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THE ECOLOGY OF BLACK GUILLEMOTS

Cepphus grylle

IN SHETLAND

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Thesis submitted for the degree of Doctor of Philosophy,
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Adult Black Guillemot in summer plumage,
Mousa, Shetland. Photo by the author.



ABSTRACT: The ecology of Black Guillemots *Cepphus grylle* in Shetland.

(Submitted for the degree of Doctor of Philosophy in Michaelmas Term 1986 by Peter John Ewins, Wolfson College, Oxford, and Edward Grey Institute of Field Ornithology, Department of Zoology).

Following a large kill of Black Guillemots in the *Esso Bernicia* oil spill in Shetland, this study was initiated to determine the population size and distribution of the species at different times of year and to investigate its ecology. The results will enable oil spill contingency plans to be made for this species and provide a base-line against which future work can be compared. This is the first major study of Black Guillemots in the UK.

There were large diurnal and seasonal fluctuations in colony attendance patterns which were investigated in relation to various factors. Reliable census techniques were devised and suitable stretches of coastline were established as monitoring units.

Black Guillemots rarely foraged in water more than 40-50 m deep, and seldom moved more than 3 km from the nest during the breeding season. The proximity of suitable breeding sites to shallow water feeding grounds accounted for the fairly regular breeding dispersion. On islands with mammalian predators only nest sites in inaccessible cliffs were used. In many areas breeding numbers were limited by nest site availability. The distribution at other times of year was more irregular. After breeding adults congregated in traditional moulting areas where they became flightless for 4-5 weeks. These flocks of up to c.600 adults constitute vulnerable "hot spots" at which the effect of oil pollution would be most severe. In winter there was some movement away from exposed coasts, resulting in concentrations in more sheltered, inshore waters.

A wide range of fish and invertebrates were eaten by adults, largely reflecting the diversity of inshore benthic communities. There appears to be a greater dependence on invertebrates during the winter months, when fish are scarcer. Chicks were fed almost exclusively on fish: their diet composition was determined primarily by local availability, although some adults specialised on particular species. When large gadoid fish became available in late summer adults were able to provide more energy per feed and consequently chicks were heavier at fledging.

Breeding parameters were quantified and analysed in relation to various factors. Breeding success and chick growth compared very favourably with results of studies elsewhere, indicating that conditions for breeding were good for Black Guillemots in Shetland. In a year of more favourable environmental conditions a greater proportion of inexperienced birds were able to reach the condition threshold for breeding. These birds tended to lay single-egg clutches, in sub-optimal sites at which egg predation was heavy and breeding success low. Some pairs of Arctic Skuas benefited considerably from kleptoparasitism of chick feeds at larger colonies, but Black Guillemot breeding success was not affected and chick growth was only depressed at high rates of piracy.

Overall, conditions in Shetland are favourable throughout the year for this seabird, whose ecology is moulded to the exploitation of an inshore feeding niche.

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CHAPTER 1. GENERAL INTRODUCTION

1.1 Project background

Exploration for oil and gas in the northern North Sea began in the early 1970's, but in 1985 approximately 128 million metric tons of crude oil were recovered from the UK sector, making Britain the 5th largest oil producing nation in the world (Shetland Islands Council 1986). Most of the oil and gas from the northern UK sector is piped directly ashore, from the Brent and Ninian field complexes in the east Shetland basin to the large Sullom Voe oil terminal in Shetland, and from the Claymore, Tartan and Piper fields to the Flotta oil terminal in Orkney (Affolter 1976; Richardson et al. 1982; Dunnet 1984; Robertson 1984; Shetland Islands Council 1986). Gas and oil are separated at the Sullom Voe terminal, stored, and then shipped out by large tankers.

Oil poses a major threat to seabirds (Bartonek & Nettleship 1979; King & Sanger 1979; RSPB 1979; Clark 1984), although toxic chemical pollution may have a more serious direct impact (Bourne 1976). Petroleum contamination of surface waters has been found in the vicinity of oil tanker routes throughout the world (Levy 1984) but the most dramatic effects have resulted from acute oil pollution near to large seabird or wildfowl concentrations [eg. the Torrey Canyon (Bourne et al. 1967; Smith 1968) and Amoco Cadiz (Hope Jones et al. 1978) incidents in the southern parts of the English channel, and others in western Norway (Barrett 1979; Rov 1982) and the Skagerrak (Anker-Nilssen & Rostad 1982).

A summary of oil spillages in the UK between 1966 and 1983 involving 144 separate incidents which affected more than 50 birds is provided by Stowe & Underwood (1984). Although many oiled seabirds are washed ashore and counted, many sink or are not found, and Gunkel & Gassman (1980) estimated that 150-450,000 seabirds die in the North Atlantic each year after being oiled. Although this is still only a fraction of the numbers dying from 'natural' causes, acute oil pollution can have devastating effects on local populations (Johnston 1984).

Shetland has some of the largest seabird colonies in the British Isles (Cramp et al. 1974; Furness 1983; Thom 1986), holding large proportions of the British breeding population for many species [eg. Red-throated Diver Gavia stellata (75%), Great Skua Stercorarius skua (c.90%), Arctic Skua S. parasiticus (67%) and Arctic Tern Sterna paradisaea (40%) (Shetland Islands

Council 1986)]. There was concern for the safety of these birds and the Shetland environment in the face of such a rapidly expanding oil industry (Bourne & Johnston 1971; Dunnet 1974; Affolter 1976; Shetland Islands Council 1978; Syratt & Richardson 1981).

Despite what was considered to be adequate safety and oil spill contingency planning (Sullom Voe Oil Spill Advisory Committee 1981), there was a spillage of 1174 tonnes of heavy fuel-oil from the Esso Bernicia tanker whilst berthing at the Sullom Voe terminal jetties on 30 December 1978 (within a month of the terminal opening). The oil spread quickly in the strong tidal currents from Sullom Voe itself into Yell Sound, and beyond (for location of places mentioned see Figure 4.1). A total of 3702 birds were found oiled and dead in the area, but the actual mortality was undoubtedly much higher since the strong currents carried some oil as far as 50 km from the terminal and large sections of coastline within this radius could not be checked for corpses. Some corpses were presumably swept out to sea and heavily oiled corpses probably sank (Heubeck & Richardson 1980). The species worst affected were Great Northern Diver Gavia immer (146 corpses, representing 37-49% of the estimated Shetland wintering population) and Black Guillemot Cepphus grylle [633 corpses, representing 27% of the number of birds seen in Shetland by the Operation Seafarer breeding season surveys (Cramp et al. 1974)].

Following this disaster, oil recovery techniques and anti-pollution surveillance measures were improved greatly. In addition to its routine programme of biological and chemical monitoring in the immediate vicinity of the oil terminal, the Shetland Oil Terminal Environmental Advisory Group (SOTEAG) initiated and funded baseline studies of three vulnerable species - Otter Lutra lutra, Red-throated Diver and Black Guillemot - which were important in a national and European context and whose ecology and distribution in Shetland was poorly understood. I was contracted through the Edward Grey Institute of Field Ornithology, at the University of Oxford to carry out a 3-year study of Black Guillemots, starting in January 1982. The fieldwork was completed in autumn 1984 and the final contract reports presented to SOTEAG on time, early in 1985.

1.2 The contract

The SOTEAG contract comprised 4 main sections:

(i) To establish how Black Guillemots use Shetland's coastal environment at different times of year, and to identify regular concentrations.
(ii) To map the breeding distribution and determine numbers.
(iii) To investigate census techniques and devise a monitoring scheme.
(iv) To ring large numbers so that in the event of any future oil spill the origins of victims could be established.

Ultimately the crucial requirement was to identify "hot spots", at which the effects of oil pollution on the Black Guillemot population would be most severe. Oil spill contingency plans could then be drawn up for such areas and oil recovery operations focussed in the event of future oil incidents.

Oil pollution may also be sub-lethal, affecting reproduction and physiology (Butler et al. 1979; Coon et al. 1979; Peakall et al. 1980; Ainley et al. 1981). Since very little was known of Black Guillemot ecology in Shetland, or indeed elsewhere in the British Isles, it was essential to collect basic information on breeding biology and feeding ecology. Any future sub-lethal effects of pollution might then be detected when comparisons were made with these baseline data.

1.3 Specific aims

The complete study aimed to:

1. Investigate seasonal and diurnal patterns of colony attendance and devise suitable census techniques (Chapter 2).
2. Determine distribution at different times of year, since this is an integral part of understanding the species' ecology and identifying the various selective pressures giving rise to the observed distributions (Chapters 3 & 4).
3. Assess (using ringing) to what extent Black Guillemots in Shetland moved away from the natal and breeding colonies (Chapter 5).
4. Document breeding biology and investigate possible factors affecting breeding parameters (Chapters 6, 7 & 8).
5. Establish the composition of adult and chick diets and identify factors influencing prey selection (Chapter 9).

In addition I describe and quantify kleptoparasitism, particularly in the breeding season (Chapter 10). In Chapter 11 consideration is given to the major points emerging from these studies, particularly in relation to the

threat of oil pollution, the general ecology of this population, and to studies elsewhere and the general Cepphus niche. Studies of taxonomy and the maturation of feeding skills will be reported elsewhere.

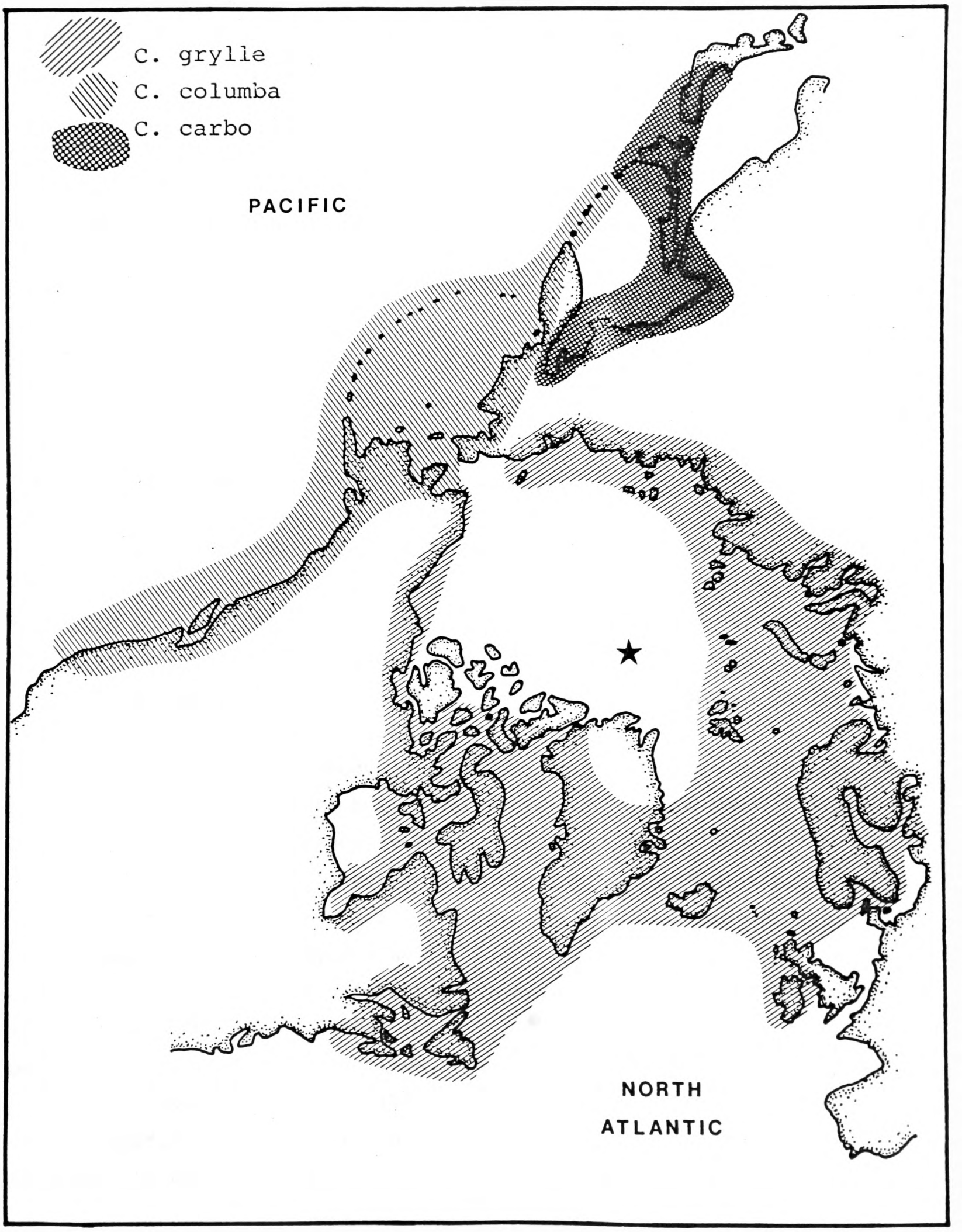
1.4 General ecology and literature review

The Black Guillemot is a boreal-arctic species breeding between 43° and 82°N in the North Atlantic and Arctic Oceans (Nettleship & Evans 1985). In the North Pacific it is replaced by the closely related (and very similar looking) Pigeon Guillemot C. columba, whilst the other member of the genus, the larger and all-dark Sooty Guillemot C. carbo, breeds from the Sea of Okhotsk down to northern Japan (Figure 1.1). Cepphus species typically occupy an inshore feeding niche, breeding as scattered pairs or in small groups at fairly regular intervals along coasts, and eating benthic fish and invertebrates caught in shallow waters. This contrasts with the more offshore niche of most auk and seabird species (Lack 1967, 1968).

The Black Guillemot is more of a cold water species than its congeners. Approximately 40% of the population breeds in high arctic waters, where the largest colonies are found, 30% in low arctic, and 30% in boreal waters (Nettleship & Evans 1985). The taxonomy of the genus is complex. Salomonsen (1944) proposed 7 subspecies of C. grylle (see review by Bedard 1985). The Pacific populations are similarly complex (Storer 1952). Salomonsen (1944) and Kartaschew (1960) regarded the Pigeon Guillemot to be a race of C. grylle, whilst Petersen (1981) considered it as a superspecies. My measurements of British skins support Salomonsen (1944) and Asbirk (1979a) in lumping Black Guillemots breeding in the British Isles, Denmark, west Sweden and Norway in the subspecies atlantis.

Winter ice forces high arctic Black Guillemots to move south in winter, but in more temperate zones the species is essentially resident. The average adult life expectancy is about 10 years, and birds breed usually at the natal colony in their third or fourth year of life. Whilst auk species which feed further offshore lay only a single egg, Black Guillemots feed relatively close to the colonies and can usually lay 2-egg clutches and often raise 2 chicks to fledging. The semi-precocial young are completely independent upon leaving the nest. The main requirements of a nest site are proximity to feeding areas and safety from predators. Most sites are in cliff cavities or crevices, or under boulders, but the species is opportunistic and tolerant of man and will nest in suitable holes in

Figure 1.1 The world breeding distribution of Cepphus species.
Compiled from information presented in:
Voous (1960), Divoky et al. (1974), Brown et al. (1975), Kuyt et al. (1976), Golovkin (1984), Hasegawa (1984) and Nettleship & Evans (1985).
★ indicates position of the North Pole



walls, buildings or piers, or amongst strand-line debris (eg. Witherby 1939; Maclean & Verbeek 1968; Kuyt et al. 1976; Asbirk 1979c; Carnduff 1981; Petersen 1981). The species is also opportunistic in its diet, preferring small benthic fish, which are usually caught amongst seaweed and crevices. A wide range of invertebrates are also eaten, especially in winter.

Much intensive research on Black Guillemots has been undertaken in the last 10 years, for research dissertations (Asbirk 1978c; Petersen 1981; Cairns 1978, 1984). Virtually all Cepphus studies have concentrated on aspects of the biology during the breeding season, due to the constraints imposed by academic requirements, the weather and accessibility of study sites. Apart from short notes and anecdotes the only studies done outwith the breeding season have been on the determination of spring diet and distribution in the Canadian North West Territories (Bradstreet 1980; Renaud & Bradstreet 1980), and winter distribution surveys along the Baltic coasts of Sweden (Nilsson 1982). For a species which is present in coastal waters at all times of year it is perhaps surprising that my work is the first to deal with the species' ecology in one area throughout the year. We know little of activities underwater, apart from a few dive-times and depths (Uspenski 1956; Kozlova 1961; Scott 1973; Piatt & Nettleship 1985).

Reviews of Black Guillemot life history studies and general literature have recently been published in The Handbook of the Birds of the Western Palearctic (Cramp 1985), and a comprehensive account of evolution, ecology and distribution in The Atlantic Alcidae (Nettleship & Birkhead 1985). The most recent status and distribution data for all three Cepphus species are presented in Croxall et al. (1984).

The first systematic study of Black Guillemot breeding activities was on Kent Island in the Bay of Fundy, New Brunswick, Canada (Hyde 1936, 1937). The work was continued by Winn (1950), and in the 1960's Preston (1968) studied the social behaviour and breeding biology for his Ph.D. thesis. Cairns (1978, 1980, 1981) carried out detailed studies of breeding biology and feeding ecology on the St. Lawrence Islands in southern Quebec, and then concentrated on the foraging ecology in his doctoral work on the Nuvuk Islands in northern Quebec (Cairns 1984). Elsewhere in North America, Divoky continues to follow breeding at Alaskan colonies (Divoky et al. 1974; Divoky & Boekelheide 1978), and in the Canadian high arctic various Canadian Wildlife Service workers have collected breeding data (see references in Nettleship & Birkhead 1985).

General life history accounts and breeding data are available from 3 areas in the Soviet Union - the Barents Sea (Belopol'skii 1957), Novaya Zemlya (Uspenski 1956), and Kandalaksha Bay in the White Sea (Bianki 1967). Data from Spitsbergen are largely confined to details in expedition reports (Lovenskiold 1964; de Korte 1972). Breeding parameters and productivity have been monitored in northern Norway [Barrett pers. comm., and data summarized by Petersen (1981)]. Studies on islands in the Gulf of Finland (Figure 1.2) documented dramatic effects of food shortage on breeding success (Bergman 1971, 1978). Two recent European studies have comprehensively covered most aspects of breeding biology and summer ecology - on the island of Norde Ronner, Denmark (Asbirk 1978b,c, 1979c), and on the island of Flatey, Iceland (Petersen 1981) (Figure 1.2).

Despite a long tradition of ornithology in the British Isles this is the first major study of Black Guillemot ecology. Most of the naturalists' accounts in the last century presented entertaining anecdotes concerning collection, persecution, superstition and breeding of the species in Scotland (eg. Bewick 1821; MacGillivray 1852; Saxby 1874; Seebohm 1885; Raeburn 1887; Evans & Buckley 1899). The breeding distribution was documented by Witherby et al. (1941), and updated by Cramp et al. (1974) and Thom (1986). The winter distribution is known in detail (Lack 1986). More detailed research has been restricted to the northern isles of Scotland: studies of census methods in Orkney (Ramsay 1976), and on Fair Isle studies of eggs (Dennis 1966), chick feeding (Slater & Slater 1972a,b; Slater 1974) and adult survival and site fidelity (Broad & Ewins 1984).

Useful comparisons are provided by studies on Pigeon Guillemots, and many results are probably applicable to Black Guillemots due to the species' close taxonomic relationship. Thoresen & Booth (1958) provided the first detailed breeding account, in Washington State, USA, but the emphasis then switched to Mandarte Island, British Columbia, Canada, where Drent (1965), Aitchison (1972) and Koelink (1972) studied basic breeding biology, behaviour, thermodynamics and energetics. Diet, colony attendance, population recovery following oil spills and breeding biology have been documented in California (Ainley et al. 1971; Ainley & Lewis 1972, 1974; Follett & Ainley 1976), whilst recent work there has concentrated on behavioural postures and vocalisations (Nelson 1982, 1984, 1985). On Naked Island, in Prince William Sound, Alaska, recent work has focussed on foraging ecology (Oakley 1981; Kuletz 1983).

The Sooty Guillemot is poorly known. Apart from a short Russian paper describing various aspects of breeding on islands in South Ussuriland

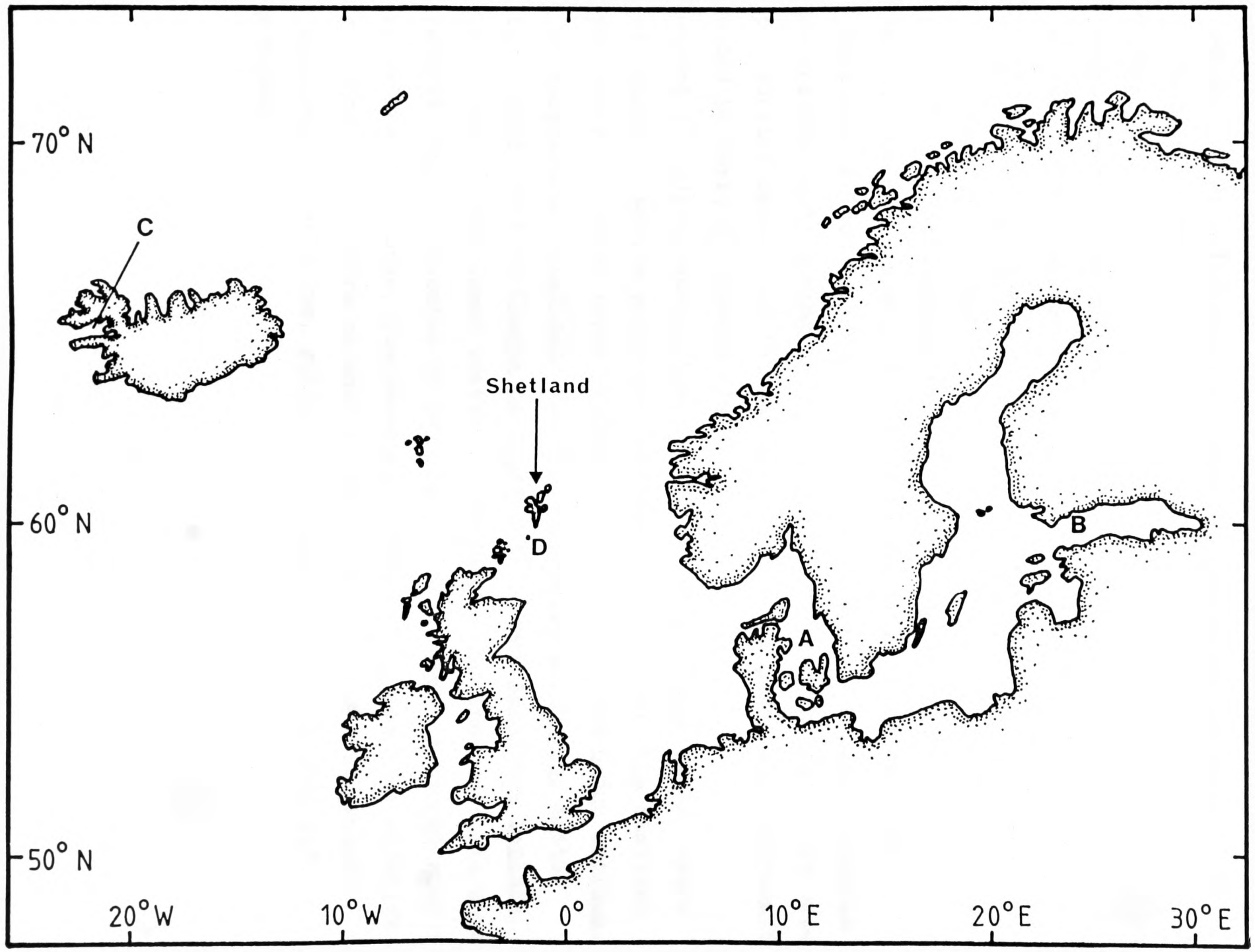


Figure 1.2 The location of Shetland, and sites of previous Black Guillemot studies in NW Europe.

A = Norde Ronner, Denmark (Asbirk)

B = Gulf of Finland (Bergman)

C = Flatey, Iceland (Petersen)

D = Fair Isle (Dennis, Broad & the Slaters)

(Nazarov & Labzyuk 1972), the only available information concerns behaviour, attendance and breeding biology during the chick stage in 1981 on Teuri Island, Japan (Thoresen 1984).

1.5 The Shetland environment

The 100-150 islands of the Shetland archipelago are the peaks of a partially drowned range of hills rising above the continental shelf, and have a complex geological history, which produced a wide range of rock types and formations (Mykura 1976). Although the total land area is c.1440 km^2, the highly convoluted coastline is at least 1450 km long and no point is more than 5 km from the sea (Flinn 1974). The strong influence of the Gulf Stream means that sea temperatures are higher than average for 60°N, and although the winters are relatively mild the summers are rather cool. Gales occur on average 58 days a year, making Shetland one of the windiest places in Britain. The oceanic influence gives Shetland the highest average monthly relative humidity (80-85%) in Britain (Berry & Johnston 1980). Most of the land is acidic moorland dominated by Calluna vulgaris and rough grasses (but lacking tree cover) and is grazed by the hardy breed of sheep. Further details of natural history and the physical environment are provided by Berry & Johnston (1980).

Shetland lies just east of the edge of the continental shelf, where upwelling increases marine productivity dramatically. The rich Shetland waters provide feeding for large stocks of fish such as Cod Gadus morrhua, Haddock Melanogrammus aeglefinus, Whiting Merlangius merlangus, Saithe Pollachius virens, Herring Clupea harengus and Sandeel Ammodytes marinus, particularly during the summer months. Accordingly Shetland supports some of the largest seabird colonies in Britain and NW Europe. Although many of the seabirds breed on large, inaccessible cliffs, the absence or relative scarcity of ground predators on many of the islands means that ground-nesting species such as terns, gulls and skuas are provided with safe breeding sites.

CHAPTER 2. COLONY ATTENDANCE AND CENSUSING

2.1 Introduction

Accurate censusing of auks at breeding colonies is difficult as numbers may fluctuate seasonally, diurnally, or in response to different weather conditions (Lloyd 1973, 1975; Birkhead & Ashcroft 1975; Harris 1976; Evans 1980; Wanless et al. 1982; Byrd et al. 1983). The Black Guillemot is no exception and a pronounced diurnal rhythm of colony attendance has been found in many areas, although there appears to be considerable variation on the basic pattern (Koskimies 1949; Asbirk 1979c; Cairns 1979, 1984; Petersen 1981). The limited British data are from two studies in Orkney and Shetland, but refer only to the later stages of the breeding season (Slater & Slater 1972b; Ramsay 1976). The closely related Pigeon Guillemot shows similar patterns and variability (Drent 1965; Ainley & Lewis 1972). The aim of this study was to examine the variation in colony attendance patterns of Black Guillemots in Shetland and to determine how and when to make counts and how to interpret these counts once made.

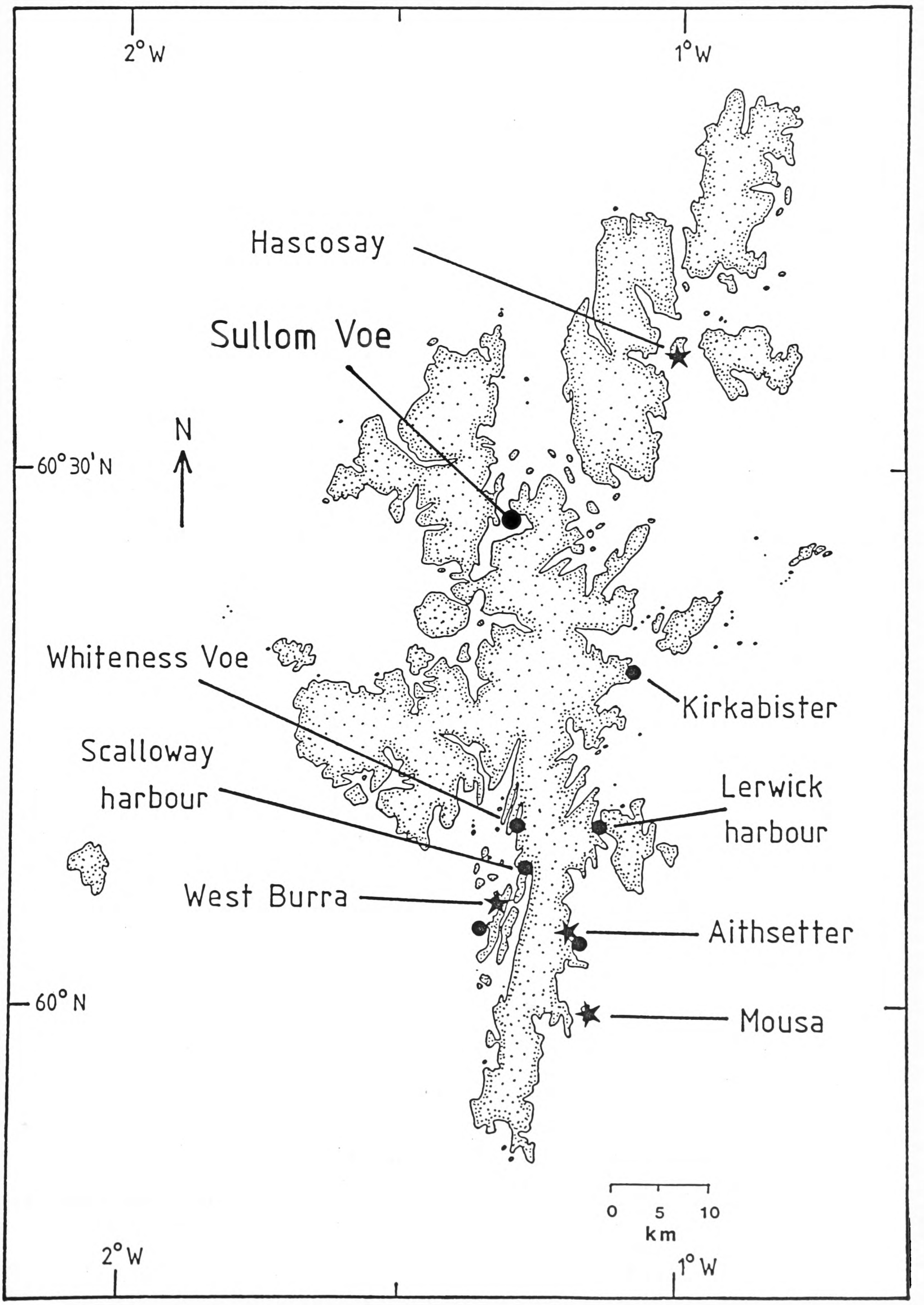
The material in this chapter has already been published (Ewins 1985b).

2.2 Study areas and methods

Black Guillemots nest both as isolated pairs and in groups, usually of less than 50 pairs. In this account a 'colony' is an aggregation of breeding individuals sufficiently separated from adjacent groups that an observer can stand between without disturbing either group (*sensu* Bullock & Gomersall 1981).

The main study colonies were on Mousa (60°00'N 1°10'W), an island of 210 ha rising to 55 m above sea level, lying 1 km offshore (Figure 2.1). Much of the coastline is steeply inclined strata of Old Red Sandstone, with a few cliffs rising to 20 m. Extensive quarrying has left large piles of discarded slates around the coast, and these now harbour many of the breeding Black Guillemots and Storm Petrels Hydrobates pelagicus. Studies were made throughout the breeding seasons of 1983 and 1984, and also in April 1984 before breeding began. The number of adults occupying sites (ie. regularly using a suitable nest cavity) was determined by observations from a hide on many occasions during the pre-breeding period; the number of

Figure 2.1 The location of study colonies (stars) and sample inshore sea areas (circles) in Shetland.



breeding attempts was obtained from daily checks of these sites. For further details of habitats and wildlife on Mousa, see Ewins (1983a, 1984a). Observations in winter and early spring were made at Aithsetter, an 800 m stretch of mainland coastline 7 km north of Mousa. The cliffs in this area were 20-50 m high, of eroded. loose Old Red Sandstone, forming a discrete bay. Counts were discontinued in late April as many birds were out of view on cliff perches by then. Comparative data were gathered at small colonies on the islands of Hascosay (60°36'N 1°00'W) and West Burra (60°06'N 1°20'W) (Figure 2.1).

The colonies chosen for study were discrete breeding areas with unrestricted views of all birds on the water within c.500 m of the centre of the colony. All Black Guillemots in this area were counted at 15 min. intervals throughout the daylight hours, with immatures and feeding birds noted separately. Most observations were made from hides ("undisturbed" counts). With the exception of the few colonies where birds were visible ashore at all times, pre-breeding counts made after adults had started to come ashore were omitted from these analyses, since unknown numbers would have been out of view. Once ashore, birds regularly occupied elevated perches, usually within 1-2 m of the nest cavity, and occupation of these "nest perches" was recorded on Mousa. "Disturbed" counts were made on Mousa during complete island censuses, the observer walking around the entire coastline, flushing all birds onto the water. Birds feeding or loafing further out and not obviously associated with breeding habitat were treated separately. Unless otherwise stated, attendance figures refer only to birds in adult summer plumage [ie. 2 or more years old (see Asbirk 1980)]. A summary of plumage types is presented in Appendix I.

Weather records were always taken at the time of observation. Wind strengths were recorded on the Beaufort scale. Tidal data have been taken from Harry's Shetland Fishing Almanacs. All times are GMT. Statistical methods throughout this and all chapters follow those of Siegel (1956), Sokal & Rohlf (1969) and Bailey (1981). The term significant is used in the statistical sense only.

2.3 Results

2.3.1 Seasonal variation in diurnal attendance

From October onwards (following completion of the autumn moult) Black Guillemots usually roost overnight in loose flocks on the sea, shifting

sites according to prevailing wind and sea conditions. In very rough winter weather they may roost on cliff ledges (R A Broad pers. comm.) but disperse rapidly at first light to feeding areas. In calmer weather groups frequently roost on the sea below breeding cliffs, remaining for up to half an hour after first light to participate in group display activities, which occur from early December onwards. This basic pattern continues until February, when some adults have acquired full summer plumage, and early morning social displays become more pronounced

Diurnal attendance patterns for five stages of the breeding season were assessed from counts made in winds of Beaufort force 4 or less and, for April only, in winds exceeding force 4 (Figure 2.2). On fine mornings in February increasing numbers of adults attended the breeding areas, usually as discrete pairs in the offshore assembly, but within an hour of first light most had dispersed. The spring increase in maximum morning attendance of adults at Aithsetter is shown in Figure 2.3. Daily maxima are presented rather than hourly means as the light regime is changing so rapidly over this period. In early March a few adults came ashore (first dates 10 and 7 March in 1983 and 1984 respectively) and by late March maximum counts approached the April peak of 60 adults. Attendance in windy weather conditions also increased but numbers reached only c.60% of those in calmer conditions. During the pre-breeding period there was an almost complete absence of birds from the vicinity of the colony during the afternoon. Morning attendance was lower and less protracted on days of winds greater than force 4 (Figure 2.2b). April attendance patterns at two smaller colonies - on Mousa (4 occupied sites) and West Burra (maximum of 12 adults) - were almost identical to that shown for this large colony (46 occupied sites).

The average duration of morning attendance by half or more of that day's maximum number increased markedly over the pre-breeding period from less than 2 hours in March to 5 hours in May (Figure 2.4). The mean value of this index of colony activity in April was lower on windy than on calmer days but not significantly so (4.45 vs. 4.85 hours; $t=1.27$, 15 df, $P>0.2$).

The undisturbed counts indicated a dramatic change in attendance pattern during incubation, with only a weak morning peak but an evening peak similar to April, though later because of the seasonal shift in daylight hours (Figure 2.2c). During the nestling period increasing numbers of single and paired prospecting adults (many probably 2 years old, as they had very worn primaries) gave rise to a slightly stronger morning peak again (Figure 2.2d). Many of the successful breeders, however, were

Figure 2.2 Seasonal variation in the diurnal pattern of attendance at colonies.

