with laying date, and so was egg size. Lack (1954: 40) suggested that young birds were less efficient feeders and the smaller clutch size was an adaptation to less food supply later in the season. Perrins (1970) and Brooke (1978) extended Lack's arguments. I argued earlier (Chapters 6 & 8) laying date and egg size, intimately linked with the general condition or fitness of the breeders. So I do concerning clutch size, arguing that late, presumably young, breeders are not necessarily less efficient in procuring food for themselves and their young, but may have less time to do so (see pp. 120-122, 163-168).

The possible adaptive values for young birds to lay one egg instead of two, has not been mentioned. In some laying periods, birds laying 1 egg were, on average, proportionally more successful than 2-egg breeders but they never fledged

actually more young (Tab. 6. VIII, p. 144). But laying 1 egg may allow young birds to start breeding earlier than they otherwise would, thus gain some breeding experience.

Anderson (1976) noted in Long-tailed Skuas that despite fluctuating mean clutch size in conjunction with density of rodent prey, the birds never laid more than 2 egg in a clutch. He suggested 3 possible explanations: (a) That the female cannot lay more than 2 eggs, (b) that the pair is not able to raise more than 2 chicks, and (c) that a larger clutch cannot be brooded. Similar arguments can be raised regarding the Black Guillemots, and I will examine these.

Although doubtful that any Black Gullemots lay more than 2 eggs per laying bout (see Chapter 6), they were obviously capable of laying more eggs in the breeding season. This was shown in birds laying replacement clutches, although the birds had to have 2 weeks to form the replacement clutch (Chapter 7).

Experiments with 3-chick broods showed that pairs were capable of raising these to fledging. Althouth their success did not exactly match that for normal broods, the number of chicks produced per pair was greater in 3-chick broods. These chicks fledged at little lower weight than chicks from normal brood sizes, which may have lead to higher post-fledging mortality. Perrins, Harris & Britton (1973) showed that chicks of low weight were at a disadvantage and survived less well than heavy chicks. Besides being lower weight, data for other stages of the breeding cycle indicated that adults had difficulties coping with 3 chicks in a brood. Although growth of tarsus and wing proceeded normally, that of culmen did not in 1975. Weight started to lag behind at the middle nestling period, which was considerably longer than normal.

Anderson (loc. cit.) concluded that Long-tailed Skuas were unable to incubate more than 2 eggs to hatching, hence did not lay a larger clutch. It was obvious in the Black Guillemot that the birds had difficulties incubating. The hatching success of 3-egg clutches was 25%, compared with 59% and 82.5% for 1-and 2-egg clutches. The eggs which did hatch, took much longer than normally, probably because they received less heat for embryonic development. Presumably greater energy expenditure by adults with 3 eggs in nest, may have lead to their poorer

condition, which in turn lead to less fledging success of their chicks (58.7%, compared with 84.7% for 1-egg clutches and 86.7% for 2-egg clutches).

In spite of these results, I believe Anderson's conclusion is wrong. If there were other inherent reasons why the birds should have a larger clutch, presumably the birds would not have difficulties evolving more than 2 brood patches, which would enable them to cover the eggs adequately. It seems more reasonable that the 2-egg clutch has evolved because of energetic reasons. Aitchison (1972: 13-18) showed that adults had to increase their feeding frequency considerably to cope with increased brood size. They appeared to have to feed in the afternoon at just as high a rate as in the morning, which is normally the peak of feeding. Koelink (1972: 64-68) suggested that adult Pigeon Guillemots were working at "optimal working capacity" feeding 2 chicks. The adults did not decline in weight, which was taken to mean that the parents did not impair their own survival for the benefit of raising extra chicks. Yet, it still seems that raising chicks is a strenuous process for the adults. If Asbirk's (1979b) information is real (no basic date were presented), then birds which fledged 1 or 2 chicks had lower survival (83%) than those that did not fledge any young (92%). Since not fledging any chicks is not a viable trait, 1 or 2 eggs are laid. Natural selection may thus have acted so as to favour clutch sizes below the one which produces most young. Adult survival in comparison with clutch size, has still to be explored in Black Guillemots.

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Appendix I: Scientific names of bird species mentioned in the thesis.