(b)-(e) show counts from colony A on Mousa, as percentages of the number of site-holding adults (84 in 1983, 92 in 1984). (a) shows counts from Aithsetter, where the number of occupied sites was not known, so the counts are expressed as percentages of the April maximum (60). Shaded sections represent counts made in winds greater than Beaufort force 4.

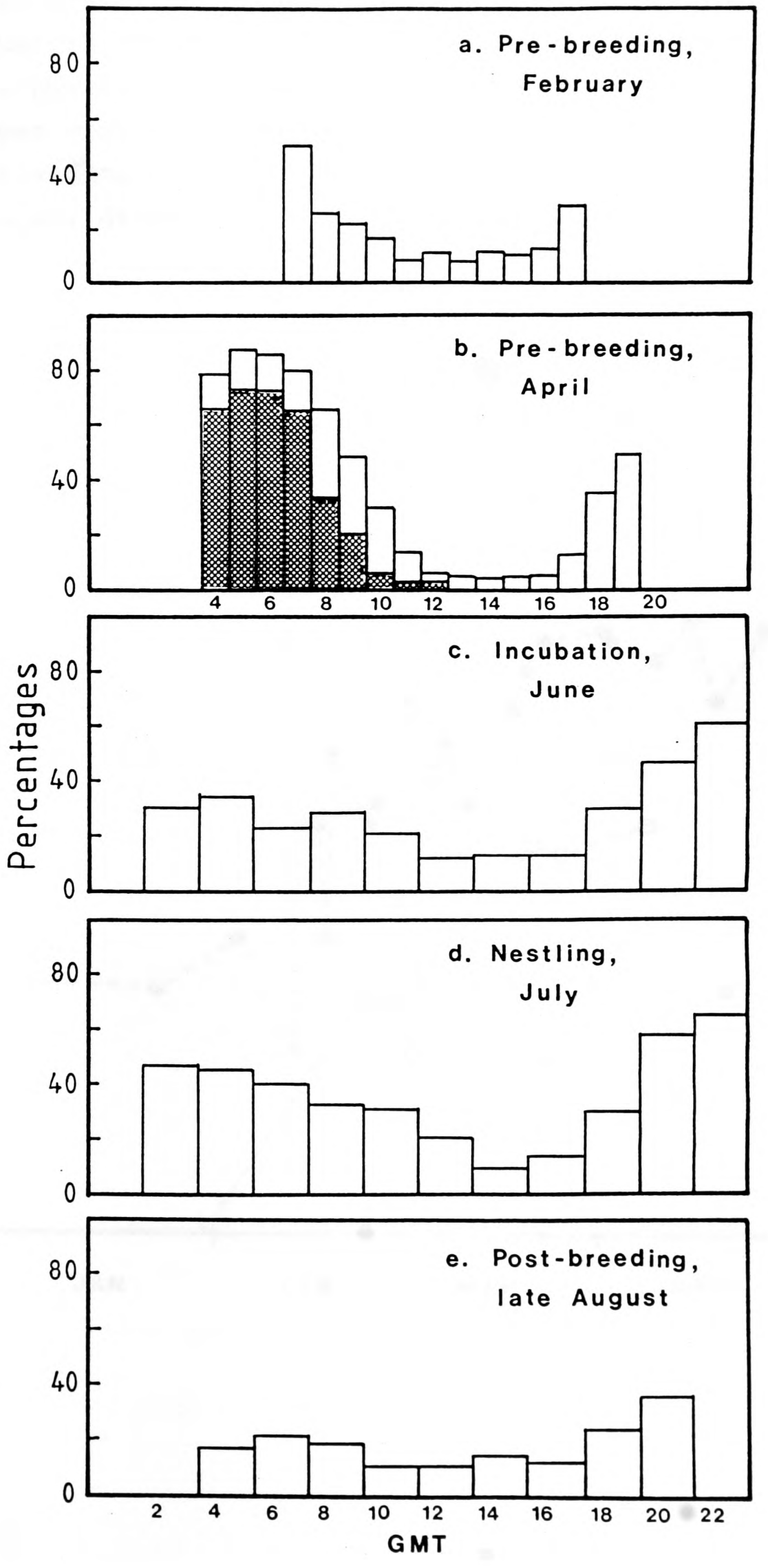

a. Pre-breeding, February
b. Pre-breeding, April
c. Incubation, June
d. Nestling, July
e. Post-breeding, late August
Percentages
80
40
0
2
4
6
8
10
12
14
16
18
20
22
GMT

Figure 2.3 Pre-breeding increase in daily maximum numbers of adults at Aithsetter, expressed as percentages of the April maximum count. Open circles refer to days with winds exceeding force 4, filled circles to calmer days.

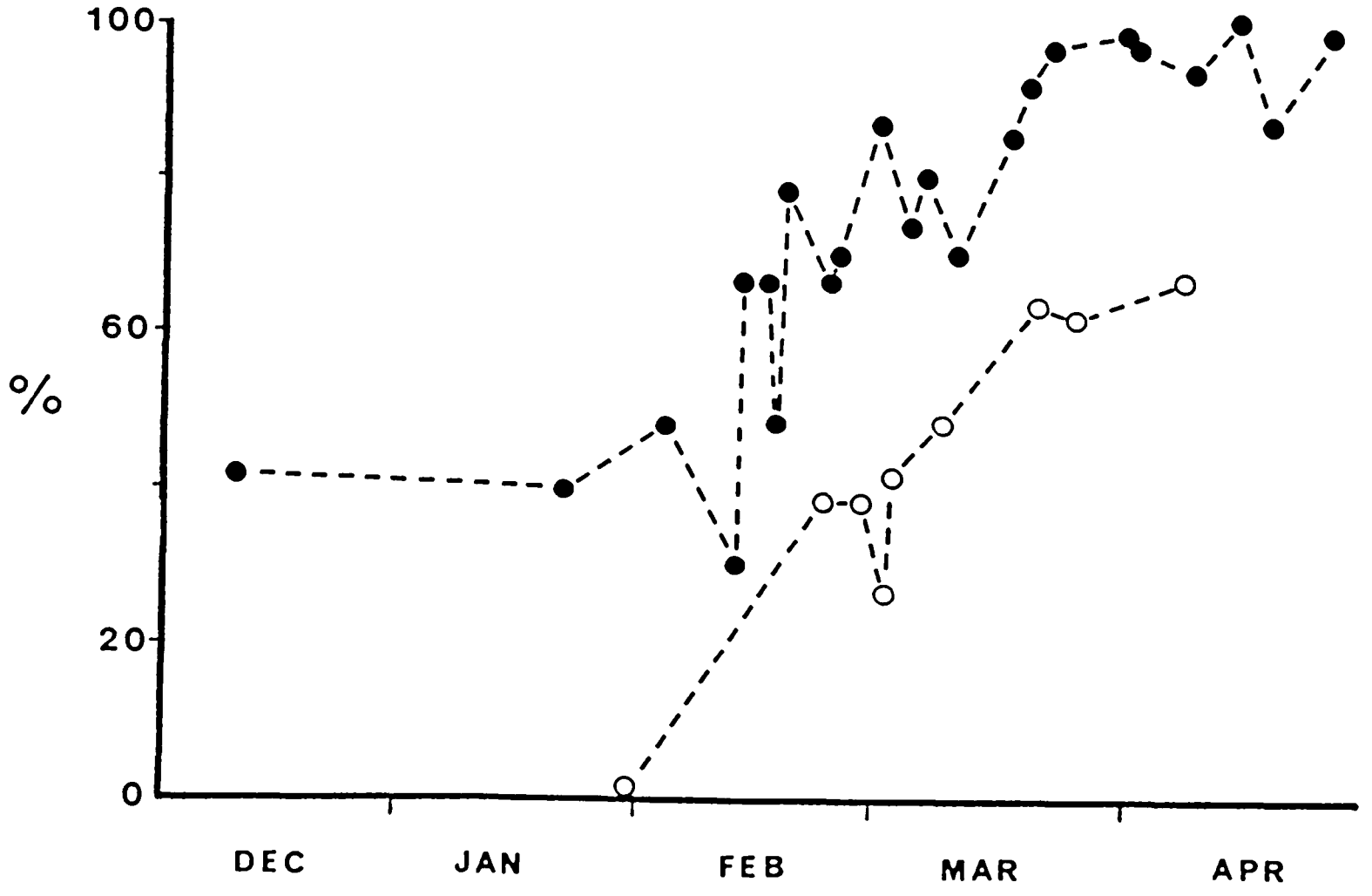


Figure 2.4 Average duration of the period each morning when half or more of the maximum number of adults seen on that day were present. The data are for days with winds of force 4 or less. Numbers show sample sizes, bars show standard errors and ranges. January - March records from Aithsetter, April - May from Mousa.

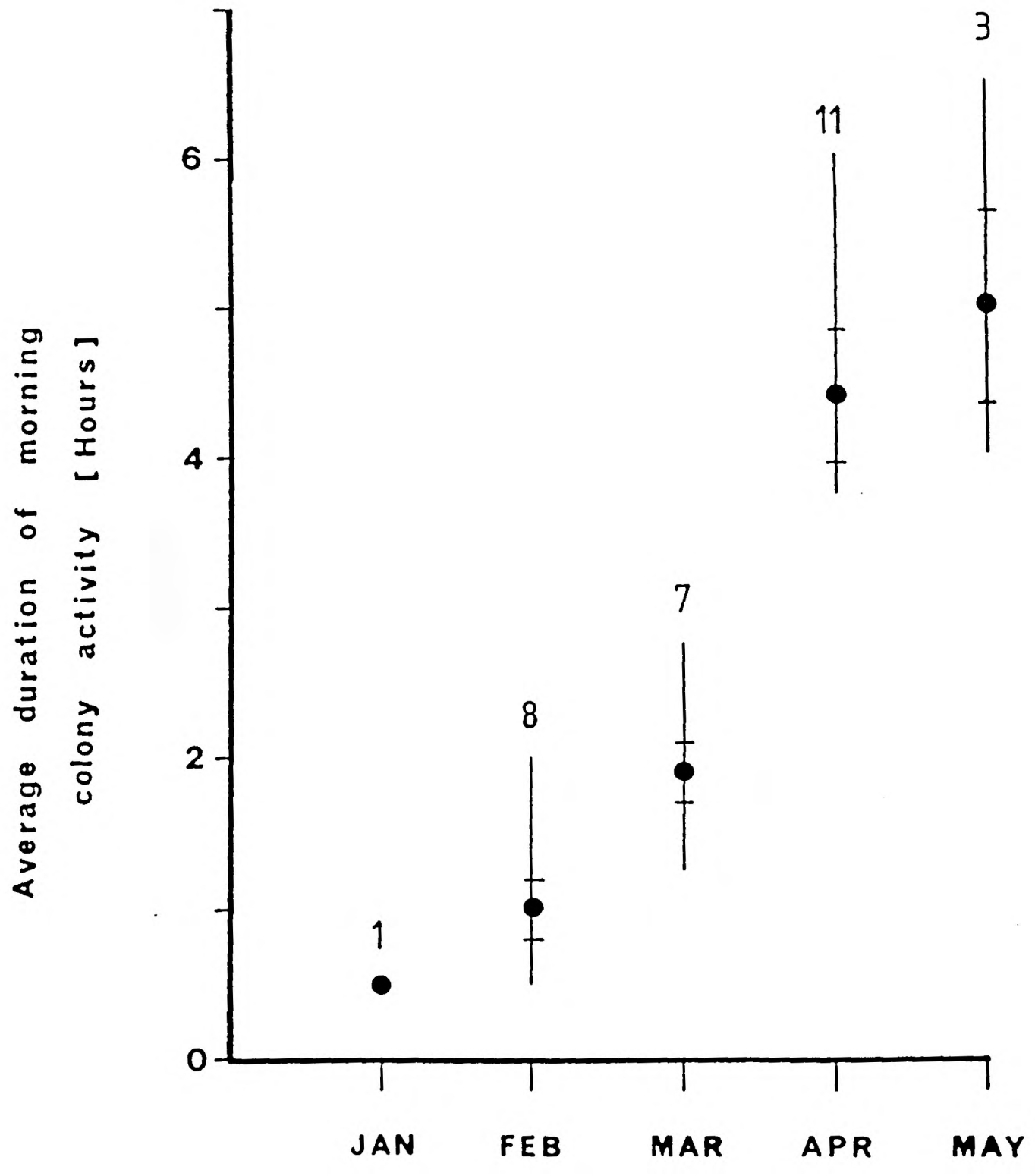


Figure 2.5 Daily variation in numbers of adults attending colony A on Mousa in April 1984. Counts in winds exceeding force 4 are excluded. Filled circles represent the means of counts during 0500-0800, and bars show standard errors. Filled triangles show maximum morning counts, open triangles minimum counts.
Br. = number of adults which later bred.

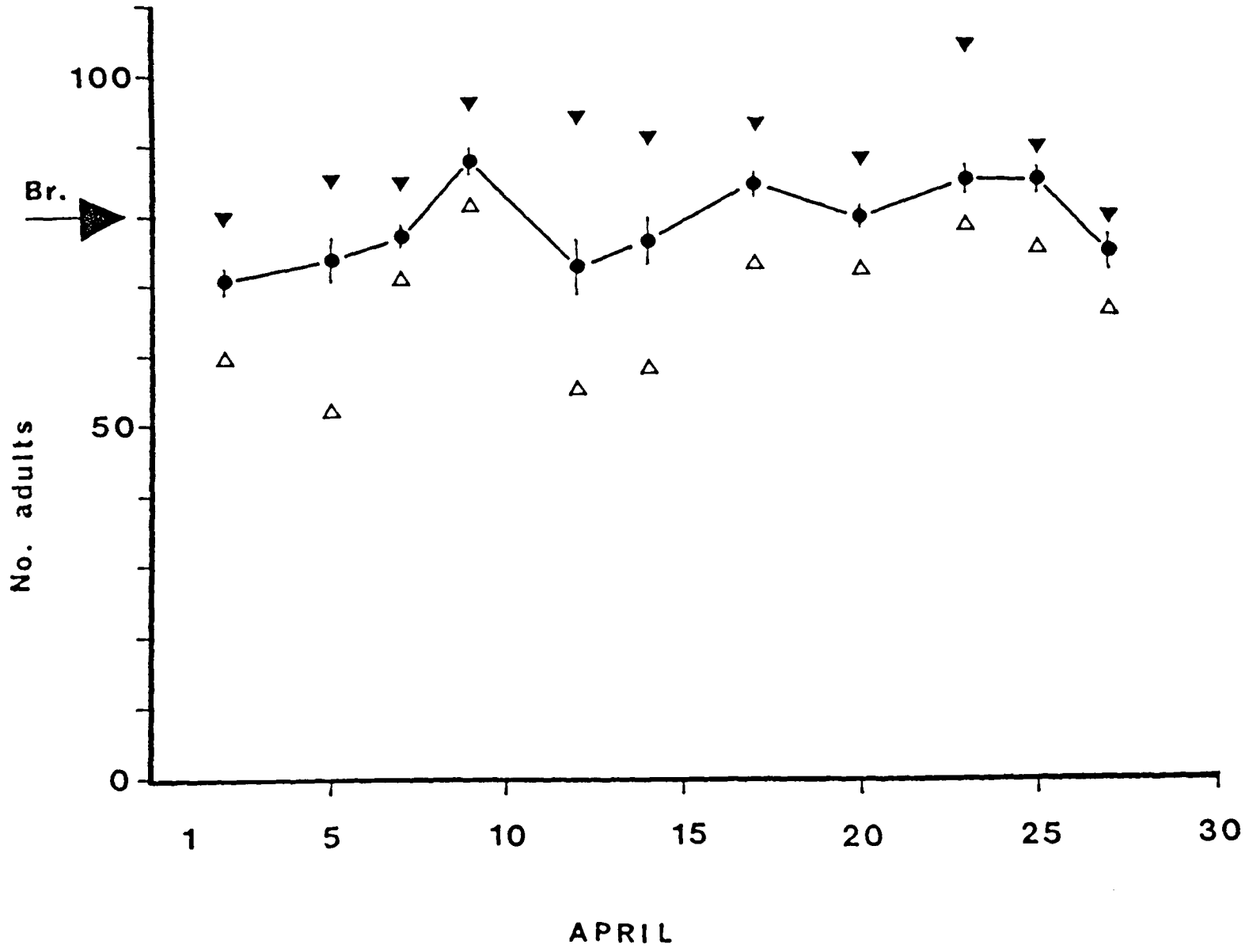


Figure 2.6 Coefficients of variation between days of hourly mean counts in April and May at colony A on Mousa.

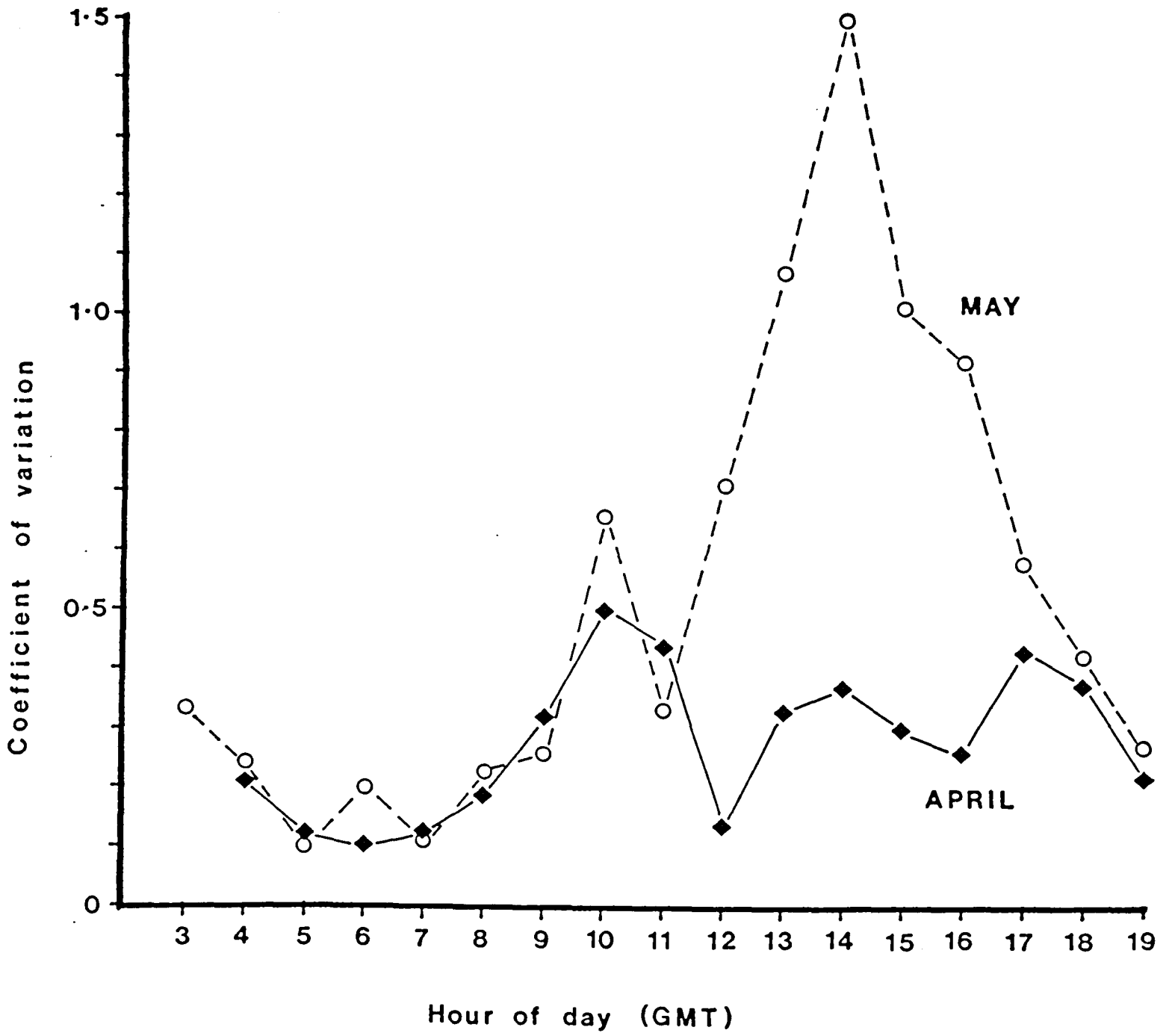


Table 2.I April attendance in relation to wind speed.

	CALM (force 4 or less)	WINDY (above force 4)
MAXIMUM ATTENDANCE		
Mean	89.6	78.4
sd	7.2	11.1
n	11	7
range	80-104	57-93
MEAN ATTENDANCE		
Mean	78.7	68.4
sd	5.8	12.1
n	11	7
range	71-88	50-83

The observations are maximum counts during 0500-0800 and mean counts during the same period. Tests of the differences between means gave: for maxima $t = 2.38$, $P<0.05$; for means $t = 2.11$, $P>0.05$. Tests of the differences between variances gave: for maxima $F = 2.41$, $P>0.05$; for means $F = 4.38$, $P<0.05$.

present for only a few minutes at a time, whilst delivering fish. The evening peak was greatest at this stage of the season, as more 2-year-olds joined breeders and immatures at the communal roost offshore and on cliff ledges. Once the young had left the nest adults continued to frequent the nest area for a few mornings (up to 1 week was recorded), but by late August most chicks had gone and many breeders had already started body moult and appeared to have moved away to moulting areas. Observations of colour-ringed birds indicated that immatures and 2-year-olds departed for the moult areas earlier than breeders and that the slight evening roost peak comprised largely breeders whose young had only recently departed.

2.3.2 April attendance

Investigations of factors affecting colony attendance were carried out in April, since most adults were attending colonies regularly at that time (Figures 2.3 and 2.5). Preliminary observations indicated that numbers were relatively stable then and that future census work might best be done in this month. The results from hide watches on calm April mornings at colony A on Mousa (40 breeding pairs in view) are summarized in Figure 2.5. The least variable counts were in the period 0500-0800 in both months (Figure 2.6) and so the attendance in this period was used in subsequent analyses. Smaller and more variable numbers of birds were present in windy weather (Table 2.I). Repeated thorough scans of the census area confirmed that the apparent reduced attendance was not an effect of lowered detectability in rougher sea conditions. Tidal effects were investigated by comparing both maximum and mean attendance during 0500-0800, with the length of time when the tide was within 3 hours of high water during 0500-0800 and also during 0400-1200. No significant relationships were found. Similarly the duration of colony activity in April (Figure 2.4) appeared to be independent of tidal state in the morning.

Occupation of nest perches was recorded on 17 mornings in April for 25 sites at which the birds subsequently bred. In 12 of the pairs concerned at least one member was individually colour-ringed, confirming that site-holders were rarely found at nest perches other than their own during the pre-breeding period. There was no significant difference in mean numbers visiting nest perches according to weather conditions (mean for calm =41.3; for windy =43.6; $t=0.8$, 15 df, $P>0.4$). The proportion of adults present on any particular day varied from 70 to 100%, with the exception of 14 April, when only 34% visited nest perches despite favourable weather and large

numbers offshore. The general pattern was of regular attendance of the nest area by breeders, with 70% or more of the perches visited on 16 of the 17 mornings. Combining the April data for pairs in which the sexes could be distinguished, there was no significant difference between the sexes in the total number of days on which the nest area was visited (paired sample test, $t=0.16$, 11 df, $P>0.8$). However, in 19 cases where only a single bird of known sex was present, 15 were males.

2.3.3 Non-breeding birds

Maximum attendance in calm weather conditions in April usually exceeded the number of breeding adults at the main study colony (Figure 2.5). On average, breeders accounted for 89% of maximum numbers (range 77-100%), so 11% of adults present at peak times did not breed in the colony. None of 25 colour-ringed adults occupying sites in other parts of the island was ever seen in the main study colony. Two colour-ringed adults which had bred unsuccessfully in 1983 regularly visited the colony from April onwards in 1984, but neither was paired nor occupying a suitable nest cavity. From June onwards increasing numbers of 2-year-olds frequented the colonies, though absent during April and May (birds of this age could be identified by colour-ring observations, confirming that the flight feathers of 2-year-olds became heavily abraded and bleached much sooner than those of breeders, because they moult earlier than adults in the previous autumn). Many 2-year-olds investigated dark recesses and cavities, but only a few formed loose pair bonds with older birds (see Chapter 5).

Only small numbers of immatures (ie. 1-year-olds) were noted in the census area during the pre-breeding period. In two springs they represented 1.0 and 1.1% of the maximum total, and in April 1984 an average of 0.8% of birds associated with all Mousa colonies were immatures. By July small numbers visited the nesting boulders but most activity was brief inspection of potential nest cavities, from which they were generally chased by older birds. Of 98 adults occupying suitable nest sites in the colony A area on Mousa in April, 12% did not make any subsequent breeding attempt that year.

2.3.4 Correction factors

Counts of birds may be converted to breeding pairs using a correction factor: $\mathbf{k}$ = Number of breeding attempts / Mean visual count

Pre-breeding counts provided the best indication of adult numbers at a colony (Figure 2.2). Morning attendance in the pre-breeding period is regular then and largely comprises breeding adults, while interpretation of counts at other times of year is complicated by breeding activities and non-breeding birds. To determine **k** values therefore, a series of disturbed counts was made in the pre-breeding period during 0500-0800 on mornings of winds force 4 or less, at colonies where the number of breeding attempts could be accurately determined. All counts from Mousa were made in April, while those from Hascosay were made from late March to early May. The data and the derived **k** values are presented in Table 2.II.

The average **k** value for Mousa of 0.51 varied little between colonies and is equivalent to 1.96 adults present per breeding attempt. The corresponding figure for Hascosay was 0.22 - an average of 4.55 adults per breeding attempt. Although both the standard error of the mean counts and the variation in k between colonies are greater for Hascosay, there is clearly a marked difference between these islands, with 57% of adult-plumaged birds at Hascosay being non-breeders, compared with only 11% on Mousa. Hascosay is close to rich and extensive feeding areas, but may have a shortage of suitable nest sites (artificially-created cavities have been rapidly occupied there in the past; R J Tulloch pers. comm.).

2.3.5 Count accuracy

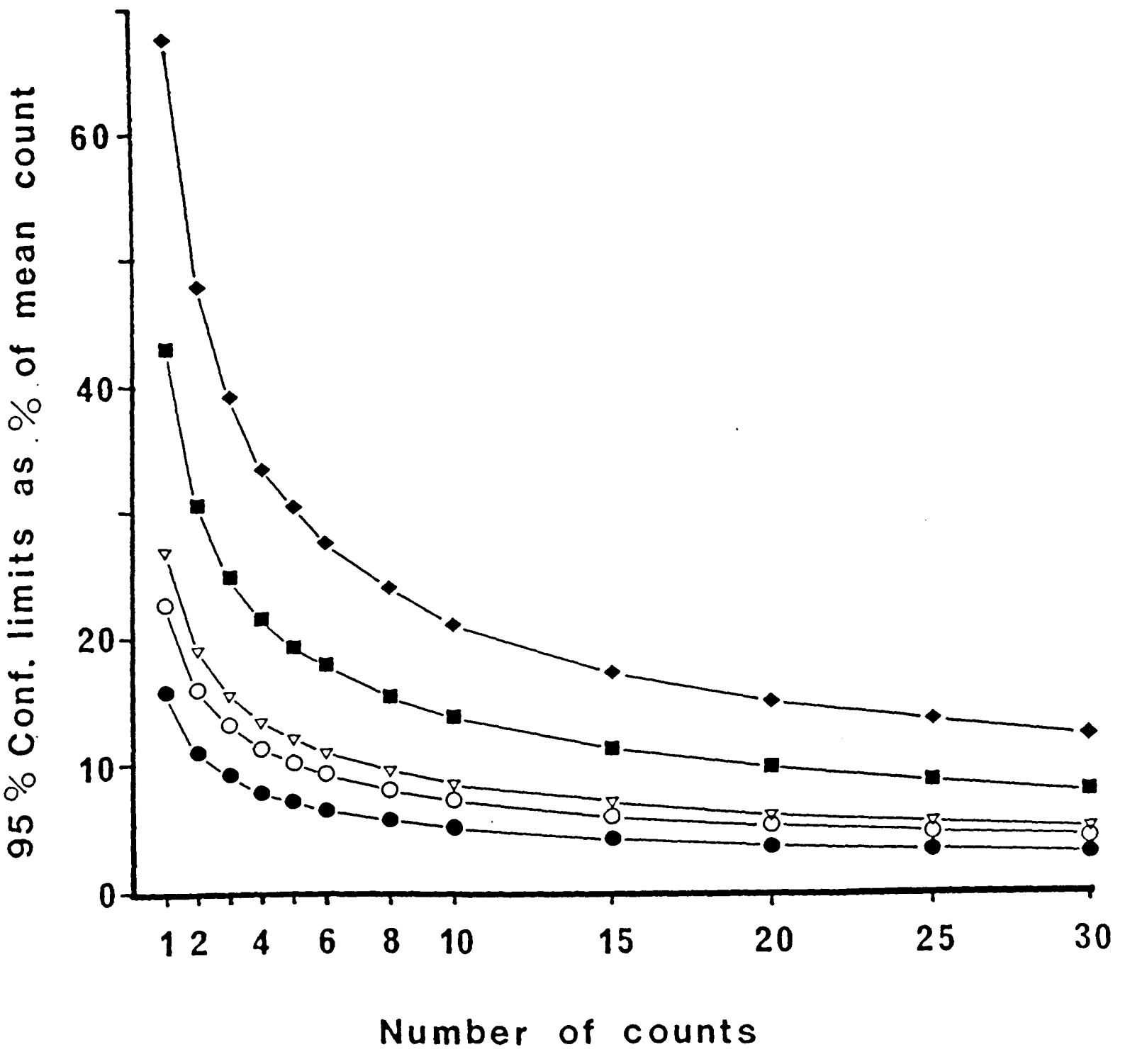
Counts were of birds on the sea, where Black Guillemots are sometimes difficult to pick out in certain light conditions. The importance of this can be seen from comparisons of simultaneous counts in discrete census areas by two observers. An observer with little previous experience of counting this species, or birds on the sea, regularly under-counted by as much as 22%, whereas one with some experience was usually within 5% of the total (determined from many repeat scans of the census area). All counts considered in this chapter were made by one experienced observer (myself), and repeat counts showed that within-observer variation rarely exceeded 5%.

The accuracy of an estimate of any mean improves with the number of counts made. If the 95% confidence limits of the mean calculated from n counts are to be within R % of the mean count (C), and SD is the standard deviation, then $R = (196 \times SD)/(C \times n)$. Using this relationship, the precision obtained by different numbers of counts is given in Figure 2.7, for 4 colonies of different sizes on Mousa, where counts were made in April during 0500-0800 in winds of force 4 or less. For colony A, undisturbed

Table 2.II Correction factors for various colonies.

Colony		Pre-breeding adult counts Mean	se	No. of breeding attempts	k
Mousa	A	82.1	3.4	43	0.52
	CGQ	39.3	1.9	21	0.53
	D	43.5	2.1	21	0.48
	E	35.4	2.3	18	0.51
	F	21.1	1.0	10	0.47
	L	19.0	1.5	9	0.47
	H	5.9	0.7	3	0.51
	J	5.6	0.6	3	0.54
	K	5.8	0.3	3	0.52
TOTAL		257.7		131	0.51
Hascosay	A	24.5	4.5	9	0.37
	B	19.0	2.0	4	0.21
	C	30.5	13.5	3	0.10
TOTAL		74.0		16	0.22

Figure 2.7 The relationship between the 95% confidence limits expressed as a percentage deviation from the mean count and the number of counts, for 4 Mousa colonies. All counts were made during 0500-0800 h in April, in winds not exceeding force 4. Circles refer to colony A, filled circles to maxima of undisturbed counts (mean 90 adults), open circles to disturbed counts (mean 82 adults). Other symbols refer to disturbed counts at colonies with means of 39 (triangles), 19 (squares) and 6 (diamonds) adults.



counts aimed at detecting maximum attendance provided a more precise estimate of the mean than did the same number of disturbed counts. Since a comparison between undisturbed and disturbed mean counts at the large colony A revealed no significant difference between the techniques (means 78.2 and 82.1 respectively; $t = 1.2$, 114 df, $P>0.2$), only the results from disturbed counts are given for the other colonies. The accuracy of the estimate of the mean increased with colony size as well as number of separate counts: at the two larger colonies (mean counts 82 and 39 adults) relatively little further accuracy would be achieved beyond 6 disturbed counts (when R was c.10%), whereas 30 or more counts would be required at the smaller colonies (mean counts 19 and 6 adults) to obtain a similar level of accuracy.

2.4 Discussion

In the pre-breeding period the basic pattern of colony attendance in Shetland was similar to that found elsewhere (Asbirk 1979c; Cairns 1979; Petersen 1981). At higher latitudes, with no darkness, the evening and morning peaks merge (Petersen 1981). At some sites birds roost overnight on cliffs or skerries some distance from the colony and only a weak evening peak is then apparent (Drent 1965). In the early spring the daily attendance at the colonies is brief but pair bonds may be established and reinforced during the early morning gatherings. Once birds have started to come ashore, occupation and defence of nest sites is probably important, particularly where good sites are in short supply, and results from Mousa indicate that the majority of breeders occupy nest perches in April. During incubation and nestling periods many of the visible birds were immatures or adults which either had not bred or had failed, and attendance patterns reflected more the activity of these elements of the population than that of successful breeders [cf. other alcids (Gaston & Nettleship 1982)]. Furthermore, an unknown proportion of birds incubate very tightly and are thus overlooked during the incubation period, even in disturbed counts.

Strong winds clearly depressed morning attendance, but they were usually accompanied by rough seas and reduced temperatures, which may be contributory factors. The influence of tidal state on attendance has been investigated in study areas with tidal ranges larger than those in Shetland (Preston 1968; Cairns 1978; Petersen 1981). In Iceland, Petersen found that an extended period of low tide in the afternoon resulted in

significantly reduced numbers at the colony in the evening. He suggested that this was due to reduced activity of benthic prey around low tide, forcing birds to feed for longer into the evening. No such effects were evident in Shetland. However, during the pre-breeding period, adults on Mousa fed on sandeels (Ammodytidae) in addition to a variety of benthic fishes (see Chapter 9), and it is possible that sandeel activity is affected more by current strength than tidal state per se (Warburton 1983).

Even in windy conditions most breeders regularly attended nest sites in the pre-breeding period, suggesting that daily variation in maximum attendance may be largely due to non-breeders. Similarly, Gaston & Nettleship (1982) found that a large number of prospecting Thick-billed Murres Uria lomvia accounted for much of the variation in colony attendance, largely determined by food availability. At colony A on Mousa 12% of adults occupying sites in April did not breed and c.1% of the total birds present were immatures. Hence c.13% of birds counted in April were non-breeders. This is of the same order as the values of 8-18% for an expanding Icelandic colony in various years (Petersen 1981), but much lower than figures elsewhere: in Canada, 50% (Winn 1950) and 45-50% (Preston 1968); and in Orkney 66% (Ramsay 1976). However, these other figures were calculated from counts made during the incubation and nestling periods, when colony attendance may not meaningfully reflect breeding numbers.

Prolonged observations from a hide of pairs occupying sites during the pre-breeding period are essential for calculating the proportion of non-breeders, since haphazard searches of likely breeding habitat are known to under-record the number of nests (Petersen 1981; pers. obs.) and some pairs losing eggs will not be detected. On Hascosay - an island where nest sites appear to be in short supply - 57% of adult-plumaged birds did not breed. Within 5 km were rich feeding areas with large stocks of sandeels and up to 1100 Black Guillemots (the largest known concentration in Britain) have been recorded in this small area, mostly feeding at the edge of tidal 'rips' (Marshall & Kinnear 1975). Excellent feeding conditions in areas where nest sites are scarce might account for such high proportions of non-breeders. The time spent at colonies by breeders and non-breeders may also be affected by local feeding conditions.

Conversion of pre-breeding disturbed counts made at Mousa colonies during 0500-0800 in winds not greater than force 4 gave a fairly reliable estimate of the number of breeding pairs, with an average of 1.96 adults per attempt. However, application of the same conversion factor to the Hascosay colonies would over-estimate the number of breeding attempts by

136%. Cairns (1979) recorded similar variation: for two Canadian colonies, k was 0.67 and 0.95. His higher k values result from counts being made throughout the breeding season, when attendance is lower than prior to breeding. For various Orkney colonies, correction factors ranged from 0.15 to 0.25 (Ramsay 1976), but these were based on counts made at various times of day during the late nestling period and so did not necessarily indicate a large surplus of non-breeders. However, the conclusions are the same: no widely applicable correction factor can be used, as the proportion of birds not breeding seems to vary regionally, depending on factors such as food supply, breeding success, and availability of nest sites.

Implications for censusing

A reasonable estimate can be made of adult numbers associated with breeding areas if an observer with some previous experience conducts disturbed counts between late March and mid May during 0500-0800 GMT in winds not greater than force 4. The period and time may vary geographically according to the timing of breeding and the light regime. Similar recommendations for censusing have been proposed by Evans (1980) and Munkejord (1983). Immatures and adults not in summer plumage should be recorded separately. In Orkney and Shetland these methods have been extended from counts at potential monitoring sites to surveys of pre-breeding distribution (Chapter 3; Ewins & Tasker 1985).

Undisturbed counts aimed at detecting maximum colony attendance provide a better estimate of the mean than the same number of disturbed counts, but they are labour-intensive and disturbed counts will usually be more practical. As fluctuation in numbers is proportionately greater at smaller colonies, it is preferable to take a larger number of birds as a monitoring unit. However, selecting large colonies alone is not recommended since these may be a result of clumping of high quality nest sites. Nests in such areas may be occupied in preference to more scattered sites of poorer quality, in which case any population changes might be detected last at large colonies. If five disturbed counts were made on different days in the specified conditions at a colony holding more than 50 adults on average, the 95% confidence limits would be within 10% of the estimated mean, whereas after 2 counts they would only be within 16%.

Proposed monitoring units in Shetland are stretches of coastline (varying from 1.5 to 8.2 km in length) which include colonies of various sizes, for disturbed counts; and a few smaller discrete colonies for

maximum attendance counts (Ewins 1985a). Ultimately it is likely that funds, manpower, and the weather will to a large extent determine the degree of accuracy obtained by such monitoring counts.

A summary of the monitoring recommendations made to the Shetland Oil Terminal Environmental Advisory Group is presented in Appendix IX.

CHAPTER 3. BREEDING DISTRIBUTION

3.1 Introduction

Black Guillemots are unusual amongst seabirds in not nesting in large colonies (Lack 1968) and unique amongst Atlantic auks in being a predominantly inshore and sedentary species (Storer 1952; Cramp 1985). The Operation Seafarer surveys in 1969-70 recorded 8343 Black Guillemots in Britain and Ireland. These were converted to the same number of pairs on the assumption that one bird per pair would be visible. The main strongholds were in Orkney (27%) and Shetland (28%) (Cramp *et al.* 1974).

The *Esso Bernicia* incident in December 1978 killed at least 633 Black Guillemots, mostly in the Yell Sound area (Heubeck & Richardson 1980), representing 27% of the Shetland population, on the basis of the Seafarer figures. A reliable base-line survey was deemed necessary. In this chapter I report the results of surveys of breeding numbers and distribution of Black Guillemots in Shetland, and investigate various factors affecting the distribution. A brief comparison of pre-breeding distribution with that at other times of year in Shetland is provided by Ewins (1985d). The material in this chapter has been published, in a comparison with results from simultaneous surveys in Orkney (Ewins & Tasker 1985).

3.2 Methods

Surveys were made during the pre-breeding period, consistent with the recommendations of Evans (1980), Petersen (1981), Munkejord (1983) and Ewins (1985b). These were carried out mainly between late March and mid May 1982-84. Counts of adults in summer plumage that were associated with potential breeding habitat were made during 0500-0800 h GMT, in winds not greater than Beaufort force 4, along lee shores whenever possible. When disturbed, birds gathered in groups on the sea below the breeding areas, where they could be counted. Birds more than c.300 m from the shore, immatures, and moulting adults are not considered here.

In all, 92% of the Shetland coastline was covered; no counts were made on the Muckle Flugga group, Muckle and Little Ossa, Holm of Maywick and Linga (Brae), though it is unlikely that any of these islands held more than a few pairs. A pre-breeding estimate was made for the North Benelip

colony by E. Tait and breeding season counts have been used for some Whalsay islands.

Counts were made either from the land or the sea. Although much of the survey was completed by myself and the project assistants (Paul Fisher and John Morton), many others were involved, and their invaluable assistance is acknowledged. Land-based counts involved observers walking the cliff-tops; up to 10 km of coast could be covered in the 3 hour period. Most sea-based counts were made from Zodiac inflatables, which enabled most of the productive geos (inlets) and caves to be investigated; up to 45 km of coast could be covered in the period. Results using these two methods are comparable since no significant difference was found between counts made at 6 coastal stretches by both methods (total land-based count = 346, sea-based count = 316; paired sample test, $t = 1.25$, 5 df, $P>0.05$). Records were kept of weather and sea conditions, cliff height and probable breeding habitat type. Presence or absence of ground predators was assessed from personal observations and information supplied by crofters and local naturalists. Water depths were obtained from Admiralty charts

A Black Guillemot colony refers to any group of adults associated with likely breeding habitat, sufficiently separated from adjacent groups that an observer can stand between without disturbing either group (see Chapter 2). An island is taken to be any piece of land larger than 750 m^2 that is permanently separated from other land by more than 100 m. Skerries regularly washed-over by heavy seas were not considered. Coastline lengths were calculated using a mapping wheel on 1:25,000 Ordnance Survey maps. Copies of the original survey data, presented in Ewins (1985a), are lodged with the Shetland Oil Terminal Environmental Advisory Group (Aberdeen University); the Nature Conservancy Council (NE Scotland Region, Aberdeen), and the Edward Grey Institute of Field Ornithology (Oxford University).

3.3 Results

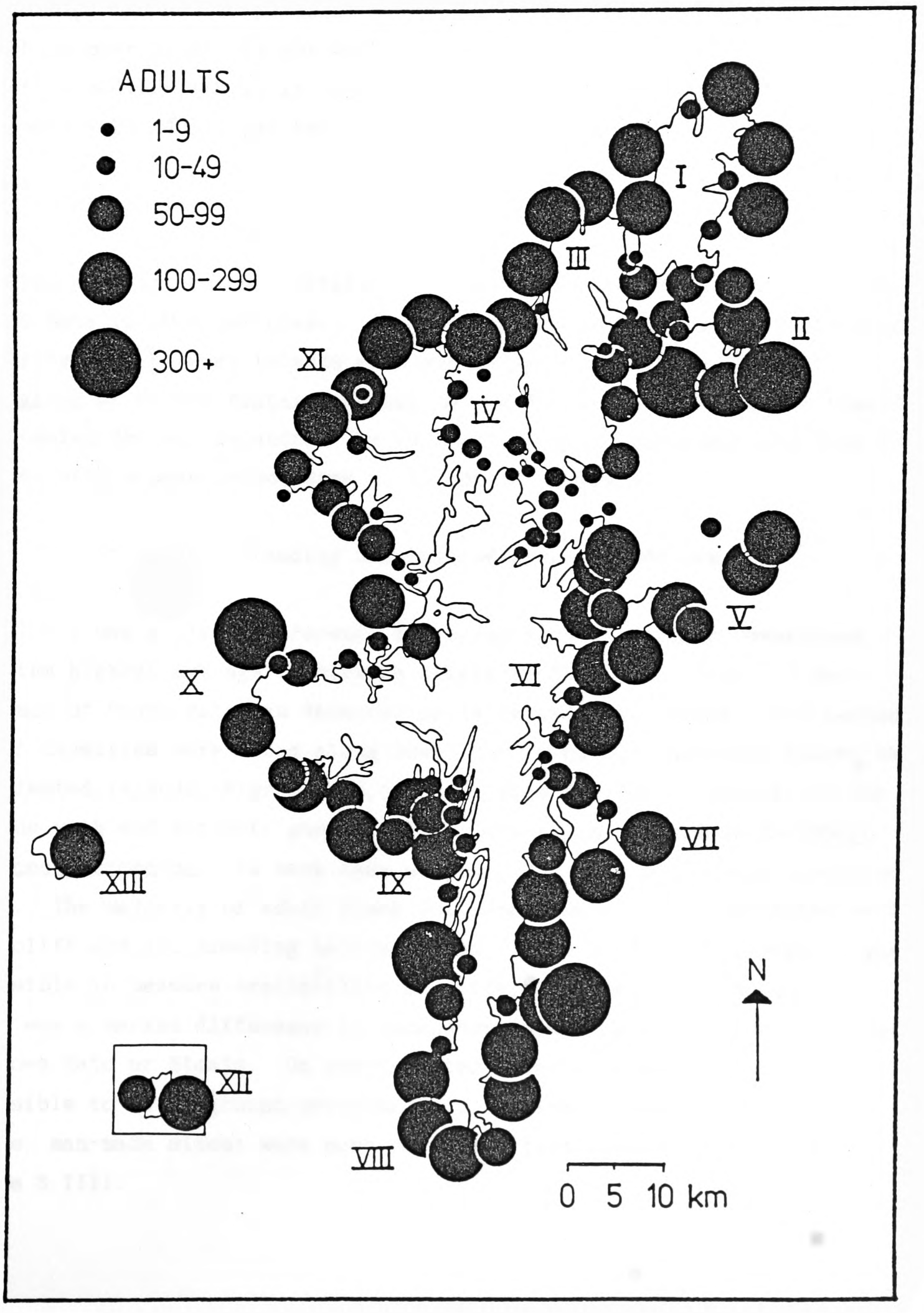
3.3.1 Numbers and distribution

A total of 12,008 adults associated with likely breeding habitat were recorded (Table 3.I). Since a few small islands were not covered, or were surveyed during the breeding season, the Shetland total is probably slightly higher than this. Although some coasts supported rather few breeding birds (eg. long voes, Yell Sound coasts, NW Unst cliffs), the overall distribution was fairly regular around Shetland (Figure 3.1). Of

Table 3.I Regional totals of adults, coastline lengths and areas of shallow water. Roman numerals correspond with those in Figure 3.1. Areas of shallow water refer to water not greater than 40 m deep, within 3 km of breeding areas.
Precise area boundaries are shown in Figure 4.1.

Area		No. of adults	Total coast (km)	Density (ads/km)	Area of shallow water (km^2)
I	Unst	1068	128	8.4	67.4
II	Fetlar	1173	51	22.8	41.8
III	North & East Yell	958	117	8.2	54.9
IV	Yell Sound	555	212	2.6	61.1
V	Whalsay group	823	65	12.6	39.4
VI	Delting	883	123	7.2	41.5
VII	Bressay & Noss	389	49	7.9	23.4
VIII	South Mainland	2139	141	15.1	57.7
IX	Scalloway Islands	998	219	4.6	55.2
X	West Mainland	1538	304	5.1	56.3
XI	Northmavine	1013	145	7.0	47.6
XII	Fair Isle	338	29	11.6	-
XIII	Foula	133	18	7.5	15.2
	TOTAL	12008	1601	7.5	

Figure 3.1 The pre-breeding distribution of adult Black Guillemots in Shetland, 1982-84. Roman numerals correspond to those in Table 3.I. The sizes of circles indicate the number of adults either at individual colonies, or in each 10 km of coast where long stretches of coast were continuously occupied.



134 islands surveyed, 105 (78%) held breeding Black Guillemots. There was a significant positive correlation between pre-breeding adult numbers and the extent of shallow water not greater than 40 m deep within 3 km of breeding areas, for 12 regions (the depth data for Fair Isle was not available) (Figure 3.2). Forty metres was chosen as the critical depth since few birds foraged in deeper water (see Figure 9.4); and 3 km since few breeders foraged further than this from the colony (see Chapter 9). The Yell Sound area supported 5% of the Shetland total, but breeding density (per km of coast) there was lower than elsewhere (Table 3.I), as was the number of adults per km^2 of suitable shallow water (Figure 3.2). Overall breeding density in Shetland was 7.5 adults per km of coastline, and roughly 21 adults per km^2 of inshore waters not greater than 40 m deep.

3.3.2 Colony size

The smallest colony contained one bird, and the largest c.100 birds (North Benelip, Out Skerries). Since there was no significant difference in colony size between islands with and without Brown Rats Rattus norvegicus or Stoats Mustela erminea ($G = 2.17$, 4 df, $P>0.05$), the results were pooled for all islands. The bulk of colonies contained less than 50 adults, with a mean colony size of 11 adults (Table 3.II).

3.3.3 Cliff height, breeding habitat and ground predators

There was a clear preference for breeding along higher coastlines, with the highest average density on cliffs 25-50 m high (Figure 3.3a). Presence of Brown Rats was detected on 14 islands, and Stoats on 3 islands. Higher densities were found along lower coasts on non-infested islands than on infested islands (Figure 3.3b,c). Analyses were also carried out for islands with and without: people, feral Cats Felis catus, and Hedgehogs Erinaceus europaeus. In each case similar, but less pronounced trends were found. The majority of adult Black Guillemots were found associated with open cliff and geo breeding habitat types (Table 3.III). Although it was impossible to measure availability of different types of breeding site, there was a marked difference in occupancy depending on presence or absence of Brown Rats or Stoats. On non-infested islands sites that would be accessible to these ground predators (ie. boulders, burrows in grassy slopes, man-made sites) were much more important than on infested islands (Table 3.III).

Figure 3.2 The relationship between adult pre-breeding numbers and area of water not deeper than 40 m within 3 km of breeding areas, for 12 regions in Shetland. Roman numerals correspond to regions in Table 3.I.

The dashed line represents the regression:

No. adults = 20.9 (Water area) - 6

$r = 0.621$, 10 df, $P<0.05$

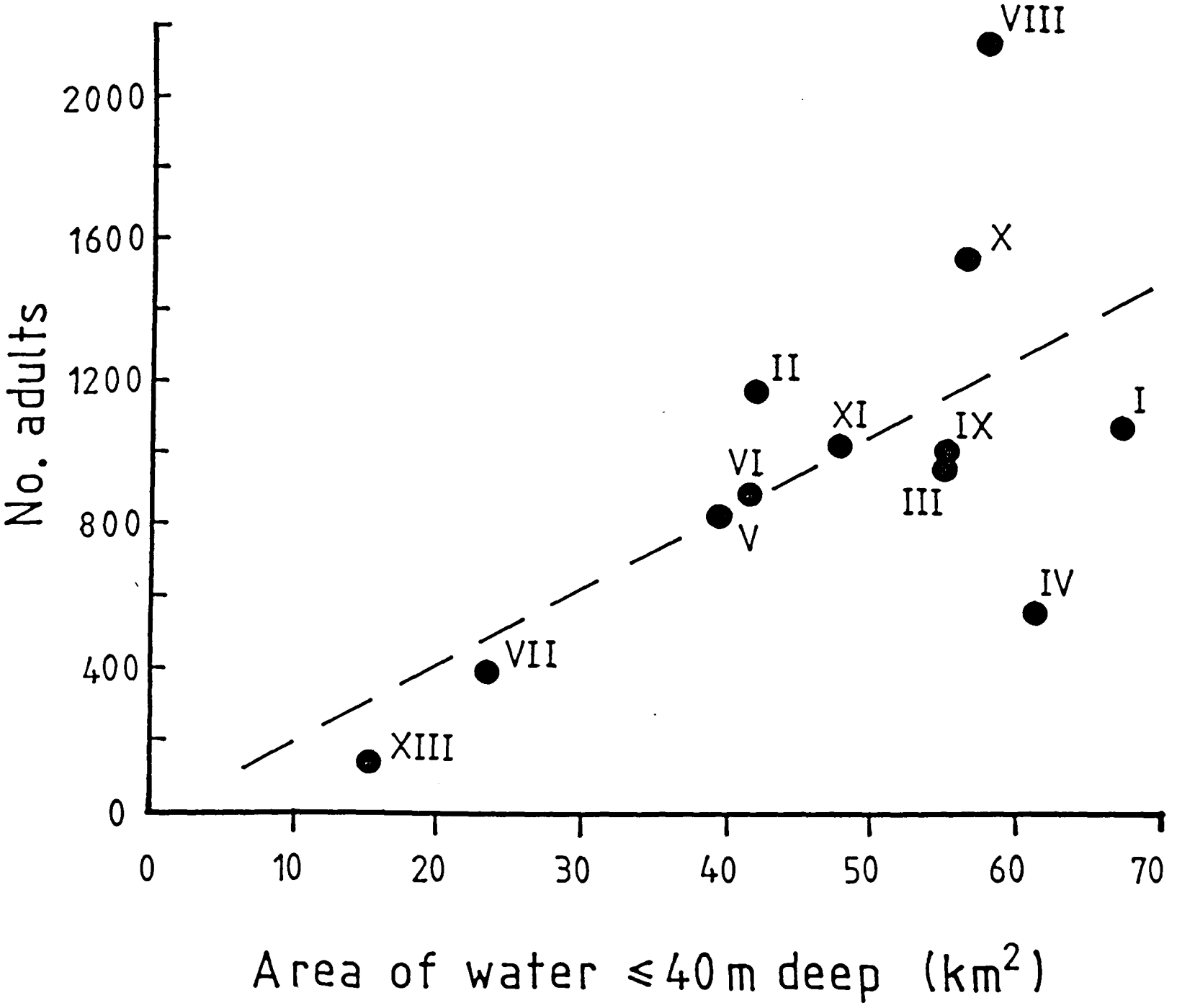


Table 3.II Size distribution of colonies in Shetland, as % of colonies containing different numbers of adults.

Colony size	%
1-2	24.0
3-9	35.6
10-19	23.2
20-49	14.9
50-99	2.1
≥100	0.1

Total no. of colonies = 1078

Figure 3.3 The pre-breeding distribution of adults in relation to cliff height, for: a) All coasts, b) Islands infested with Brown rats or Stoats, c) Non-infested islands.

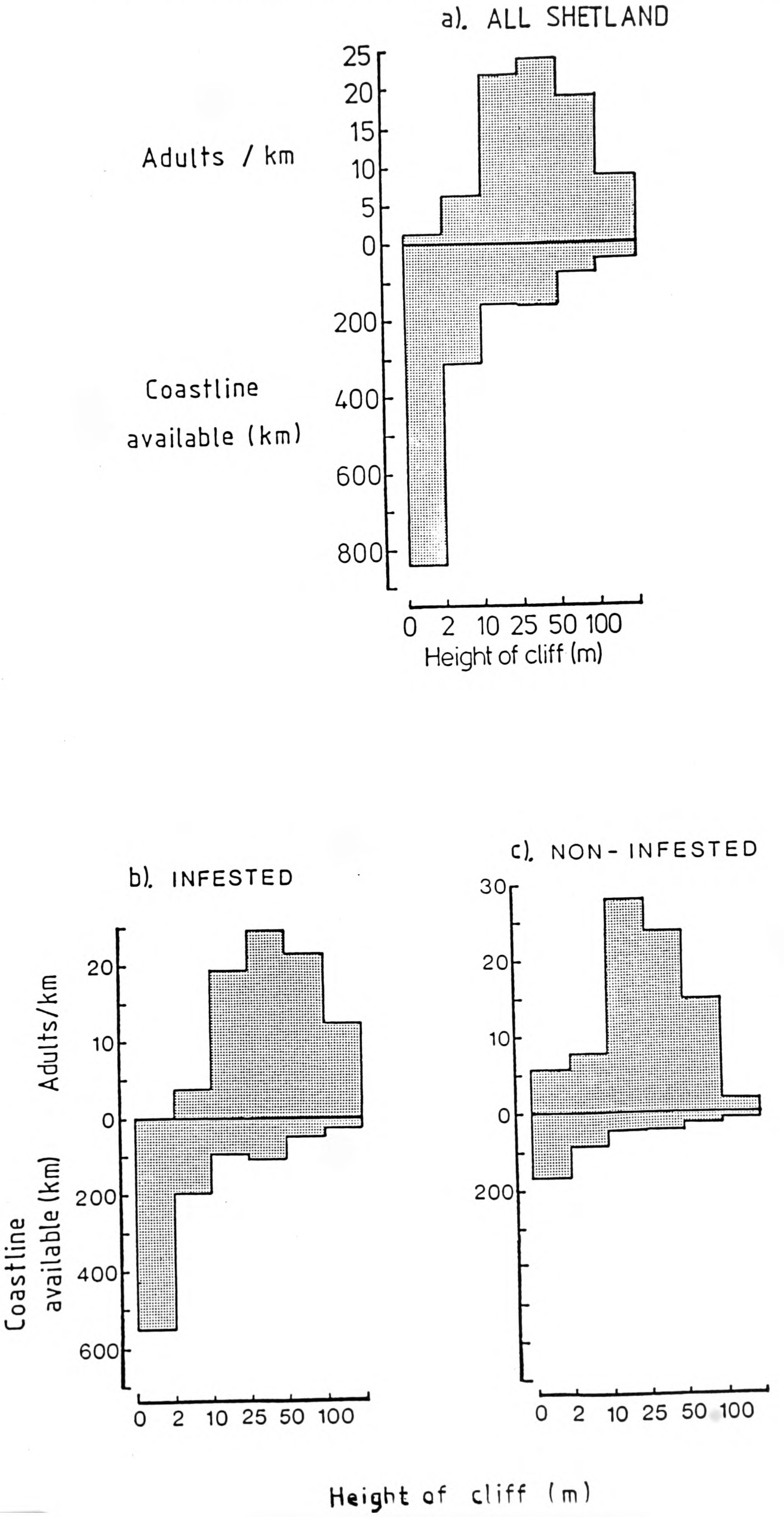


Table 3.III The percentage of adults associated with various types of breeding site in Shetland, in relation to infestation with Brown Rats or Stoats. Islands where ground predator status was uncertain have been excluded.

	Open cliff	Geo	Boulders	Grass slope	Man-made	Total no. of adults
Islands with rats or Stoats	50	48	2	<1	<1	6729
Islands without rats or Stoats	32	36	27	2	3	4571
TOTAL	43	43	12	1	1	11300

A number of factors other than ground predators could also contribute to the results presented in Figure 3.3. Non-infested islands were smaller (coastline length was less than 5 km for 20% of infested islands, but 80% of non-infested islands) and they tended to be more isolated from other breeding areas than coasts on larger islands. Further investigation of ground predators was therefore made on 10 small islands of similar size (1-6 km coastal lengths) in the Scalloway Islands group (area IX in Figure 3.1). All were uninhabited and in a relatively uniform area of inshore, sheltered water, and three had Brown Rats. Analysis of breeding density in relation to cliff height was not possible as lengths of higher coastline were small and on non-infested islands large numbers bred in raised beaches above 2-10 m cliffs. However, cliff heights were similar and boulder areas and walls appeared to be equally available on infested and non-infested islands. Black Guillemots bred on cliffs, but not in sites accessible to ground predators, on islands infested with Brown Rats (Table 3.IV).

3.3.4 Nest sites

Direct observations confirmed that the majority of nests on larger islands were amongst loose rocks and crevices in geos and on cliffs. Sites accessible to ground predators were used only on smaller, uninhabited islands. Nests were also recorded in talus, boulder piles at the foot of cliffs, in raised beaches and in boulder beaches. Occupied nests occurred from c.40 m above sea level down to less than 1 m above high water mark (by the sheltered tidal pool on Mousa). A few nests were found in grassy slopes, usually in disused burrows of Rabbits Oryctolagus cuniculus or Puffins Fratercula arctica. On Linga (Bluemull Sound), many nests were in burrows in low peat cliffs, and may well have been excavated by Black Guillemots themsleves [as found in Denmark by Asbirk (1978a)]. Dry-stone walls and derelict brochs and houses were sometimes used, particularly on smaller islands. On Mousa many nested amongst piles of sandstone slabs, relicts from past quarrying. Artificially-created nest sites have been used in Shetland, and breeding was once attempted (unsuccessfully) on an inter-island ferry (R J Tulloch pers. comm.; pers. obs.).

3.4 Discussion

Black Guillemots were found to be far more numerous in Shetland than had previously been thought, almost certainly due to the greatly improved

Table 3.IV The percentage of adults associated with different types of breeding sites on various Scalloway Islands, in relation to rat infestation.

	Open cliff	Geo	Boulders	Grass slope	Man-made	Total no. of adults
Islands with rats	94	0	6	0	0	48
Islands without rats	11	16	61	4	8	263

census methods. The total represents c.2% of the recent tentative estimate of 270,000 breeding pairs for the North Atlantic and adjacent seas (Nettleship & Evans 1985). The general picture was of fairly even breeding dispersion around the archipelago, except for gaps along stretches of low coastline on larger islands which lacked suitable breeding sites, and coasts with very little shallow water nearby (eg. at Hermaness, NW Unst). The average breeding density in Shetland was similar to that in Orkney - 7.5 and 7.6 adults per km respectively (Ewins & Tasker 1985). The only comparable figures in other regions are provided by Evans (1985): sample stretches of coastline in Greenland held densities ranging from 1 to 25 pairs per km, with highest densities in areas with many islands. The largest known breeding concentration is in the Canadian Arctic, where an estimated 10,000 pairs bred along a 22 km stretch of cliffs on Devon Island (Nettleship & Smith 1975). Ramsay (1976) suggested that the total breeding population in Britain and Ireland was actually lower than that recorded in Operation Seafarer, but this was based on studies during the late breeding season, when counts at the colonies may bear little relation to breeding numbers (Ewins 1985b).

Breeding densities were highest along coasts with cliffs over 10 m high. Since relatively short lengths of higher cliffs usually occur between long stretches of low, sheltered coastlines of voes and bays, availability of suitable sites may have a strong influence on breeding dispersion. The geology of Shetland is complex (Mykura 1976), and results in a heavily indented coastline with many geos. Geos have many loose rocks and crevices which provide excellent breeding sites for Black Guillemots, and it is not surprising that this type of breeding habitat is usually occupied whenever available. Although availability of food resources also influences breeding numbers (as indicated by the importance of shallow water areas in Figure 3.2), the summer distributions and availability of stocks of sandeels and gadoids (Gadidae) are probably also important since these fish are common in the chick diet (Chapter 9).

A wide variety of nest site types was recorded in Shetland, and availability of suitable sites is clearly an important proximate factor in determining breeding distribution. Along coastlines with suitable shallow foraging areas but without suitable nest sites, Black Guillemots did not breed. Elsewhere in the range the species has been quick to occupy suitable sites provided (often inadvertently) by man, eg: in piers and harbour walls (Witherby 1939; Ewins & Tasker 1985; M Stewart pers. comm.), buildings (Kuyt et al. 1976; Carnduff 1981), or amongst driftwood (Divoky

et al. 1974; Divoky & Boekelheide 1978; Asbirk 1979c). In some cases this opportunism has permitted an extension of the breeding range (Divoky et al. 1974; Kuyt et al. 1976).

The utilisation of breeding habitats is influenced not only by their availability but by the distribution of mammalian ground predators. Although Otters Lutra lutra are widespread in Shetland and will occasionally take Black Guillemots (Ewins 1985f), they are unlikely to affect breeding distribution as much as do Brown Rats or Stoats. On low islands lacking rats or Stoats, Black Guillemots nested amongst boulders, in burrows, or in stone walls (and also in cliffs if present), but on infested islands breeding in these accessible sites was rare. Although I have no direct evidence of predation by rats or Stoats there is strong circumstantial evidence: accessible breeding sites on Wyre (Orkney) and Flotta (Shetland) were abandoned following colonisation by rats (M Flaws pers. comm.; Venables 1952; pers. obs.). The spread of North American Mink Mustela vison to offshore islands in many parts of the Black Guillemot's range has resulted in major distribution changes, and almost certainly led to reduced breeding numbers (Olsson 1974; Asbirk 1978a; Petersen 1981; Folkestad 1982). Although Mink are now widespread throughout much of the British Isles, Shetland (and Orkney) are still Mink-free, and every attempt should be made to discourage Mink farming here. Although Hedgehogs are not thought to be a serious predator of Black Guillemot nests in Shetland, their recent introduction and population explosion on North Ronaldsay (Orkney) has caused breeding failure of most ground-nesting birds, including Black Guillemots (M Gray pers. comm.).

It is difficult to make any firm comments on status, since reliable survey methods were previously not available. However, there is some indication of relatively stable numbers at a few sites in more recent times (Perry 1948; Broad & Ewins 1984). Life may well have been more hazardous for the Black Guillemot during the last century though, since Saxby (1871) noted that it was "sadly persecuted by Shetlanders of every class.... ..although it is utterly worthless to them once killed". As a possible explanation for this, Mrs. J M E Saxby (quoted by Raeburn 1887) suggested that Black Guillemots had become associated with calamity due to their habit of frequenting areas of broken water close inshore, where fishermen had lost their lives. In addition, large young were sometimes taken from accessible nests and roasted on a spit, making good eating (J Fullerton pers. comm.).

Marked declines attributable to oil pollution have been noted in Norway (Rov 1982), Denmark (Asbirk 1978a), and for Pigeon Guillemots in California (Ainley & Lewis 1974), although numbers later returned to former levels in the last two cases. Corpses from the Esso Bernicia incident in Shetland in 1978 comprised 85% of the British total of Black Guillemots affected by oil pollution incidents from 1971-83 (Stowe & Underwood 1984). Many adults were affected - 79% of a sample of 91 corpses were in adult plumage - and surveys during the summer in Yell Sound recorded a substantial decrease, although systematic methods were not used (de Camara et al. 1978; McKay et al. 1980). Whilst numbers feeding in Sullom Voe itself have returned to pre-spillage levels (Ewins & Perrins 1984; Figure 4.9), the current situation in Yell Sound is unclear, since no previous systematic counts are available for comparison. The breeding density in Yell Sound (2.6 adults per km) was much the lowest in Shetland. This was partly due to a high proportion of low coastline, lacking suitable breeding sites, but local information suggests that at least some former breeding sites on the Yell Sound islands are only slowly being re-colonized and that breeding numbers may still be lower than prior to the Esso Bernicia spillage (Fowler et al. 1984; R J Tulloch pers. comm.).

CHAPTER 4. DISTRIBUTION OUTSIDE THE BREEDING SEASON AND TIMING OF MOULT.

4.1 Introduction

Although the main breeding concentrations of Black Guillemots occur in the high arctic (Nettleship & Evans 1985), the restricted light conditions and increased ice cover in winter forces many of these birds from the northern populations to move south. Very little information exists on Cepphus distribution or ecology outside the breeding season. Renaud & Bradstreet (1980) conducted winter surveys in Baffin Bay, and concluded that "only a small proportion of the summer population overwinters in the high arctic". A few wintering birds have been noted as far north as 80°N (Nanssen 1898; Lovenskiold 1964), but the general pattern is of greater dispersal in higher latitudes (Cramp 1985). The limited accounts of winter distribution further south in the range suggest a regular dispersion in shallow inshore waters (Andersen-Harild 1969; Haftorn 1971; Nilsson 1982; Lack 1986), with some immatures wintering well away from the natal colony (Salomonsen 1967; Myrberget 1973; Petersen 1981). Within the British Isles, Witherby et al. (1941) considered that some individuals from northern areas moved south in winter, "though not as a rule to any great distance beyond the normal breeding range", and the BTO Winter Atlas project has recently confirmed these views (Lack 1986).

The Esso Bernicia incident highlighted the vulnerability of seabirds in Shetland to oil pollution during the winter months (Heubeck & Richardson 1980). It was therefore necessary to determine the dispersion of Black Guillemots in Shetland in winter as well as during the breeding season. Furthermore, it was known from a few accounts that adults congregate in moult flocks following breeding (Bianki 1967; Heubeck 1981; Petersen 1981); they shed all their flight feathers simultaneously and remain flightless for a few weeks (Salomonsen 1944; Storer 1952). In the event of an oil spill, such large concentrations of flightless adults would be unable to fly away. In the aftermath of the Amoco Cadiz oil incident off Brittany in March 1978, Puffins were worst affected since they were undergoing primary moult at that time of year, whereas other auk species in the area had completed wing moult the previous autumn (Hope Jones et al. 1978; Harris 1984). Thus, a survey of Black Guillemot distribution in Shetland during the autumn moult was also required.

This chapter summarizes the results of surveys of distribution in autumn and winter, which were intended to complement the pre-breeding surveys reported in Chapter 3. Direct comparisons are made with pre-breeding numbers, and various factors which may influence distribution outside the breeding season are considered. Seasonal movements of adults and immatures are dealt with in Chapter 5. These survey results and some additional material have been presented by Ewins & Kirk (1985).

4.2 Methods

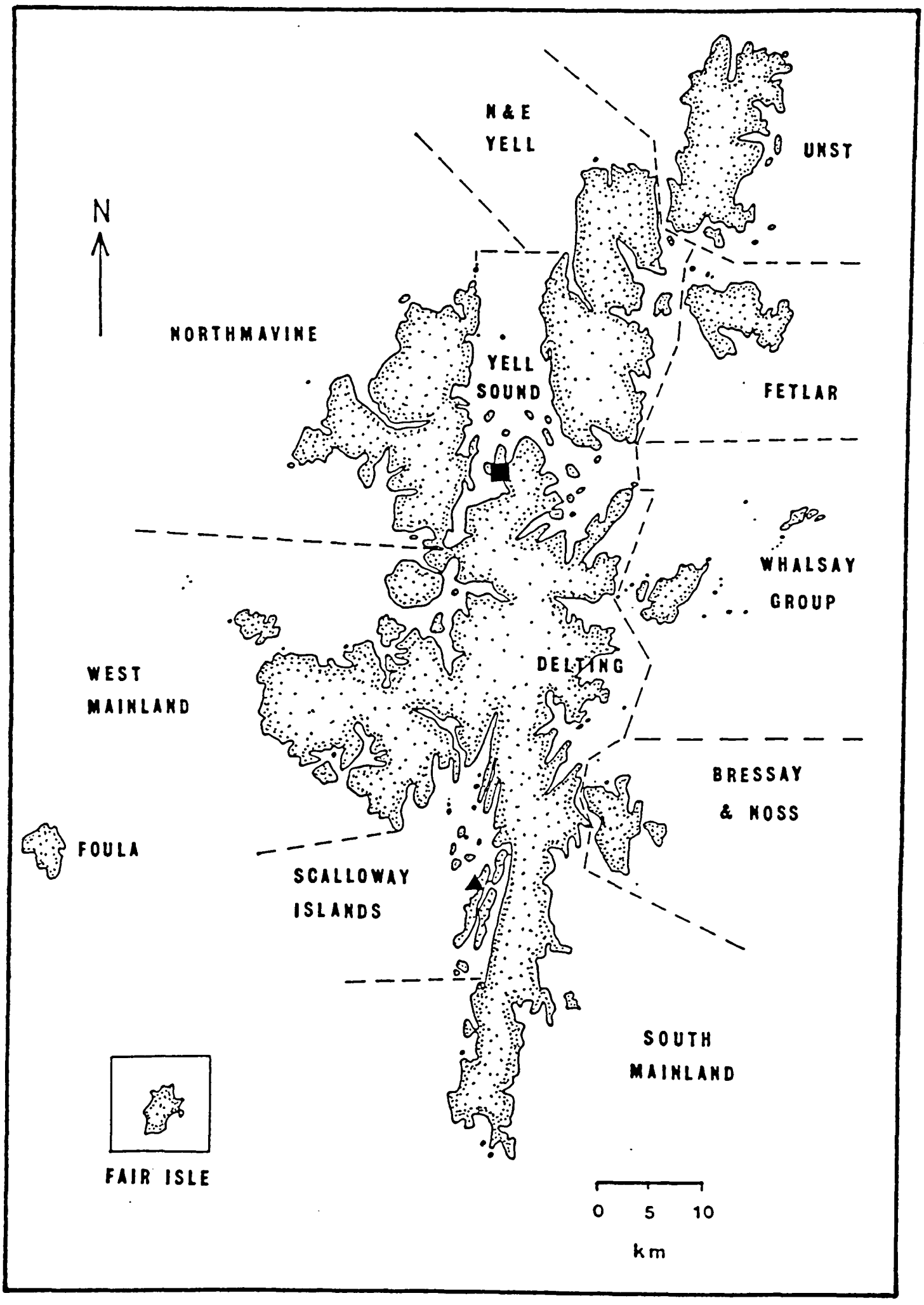
4.2.1 Moult

Plumage type was scored in four categories for both adults and immatures, ranging from full winter to full summer plumage. For the purpose of this analysis juveniles were grouped with immatures in winter plumage. Typical examples of each plumage type are shown in Appendix I. Observations were made from boats or the shore, usually only of birds within 200 m, for which the age could be accurately determined (ie. by the presence or absence of brown tips to the white upper-wing coverts). Samples included birds on foraging areas, and in the vicinity of breeding colonies. Comparative data were obtained from 193 skins collected in Shetland and lodged in: the British Museum of Natural History, Tring; Royal Scottish Museum, Edinburgh; and Fair Isle Bird Observatory, Shetland.