Emperor Penguin	Aptenodytes forsteri
King Penguin	A. patagonica
Yellow-eyed Penguin	Megadyptes antipodes
Red-throated Diver	Gavia stellata
Laysan Albatross	Diomedea immutabilis
Fulmar	Fulmarus glacialis
Manx Shearwater	Puffinus puffinus
Short-tailed Shearwater	P. tenuirostris
Fork-tailed Storm Petrel	Oceanodroma furcata
Brown Pelican	Pelecanus occidentalis
Gannet	Sula bassana
Double-crested Cormorant	Phalacrocorax auritus
Cormorant	P. carbo
Shag	P. aristotelis
Whooper Swan	Cygnus cygnus
Grey-lag Goose	Anser anser
Lesser Snow Goose	A. caerulescens
Barnacle Goose	Branta leucopsis
Mallard	Anas platyrhynchos
Teal	A. crecca
Widgeon	A. penelope
Long-tailed Duck	Clangula hyemalis
Eider Duck	Somateria mollissima
Red-breasted Merganser	Mergus serrator
Goshawk	Accipiter gentilis
White-tailed Eagle	Haliaëtus albicilla
Gyrfalcon	Falco rusticolus
Peregrine	F. peregrinus
Oystercatcher	Haematopus ostralegus
Ringed Plover	Charadrius hiaticula
Golden Plover	Pluvialis apricaria
Whimbrel	Numenius phaeopus
Snipe	Gallinago gallinago
Redshank	Tringa totanus
Dunlin	Calidris alpina
Grey Phalarope	Phalaropus fulicarius

Red-necked Phalarope	Phalaropus lobatus
Great Skua	Stercorarius skua
Arctic Skua	S. parasiticus
Long-tailed Skua	S. longicaudus
Great Black-backed Gull	Larus marinus
Lesser Black-backed Gull	L. fuscus
Herring Gull	L. argentatus
Glaucous Gull	L. hyperboreus
Red-billed Gull	L. novaehollandiae
Western Gull	L. occidentalis
Black-headed Gull	L. ridibundus
Kittiwake	Rissa tridactyla
Arctic Tern	Sterna paradisaea
Sandwich Tern	S. sandwicensis
Roseate Tern	S. dougallii
Common Tern	S. hirundo
Common Guillemot	Uria aalge
Brünnich's Guillemot	U. lomvia
Razorbill	Alca torda
Black Guillemot	Cepphus grylle
Spectacled Guillemot	C. carbo
Pigeon Guillemot	C. columba
Puffin	Fratercula arctica
Little Auk	Plautus alle
Cassin's Auklet	Ptychoramphus aleutica
Ancient Murrelet	Synthliboramphus antiquum
Woodpigeon	Columba palumbus
Eagle Owl	Bubo bubo
Snowy Owl	Nyctea scandica
Short-eared Owl	Asio flammea
Swift	Apus apus
Wheatear	Oenanthe oenanthe
Meadow Pipit	Anthus pratensis
Raven	Corvus corax
Hooded Crow	Corvus corone cornix
Great Tit	Parus major
Redwing	Turdus iliacus
White Wagtail	Motacilla alba
Snow Bunting	Plectrophenax nivalis

Appendix IV: Some technical terms used in the thesis.

Nesting area = The division of Flatey into subsections within which Black Guillemots had their nests. These areas were 15 in all, numbered I - XV (see Fig. 2.2, p. 23).

Nesting group = Nesting aggregation = Undetermined number of Black Guillemots nesting together, separated by a much longer gap between groups (aggregations) than found between nests within a group (aggregation).

Chick = Young = Nestling = A bird of the year in nest.

Yearling = A bird in first summer after it fledged = First-year bird.

Full-grown bird = Fully fledged bird, usually from previous year or more.

Adult = Bird which has bred one or more times = Mature bird.

Adult-plumaged bird = Bird which has developed a plumage indistinguishable from that of adults, mature or not, two-years old or older.

Non-breeding adult = An adult not laying eggs one year although may have done so in previous years.

Flatey breeding population = Refers to all Black Guillemots breeding on Flatey.

Area fidelity = Nesting at same nesting area as the year before.

Nest-site fidelity = Nesting at same nest-site as the year before = Site tenacity.

Mate fidelity = Paired with same individual as the year before.

Nest = The cup where the eggs are deposited.

Nest-site = The whole cavity within which the nest is found.