Detailed work was carried out on a moult flock in the west-facing bay adjacent to the small study colony at Meal, West Burra (for location see Figure 4.1). The flock was always located within the bay area (1 km^2), and regular counts were made from the surrounding elevated vantage points only in winds of Beaufort force 4 or less, and in good light conditions.

The wing lengths of adult specimens in the museum collections, which had been collected in Scotland between August and November, were measured by the maximum flattened chord technique (Svensson 1984). This provided an indication of the duration of the period of flightlessness. The chord for wings lacking remiges was taken to the tip of the longest covert. These were compared with the mean length of dry wings, not in moult, collected on Shetland beaches during the study years. A correction factor of +1.5%, allowing for shrinkage post-mortem, must be applied if wing lengths of live birds are compared with these lengths (Ewins 1985e).

Figure 4.1 Regional boundaries and the location of sites mentioned in the text. Square = Sullom Voe oil terminal; triangle = Meal bay, West Burra.



4.2.2 Autumn surveys

Much of the Shetland coastline was covered between mid August and late September 1982-84 in searches for moult concentrations, but a few counts from 1980-81 have also been used (supplied by M Heubeck). Coverage was poor or lacking in NW Unst, NW parts of Northmavine, Foula, West Sandness and Swarbacks Minn (West Mainland). Boundaries of regions mentioned in the text are shown in Figure 4.1. Preliminary observations showed that birds rarely occurred in water deeper than 40 m during the autumn moult period, and thereafter surveys were restricted to water areas of these depths. Since white and grey birds were often difficult to detect on the water, counts were not attempted when winds exceeded force 4, or sea states rose above 2 (International Sea State Code), and lee shores were selected whenever possible. Shallow water areas amongst offshore islands were surveyed from a slow-moving boat: at large concentrations of birds the engines were stopped and a number of 360° scans were made. Counts from land were made by walking the coastline and making repeated, slow scans from vantage points at c.200 m intervals. A telescope with a 20x wide angle lens, mounted on a tripod, proved invaluable for this work. Attention was focussed on bays, mouths of voes (long, fjord-like inlets) and offshore island groups, since it quickly became apparent that moult flocks favoured such areas. Much of this work was completed by myself and the 1984 project assistant, Dave Kirk, but many others assisted at various stages.

4.2.3 Winter surveys

Counts were made in those 10-km squares for which coverage of water less than 40 m deep could be completed, usually by combining boat and land-based counts. Black Guillemots rarely dived in water deeper than 40-50 m in Shetland at any time of year (Chapters 5 & 8). Survey methods were similar to those for the autumn moult work. Most of the survey was conducted by myself between late October and mid February in the 1982-83 and 1983-84 winters. During this period there is a daily movement of birds from communal overnight roosts on the sea, usually in the lee of islands or large cliffs affording some protection from heavy seas, to the foraging grounds. These may be anything from 0.5-8 km apart. Thus winter counts were made of birds on the foraging areas, between 1 hour after sunrise and 1 hour before sunset. Whenever possible a 10-km square was completely

covered in one day. Paul Fisher provided data for square N, and Martin Heubeck for square R (see Figure 4.7).

4.3 Results

4.3.1 Moult

The transition between the various age and plumage types depicted in Appendix I has been examined in depth by Salomonsen (1944), and the basic moult sequence in adults and immatures summarized by Storer (1952). Their accounts apply to all Black Guillemot subspecies, although the exact timing of the various stages varies with latitude and sea temperature. Storer's summary outlines the major moult stages:

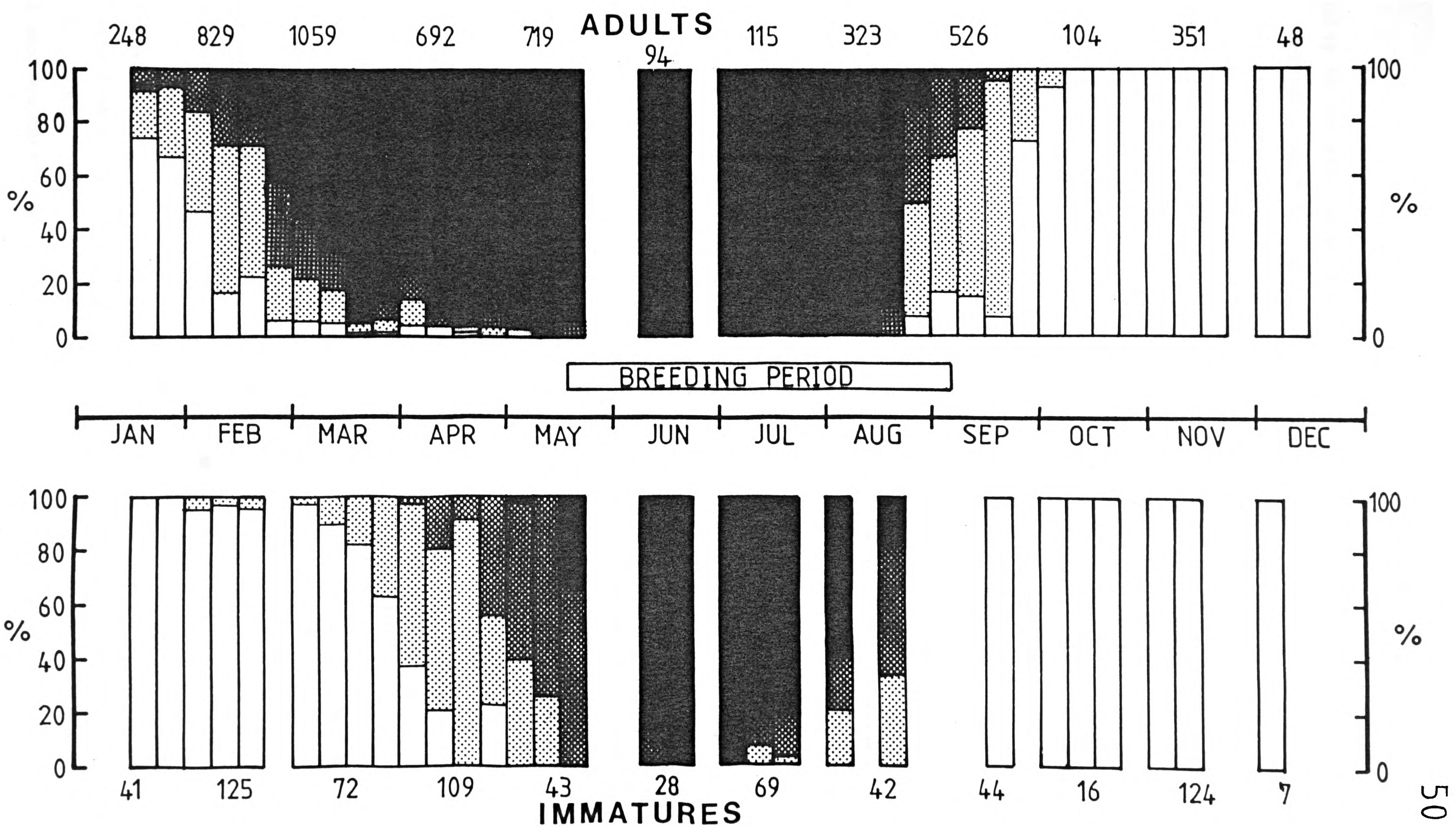
> "The juvenile plumage is nearly complete at the time the young leave the nest and the primaries are the last feathers to finish growth; almost as soon as their growth has stopped, there is a complete moult of the body feathers and the first winter plumage is assumed. Another complete or nearly complete moult of the body feathers occurs in the spring, producing the first nuptial plumage. After the breeding season there is the usual complete annual moult, during which the remiges are all shed at one time and the birds are flightless. The rectrices are also shed together shortly after the new remiges have begun to grow. The annual moult results in the adult winter plumage, which is replaced in winter (as early as November) or spring by a complete moult of the body feathers, producing the nuptial plumage. The latter two moults are repeated annually thereafter throughout the life of the bird".

In Shetland immatures (ie. birds in their first year) commenced their spring body moult later than, and the autumn moult earlier than adults (ie. birds 2 or more years old). The summer plumage attained by immatures was a matt dark chocolate brown colour, lacking the iridescent sheen of the adults' black summer dress. The period during which 80% or more of the immatures were in summer plumage was less than 2 months (June-July), whereas for adults it was 5 months (mid March - mid August) (Figure 4.2). Although some adults already showed signs of body moult by mid January, the first bird in full summer plumage was not seen until early February. Observations at breeding colonies on Mousa suggested that the small numbers of adult-plumaged birds still moulting body feathers during April and May were probably 2-3-year-olds, since virtually all breeders (first breeding

Figure 4.2 The timing of moult for adults and immatures in Shetland, expressed as the frequency of occurrence of plumage types in ¼-month periods.

Unshaded = winter plumage (white);
Stippled = white with some black;
Hatched = black with some white;
Black = summer plumage (black).

Plumage details are shown in Appendix I.
Monthly sample sizes and the extent of the breeding period are also given.


ADULTS
248
829
1059
692
719
94
115
323
526
104
351
48
100
80
60
40
20
0
%
BREEDING PERIOD
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
41
125
72
109
43
28
69
42
44
16
124
7
IMMATURES

is usually in the 4th. year) were in full summer plumage by at least early April. However, two breeding individuals on Mousa retained a few white feathers (less than 30 in both cases) on the underparts throughout both the 1983 and 1984 breeding seasons. Similarly some winter birds retained a few black feathers on the underparts. In these cases the birds were still scored as having full summer or full winter plumage.

In late July active moult was visible on the chin and throat of some breeding birds still feeding young, but most adults commenced moult only after chicks had left the nest. Few immatures were noted in the vicinity of breeding areas after mid July; presumably they moved off to moulting areas before adults, which is consistent with their earlier moult. Examination of the plumage of 193 museum skins of Shetland birds confirmed that the timing of moult was as shown in Figure 4.2.

Regular counts made at the moult flock at Meal, West Burra in 1983 indicated that numbers increased from mid August, peaking in early September, followed by a decline towards late September as birds moved away from the area (Figure 4.3). Although I was unable to carry out similar work at other moult areas, the general impression gained was that moult flocks seldom occurred outside the mid August - late September period. During bouts of bathing and preening in September, adults in moult flocks often stretched their wings, revealing regrowing or absent flight feathers. However, the exact period of flightlessness could only be inferred - flying adults were not noted at Meal between late August and 23 September in 1983, a period of c.4 weeks. Measurements of adult wing length from 37 museum skins collected in Scotland between August and November suggested that flightlessness occurred between 1 September and 5 October, a 5 week period (Figure 4.4). Comparative data for 18 adult skins in the British Museum collected between July and November on the Norewgian Skaggerak coast (58°N) indicated a 5-6 week flightless period.

4.3.2 Autumn moult distribution

Concentrations of moulting adults occurred throughout Shetland, but were dispersed in a rather irregular fashion when compared with the pre-breeding distribution (Figure 4.5). Since the moult areas appeared to be traditional, with a significant correlation between years for moult counts at 10 sample sites ($r = 0.98$, $P<0.001$), pooling the data from a number of years is probably justified. Although some areas were poorly covered, the sum of maximum counts for each moult area (Foula excluded) was 9609 birds,

Figure 4.3 Fluctuations in the number of Black Guillemots in the autumn moult flock at Meal, West Burra, August-October 1983. When more than one count was made on a date, the range is indicated by a vertical bar. All counts were made in winds not exceeding Beaufort force 4, sea state 2 or less, and in good light conditions.

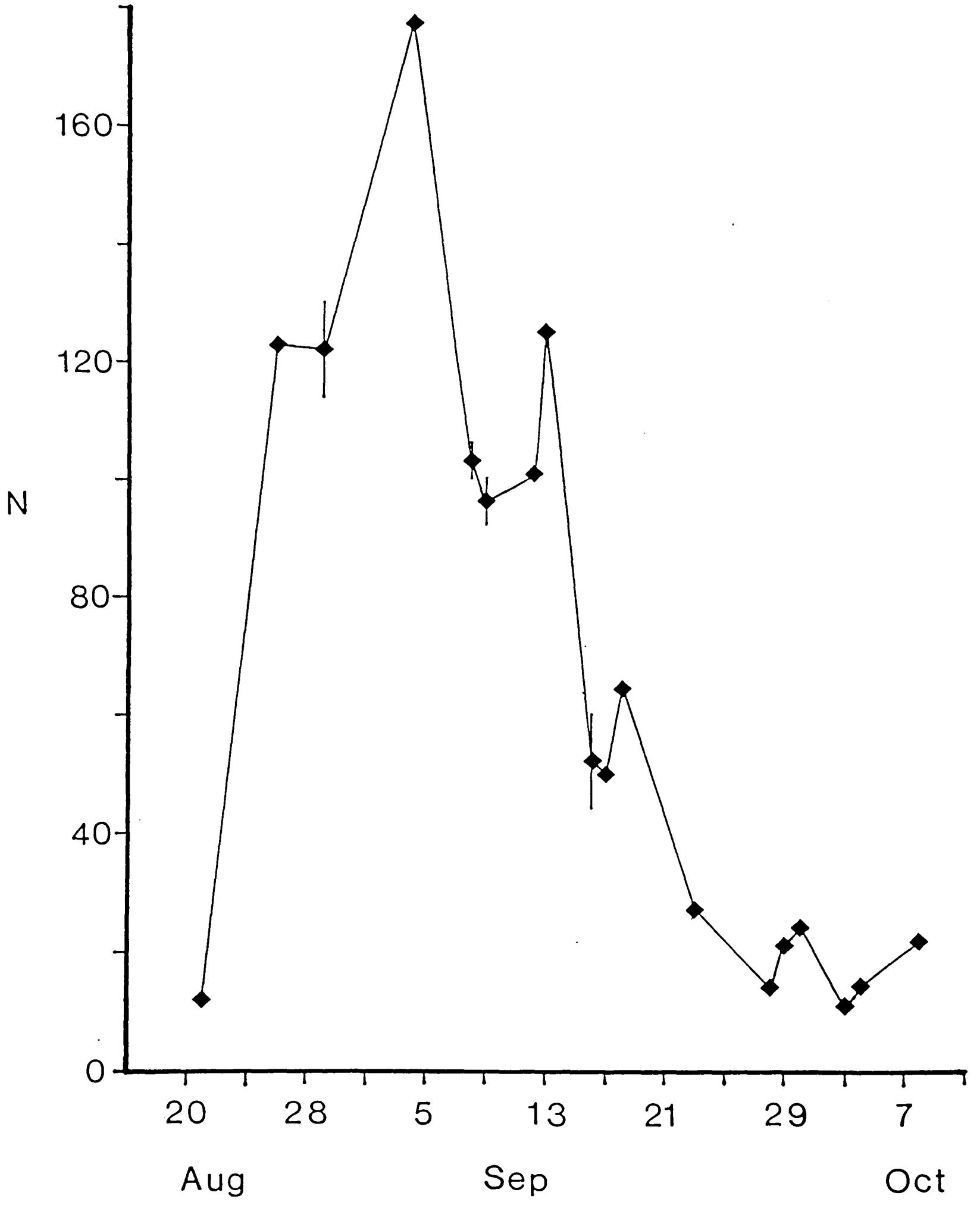


Figure 4.4 Wing lengths of 37 skins of Black Guillemots collected in Scotland between August and November, in relation to the mean length of dried wings of Shetland adults. Filled circles represent old flight feathers; open circles represent absent or growing feathers.

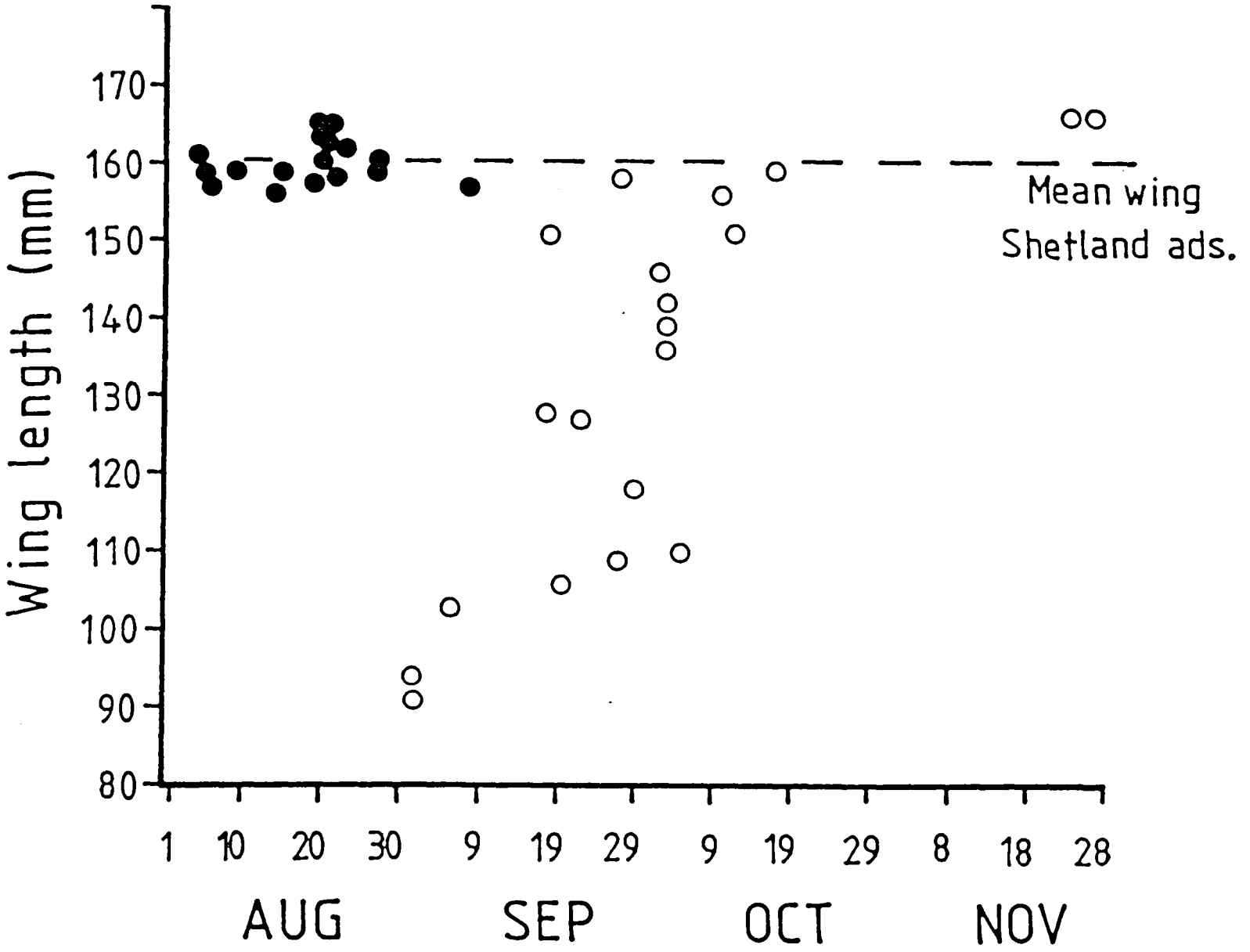
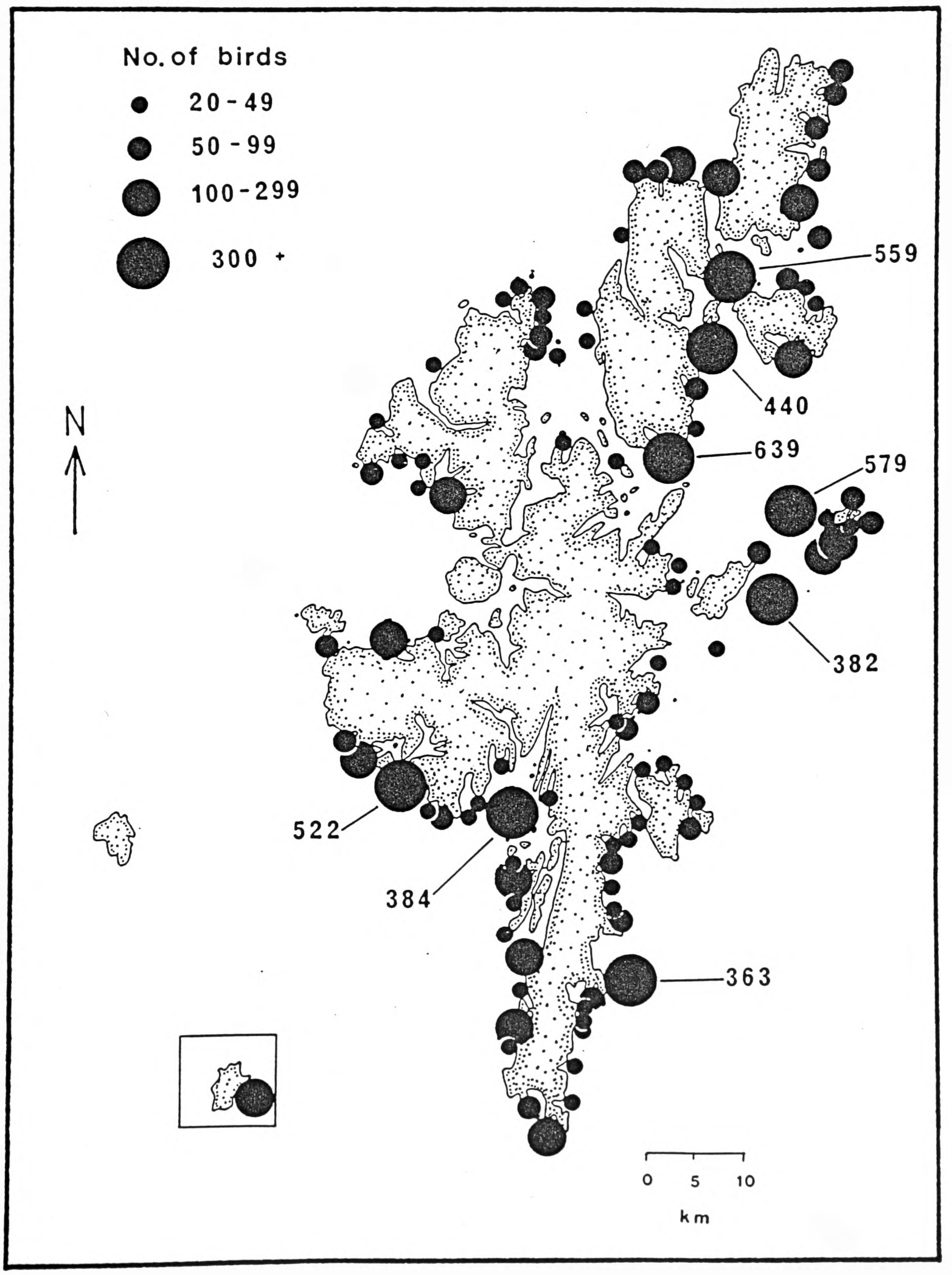


Figure 4.5 The size and distribution of autumn moult concentrations in Shetland, mid August - late September, 1980-84. Only the maximum count for each site has been used.



mostly adults. This figure represents 81% of the pre-breeding adult number, and suggests that few major moult concentrations were overlooked. Flocks usually occurred in water less than 40 m deep in bays, at the mouth of voes, and amongst offshore island groups - sites which afforded suitable feeding conditions as well as some protection from heavy seas. The cohesiveness of the moult flocks changed according to the birds' activities - compact when roosting but more dispersed when feeding. In general, densities were often similar to those seen off the colonies in the pre-breeding period. Most adults were observed in moult flocks of more than 20 birds. For 97 separate flocks, 52% contained 20-49 birds, 27% had 50-99, 13% had 100-299, and 8% contained more than 300 birds.

A comparison between autumn moult flock and pre-breeding numbers in 11 of the regions revealed no significant correlation ($r = 0.26$, $P>0.1$), emphasizing the lack of any tendency to moult near to breeding sites (Figure 4.6). The extent of shallow water areas did not appear to influence moult distribution, since there was no significant correlation between area of water less than 40 m deep and adult moult totals in the 11 regions ($r = 0.39$, $P>0.1$). Although regions such as South Mainland, West Mainland, Unst, Fetlar etc. have some large areas of shallow water, they occur mainly along coastlines exposed to the open sea. In contrast, the four regions in Figure 4.6 lying above the y=x line all have groups of small islands, amongst which shelter could be found during rough autumn weather, from any direction.

The proportion of juveniles was significantly lower in moult flocks than in other areas (excluding the immediate vicinity of the oil terminal) during the autumn moult period [mean $\pm$ se(%): 4.7 $\pm$ 1.6, and 24.2 $\pm$ 7.4 respectively; $t = 2.39$, 11 df, $P<0.05$], although there was considerable variation in areas away from flocks, possibly due to small sample sizes (Table 4.I). In the vicinity of the oil terminal (ie. Sullom Voe and the central Yell Sound islands area) juveniles accounted for a higher percentage (32.4%) of birds aged, although this was not significantly different from elsewhere ($G = 3.26$, 1 df, $P>0.05$).

4.3.3 Winter distribution

Complete coverage was achieved for nineteen of the 10-km squares. Marked differences were found in total numbers between squares (Figure 4.7). Total numbers are given since poor light conditions permitted ageing of only a small proportion of birds. The sheltered shallows between

Figure 4.6 The relationship between autumn moult flock totals and adult pre-breeding numbers for 11 regions of Shetland. Locations of regions are shown in Figure 4.1.

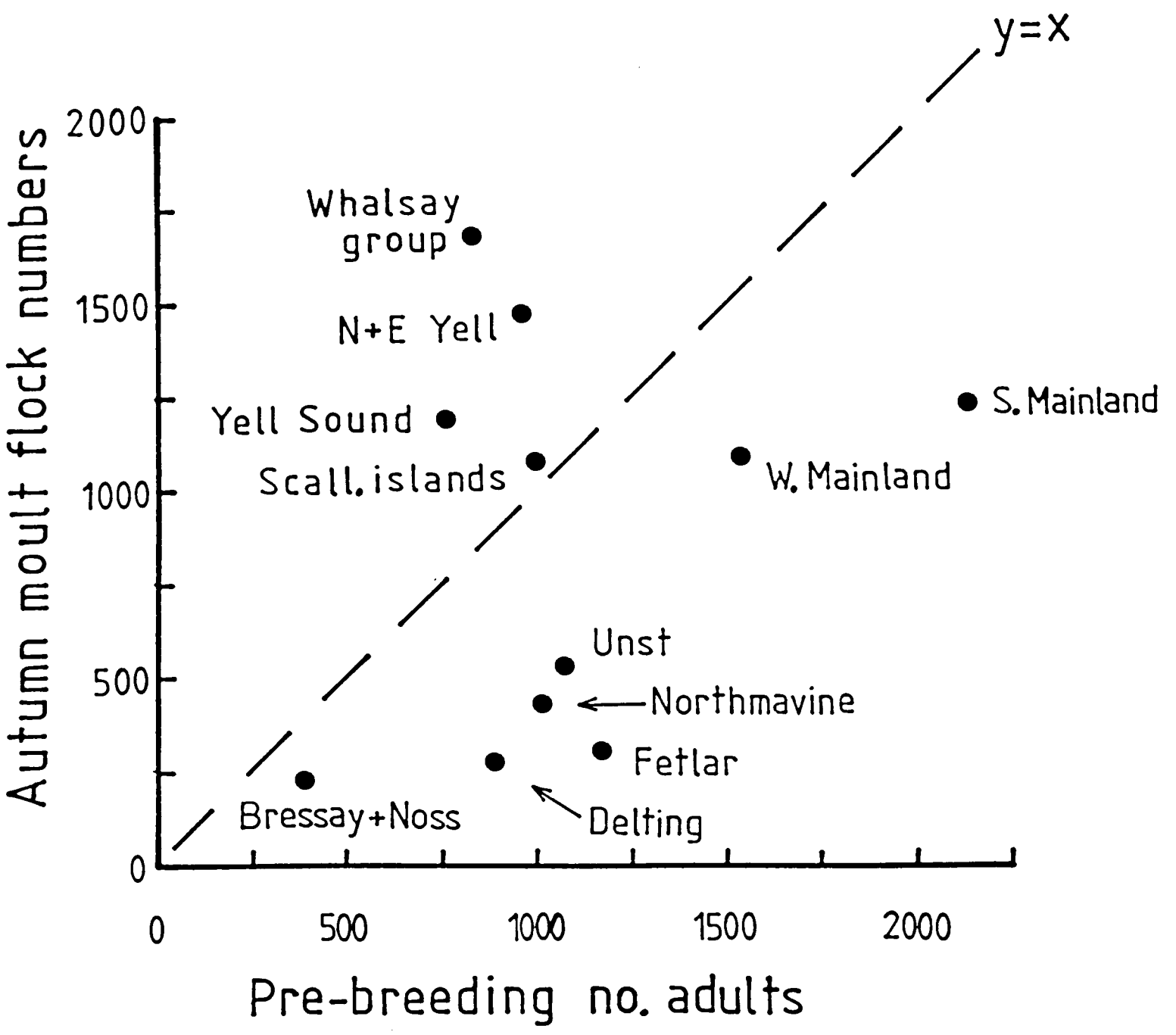


Table 4.I Age composition of moult flocks and birds in other areas during the autumn moult period, 1982-84.

	No. adults	No. juvs.	% juvs.
MOULT FLOCKS			
Mousa	112	6	5.1
Meal	114	13	10.2
Sandwick (Unst)	163	0	0
Fethaland (Northmavine)	98	1	1.0
East Yell	36	3	7.7
E. Yell Sound	141	6	4.1
OTHER AREAS	12	2	14.3
	9	10	52.6
	4	4	50.0
	10	3	23.1
	12	1	7.7
	19	4	17.4
	22	1	4.3

Fetlar, Unst and Yell were clearly important foraging areas in winter. There was a highly significant positive relationship between winter totals and the area of water (km^2) not deeper than 40 m within the square: (Total no. birds) = 12.1x(Shallow water area) + 12.7; r=0.8, 17df, P<0.001. Combining results for all squares surveyed, the average density of birds on foraging areas in winter was 13.1 birds per km^2 of water not greater than 40 m deep. The total number of birds recorded during pre-breeding surveys in each square (ie. adults associated with breeding areas, plus immatures and other adults away from the colonies) was also significantly correlated with winter numbers (r = 0.71, P<0.001) (Figure 4.8). The total number of birds recorded in the squares in winter (3308) was only 74% of the pre-breeding total (4478), but some squares contained greater numbers in winter (eg. D,F,G,K,L etc.).

To investigate the importance of shelter in winter, I used the results of surveys of coastline exposure conducted by the Institute of Terrestrial Ecology (ITE 1975), in which coastal exposure was scored on a scale from 1 (sheltered) to 8 (very exposed) at each point along the coast intersected by the 1-km Ordnance Survey grid. I calculated the percentage of intersections within each 10-km square for which the exposure rating was 6 or above, to give an index of coastal exposure for the square. The ratio of winter : pre-breeding numbers was negatively correlated with this exposure index (r = -0.53, 17 df, P<0.05), indicating that more exposed coastlines supported fewer Black Guillemots in winter. Cursory examination of Figure 4.7, in conjunction with Figure 4.8, bears this out: squares D,F,G,K,L and P have large areas of sheltered inshore waters, and support more birds in winter than in summer.

The mean ($\pm$ se) percentage of immatures in winter (excluding the central Yell Sound islands area), based on ageing of a randon sample of at least 10 birds in each of 12 squares, was 13.1 $\pm$ 2.8%. The % immatures in winter in the central Yell Sound islands area (42.6%) was significantly greater than elsewhere in Shetland (G = 125.7, 1 df, P<0.001). When this sample was included, the overall winter figure rose to 18.2 % immatures. That the age composition in winter in the vicinity of the oil terminal was somewhat unusual, and not simply a result of immatures congregating in sheltered inshore waters, was supported by the significantly lower percentage immatures in the superficially similar inshore area between Fetlar, Unst and NE Yell (11.6% immatures; G = 73.0, 1 df, P<0.001). Although after 6 years, Black Guillemot numbers in Sullom Voe itself had nearly returned to pre-spillage levels, with highest numbers present during

Figure 4.7 Black Guillemot numbers in selected 10-km squares during winter 1982/83 and 1983/84. Letters correspond with those in Figure 4.8.
● = 1-99 birds; ●● = 100-199 birds;
●● = 200-299 birds, etc.
●

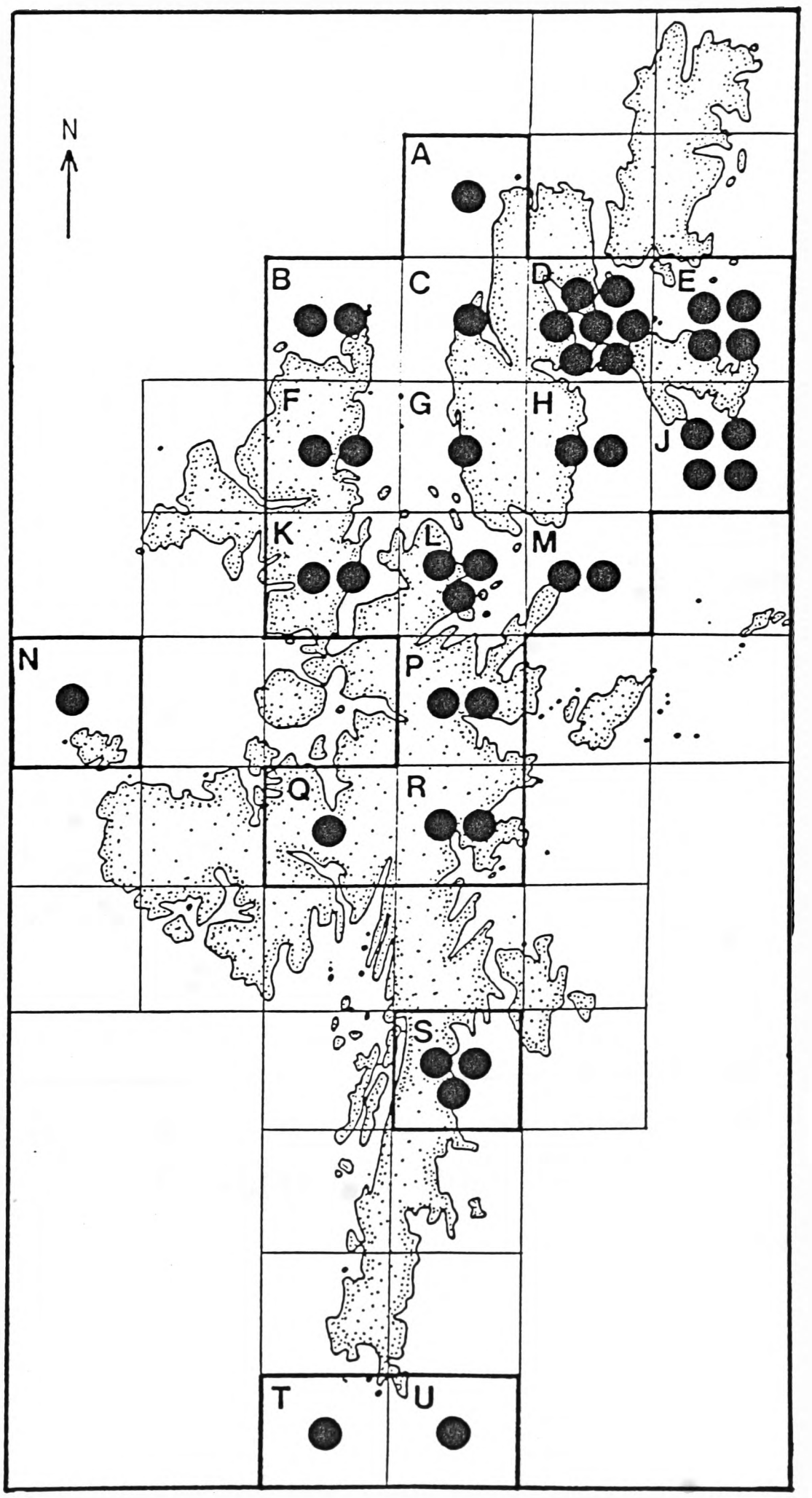


Figure 4.8 The relationship between winter numbers and the total number of birds recorded during pre-breeding surveys in nineteen of the 10-km squares in Shetland. Letters refer to squares shown in Figure 4.7.

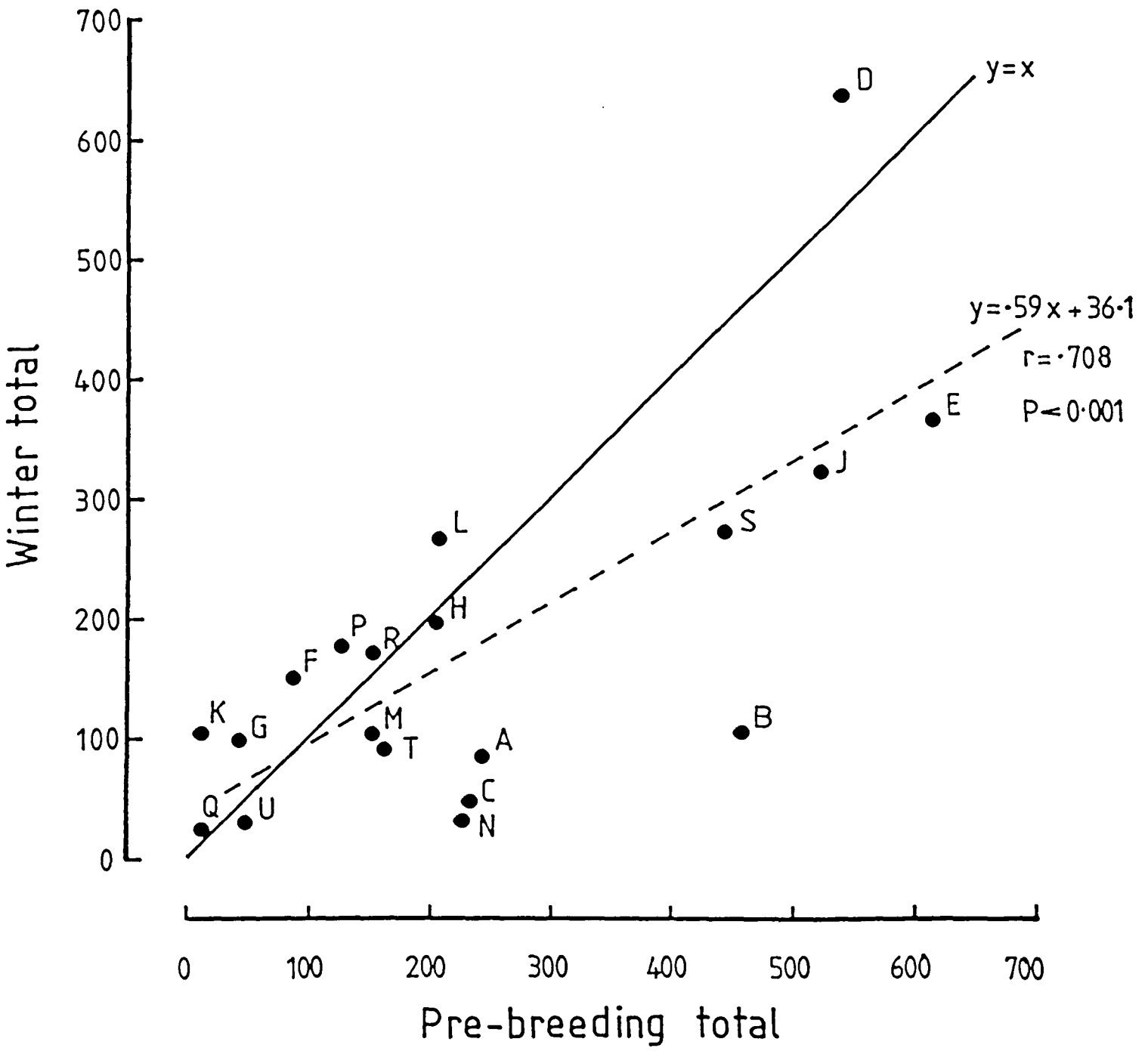
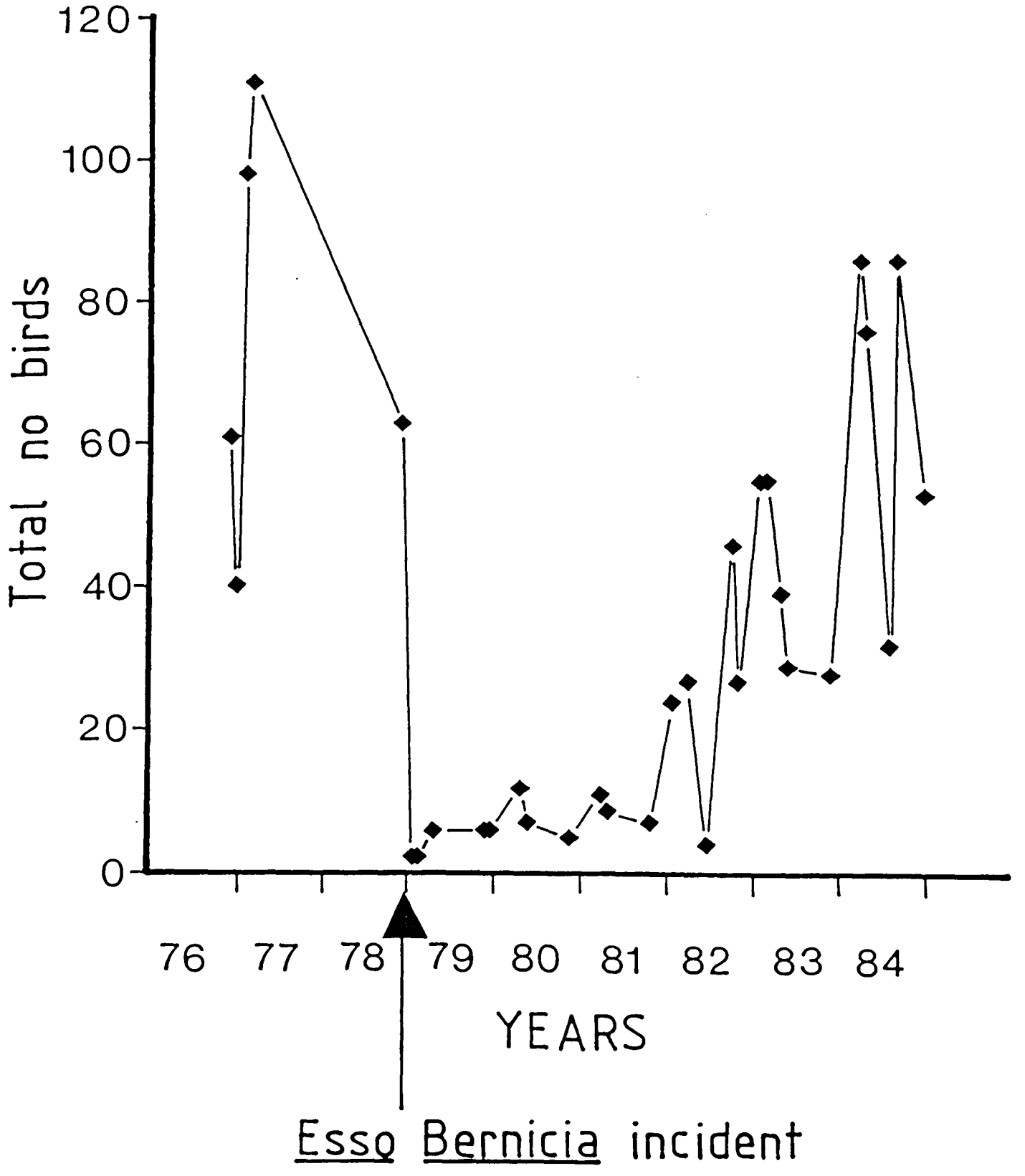


Figure 4.9 Total numbers of Black Guillemots foraging within Sullom Voe, between 1976 and 1984.



winter months (Figure 4.9), the percentage of immatures in the area prior to the oil spill was not known. However, in a sample of 91 corpses collected in January and February 1979 following the Esso Bernicia incident, 21% were immatures - significantly lower than the 43% recorded during the 1983-84 winter in the same area ($G = 5.89$, 1 df, $P<0.05$).

4.4 Discussion

Moult and autumn distribution

The sequence and timing of moult in Shetland is similar to that reported from western Sweden and Norway (Salomonsen 1944) and Denmark (Asbirk 1979a), for the same subspecies. Some adults acquired the full summer plumage as much as 3 months prior to the start of laying, coincident with intensive display and protracted morning attendance at the breeding colonies. However, heterosexual behavioural postures were also adopted by adults still in winter plumage, in December and January, both at the overnight communal roosts and on the foraging grounds. Saxby (1874) correctly noted that adults in Shetland acquired the summer plumage earlier than immatures. This is in agreement with all later studies. He also remarked that males commenced (spring ?) moult earlier than females. Unfortunately no data were given, so this remains the only suggestion of a sex difference in the timing of moult.

Both my field observations and the examinations of museum skins, relating to flightlessness, refer to groups of birds and not to individuals. Indeed the period during which a group of birds are flightless is obviously longer than that taken by any one individual to regain flight ability; 1-year-olds start their first complete moult earlier than adults, and there will be individual variation in the timing of adult moult. Nine captive Guillemots showed considerable variation in the time taken to renew flight feathers: the mean was 63 days, and the range 42-90 days (Birkhead & Taylor 1977). These authors considered that flight would be possible when primaries were at least 70-80% grown, thus making the flightless period approximately 6-7 weeks. Since the wing loading of Black Guillemots (average of 1.6 g cm^{-2} for 7 fresh Shetland corpses) is lower than for Guillemots [c.1.7 g cm^{-2}, extracted from plot given by Warham (1977)], flight may be possible at wing lengths of 110-120 mm. Therefore adult Black Guillemots in Shetland are probably flightless for 4-5 weeks,

mostly during September, when they are extremely vulnerable to rough seas and oil pollution.

This appears to be the first detailed study of moult flocks in this species. Seebohm (1885) wrote that "in autumn the young appear to congregate in flocks apart from the adult birds, and wander far from their birth place"; Bianki (1967) noted that adults disappeared for 4-6 weeks from their White Sea breeding areas in autumn, to moult; and Petersen (1981) found four small groups of adults (each 20-30 birds) in Iceland in late August, which were presumably moult flocks. Although the phenomenon of autumn moult concentrations of Black Guillemots has been known for some time in Shetland (Gammack & Richardson 1980; Heubeck 1981), no published accounts exist. The majority of adults congregated in moult flocks after breeding, whereas juveniles dispersed more evenly around the coastline. Juveniles noted in deeper water were presumably moving between islands (Chapter 5).

A few adults completed the autumn moult in groups of fewer than 20 birds, but most occurred in larger flocks, which were dispersed rather more irregularly around the coast than were adults in the pre-breeding period. The largest moult concentrations occurred amongst groups of small islands or in sounds between larger islands - areas which were sheltered from heavy seas and autumn gales from any direction. Flightlessness imposes several restrictions, perhaps the most important being the inability to move quickly to alternative feeding areas and sheltered roost sites. It prevents birds from feeding in strong tidal currents (which are often favoured foraging areas) because they would be unable to fly back up-current to resume the diving sequence. Diving capabilities are probably little affected by lack of flight feathers however, since observations in winter showed that birds propelled themselves underwater with half-closed wings, with the primaries folded back beneath the secondaries.

Moult flocks occurred in areas of water less than 40 m deep, away from strong tidal currents, and in situations providing shelter from heavy seas. Despite apparently suitable conditions in the Delting (East Mainland) region, no major moult concentrations were found here, and it is possible that many of the birds breeding here moved east to the Whalsay islands group to moult. The apparent absence of moulting birds in northern parts of West Mainland (Figures 4.1 & 4.5) may reflect poor coverage however, since some suitable-looking areas were not surveyed.

The reason why adults undergo the autumn moult in flocks is unclear. Flocking behaviour is often considered to be a response to predation

pressure, minimizing the risk to an individual of predation (Powell 1974; Perrins & Birkhead 1983), but as far as I am aware Otters, Great Skuas Stercorarius skua and man are the only recorded predators of fully-grown Black Guillemots in Shetland. In many hundreds of hours observing birds on the water (both in flocks and as scattered individuals) I never witnessed any attempted predation. Although Grey Seals Halichoerus grypus will attempt to take auks and other seabirds on the water (Corbett & Southern 1977; del-Nevo 1986; Morgan 1986), and frequently occur along with the more numerous Common Seal Phoca vitulina in the vicinity of Black Guillemot moult flocks, I never saw any attempted predation (by either species), and seals were tolerated at very close quarters. I think it unlikely that predation constitutes a sufficiently strong selective pressure to be a major factor accounting for widespread flocking behaviour during the autumn moult period. It is possible that adults simply congregate to moult at rich feeding areas in suitable sheltered conditions. The regular use of similar environments in different areas lends support to this as the main reason for autumn moult flocking.

Winter distribution

Interpretation of the finding that numbers in winter in the areas sampled were only 74% of those in the pre-breeding season is complicated by various sources of bias. I tended to concentrate winter survey work on 10-km squares with more sheltered, inshore waters since coverage could usually be achieved in one day. However, suitable breeding habitat was often scarce in such areas and although total numbers were compared, pre-breeding surveys were not of birds on the foraging areas. Poor light conditions and the problems of detecting winter-plumage birds on the sea may have led to under-estimation of numbers then. In the pre-breeding surveys, most birds occurred within 300 m of the shore, whereas in winter birds were scattered throughout shallow areas, and some were undoubtedly overlooked even on the calmest days. However, bearing in mind that winter numbers were actually somewhat higher than recorded, the overall density of birds in water not deeper than 40 m was c.13 per km^2, compared with c.23 per km^2 in spring/summer.

In late winter surveys in the Canadian arctic found densities of only 0.17 birds per km^2 along offshore pack ice edges (Renaud & Bradstreet

1980), and along the Baltic coasts of south and east Sweden, Nilsson (1982) recorded similar low densities of between 0.01 - 0.2 birds per km^2. The high winter densities in Shetland probably reflect the relatively sedentary habits of Black Guillemots there (ultimately related to the warming influence of the gulf stream, and food availability), compared with more northerly populations which show greater dispersal in winter, often in response to ice conditions (Cramp 1985). The winter distribution in Britain and Ireland closely matches that in summer although a few birds (probably mostly immatures) winter south of the breeding range (Sharrock 1976; Lack 1986).

The relative importance of different areas in winter can be assessed from these results. The Fetlar-Unst-NE Yell area is probably the most important concentration in Shetland, but some birds are found along all coasts. In winter, sheltered inshore areas support greater numbers than during the pre-breeding period, and exposed coastlines open to heavy seas are frequented by relatively few birds (seasonal movements between different coastal types are analysed further in Chapter 5). Although only a few Black Guillemots were found dead on beaches following severe gales, Formosov (1946) has recorded large numbers perishing in winter storms. Movement to sheltered inshore waters in winter has not previously been documented for this species, but some Pigeon Guillemots breeding along 'open' Pacific coasts migrate to inshore wintering grounds, protected from heavy seas (Scott 1973; Oakley 1981). Prey availability may be reduced along exposed coasts in winter since some inshore fish species are known to migrate to deeper water then, possibly due to increased water turbulence (Gibson 1969).

Immatures accounted for 43% of wintering birds in the vicinity of the Sullom Voe oil terminal, but only 13% in the rest of Shetland. If the sample of corpses found after the Esso Bernicia spill was representative, the significantly higher proportion of immatures in 1983-84 in the central Yell Sound islands area and Sullom Voe suggests that there were still relatively few adults wintering in the area, even though total numbers feeding in Sullom Voe had returned to pre-spillage levels.

CHAPTER 5. MOVEMENTS AND MORTALITY

5.1 Introduction

Black Guillemots nesting in northern areas tend to move southwards in winter, seeking ice-free inshore waters and increased daylight hours in which to forage (Salomonsen 1944; Lovenskiold 1964; Renaud & Bradstreet 1980; McLaren 1982). Further south the species is relatively sedentary (MacGillivray 1852; Witherby et al. 1941; Andersen-Harild 1969; Cramp 1985), although birds ringed in Scandinavia have been recovered hundreds of kilometres to the south of their breeding areas in winter (Myrberget 1973), and a chick ringed on Fair Isle, Shetland, was shot over 800 km south in its first winter (Mead 1974). Overall, Black Guillemots ringed in Britain are recovered nearer the natal colony than are Razorbills, Guillemots and Puffins (Birkhead 1974a; Lloyd 1974; Harris 1984).

More recoveries during the past decade in Britain and Ireland now allow a meaningful analysis to be made for this species. I also consider seasonal movements between different types of coastal waters in Shetland, and the extent of philopatry [ie. natal dispersal, *sensu* Campbell & Lack (1985)] and nest-site fidelity in relation to breeding success. Annual mortality rates are calculated for breeding adults on Mousa and Fair Isle, and causes of mortality are discussed. Full details of all recoveries of Black Guillemots ringed in Shetland, that had been reported to the British Trust for Ornithology (BTO) up to March 1985, were given by Ewins & Kirk (1985). Since seasonal movements lead to variations in distribution at different times of year, I also discuss the survey results presented in Chapters 3 and 4 here.

5.2 Methods

The analysis of movements of Black Guillemots ringed in Britain and Ireland was based on recoveries reported as of July 1985. Birds ringed with a BTO ring only, and retrapped at the natal colony were not considered, since colour-ringing shows that most birds return to breed at their natal colony: such retrap data merely reflects trapping effort. Birds caught alive elsewhere (eg. in fishing gear) and subsequently released, were included as 'recoveries'. All ringed fledged birds found dead were regarded as recoveries, even if remains were found in the

immediate vicinity of the natal colony. Since the bulk of Black Guillemots in this country have been ringed on Orkney, Fair Isle, Foula, and (since this study began) in the main group of Shetland islands, attention was focussed on these northern British populations.

Until the present study most ringing effort in Shetland had been concentrated on Fair Isle and Foula. Since both are somewhat unusual in being small islands, c.30 km from the nearest land, recoveries have been analysed separately. Black Guillemots first breed when 3 or 4 years old (Petersen 1981; in litt.), and the heaviest mortality occurs during the first two years of life (section 5.4.3). Recoveries in the first 2 years of life are therefore analysed separately from those later in life.

On Mousa in 1982 and 1983, 51 breeding adults were individually colour-ringed, with a double spiral of stout 'Darvic' plastic. Between 1982-84 all accessible young were given a year-specific colour-ring, in addition to the monel ring. Throughout both pre-breeding and breeding periods hide watches and intensive searches were made for colour-ringed individuals. Similar methods were used by Roger Broad on Fair Isle from 1974-77 during his detailed study at the Busta Geo colony of 12-15 breeding pairs [further details given in Broad & Ewins (1984)]. I watched at Busta Geo in the pre-breeding periods of 1982-84. Although after 6-7 years a few birds had lost a colour ring, I deduced their identity and could thus use these data to estimate adult mortality rates.

From May 1982 to June 1984 monthly counts were made of birds on foraging areas along sample stretches of coast of different exposures. Counts were made in winds not exceeding force 4, in good light conditions, between 1000 and 1600 h GMT, and as near to the middle of the month as possible. Coastal exposure ranged from 1 (very sheltered) to 8 (fully exposed to heavy seas), as outlined in Chapter 4 (Methods). 'Exposed' coasts refer to those with values from 6-8, and 'sheltered' those from 1-5. The lengths of coastline for sample stretches of exposed coast were: Aithsetter 2.5 km, Kirkabister 5 km. West Burra 4.5 km; and for sheltered coasts: Scalloway harbour 4 km, Whiteness Voe 8 km (locations shown in Figure 2.1). Methods used for these counts were similar to those for land-based counts during the autumn and winter distribution surveys (Chapter 4). Birds clearly associated with breeding areas (eg. incubating birds flushed off the nest) were omitted. Additional counts made at four other sites confirmed the general pattern but, since weather conditions prevented counts being made in every month, these data are not presented. Birds seen clearly within 200 m and in good light and weather conditions were aged.

Monthly variation in mortality was investigated using data from:

(i) Shetland beached bird surveys, 1980-84 (data provided by M Heubeck, SOTEAG)

(ii) Corpses and remains found by myself and others in Shetland, 1982-85 [excludes (i)]

(iii) Orkney beached bird surveys, 1976-84 (data supplied by L Underwood, R.S.P.B.)

(iv) UK ringing recoveries (birds found as "long dead" were considered to have died in the previous month)

Full details of beached bird survey methods are given by Hope Jones (1980) and Heubeck (in press). Wherever possible the causes of mortality and percentages of oiled corpses were determined from these data sets. August 1st has been taken as the beginning of the Black Guillemot year, since the median fledging date in Shetland was 12-13 August, with the first chick leaving the nest on 26 July (Chapter 7).

5.3 Results: Movements

5.3.1 Ringing recoveries

The total of 64 recoveries of Black Guillemots ringed in Britain and Ireland represents 1.2% of the 5333 ringed. For birds ringed as chicks and recovered within 2 years, Fair Isle and Foula individuals were recovered significantly further from the natal colony than those ringed elsewhere in Shetland (and Orkney): median recovery distances were 68.0 and 7.5 km respectively, n = 12,14; Mann-Whitney test, W = 136, $P<0.01$. This difference was not due to biases in the season of recovery as there was no significant difference in the variance of the month of recovery between the two data sets ($F = 1.83$, n = 12,14). Some Black Guillemots from Fair Isle and Foula dispersed widely during their first 2 years (Figure 5.1), but no bird ringed elsewhere in Shetland was recovered outside the main group of islands. Results from Mousa were typical, most recoveries being within 5 km of the natal colony (Figure 5.2). Similar results were found in Orkney, where the only 2 recoveries outside the main island group were on the nearby Caithness coast (Ewins & Kirk 1985).

Combining Shetland and Orkney main island groups, 1-2-year-olds moved significantly further than older birds (median distances = 7.5 vs. 4.5 km respectively, ranges = 0-67 and 0-17 km; n = 14,12; Mann-Whitney test, W =

Figure 5.1 Recoveries of Black Guillemots ringed as adults (dashed line) and chicks (solid line) on Fair Isle and Foula. The symbol at each recovery site of birds ringed as chicks represents the age at death: ▲ 1st yr; ● 2nd yr; ■ 3rd yr; ◆ 4th yr; ◇(n) nth yr. The month of recovery is given next to each symbol.

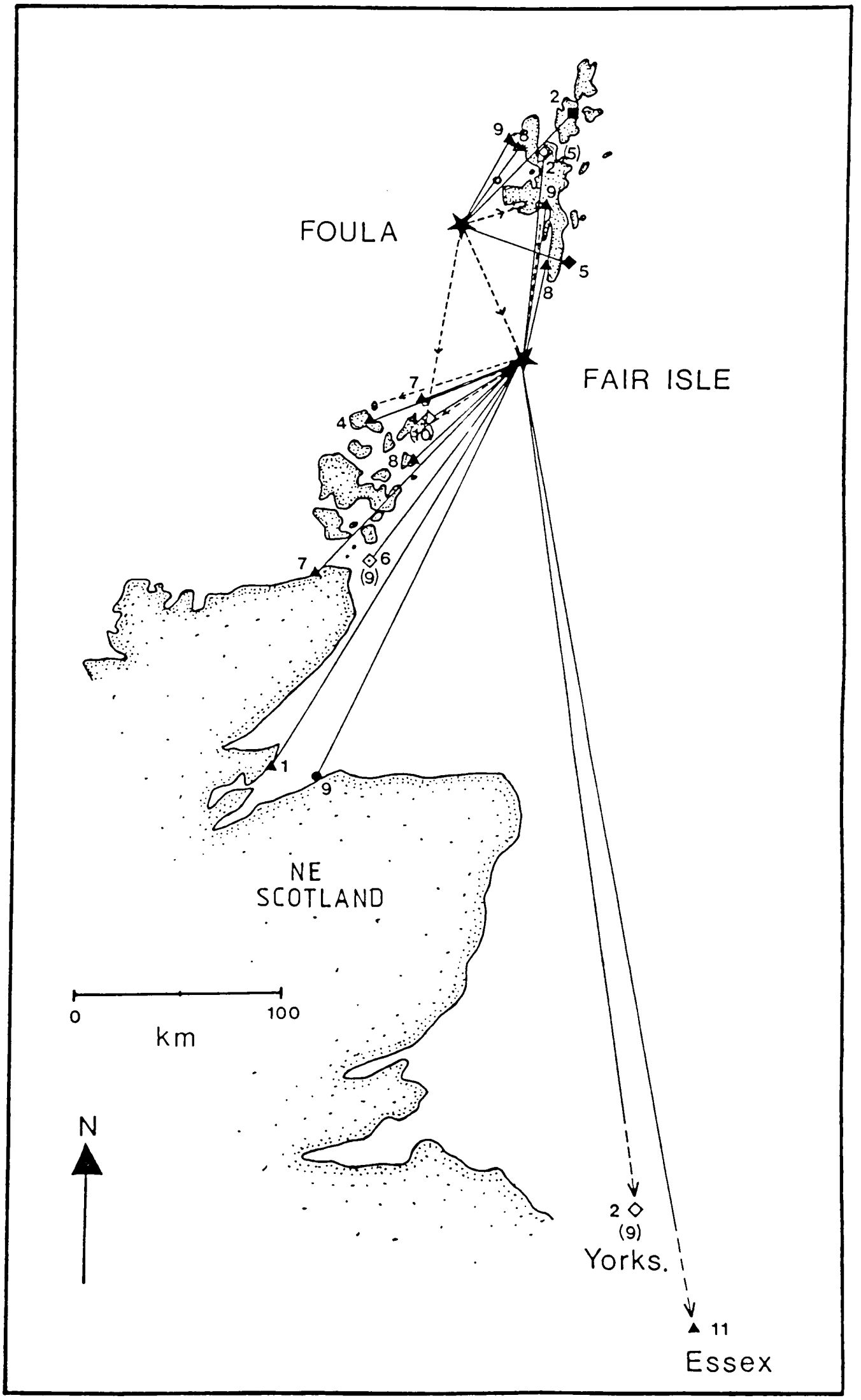
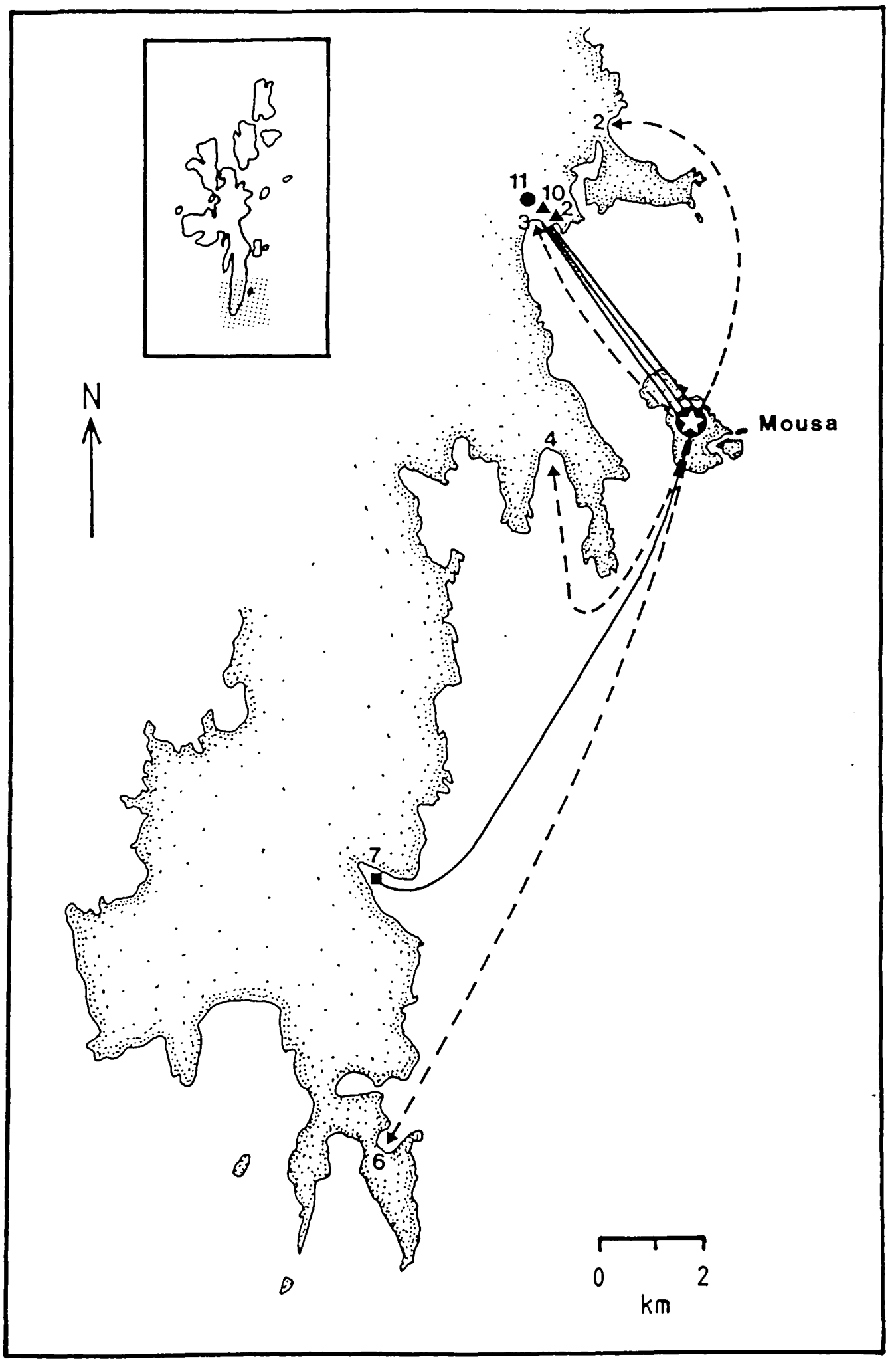


Figure 5.2 Recoveries of Black Guillemots ringed on Mousa. Details as for Figure 5.1.



230, P<0.05). Again there was no significant bias caused by the season of recovery. For Fair Isle and Foula recoveries, median recovery distance was greater for 1-2-year-olds (68 km) than for older birds (54 km), but the difference was not significant. In neither case was there any obvious relationship between recovery distance and time of year. There are no foreign recoveries of Black Guillemots ringed in Britain and Ireland. Although a few birds from north Scottish colonies move down the east coast of Britain in the autumn and winter, the winter and summer distributions are similar (Sharrock 1976; Lack 1986). The few birds seen in southern England probably originate from southern Scandinavia, as two Swedish chicks were recovered in their first autumn in east England. Small numbers regularly occur in autumn and winter in northern France, one was a first-winter bird from a south Norwegian colony (Hemery & Pasquet 1983).

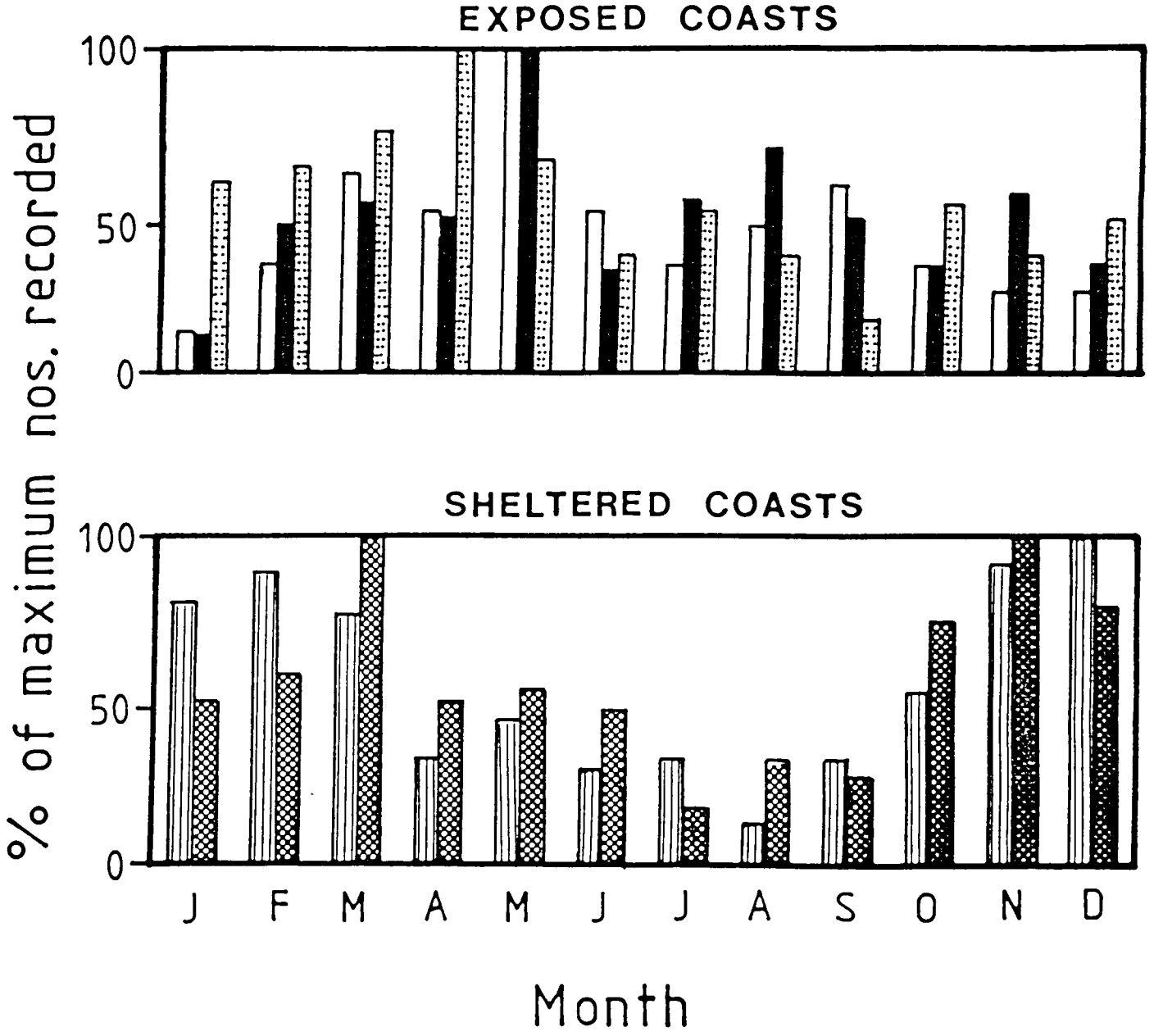
5.3.2 Seasonal movements

Monthly counts on sample foraging areas revealed fundamental differences in the pattern of usage through the year between exposed and sheltered coasts. The 3 sample stretches of exposed coastline each supported breeding concentrations, the birds feeding in the relatively narrow belt of shallow water immediately offshore. The 2 sheltered coastline sites contained no suitable breeding habitat (nearest breeding sites were at least 1 km distant) and both contained large expanses of shallow waters.