Pre-laying period = The period from which Black Guillemots started attending nesting area regularly every day until the first egg was laid in the population.

Laying season = The period over which eggs were laid in the population.

Breeding season = The period from the first egg being laid in the population till the last chick fledged, in practice taken as May-August.

Laying date = The day on which the first egg (the a-egg) of a clutch appeared in nest.

First clutch = The first clutch laid by a pair in a breeding season.

Replacement clutch = A clutch laid after the pair's first clutch had failed completely that same breeding season.

Replacement time = The time taken by a pair to replace a lost clutch, day 0 being that in which the lost clutch failed (or in experiments, were removed), calculated until the a-egg of the replacement clutch had appeared in nest.

The a-egg = The first egg of a clutch.

The b-egg = The second egg of a clutch.

Laying interval = Number of days between eggs in a clutch = The day on which the a-egg appeared (the day 0 of that egg) to the day the b-egg appeared (the day 0 of that egg).

Hatching weight = The weight of chick on day 0.

Length of the incubation (or nestling) period = The day egg (or chick) appeared in nest (based on daily checks) is day 0, the next day 1, counted until day 0 of the chick from that egg (or until first day the chick was not recorded in the nest).

Fledging = The leaving of a nest for the sea by a chick.

Fledging age = Same as the length of the nestling period.

Fledging weight (culmen, tarsus, wing) = The weight (measurements) of a chick on the last day before fledging.

Fledgling = A bird just recently out of nest.

Mean clutch size = The average number of eggs laid per nest, for all nests in which the number of eggs laid per laying bout, was accurately determined.

Mean number of chicks hatching = The average number of chicks which hatched from all nests for which the number of chicks was accurately determined and had known-sized clutch.

% hatching success = The percentage number of chicks which hatch from all clutches in all nests for which the numbers hatching was accurately determined and clutch size was known.

Mean number of chicks fledging = The average number of chicks fledging per nest of those hatching in all nests for which clutch size and numbers hatching were known.

% fledging success = The percentage number of chicks which fledged for all broods for which numbers of chicks hatching and clutch size were accurately determined.

% breeding success = The success of chicks fledging as percentage of all eggs for which the clutch size was accurately determined.

Methods of measurement of: Wing: The maximum chord method, with a stoppered metal ruler. Culmen: Taken from the growth line at the top of the upper mandible to the tip of the bill, using pointed calipers accurate to 0.1 mm. Tarsus: Taken from behind the intertarsal joint on right leg to tarso-phalangial joint of the middle toe, using pointed calipers accurate to 0.1 mm. Weight: Taken with Pesolas, chicks with 50, 100, and 500 g ones (accurate to 0.5, 1, and 5 g), adults with a 500 g one.

Appendix V. Materials used for calculating pre-breeding survival of Black Guillemots ringed within various ringing schemes.

Greenland: Recoveries from 1946-1966 (?). Total number of recoveries: 736. Sources: Unpublished data per Finn Salomonsen through Sten Asbirk, Zoologisk Museum, Copenhagen. (See also Salomonsen (1967: 282).

Norway: Recoveries from 1936-1975. Total number of recoveries: 60. Sources: (i) Unpublished material per Holger Holgersen, Stavanger Museum. (ii) Published materials in Stavanger Mus. Årb., Meddr St. Viltunders., Nytt Mag. Naturv., and Sterna.

Sweden: Recoveries from 1929-1971. Total number of recoveries: 135. Sources: (i) Unpublished data per Sten Österlöf, Ringmärkningscentralen, Riksmuseet, Stockholm. (ii) Published material in Årstr. Göteborgs Mus., Fauna Flora, Upps., Viltrevy, and Vår Fågelvärld.

Denmark: Recoveries from 1930-1967. Total number of recoveries: 156. Sources: (i) Published material in Vidensk. Meddr dansk naturh. Foren., Dansk orn. Foren. Tidsskr., and Danske Fugle.

Finland: Recoveries from 1915-1967. Total number of recoveries: 262. Sources: (i) Unpublished data per J. Ruoho and P. Saurola, Zoological Museum, Dept of Bird-Ringing, Helsinki University, Helsinki. (ii) Published material in Ornis Fenn., Memo. Soc. Fauna Flora fenn., and Suomen Riista.

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