Along exposed coasts numbers increased from January to April-May, then declined from June onwards. In contrast numbers in sheltered inshore waters were highest through the winter, declined steadily until July-August, then rose steeply in the late autumn (Figure 5.3). The total number of individuals foraging along the exposed coasts during the breeding season was much higher than indicated because birds associated with breeding sites were omitted from these counts, an unknown number sat tight on eggs, and others may have foraged outside the census area. Thus the highest numbers occurred along exposed coasts in summer, and along sheltered coasts in winter, suggesting some degree of movement inshore away from exposed coasts in late autumn/winter.

The mean proportion of immatures present at the 5 sample sites, and in a total of 15 other areas (excluding the Yell Sound area, because the age structure of the population there may still be recovering from the Esso Bernicia incident - Chapters 3 and 4) was calculated for 2-month periods,

Figure 5.3 Monthly variation in numbers foraging along sample stretches of exposed and sheltered coastline in Shetland, expressed as percentages of maximum numbers recorded at each site. Maxima were, for exposed coasts: ▯ Aithsetter = 24; ▮ West Burra = 50; ▯ Kirkabister = 44; and for sheltered coasts: ▯ Scalloway harbour = 25; ▯ Whiteness Voe = 87. Site locations are given in Figure 2.1.



based on a reliable ageing of a minimum of 10 birds at each place. In each period the mean proportion of immatures was significantly higher along sheltered than along exposed coasts (Two-way ANOVA, F = 14.0, P=0.014) (Figure 5.4). The apparent increase in the proportion of immatures along sheltered coasts in June-July was probably due to the relative absence of breeding adults from these areas then, since most breeders foraged within 2-3 km of the colony (mostly located away from sheltered waters) whilst feeding young (Chapter 9). The similar rise in June-July on exposed coasts may be due to immatures visiting colonies then. Excluding the June-July counts, linear regression analyses revealed a nearly significant trend from August onwards for decreasing proportion of immatures on foraging areas along both sheltered (P=0.054) and exposed (P=0.07) coasts.

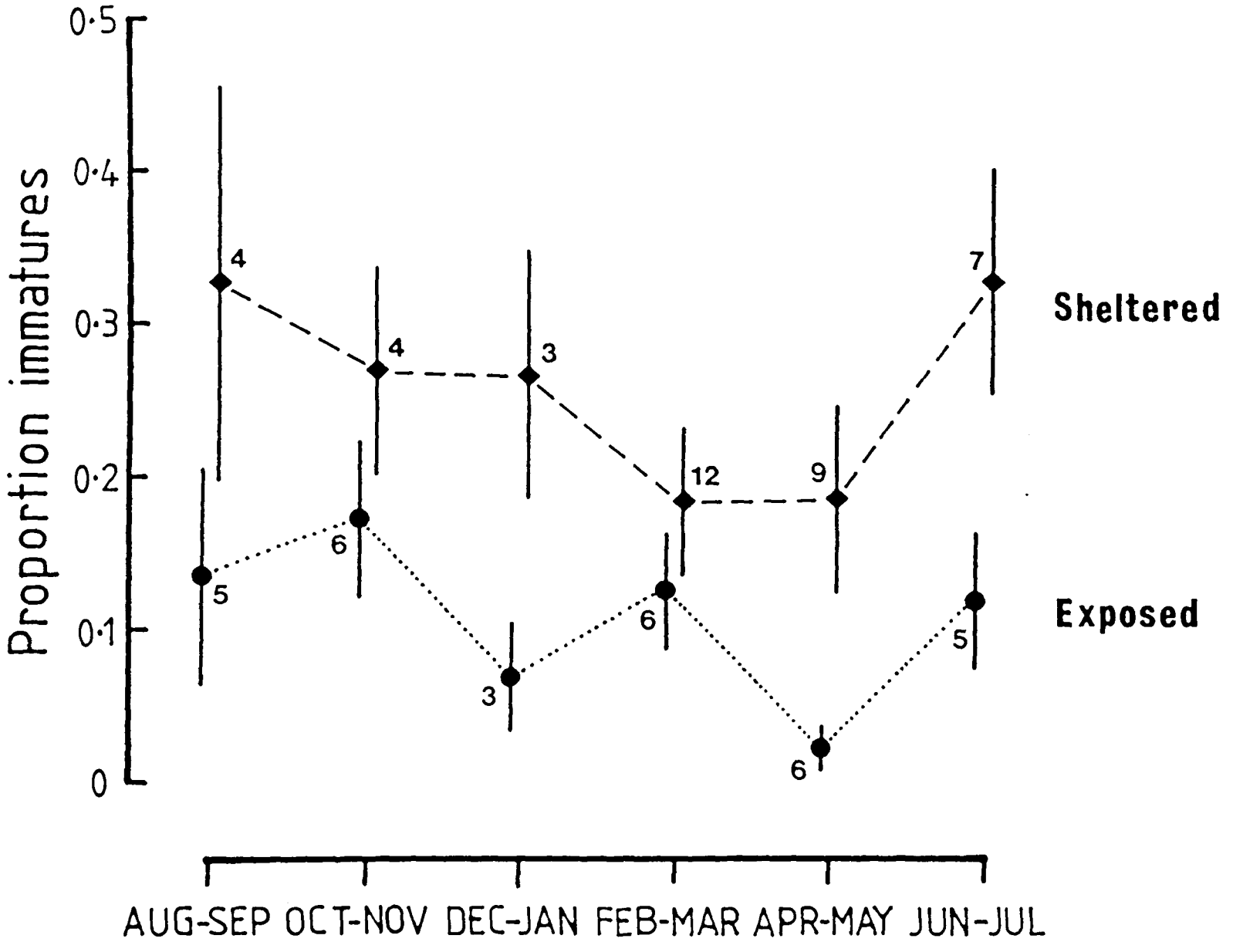
During numerous boat journeys in Shetland I rarely noted birds in water deeper than 40-50 m, or more than 2 km from land. These observations agree with those of Petersen (1981) and Piatt & Nettleship (1985), suggesting that this species seldom forages on the sea bed in water more than 50 m deep. However, some birds do move south in autumn, eg. there was a "spectacular influx" on Fair Isle on 20-21 October 1981, including a flock of 119 (F.I.B.O. 1982), and small numbers were seen flying south past Fair Isle during autumn seawatches (A del-Nevo pers. comm.). During extensive surveys of seabird distribution in the UK sectors of the North Sea from 1980-85 inclusive, Black Guillemots were seen more than 5 km from the coast on only 3 occasions: one on 1 June 1981 flying NW midway between Foula and Orkney (53 km from land, in water 70 m deep), one bird 15 km NE of Noss, Shetland on 12 June 1981, in water 110 m deep, and one near the Bell Rock, Fife on 19 January 1982, 53 km from the coast, in water 40 m deep (Blake et al. 1984; M Tasker pers. comm.).

5.3.3 Philopatry and nest site fidelity

Most birds more than 2 years old were probably close to their breeding (or prospective) colony from at least May to July. Of 11 recoveries of such 'adults' in this period, 7 (64%) were at the natal colony and 4 (36%) were elsewhere - at distances of 17, 51, 90 and 120 km. The last bird was a Fair Isle chick seen 8 years later on the Pentland Skerries, Orkney, where it was probably breeding.

Observations of colour-ringed birds on Mousa indicated that small numbers of immatures, and greater numbers of 2-year-olds frequented the natal island during the later stages of the breeding season. Neither age

Figure 5.4 The variation in mean proportion of immatures amongst Black Guillemots foraging along sheltered (diamonds) and exposed (circles) coasts in 2-month periods.
Mean ± se and sample no. of areas are given.



class was noted ashore in the colonies in April or May. Although immatures were present offshore throughout the year the first sighting of a colour-ringed individual was on 28 June in both 1983 and 1984. The earliest 2-year-old was ashore on 6 June in 1984. Immatures spent their time ashore at shore perches during morning peaks of colony attendance, with the occasional inspection under boulders close to the shoreline. They were usually driven from nest areas by adults. There was no indication that any immature had established a pair bond with another bird. Birds in their 2nd year spent protracted periods ashore, particularly in July, and regularly inspected potential nest cavities. Once, two 2-year-olds adopted behavioural postures characteristic of a pair [ie. circling, hunch-whistling (Asbirk 1979a)]. An adult male (probably at least 3 years old) attempted to copulate with a 2nd year female, but was unsuccessful. This pair were often present in the colony area in July although they did not defend a site. No immature or 2-year-old bred on Mousa. More colour-ringed immatures and 2-year-olds regularly roosted at overnight communal roosts on cliff ledges and offshore stacks. Presumably many more young birds returned to the vicinity of the natal colony than actually came ashore in the breeding areas.

Although little ringing had previously been done on Mousa, 2 of the adults breeding during my study years were already ringed: both had been ringed as chicks on Mousa in 1973.

Only two of the 51 colour-ringed adults were seen at a colony other than that in which they had originally been caught as a breeder. One bred successfully in 1983, but in 1984 its site was occupied by an unringed pair and this individual remained unpaired and frequented both its former colony and another 700 m distant. A second bird bred successfully in 1982 but failed in the same site in 1983. In 1984 it was unpaired and similarly frequented the same two colonies as the first bird. It caused considerable disturbance and aggressive interactions amongst established pairs in both colonies as it wandered amongst the boulder areas.

Of 37 successful breeders alive the next year 34 (92%) bred in the same site the following year. However, only 6 (67%) of 9 unsuccessful birds attempted to breed at the site the following year. (In cases where both members of a pair were colour-ringed only one has been considered in this analysis). Overall, nest site fidelity on Mousa was high, at 87%. One pair whose nest site was destroyed by heavy winter seas shifted to another site in the same colony. There were only 4 cases of birds breeding in

different sites in successive seasons, all within the same colony. Distances moved were 7, 20, 230 and 250 m.

Two colour-ringed birds changed site within a season. One laid a second clutch in an artificial site 17 m away from the original nest after its first clutch was lost. Another pair moved to defend a site 230 m away in the same colony after losing their first clutch, but no replacement eggs were laid.

5.4 Results: Mortality

5.4.1 Seasonal variation

Analyses of beached bird surveys, corpses found during the present study, and ringing recoveries indicated both seasonal and age differences in mortality (Figure 5.5).

The mean number of corpses found per km during the monthly beached bird surveys in Shetland (March 1980-February 1984 inclusive, total 86 corpses) dropped rapidly from a peak in August, with a smaller peak in February. Although analysis of 8 years of Orkney beached bird survey data (January 1976-December 1984 inclusive, total 102 corpses) also indicated a mid winter increase in mortality, there was no August peak (Figure 5.5a). There was no overall significant difference between average monthly numbers of corpses per km on Shetland and Orkney beaches (0.035 vs. 0.031 respectively, $t = 0.7$, 22 df, $P>0.1$). Corpses were not aged during these surveys. I aged the 78 dead birds found in Shetland however; over 50% of the immatures were found in August and September, whereas 42% of adults were found in June and July (Figure 5.5a). Although there was no seasonal search bias in the case of immatures, the large number of adult corpses found in the breeding season reflected, at least in part, the high chance of a bird dying at a breeding colony being found.

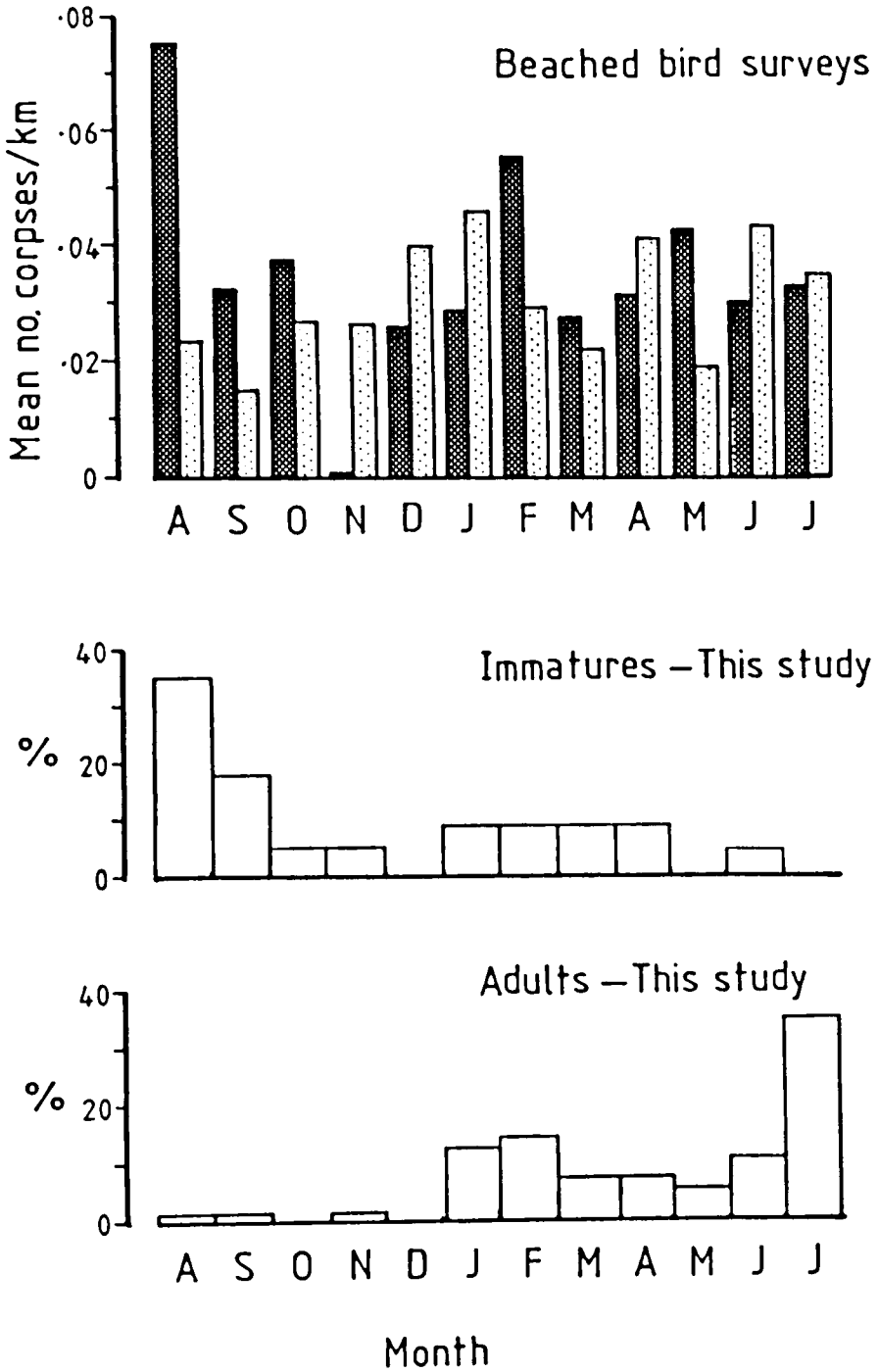
For 57 recoveries of Black Guillemots ringed in the UK, the seasonal pattern of mortality for immatures and adults was similar to that found in this study. August-September accounted for 57% of the immature mortality, whereas greater numbers of adults were recovered in June and July (18% in each month) (Figure 5.5b). However, the same seasonal biases apply to these data. When all the ringing recoveries were pooled no seasonal variation in mortality was apparent.

Figure 5.5 Monthly variation in mortality, as indicated by:

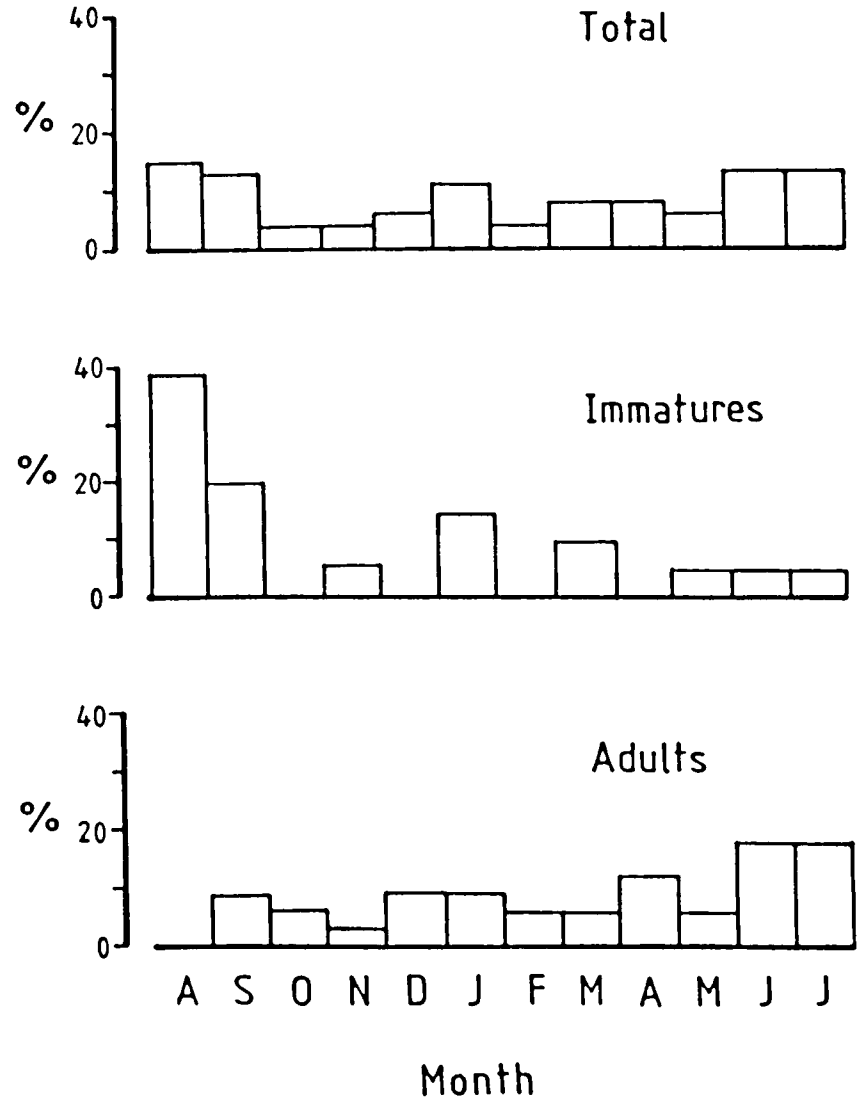
a) Mean number of corpses found per km during beached bird surveys in Shetland (▓), and Orkney (▒); and the % of immature and adult corpses found in each month during this study elsewhere in Shetland.

b) The percentage of ringing recoveries reported in each month. Sample sizes are given in brackets.

a. CORPSES FOUND



b. UK RINGING RECOVERIES



5.4.2 Causes of mortality

The likely cause of death was noted whenever possible and results compared with ringing recovery details. A wide variety of mortality factors was identified, but in both analyses the majority of corpses were recorded as "cause unknown" (Table 5.I). Remains usually consisted of a pair of wings and sternum, only occasionally with the legs still attached.

The birds caught in Salmon nets were all off the west coast of Ireland. Although illegal gill-netting still occurs in Shetland I received no reports of entangled Black Guillemots. An Otter Lutra lutra killed incubating adults in 1982 at a boulder colony on Mousa. Most birds were found decapitated in the nest cavity, none had been eaten. Although suspected in a few other areas such predation is probably uncommon. This one incident possibly involved a single Otter investigating under large boulders for suitable couches/holts, and surprising incubating adults in the process (Ewins 1985f). Predation by a feral cat was suspected at one site in a talus slope near to houses in the East Mainland; this has also been noted on Fair Isle (R A Broad pers. comm.).

Common and Grey Seals were seen pursuing Black Guillemots at the water surface in the summer months but no predation was recorded. In most cases the behaviour was thought to be 'play' rather than overt attack, but attempted kleptoparasitism was suspected on Mousa (Chapter 10). Black Guillemots breeding in a boulder beach colony on Foula during the 1970's suffered heavy adult predation from a pair of Great Skuas nesting nearby, resulting in a marked population decline (Furness 1983).

Oil pollution is underestimated as a cause of mortality by Table 5.I. From the years 1980-84, 7% of Black Guillemots found dead on Shetland beaches were oiled. Between March and September 1985 however, there were 2 cases of chronic oil pollution in inshore waters and 14 of the 29 corpses (48%) found on the surveys were oiled (M Heubeck pers. comm.). Although relatively few Black Guillemot corpses were found on these surveys in winter 1978-79, 633 oiled corpses were found then along the Yell Sound shores after the Esso Bernicia oil incident (Heubeck & Richardson 1980). Local breeding populations were reduced and numbers were still recovering 6 years later (Chapter 3). In Orkney between 1980 and 1984, 6% of the 54 corpses found on the beached bird surveys were oiled. However, in 1978-79, 45% of the 29 corpses found were oiled, coinciding with a series of spillages following the opening of the Flotta oil terminal there in 1977 (eg. R.S.P.B. 1977).

Table 5.I Causes of mortality as determined by details accompanying ringing recoveries, and corpses found in Shetland in this study.

CAUSE OF MORTALITY	UK RINGING RECOVERIES No.	%	SHETLAND 1982-84[a] No.	%
Unknown	48	75	80	87
Oiled	7	11	1	1
Shot	1	2	1	1
Caught in fishing gear [b]	5	8	1	1
Gt. Black-backed Gull [c]	2	3	1	1
Otter	-	-	8	9
Road casualty	1	2	-	-
	64		92	

Notes:
[a] Excludes Shetland beached bird survey data
[b] Includes 2 dead in Lobster pots, 3 in Salmon nets (2 were released alive), and one trapped in monofilament nylon line amongst boulders in a breeding colony
[c] *Larus marinus*

5.4.3 Adult survival rates

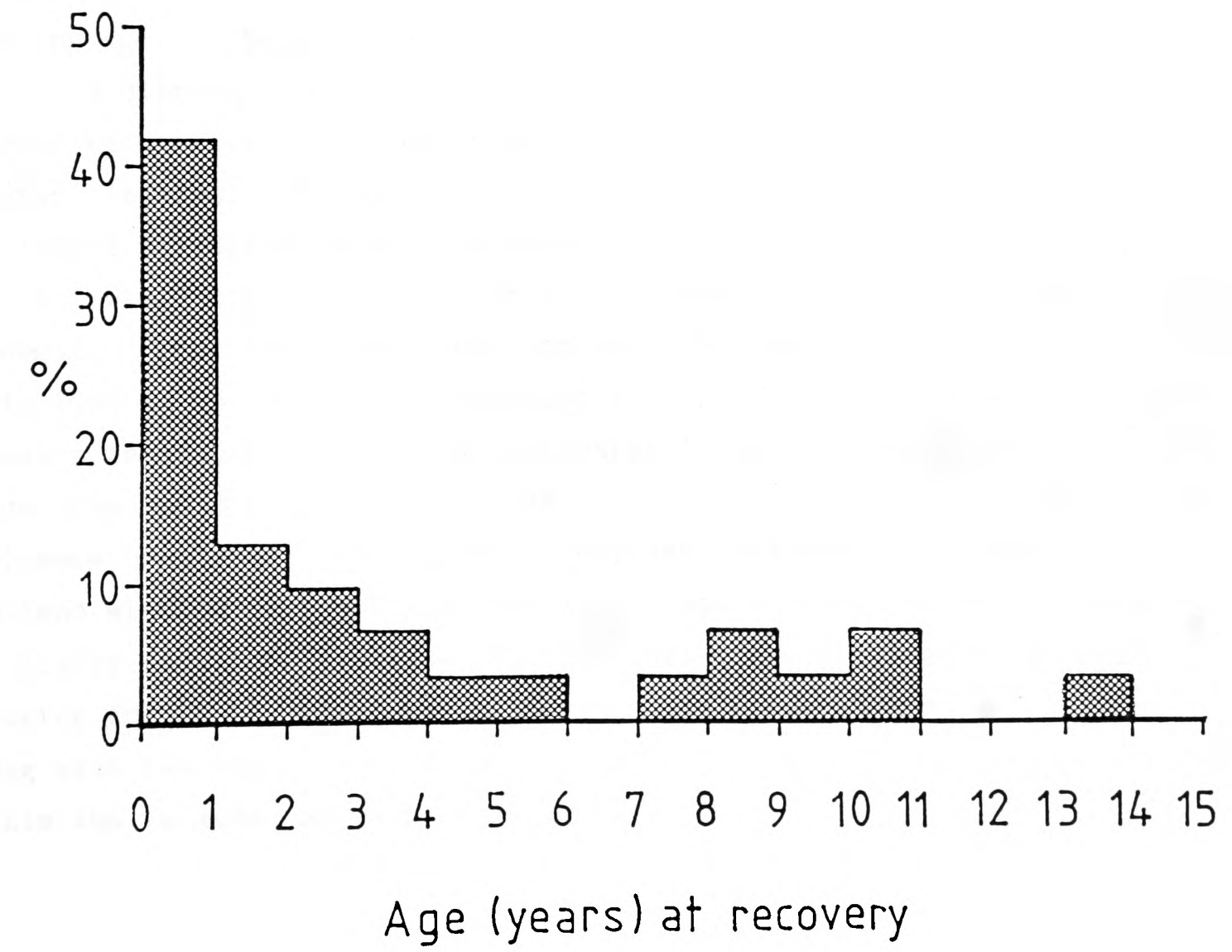
Of the 31 recoveries of chicks ringed in the UK before 1976, and reported dead by July 1985, 42% of birds died in the first year of life, 55% in the first 2 years, and mortality then levelled off (Figure 5.6). Since only one bird was recovered in its 10th year, taking 1975 as the last cohort meant that there was an equal likelihood of recoveries being made for all age groups. A bird ringed as a chick on Fair Isle in 1965 was still paired there in 1984, 19 years later.

The survival rate of colour-ringed adults was higher on Mousa than on Fair Isle. Of 51 adults breeding in July 1983 on Mousa, 48 were alive in July 1984 - an annual survival rate of 94%. At Busta Geo, Fair Isle, of 10 adults colour-ringed in August 1983, 90% were alive the following May. Of 20 marked adults alive there in summer 1977, 8 were present in summer 1983 - a mean annual survival of 86%. Annual adult survival is probably c.90% in Shetland, ie. an adult life expectancy of 9.5 years.

5.5 Discussion

During the breeding season Black Guillemots require both a suitable breeding site and sufficient food supplies nearby in order to rear young. The overall regular breeding distribution (Chapter 3) reflects these two main requirements and the even dispersion of shallow foraging areas in Shetland. Outside the breeding season, however, food is of prime concern and probably the major factor accounting for movements to wintering areas. Inshore fish are less abundant in shallow water in winter since some species migrate to deeper water then (Gibson 1969), or are less active in response to lower temperatures and light intensities (Woodhead 1966). Winter gales and heavy seas cause tremendous water turbulence, especially along exposed coasts, increasing energy demands and presumably hampering underwater foraging of diving birds. Increased water turbulence also makes benthic organisms seek shelter in deeper waters or crevices ("thigmotropism", Sverdrup *et al.* 1942). Thus, with reduced prey availability in winter along exposed coasts, some Black Guillemots move to more sheltered inshore foraging areas (Figure 5.3). The same conclusion was reached by comparison of pre-breeding and winter distributions in 10-km squares (Chapter 4). These results suggest inshore winter movements away

Figure 5.6 Frequency distribution of the age at recovery of chicks ringed before 1976 in the UK. (Based on a total of 31 recoveries).



from more exposed coasts, as described by Scott (1973) and Oakley (1981) for Pigeon Guillemots.

Fair Isle and Foula have little sheltered water during winter gales and heavy seas. Birds roost ashore more regularly here than elsewhere outside the breeding season (R A Broad pers. comm.; pers. obs.), and I suspect that both islands are inhospitable in winter to Black Guillemots, especially those inexperienced in foraging skills. Unfortunately there is no reliable winter census for either island, but post-fledging dispersal is probably greater and more widespread than in the main island groups of Shetland or Orkney. Severe winter storms are known to have caused heavy mortality of this species in the Soviet Union (Formosov 1946).

Although the pattern of greater dispersal during the first two years of life (than subsequently) was evident from all analyses, the Fair Isle and Foula ringing recoveries are unrepresentative of the northern Scottish populations. Most Black Guillemots in Shetland probably undergo limited dispersal in their first two years, then remain within 5-10 km of the breeding colony thereafter. Petersen (1981) found that in Iceland 1-2-year-olds dispersed more widely than adults, although there are still no ringing recoveries of adults in winter there (Petersen in litt.). Similar greater dispersal of immatures and 2-year-olds has been found in both Guillemots (Birkhead 1974a) and Razorbills (Lloyd 1974).

Elsewhere there is variation in the extent of post-fledging and winter movements. Some Norwegian birds appear to be sedentary whilst others move up to 1500 km to the south (Myrberget 1973), and in the Kattegat, Danish breeders tend to move slightly southwards in winter, being joined by some birds from the Baltic and Skagerrak colonies (Andersen-Harild 1969). The influence of the Gulf Stream is largely responsible for the mildness of Shetland winters (Berry & Johnston 1980), and although gales are regular, the highly indented coastline provides large areas of sheltered inshore foraging for Black Guillemots. The high winter densities in Shetland, along with the indications from ringing recoveries of only limited movement within the islands, suggests that overall, conditions are good for over-wintering by Black Guillemots in Shetland.

Like most seabirds, alcids appear to be highly philopatric (Ashmole 1971). On Skokholm for example, only 0.6% of adult Razorbills caught had been ringed elsewhere (Lloyd & Perrins 1977), but 5% of ringed adults were retrapped at other colonies (Lloyd 1976). No Puffin from Skomer was found resident at another colony (Ashcroft 1976). However, this situation can change. Severe erosion of breeding areas on the Farne Islands forced many

young Puffins to move to breed on the Isle of May, 100 km to the north (Harris 1983a). Similar variability is evident for Black Guillemots. On Fair Isle no adult was ever seen at a colony other than that in which it had been ringed as a breeder (Broad & Ewins 1984), and on Mousa only 2 of 51 marked birds ever frequented other colonies on the island (both were non-breeders). Asbirk (1979c) and Petersen (1981) found pronounced philopatry amongst breeding adults, although in Petersen's expanding Icelandic study population colour-ringed 1-2-year-olds regularly frequented breeding areas on islands a few km from the natal colonies. Large scale shifts have occurred however in areas colonized by Mink (Olsson 1974; Asbirk 1978c; Petersen 1981; Folkestad 1982), and philopatry of both adults and young must have been greatly reduced in the infested areas.

Nest site fidelity was high on Mousa (87%) when compared to figures elsewhere: Iceland 90% (Petersen 1981); White Sea 78% (Bianki 1967); Canada 68% (Preston 1968); Denmark 56% and 79% (Asbirk 1979c). This variation largely reflects the degree of permanence of the nest sites and annual fluctuations in breeding success. Thus, on Mousa and at Petersen's Icelandic colonies there was little physical change to nest sites between years, whereas on Asbirk's Danish study island sites amongst driftwood and sand dunes around the high water mark often shifted as a result of heavy winter seas (Asbirk 1979c). Unsuccessful breeding in one year meant that there was a greater likelihood of a bird not attempting in that site the following year. A similar effect has recently been found in Herring Gulls Larus argentatus (Graves et al. 1986) and is well-established in Yellow-eyed Penguins Megadyptes antipodes (Richdale 1957). Sample sizes were too small to permit further analysis, but Petersen (1981), finding a similar but more marked difference in site fidelity according to breeding success, suggested that divorce was more likely in unsuccessful pairs. Further, Broad & Ewins (1984) suspected that following divorce a surviving male was more likely to remain at the original site than was a surviving female.

The distance moved between successively occupied sites largely reflects local topographic features and the distribution of available sites. Preston (1968) found all such moves to be within 25 ft. of the original site, and Petersen (1981) gave the mean straight-line distance moved by 10 individuals as 12 m (range 2-28 m), stating that new sites were always in the same nesting area (ie. 'colony') as the old site. The more scattered nature of some Mousa colonies explains the larger distances moved between sites there (range 7-250 m).

The pattern of immature and 2-year-old Black Guillemots frequenting nesting areas progressively earlier and with increasing regularity as sexual maturity approaches is also found in other alcids (Lloyd 1974; Birkhead & Hudson 1977; Harris 1984). Petersen (1981) correctly pointed out that the occurrence of immature Black Guillemots at nesting areas in the pre-breeding period is unusual when compared to the situation in Guillemot, Razorbill and Puffin, and he suggested that this difference may relate to the earlier onset of maturity in Black Guillemots. Results on Mousa lend no support to this suggestion. During the pre-breeding period (as at all other times of year) immatures forage around all Shetland coastlines. The presence of c. 1% of immatures in the morning peaks of colony attendance (Chapter 2) is explained by their foraging distribution alone. In this period the only social activity which involved immatures was their being chased away by adults in the offshore gatherings. I suggest that the 'absence' of immature Guillemots, Razorbills and Puffins from pre-breeding gatherings at the colonies (Lloyd 1974; Petersen 1976; Birkhead & Hudson 1977; Harris 1984) largely reflects the more distant foraging areas of these species, compared to the inshore niche of Black Guillemots.

The recovery rate of 1.2% is similar to the 1.9% found in western Iceland (Petersen 1977), but both values are considerably lower than that in Denmark - 14% (Andersen-Harild 1969) and Norway - 6% (Myrberget 1973). The reasons for this are unclear, but may be related to shooting and fishing nets being far commoner in Denmark and Norway (see below).

Since the cause of death was unknown for such a high proportion of corpses, it is difficult to assess the relative importance of different mortality causes. Many Black Guillemots are killed in (benthic) nets set for Lumpsuckers Cyclopterus lumpus in Iceland (Petersen 1981), and in monofilament fishing nets in Norway (Myrberget 1981). Analyses of ringing recovery details show that in Denmark 49% were recorded as shot, 34% drowned in fishing gear, and 4% were oiled (Andersen-Harild 1969). In Norway 43% were shot and 25% caught in fishing gear (Myrberget 1973). Both inshore gill-netting and shooting were much more widespread in Scandinavia than in Britain in this period, and are probably not significant causes of mortality in this country. However, the rapid expansion of the salmon farming industry in Shetland over the last 3-4 years has resulted in some mortality of Black Guillemots, mostly becoming entangled in anti-predator nets (although precise figures are difficult to obtain). Predation by mammals and larids is probably only occasionally important on a local

scale, but in recent years oil pollution has clearly been an important mortality factor in Shetland and Orkney.

The apparent seasonal variations in mortality can best be explained by considering immatures and adults separately. The sharp decline in immature mortality after August (ie. when young leave the nest) is characteristic of a species lacking post-fledging parental care. Success rates whilst foraging (fish brought to the surface) were significantly lower for immatures than for adults (pers. obs.), emphasizing that considerable skill is necessary to catch and handle benthic fish. Although breeding imposes additional stress on most adult animals (Frank et al. 1957; Bryant 1979), non-breeding by Puffins does not appear to influence adult survival (Harris 1984). The biases inherent in my data make interpretation of the breeding season peak in adult mortality difficult. However, the indication of a second peak of adult mortality in January-February coincides with greatest numbers of other auks found on the Shetland beached bird surveys (Heubeck 1982, 1984) and lowest monthly air temperatures and strongest winds (Shetland Islands Council 1986).

The estimates of adult survival rate in Shetland (86-94%) are slightly higher than those found elsewhere, vis.: Iceland 83-92% (Petersen 1981); Canada 80% (Preston 1968); Denmark 82-89% (Asbirk 1978a). However, the validity of Preston's low figure is questionable since he did not use colour rings but relied on retrapping of birds banded with a metal ring only. Clearly any trap shyness or insufficient trapping effort would have deflated the survival estimate. There are a number of reasons for treating my estimates with caution. Sample sizes are rather small for Fair Isle (though similar to those used by Preston), and estimates based on only one winter may simply reflect the severity of that particular winter. However, the 1983-84 winter was not exceptional in any sense (records from Lerwick Met. Station). Ring loss, emigration and non-breeding are factors which may have led to an under-estimate of survival (some loss of colour-rings had occurred on Fair Isle birds). Taking any of these factors into account would actually increase the survival estimate further, and my supporting conclusion is that adult survival may well be higher in Shetland than in some parts of the range.

CHAPTER 6. BREEDING BIOLOGY: THE EGG STAGE.

6.1 Introduction

The main studies of the breeding biology have been made in Finland (Bergman 1971), Denmark (Asbirk 1978b,c; 1979b,c), Iceland (Petersen 1981), and Canada (Preston 1968; Cairns 1978; 1981). The only British work is that of Dennis (1966) on Fair Isle, Shetland (which deals with eggs only), continued by R A Broad in the 1970's (Broad & Ewins 1984). Past data are summarized by Cramp (1985) and Harris & Birkhead (1985). Other accounts are more anecdotal and descriptive, but a few useful comparisons can be made, with clutch sizes and the timing of breeding for example in Shetland in the last century (MacGillivray 1852; Saxby 1874).

Chapter 6 deals with the egg stage, Chapter 7 with the chick stage, and Chapter 8 considers the various factors affecting breeding success. The study area and methods sections below also apply to Chapters 7 and 8.

The laying period of most birds appears to be timed to enable young to be raised when food is most readily available (Lack 1954, 1968). However, egg laying may be delayed if female reserves are insufficient to form the egg(s) (Perrins 1970) and to see her through the incubation period (Brooke 1978). Clearly the most important ultimate factor affecting the timing of breeding is food availability (Jones & Ward 1976), but for some seabirds daylength (Murton & Westwood 1977), and sea temperature (Salomonsen 1943, 1955) may be proximate factors.

In my study there was sufficient variation in laying dates between years and sites to allow further examination of the effects of factors such as environmental conditions, female size, nest site quality and colony size on laying date and egg size. Details are presented of egg biometrics, colouration and pollutant concentrations, and the frequency and interval of egg replacement. I also consider differences in the length of the incubation period, and the importance of hatching synchrony to subsequent chick growth and fledging success.

6.2 Study areas

The main study was carried out on Mousa, and comparative data were collected on Hascosay and other low-lying islands along the eastern side of Shetland (Figure 2.1). Although most Black Guillemots in Shetland breed in

cliffs and geos, rather than amongst boulders in more accessible situations (Chapter 3), studies of such colonies are impractical. Mousa had some 313 adults in the pre-breeding period (Ewins 1985a), at the high mean density of 38 birds per km of coastline (see Table 3.I). The island is uninhabited although visited by over 2000 tourists between May and September each year. Otters are the only ground predators.

Vast numbers of sandeels in the productive shallow seas nearby (Figure 6.1) provide rich summer feeding for many seabirds, but have been subject to intensive industrial fishing over the last decade (Warburton 1983). In 1984 Mousa had 16 breeding seabird species, the commonest being Storm Petrel (guessed at 1-9,000 pairs), Arctic Tern Sterna paradisaea (1300 prs.), Arctic Skua Stercorarius parasiticus (17 prs.). Lesser Black-backed Gull Larus fuscus (c.100 prs.), Herring Gull L. argentatus (c.60 prs.), and Eider Somateria mollissima (c.100 prs.) (Ewins 1983a, 1984a). Black Guillemot colonies were scattered around the island, with the largest towards the south-east corner, amongst boulders and piles of sandstone slabs discarded from previous quarrying (Figure 6.2). In both 1983 and 1984, c.13% of the sites on Mousa at which breeding was proven or suspected were inaccessible, most being in cliff crevices on the western side of the island.

About 25 breeding attempts were made on Hascosay each year, in scattered small colonies or as isolated pairs. Most nests were amongst talus scree or in disused Rabbit Oryctolagus cuniculus burrows at the cliff edges. The island was uninhabited and Otters were the only ground predator. Small numbers of gulls, skuas and Arctic Terns also bred.

6.3 Methods

In 1982, Mousa and Hascosay were each visited regularly between 7 May and 5 September. In 1983 and 1984 attention was focussed on Mousa, with continuous coverage during both breeding seasons.

Nest cavities were located by morning hide watches in the pre-breeding periods. A permanent stone hide was built at the large colony A (see Figure 10.1), and portable canvas hides were used elsewhere. Regularly occupied nest perches (*sensu* Asbirk 1979c) and cavities were plotted on sketch maps and inspected later. A few 'new' nests were found later on in each season and these sites are omitted from many of the breeding anlayses. Scraping activity was usually obvious, in the form of small flat stones arranged in a nest cup depression (subsequently referred to as the

Figure 6.1 Submarine contours in the Mousa area.

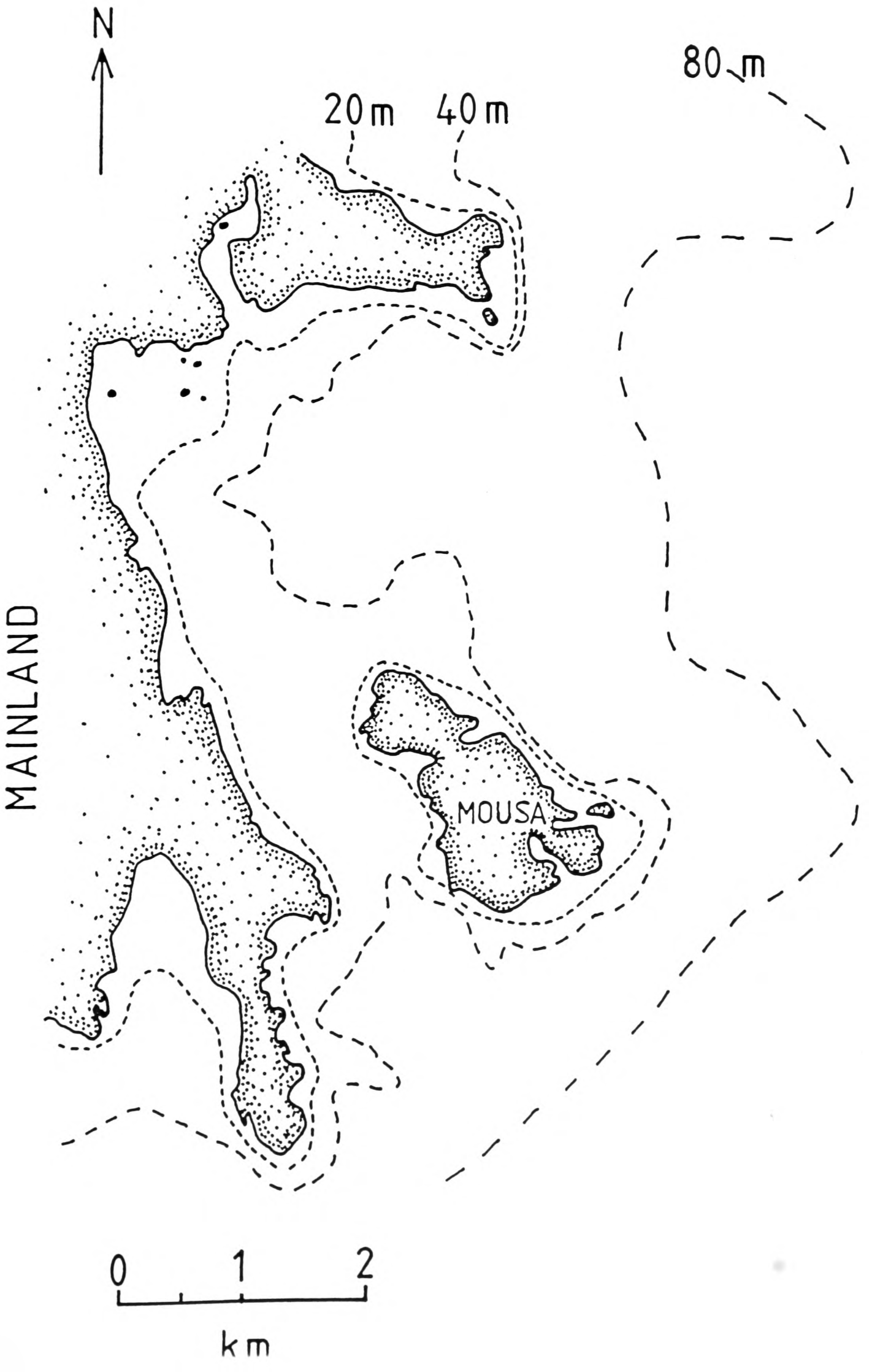
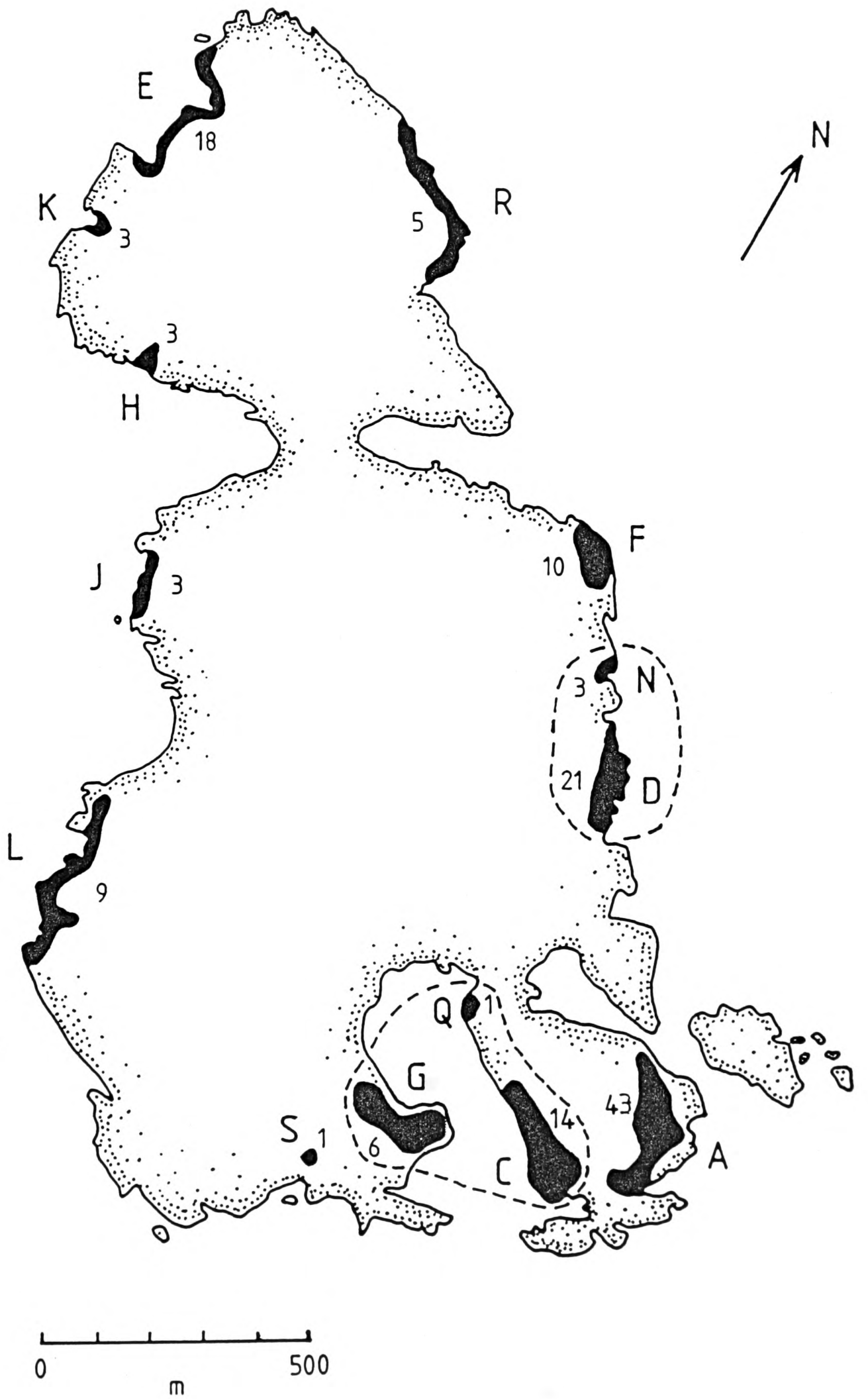


Figure 6.2 The location of Black Guillemot breeding areas on Mousa. The number of breeding attempts in 1984 are given beside each lettered colony. Breeding aggregations enclosed within dashed lines were treated as single colonies in the analyses.



'scrape') by the adults' shuffling motions. The extent and form of nest scrapes often changed dramatically from day to day in the few weeks prior to laying. Nests were usually inspected between 1300-1800 h BST, when colony attendance was lowest, to minimize disturbance. The time spent at any colony never exceeded 30 minutes, and in cold and wet conditions visits were cut short to allow adults to return quickly to incubate or brood. The frequency of nest checks varied according to stage of the breeding cycle. Daily checks were made to determine laying and hatching dates. Day 0 for eggs was the first day an egg was noted; for chicks it was the first day a chick was completely free of the shell. In 1983, eggs were weighed every 5 days during incubation. Incubation was considered to be occurring if the eggs were warm or if an adult was present in the nest cavity. Nestlings were measured every 3 days, but daily in the 7-10 days prior to fledging.

Human disturbance of auk colonies during the egg stage can lower breeding success and extend the incubation period (Sealy 1984; Pierce & Simons 1986). Colony CGQ received almost daily disturbance from photographers, picnickers and general tourists (additional to my daily nest-rounds of much shorter duration). Some incubating birds were probably kept off the nest for up to 1 hour each day, but rarely at all in bad weather conditions because visitors did not come to the island then.

Most adults flew onto the sea when disturbed but c.5% regularly sat tight, and these were usually not disturbed further, especially during the first 10 days of incubation or whilst brooding very small chicks. Where an adult ran to the rear of a large cavity, the eggs were removed and placed in a container, then the adult extracted either by hand or with a wire crook hooked around the tarsus. Other adults were caught in mist nets when feeding chicks. Measurement of weight, wing length and colour-ringing were the priorities. Taking additional biometrics would have increased the stress time unnecessarily. A summary of trapping methods and caution required when ringing this species is provided in Appendix II.

Examination of nest contents usually required a torch and/or a mirror. Use of an optical fibrescope (as recommended by Cairns 1983) would have increased sample sizes only slightly on Mousa. At the end of each breeding season many nest chambers were modified so that young could be more easily caught.

The a-egg (ie. first-laid) was marked with nail varnish or permanent ink at the blunt end to permit distinction from subsequent eggs in the scrape. The first chick to hatch was given a small spot of nail varnish on the dorsal down. This persisted for at least a week, by when the chick

could be ringed. Causes of breeding failure were noted whenever possible. Nests at which my interference (eg. via trapping of an adult) was thought to have prompted desertion have been omitted from the relevant analyses.

Pesola balances were checked against standard weights, and measurement of eggs and wing lengths practised before each field season. Egg dimensions were measured to 0.1 mm with vernier calipers. Eggs were weighed to 0.1 g, and nestlings to the nearest 1 g. The weighing bag was weighed regularly during the nest-round, since its weight increased by as much as 150% over 3 hours in wet weather conditions.

Ten eggs were taken under licence in June 1983, within a week of laying, from a colony at Brindister, 12 km north of Mousa. These were analysed for pollutant residues by the Institute of Terrestrial Ecology at Monks Wood, England, as a contribution to their data bank on pollutant levels in bird eggs. Egg volume index (length x breadth^2) is given in cm^3, and a good approximation to actual egg volume may be obtained by multiplying by the constant K_v = 0.507 (Hoyt 1979).

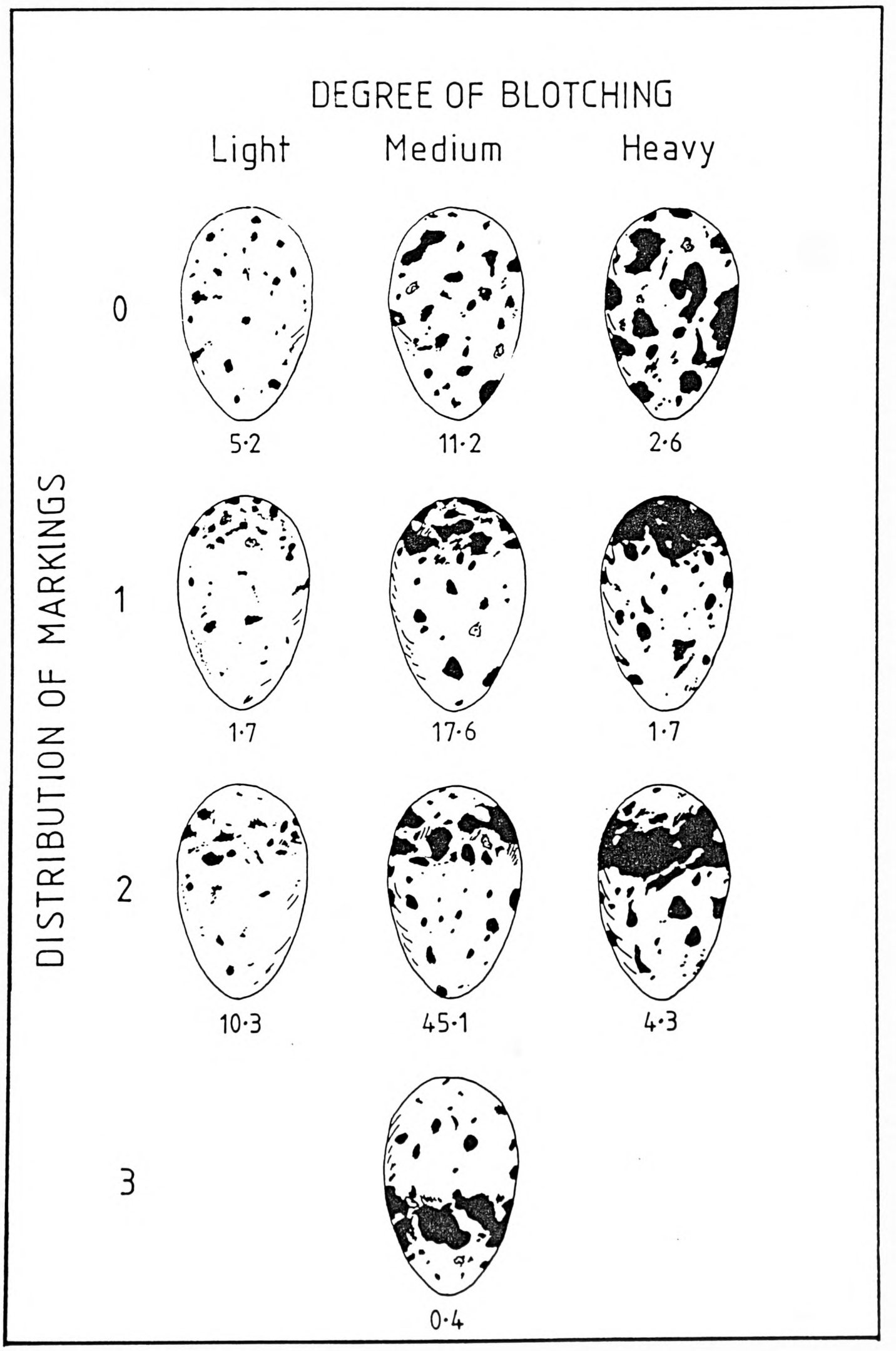
Meteorological data used in the analyses are from the Lerwick Met. Station. Average monthly sea-surface temperatures were recorded at Fair Isle (50 km south of Mousa), and are presented in Appendix III.

6.4 Results

6.4.1 Eggs

The ground colour, patterning and degree of blotching was scored for a sample of 233 eggs on Mousa. The shape of most eggs was as shown in Figure 6.3, ie. elliptical ovate (cf. Nettleship & Birkhead 1985), with a blunt end always distinguishable. Two eggs were abnormally elongated at the pointed end. Ground colour was usually pale blue-green, shading to off-white (96% of eggs), with fawn (3%) and olive-brown (1%) being uncommon. Markings were mostly dark brown or black, with some shading of grey and reddish brown. The commonest patterning was medium blotching concentrated in a ring toward the blunt pole. Overall 74% of eggs had medium blotching and 60% had a marked polar ring (marking type 2, Figure 6.3). There was a significant tendency for eggs in two-egg clutches to have the same ground colour, blotching and marking score (67% identical versus 33% different; G = 20.2, 1 df, $P<0.001$), but occasionally the two eggs differed substantially in pattern of marking [contrary to Asbirk (1979c) who stated that "eggs of the same clutch always have the same pattern of spots"].

Figure 6.3 The range of variation in egg markings. The percentage frequency of each type, in a sample of 233 Mousa eggs, is given beneath each egg.



Although there was a tendency for eggs in successive years at the same site to be of the same type this trend was not significant. Many of the differences were of only one point on the scales used however, and although sites at which a female change was known to have occurred were excluded, some sites may still have held different females in different years.

In two-egg clutches (c2) eggs were, on average, larger in all dimensions in 1984, though this was only significant for breadth and volume index of a-eggs (Table 6.I). Similarly the a-egg was usually significantly larger than the b-egg in all dimensions. Asbirk (1979c) found single eggs to be significantly smaller than those in two-egg clutches, but on Fair Isle, Dennis (1966) reported the reverse, although no statistical analysis was provided. Comparison of the a-egg in c2 with c1 eggs showed that both breadth and volume index were smaller in c1 eggs, although this was only significant for breadth in 1984 ($P<0.01$). When all eggs were pooled and comparison made between years, both mean ($\pm$ sd) breadth (38.9 $\pm$ 1.2 : 39.3 $\pm$ 1.1 mm; $t = 2.46$, 184 df, $P<0.02$) and volume index (86.5 $\pm$ 7.0 : 89.3 $\pm$ 7.2 mm; $t = 2.65$, 184 df, $P<0.01$) were significantly greater in 1984. This was not simply due to proportionately fewer single eggs measured in 1984, since sample size for c1:c2 eggs did not differ significantly between years ($G = 0.63$, 1 df).

Eggs measured elsewhere in Shetland in 1982-83 had significantly greater mean volume index than 1983 Mousa eggs ($t = 2.01$, 132 df, $P<0.05$), but were not significantly different from 1984 Mousa eggs (Table 6.II). These pooled measurements are presented with those I made of eggs in collections in the Royal Scottish Museum, Edinburgh, and other published values for British Black Guillemots in Table 6.II. The Shetland and British egg sizes differed little from those in Denmark (Asbirk 1979c), Bay of Fundy, Canada (Winn 1950), and Iceland (Petersen 1981), but were notably smaller than those further north, from the northern Soviet Union (Uspenski 1956; Kozlova 1961), where adult Black Guillemots are larger (Salomonsen 1944; Cramp 1985).

There was a highly significant correlation between fresh egg weight (g) and egg volume index (cm^3) in both 1983 and 1984 ($P<0.001$). Fresh a-eggs were significantly heavier than fresh b-eggs in both years (on average by 3.7% in 1983, and 4.0% in 1984). However, although mean weights of fresh eggs in all categories were greater in 1984 than in 1983, the difference between years was only significant when all eggs were pooled ($t = 2.62$, 176 df, $P<0.01$) (Table 6.III). Mean fresh a-egg weight was significantly greater than that for single eggs in 1983 ($t = 2.25$, 41 df,

Table 6.I Comparison of egg dimensions in single-egg and two-egg clutches on Mousa in 1983 and 1984. Length and breadth are given in mm, volume index in cm^3. Significance levels from t-test analyses are denoted by: * P<0.05, ** P<0.01.

			1983				1984			1983-1984
			Mean	sd	n		Mean	sd	n	comparison
c1	Length		57.3	1.4	8		56.7	2.5	7	ns
	Breadth		38.4	0.9	8		38.3	1.0	7	ns
	Vol.index		84.5	5.7	8		83.5	7.5	7	ns
c2	Length	a	57.6	2.5	38	ns	58.3	2.2	52	* ns
		b	56.9	2.3	36		57.4	2.0	45	
	Breadth	a	39.0	1.3	38	ns	39.6	1.2	52	* *
		b	38.7	1.0	36		39.1	0.9	45	ns
	Volume index	a	88.3	7.2	38	*	91.6	7.5	52	** *
		b	85.1	6.7	36		87.7	5.9	45	ns

Table 6.II Dimensions of British Black Guillemot eggs, (irrespective of clutch size, laying date or order). Mean, sd, and ranges (in brackets) are given.
RSM = Royal Scottish Museum collections.

Area	Years	Source	No.	Length(mm)	Breadth(mm)	Volume Index(cm^3)
Mousa	1983	This study	82	57.2±2.5	38.9±1.2	86.5±7.0
Mousa	1984	" "	104	57.8±2.2	39.3±1.1	89.3±7.2
Rest of Shetland	1982-83	" "	52	58.7±2.0	38.9±1.1	89.0±6.5
Shetland	1982-84	" "	238	57.8±2.3 (52.7-65.1)	39.1±1.1 (34.5-43.0)	88.3±7.1 (70.0-110.4)
Shetland	-	RSM	40	58.2±2.9 (54.0-71.5)	38.9±1.0 (37.2-40.7)	88.1±6.0 (75.5-102.2)
Orkney/NW Scotland	-	RSM	89	58.5±2.7 (52.0-68.2)	39.4±1.1 (36.5-42.0)	90.9±7.0 (69.3-108.0)
Fair Isle	1960's	Dennis (1966)	79	57.5±2.3 (52.4-64.7)	39.2±1.2 (36.3-42.7)	-
Britain	-	Witherby et al. (1941)	100	58.1 (54.3-62.4)	39.5 (33.9-41.6)	-

Table 6.III Comparison of fresh egg weights (g) in one-egg and two-egg clutches in 1983 and 1984. t-test differences: * P<0.05, ** P<0.02, *** P<0.01.

		1983		1984		1983-84 comparison
c1	Mean	44.9		46.4		ns
	sd	4.6		3.8		
	n	7		6		
	range	36.5-52.1		43.4-53.5		
c2		a-egg	b-egg	a-egg	b-egg	
	Mean	48.4 *	46.7	49.9 **	47.9	y
	sd	3.6	3.5	3.9	3.2	
	n	36	34	51	44	
	range	40.9-58.0	40.6-54.0	42.1-60.1	41.2-55.9	
All eggs:						
	Mean	47.3		48.8		***
	sd	3.8		3.8		
	n	77		101		
	range	36.5-58.0		41.2-60.1		

Note: **y** No significant difference between years for either a or b eggs

P<0.05) and 1984 (t = 2.08, 55 df, P<0.05), and even b-eggs were on average heavier than single eggs. The Shetland average weights fit in well with a trend of increasing fresh egg weight with latitude: Denmark 47.9 g (Asbirk 1979c), Iceland 49.7 g (Petersen 1981), Murmansk 53.7 g (Belopol'skii 1957).

A comparison of fresh egg weights in 77 two-egg clutches revealed that for 1983 and 1984 pooled data (since there was no significant difference between years), the fresh a-egg was at least 1 g heavier than the b-egg in 62% of clutches, within 1 g in 30%, and over 1 g lighter in only 8%. Similar results were obtained in Iceland by Petersen (1981).

Adult weights differed significantly between years (mean ± sd in 1983 = 388.2 ± 22.6 g, n=43; in 1984 = 410.8 ± 32.3, n=8; t = 2.42, 50 df, P<0.02). In 1983 at least, there was no significant sex difference in average post-laying weight (males = 387.2 ± 27.3 g, n=13; females = 399.9 ± 19.1, n=8; t = 1.15, 20 df, P>0.1). Further, there was no significant seasonal decline in adult weight on Mousa (Chapter 9), or on Fair Isle (sample of 80 adults between 7 June and 18 August; data from Fair Isle Bird Observatory Ringing logs). Therefore the average fresh egg weight on Mousa in 1983 and 1984 was respectively 12.2% and 11.9% of average adult (female) post-laying weight. Similar values (12-13%) have been found elsewhere (Belopol'skii 1957; Asbirk 1979c; Petersen 1981).

Since some females were individually ringed it was possible to compare female body size with fresh egg weight and egg breadth. Petersen (1981) found that weight (and tarsal length) was a more reliable indicator of body size than wing length. On Mousa female weight and wing length were significantly correlated (r = 0.648, 10 df, P<0.05). Female weight (post-laying) was significantly correlated with fresh weight of the first egg laid (r = 0.705, 10 df, P<0.02), as was wing length (P<0.05).

Egg breadth may be used as a reliable indicator of female age (eg. Richdale 1949, 1955; Coulson 1963; Coulson et al. 1969), and in Black Guillemots Asbirk (1979c) found an increase in egg breadth with adult age. Although adult ages were not known on Mousa, there was a significant correlation between female (post-laying) weight and egg breadth (r = 0.658, 10 df, P<0.02). Therefore larger females laid broader and heavier eggs. Further, eggs in two-egg clutches were on average broader than those in single-egg clutches in both 1983 (38.92 : 38.38 mm) and 1984 (39.35 : 38.33 mm), although the difference was only significant in 1984 (P<0.02).

The eggs contained only trace concentrations of the commonly encountered organochlorine pollutants (Table 6.IV). Mercury levels were

Table 6.IV Results of chemical analysis of 10 fresh Black Guillemot eggs collected in Shetland in 1983.

Ref. no.	Fresh egg wt. (g)	Shell Index	% Lipid of wet weight	HCH/HCB	HEOD	DDE	PCB	Hg
G571	46.7	1.50	7.54*	.06(.80)	ND	.14(1.86)	<0.1	3.32
G572	45.0	1.43	9.50	.08(.84)	ND	ND	.11(1.16)	2.26
G573	51.0	1.51	9.45	.06(.64)	ND	.22(2.34)	.34(3.62)	2.43
G574	51.6	1.93	8.54	.56(6.56)	ND	ND	<0.1	1.49
G575	42.1	1.53	8.44	.06(.71)	ND	ND	ND	1.17
G576	48.0	1.78	12.63*	.07(.55)	ND	.09(.71)	<0.1	1.63
G577	45.1	1.89	14.20	.05(.35)	.1(.7)	1.12(7.89)	<0.1	1.33
G578	53.4	1.74	8.84	.05(.57)	ND	.09(1.02)	.15(1.70)	2.16
G579	55.0	2.02	8.73	<.05	ND	ND	ND	1.76
G580	44.7	1.82	10.39	<.05	ND	ND	ND	1.59

Notes: Organochlorine concentrations are given as ppm wet weight (ppm in lipid is given in brackets).
Mercury (Hg) concentration given as ppm dry weight.
Shell index = weight of dry shell (mg) / egg length x breadth(mm)
HCH/HCB = isomers of benzene hexachloride.
HEOD = breakdown product of aldrin and dieldrin.
DDE = main metabolite of DDT.
PCB = polychlorinated biphenyls.
* = cracked in transit.

ND = none detectable.

also low, although insufficient is known at present to assess the toxic importance of these concentrations (M B Haas in litt.). It is unlikely that the trace levels of pollutants found in fresh Black Guillemot eggs from Shetland are having any damaging effect on the population at present. The % lipid of wet weight of intact eggs varied from 8.4-14.2 %. DDE is generally considered to be largely responsible for egg shell thinning (Cooke 1973). There was no relationship in this sample between shell index and the small DDE residues.

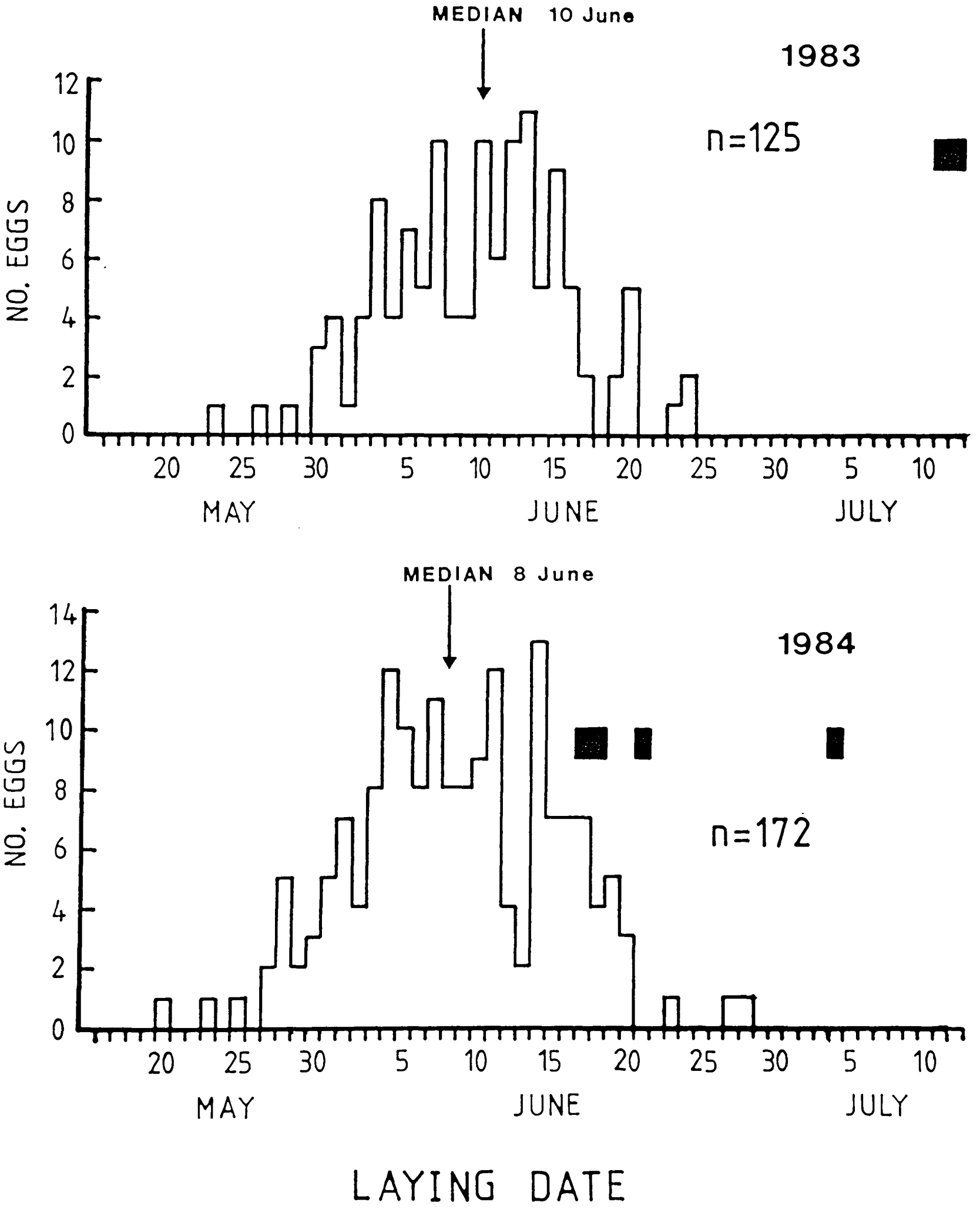
Multiple measurements of shell thickness made on 3 Black Guillemot eggs with a micrometer (accurate to 0.001 mm), confirmed the findings of Olsson (1936) with hens' eggs, that the shell was significantly thinner at the blunt end, and thicker at the pointed end, than in the middle zone. A longitudinal strip c.20 mm long was cut from the mid zone (ie. where shell curvature was minimal) of 25 eggs which had hatched successfully, and each crushed into many pieces 1-2 mm across. The thickness of 12 haphazardly selected fragments was measured for each egg (ie. shell + membrane thickness), broadly following the methods of Tyler (1961a,b). Similar measurements were made for 5 eggs, first with, then without the membrane attached, and the mean membrane thickness so deduced. For egg shell in the mid-zone, mean thickness ($\pm$ sd) of shell with membrane was 0.374 $\pm$ 0.015 mm (n=25). Mean membrane thickness was 0.101 $\pm$ 0.017 mm (n=5), and thus mean shell thickness was 0.273 mm. The corresponding values in Denmark varied from 0.26 to 0.29 mm for shell thickness, and 0.34 to 0.35 mm for shell with membranes (Asbirk 1978a).

6.4.2 Timing of laying

The laying of first clutches on Mousa spanned 5 weeks in 1983 and nearly 6 weeks in 1984. However, c.90% of eggs were laid during the first 3 weeks of June in both years. Although the median laying date was 2 days later in 1983 (10 June) than in 1984 (8 June), this difference was not statistically significant. In 1983 the first egg was laid on 23 May, and in 1984 on 20 May (by the same female) (Figure 6.4). However, when median laying dates of first eggs were compared in different clutch sizes, birds laying single eggs started laying significantly later than those laying two-egg clutches in 1983 (13 vs. 8 June; Mann-Whitney test, U=218; n=16, 68; $P<0.001$) and 1984 (11 vs. 7 June; U=342, n=15, 80; $P<0.01$).

Laying dates for 1982 were mostly back-calculated from the hatching date, which itself was subsequently estimated using the chick wing length

Figure 6.4 The timing of laying of Black Guillemot eggs on Mousa in 1983 and 1984.
Solid bars represent replacement clutches.



and the wing growth curves for 1983-84 (see Figure 7.1). The estimated median laying date of 43 eggs on Mousa in 1982 was 6 June, exactly the same as for a sample of 147 eggs on various other islands (island locations given in Ewins & Perrins 1982), indicating that the timing of breeding on Mousa was similar to that elsewhere in Shetland. The corresponding median dates of laying of the first egg in clutches on Mousa were: 6 June in 1982, 10 June in 1983, and 7 June in 1984. Since the frequency distribution of laying dates did not differ significantly from normality, mean laying dates have been used in the subsequent analyses.

Differences between colonies on Mousa

At 4 colonies with sufficient sample sizes, mean laying dates varied significantly between colonies in both years (Table 6.V). Laying at colony DN was significantly later than at other colonies in both years, possibly as a result of Otter predation of incubating adults there in 1982 (Chapters 5 & 8). Omitting this colony, mean laying dates still varied significantly between colonies in 1983 ($F = 4.2$; 2,82 df, $P<0.02$), but not in 1984 ($F = 2.3$; 2,107 df). The mean laying date for individual colonies were similarly ranked relative to the overall Mousa average, in both years.

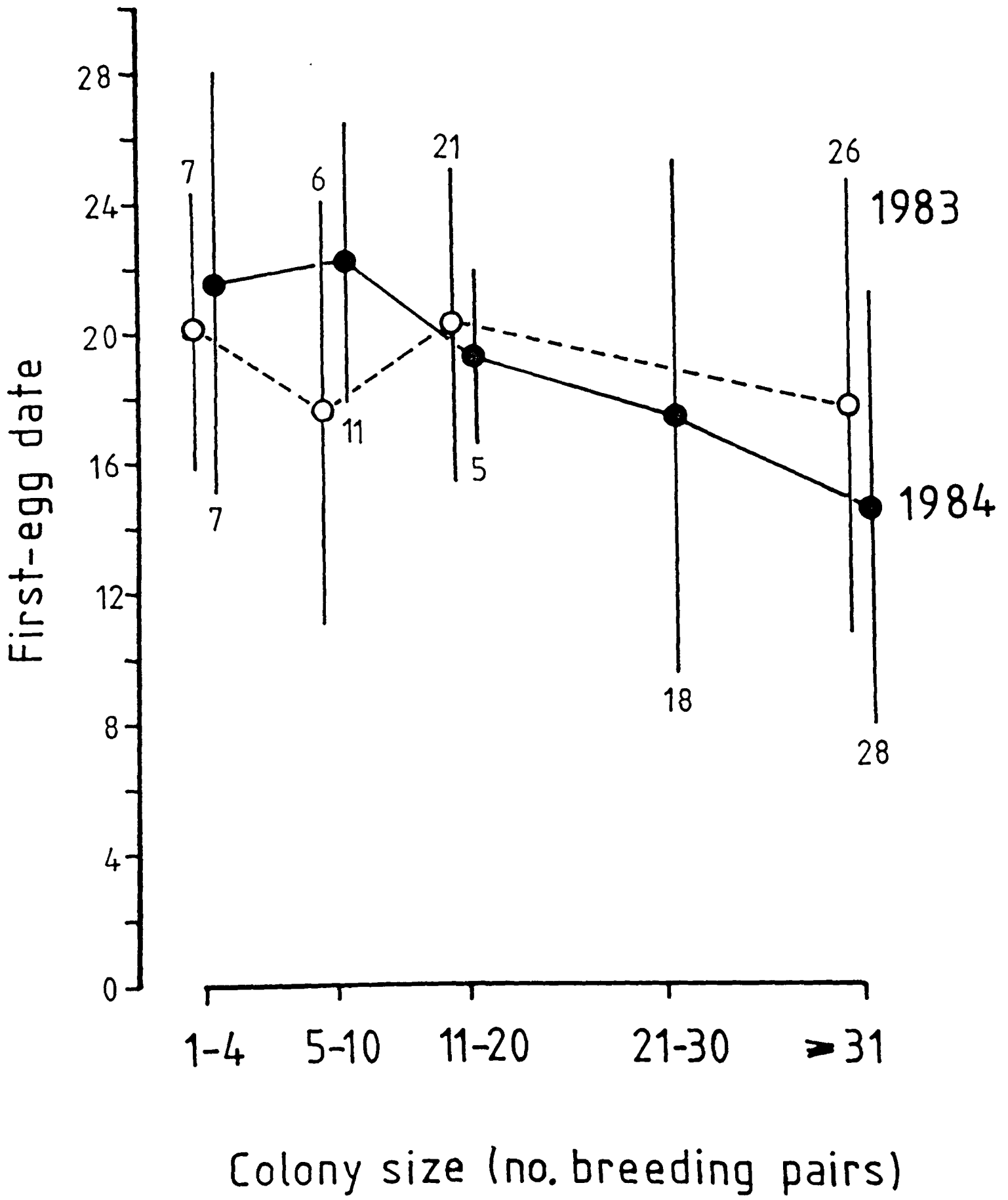
In 1984 there was a significant trend for earlier laying of first-eggs with increasing colony size ($r = -0.418$, 67 df, $P<0.001$), though no significant relationship was found in 1983 (Figure 6.5). For Razorbills, Lloyd (1976) similarly found a significant relationship in one year but not in another. However, colony size *per se* (ie. number of breeding attempts) may not be as important as other related factors. For example, colony size was significantly correlated with mean nest distance from the sea ($r = 0.85$, 12 df, $P<0.001$), and median nearest neighbour distance (NND) was smaller in the larger colonies, though not significantly so. Therefore a multiple regression analysis was performed on the data for each colony, with mean first-egg date (at each nest) as the dependent variable, and colony size, median NND, and mean nest distance from the sea (high water mark) as the independent variables. Overall a significant relationship was found ($F = 9.67$; 3,7 df, $P<0.01$), but the three variables accounted for only 24% of the variation. Both colony size ($P<0.02$) and mean distance from the sea ($P<0.01$) were significant variables, both negatively correlated with laying date, accounting for 9% and 13% of the variation respectively.

Table 6.V First-egg dates at nests in different Mousa colonies, 1983-84. Mean, sd (in days), and number of eggs are given.

	1983			1984		
Colony	Mean	sd	n	Mean	sd	n
A	7 June	6.9	45	5 June	6.7	66
CGQ	10 June	4.7	30	6 June	6.7	34
E	12 June	5.6	11	9 June	3.0	10
DN *	14 June	4.2	14	13 June	4.6	28
	F = 6.7, P<0.001			F = 11.3, P<0.001		
All Mousa	9 June	6.1	125	8 June	6.8	172

Note: * Otter predation of some nests in this colony in 1982 (see Chapter 8).

Figure 6.5 Mean first-egg dates in colonies of different size, 1983 (open circles) and 1984 (closed circles). Standard deviation (bars) and sample sizes are given. First-egg date of 0 = May 20th.



A multiple regression analysis of laying date of first-eggs against a variety of physical characteristics of each individual nest site (see Chapter 8 for details) revealed that only nest distance from the sea ($P<0.01$) and height above sea level ($P<0.02$) were significant variables, accounting for only 6.4% and 2.3% respectively of the variation however. For the key physical characteristics of the cavities themselves (see Table 8.VI) the maximum vertical dimension of the nest entrance proved to be significantly smaller in colonies A and CGQ than elsewhere on the island (11.5 vs. 14.0 cm, $U = 548$, $n=60, 26$, $P=0.03$), reflecting the low, flat sandstone slabs above nest scrapes there.

Laying was earlier at larger colonies and was more protracted (Table 6.V, Figure 6.6), although the regression of standard deviation of mean first-egg dates against colony size was not significant ($r = 0.43$, 9 df). Similarly no significant relationship existed between standard deviation of mean laying dates and median nearest neighbour distances for the different colonies, ie. nest density had no significant affect on laying dates. However, the significant increase in total spread of first-egg laying dates with the logarithm of colony size (Figure 6.6) indicated greater laying synchrony in the larger colonies. Breeding synchrony is discussed later in relation to possible selective advantages such as swamping of predators and kleptoparasites, and the 'Fraser Darling effect' (Darling 1938).

Differences between years

Laying was earlier in 1984 than 1983 (Figure 6.4). Although there were significant colony differences in mean laying dates, this factor did not account for the overall difference between years since the number of nests sampled in each colony did not vary significantly between years ($G = 2.1$, 4 df). Another way of looking at this difference is to compare first-egg dates at the same nest in the two years. There was a significant positive correlation between the laying dates of first eggs in the two years, and the regression line differed significantly from $y=x$ ($t = 3.23$, 50 df, $P<0.01$) (Figure 6.7). A mate change, or new pair at a site did not necessarily delay laying. A similar conclusion was reached by Asbirk (1979c), contrary to results for other seabirds (eg. Coulson 1966; Davis 1976).

Strong winds cause heavy seas and increased water turbulence and might well reduce the foraging success of Black Guillemots, although this has been properly demonstrated for only a few seabirds (eg. Dunn E.K. 1975;

Figure 6.6 The spread of first-egg laying dates in relation to log. colony size (given as the number of breeding attempts). Data for 1983 (closed circles) and 1984 (open circles).

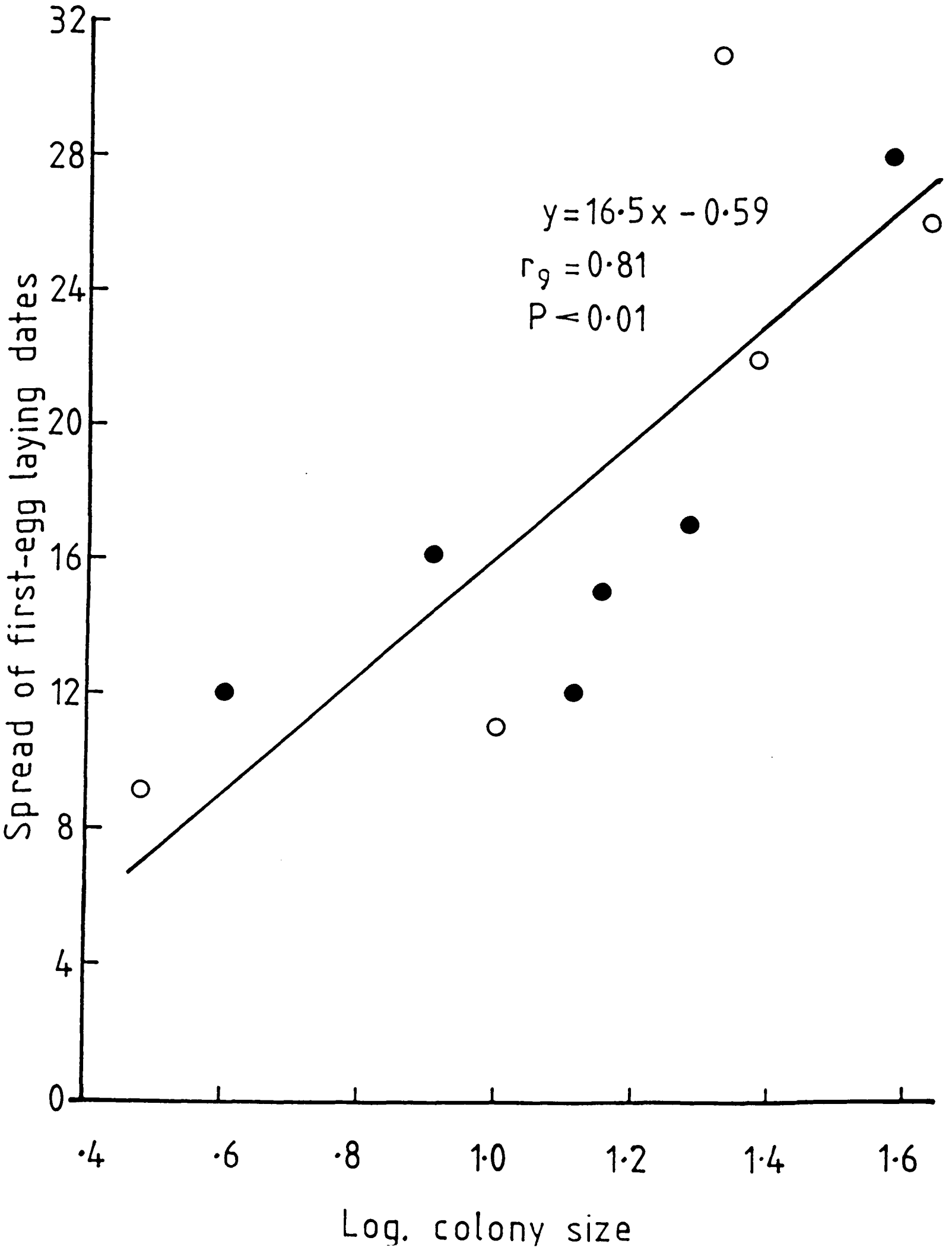
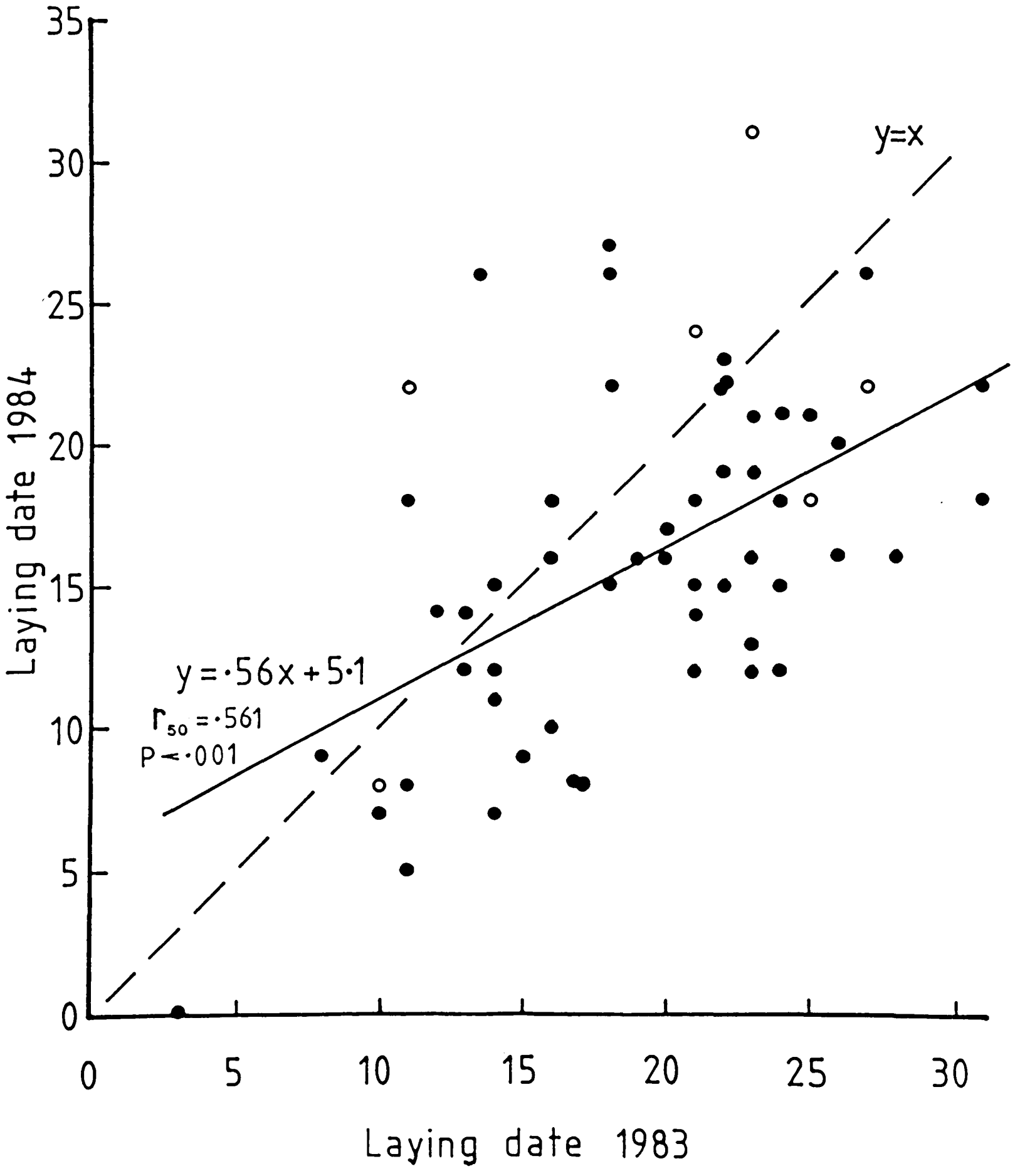


Figure 6.7 Comparison of dates of laying of first-egg at sites in 1983 and 1984. May 20 = Day 0. Filled circles = no known change of birds at site; open circles = definitely not the same pair in both years.



Birkhead 1976). Reduced air temperatures will also increase energy demands via increased heat loss. Therefore I investigated the effect of annual variations in wind speed and air temperature in the pre-laying period on the mean laying date. Since egg formation in the auks appears to take 2-3 weeks [Asbirk 1979c; Petersen 1981; Harris & Birkhead 1985; Birkhead & del Nevo (in press)], I analysed mean daily wind speeds and minimum day-time air temperatures in the period 10-31 May to assess the influence on laying dates of weather conditions during the egg formation period. Both wind speed and temperature varied significantly between years; late laying was associated with stronger winds and lower day-time temperatures (Table 6.VI). In most months average sea-surface temperatures varied little between the study years (Appendix III), but the sea-surface in April 1984 was slightly cooler (6.9°C) than in 1983 (7.5°C).

The frequency of copulation attempts increased during the month, reaching a plateau during the third week of April (Figure 6.8). The mean (± sd) duration of 99 copulations was 41.2 ± 28.6 s, ranging from 2-147 s, but most were 10-80 s in length. For 14 recognisable pairs in colony A, the mean (± sd) interval between the first observed copulation attempt and date of laying of the first egg was 45 ± 4 d (range 37-52 d). There was a significant positive relationship between the first observed copulation and the first egg date (Figure 6.9), indicating that birds laying earlier came into breeding condition earlier. Female condition may be important in addition to weather conditions and food supply, perhaps even as early as April.

The average interval between laying of eggs in two-egg clutches was 3.2 d in 1983 but only 3.0 d in 1984. Although this difference was not quite statistically significant ($t = 1.959$, 134 df), it did lend support to the idea that feeding conditions in the pre-breeding period may have been better in 1984, enabling females to lay the b-egg sooner and commence incubation slightly earlier than in 1983. There was no significant relationship between the laying of first and second eggs in either year. However, in both years the fresh-egg weight difference (a - b eggs, divided by the a-egg weight, to control for egg size variation between females) decreased with increasing laying interval, although the correlation was only significant in 1984 ($r = -0.309$, 42 df, $P<0.05$). In other words, a greater interval between laying of a and b eggs resulted in a smaller fresh-egg weight difference within the clutch (N.B. the b-egg was heavier than the a-egg in 8% of clutches).

Table 6.VI Mean laying dates on Mousa, 1982-84, in relation to weather conditions in the pre-laying period 10-31 May (as measured at Lerwick Met. Stn., 15 km north of Mousa).

Year	Mean first-egg date	WIND (knots) [a] Mean	sd	range	TEMPERATURE (°C) [b] Mean	sd	range
1982	6 June	9.8	3.4	4.7-18.2	7.6	1.6	3.7-10.3
1983	10 June	13.4	6.1	5.4-28.2	6.7	0.7	5.5-7.8
1984	7 June	11.4	4.0	6.5-20.1	6.8	1.1	4.4-8.1
		F = 3.46, P<0.05			F = 3.9, P<0.05		

Note: [a] Daily mean of mean hourly wind speeds.

[b] Minimum day-time temperature.

Figure 6.8 Daily variation in the number of copulation attempts recorded during the morning attendance at colony A in 1984.

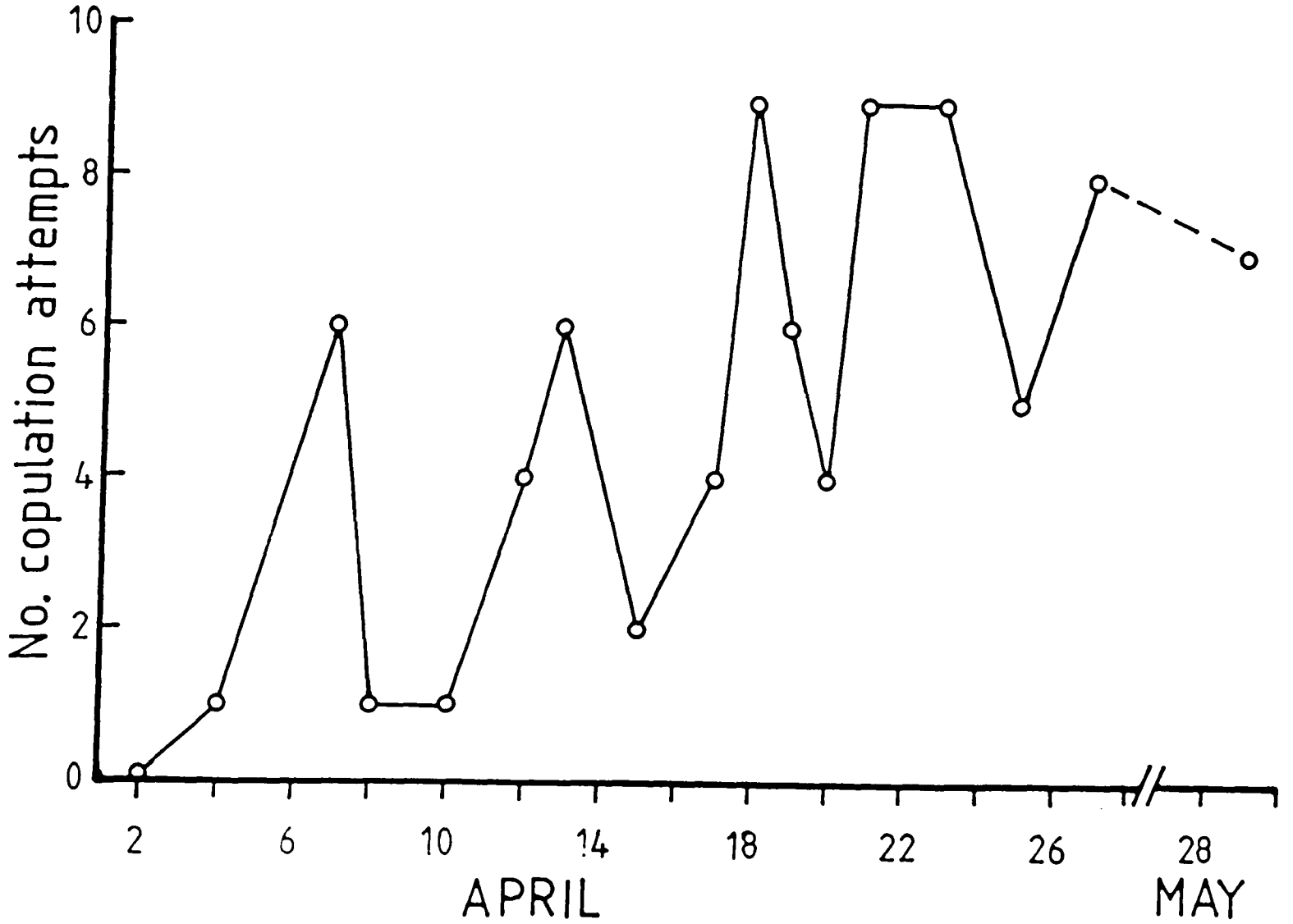
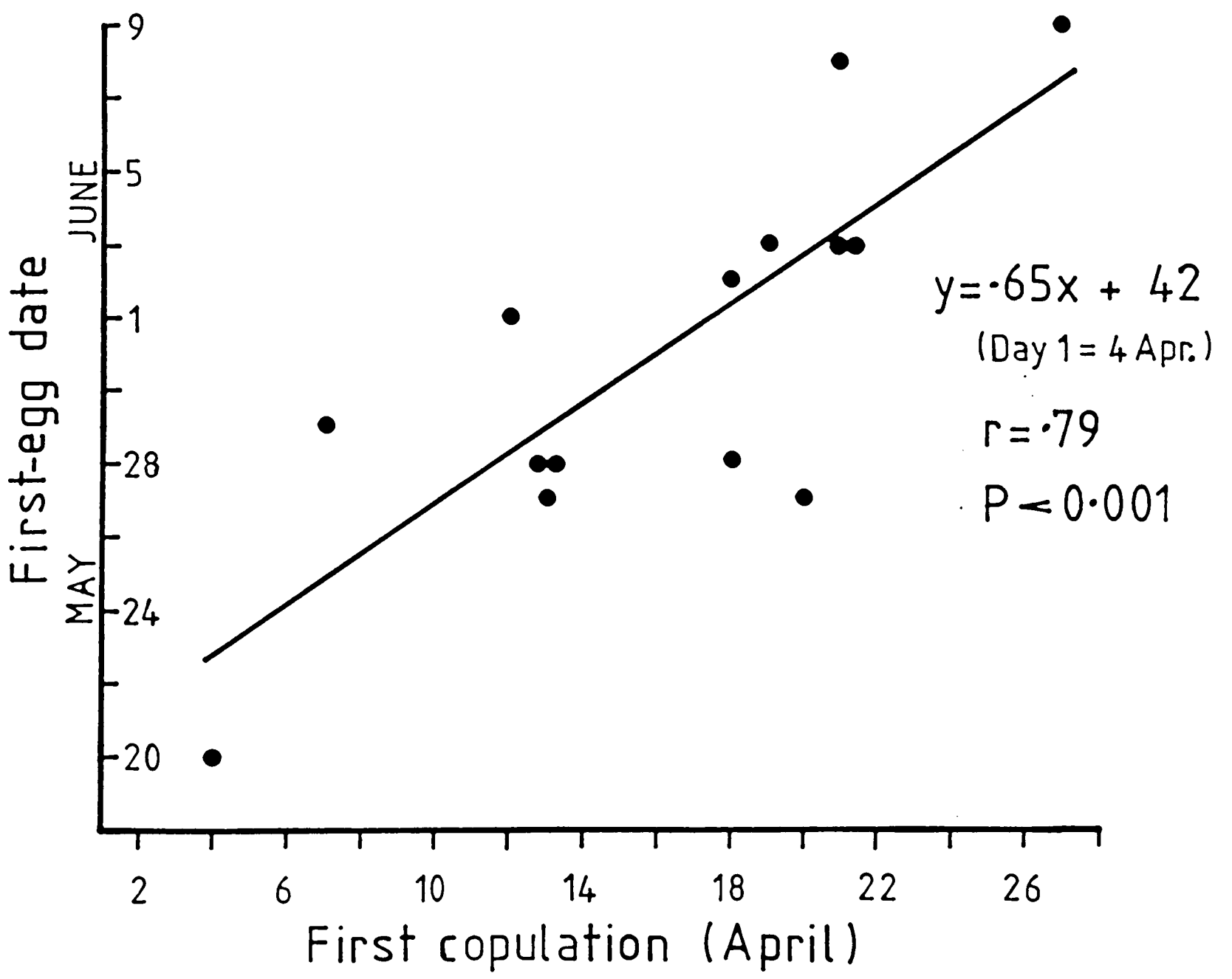


Figure 6.9 The relationship between dates of laying of first-egg and first attempted copulation for 14 pairs at colony A in 1984.



When all eggs were pooled, irrespective of clutch size (there was no significant difference between years in the proportion of c1:c2 eggs measured), there was a trend for decreasing fresh-egg weight with later laying in both years (Figure 6.10). Although the differences between laying periods were not significant for either year overall, eggs in 1984 were significantly heavier than in 1983 ($F = 6.83$; 1,178 df, $P<0.01$).

6.4.3 Incubation

To assess the extent of incubation of the a-egg prior to laying of the b-egg in two-egg clutches, the a-egg temperature was scored as cold or warm during each afternoon nest-check. Each clutch was then placed in a category according to the proportion of days on which the a-egg was warm, vis: cold each day; warm on 1/4 - 1/3 of the days; warm 1/2 - 2/3 of days; warm each day. Since the proportions of clutches in each category did not vary significantly between years ($G = 2.06$, 2 df), results from 1983 and 1984 were pooled. In a total sample of 72 two-egg clutches, the a-egg received no prior incubation in 50%, a little in 28% (ie. warm on 1/4 - 1/3 of days), a substantial amount in 15%, and apparently full incubation in 7% of cases (ie. a-egg warm whenever checked).

Full incubation usually started within a day of laying of the last egg in a clutch. In 12 single-egg clutches full incubation started on average ($\pm$ sd) 0.67 ± 0.89 d (range 0-2 d) after laying, whereas in 88 two-egg clutches the mean for a-eggs was 2.94 ± 1.53 d (range 0-9 d) and 0.40 ± 1.03 d (range 0-6 d) for b-eggs. The amount of incubation of the a-egg prior to the laying of the b-egg affected the degree of hatching asynchrony (see below). Although not significantly different, the onset of incubation in single-egg clutches was slightly delayed, perhaps due to some 'uncertainty' over the laying of a second egg.

Some eggs initially received intermittent incubation. Therefore I have taken the 'incubation period' to be the interval between the laying and hatching of an egg. For two-egg clutches in 1984 the average incubation period was shorter for both a and b-eggs than in 1983, but longer for single-egg clutches (Table 6.VII). There were no significant differences between years, nor between single eggs and b-eggs in two-egg clutches, in either year. Eggs which were infertile, or in which the embryo had died, were incubated significantly longer (mean incubation time 35.6 ± 7.5 d, n=10, maximum recorded = 48 d) than successful eggs in clutches of 1 or 2 eggs, in either year (see Table 6.VII), ($P<0.001$).

Figure 6.10 The seasonal decline of fresh egg weights in 1983 (open circles) and 1984 (filled circles). Mean, standard error and sample size given for each 7-day period. Period I = 20-26 May; II = 27 May - 2 June etc., V = 17-23 June.

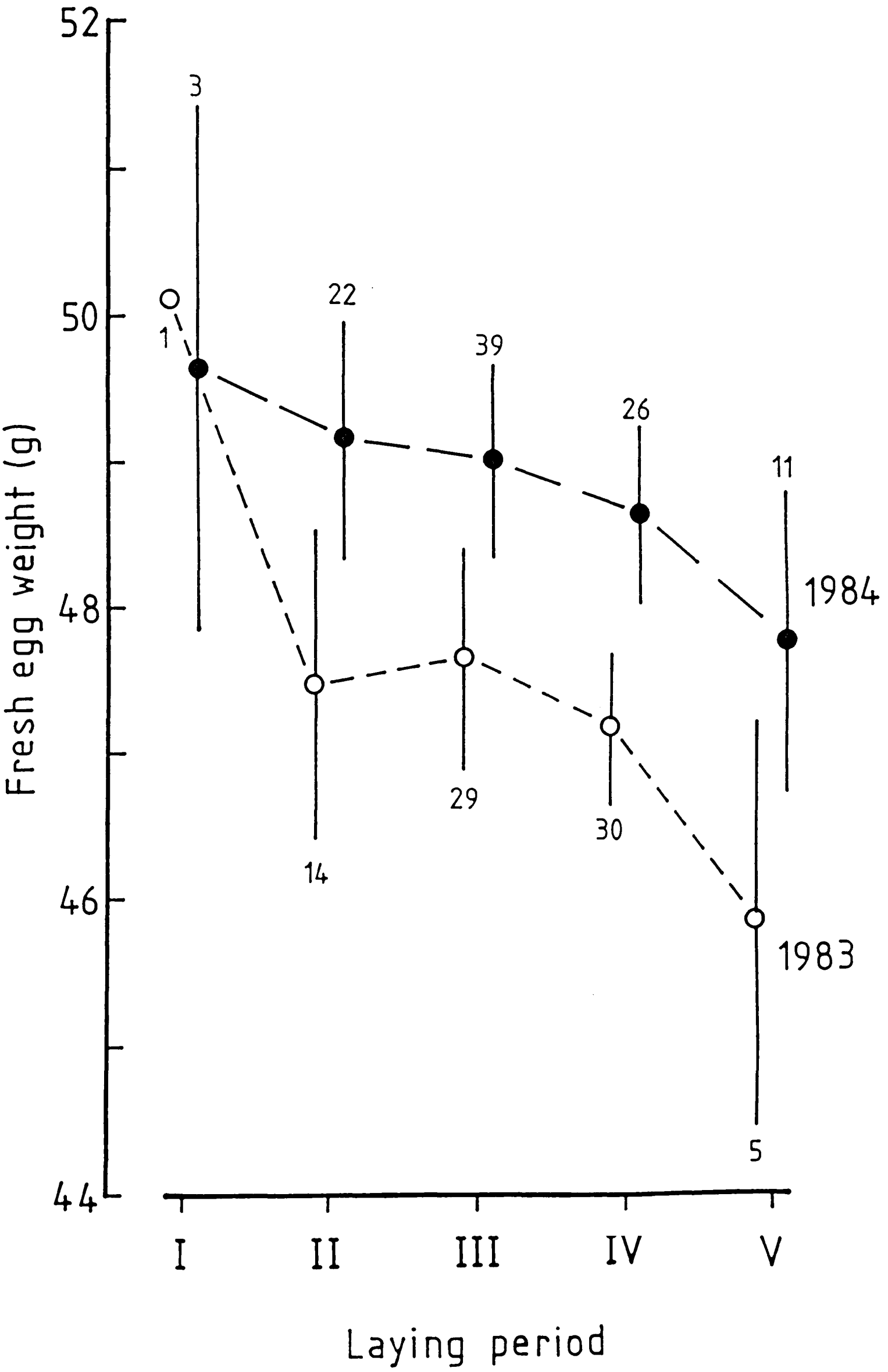


Table 6.VII The length of the incubation period (days) on Mousa, 1983-84.

	1983		1984	
1-egg clutches:				
Mean	28.1		29.0	
sd	1.6		1.6	
n	7		4	
range	26-31		27-31	
2-egg clutches:	a-egg	b-egg	a-egg	b-egg
Mean	30.4	28.2	29.9	27.8
sd	1.7	1.4	1.6	1.4
n	39	39	55	55
range	28-36	26-33	27-35	26-33

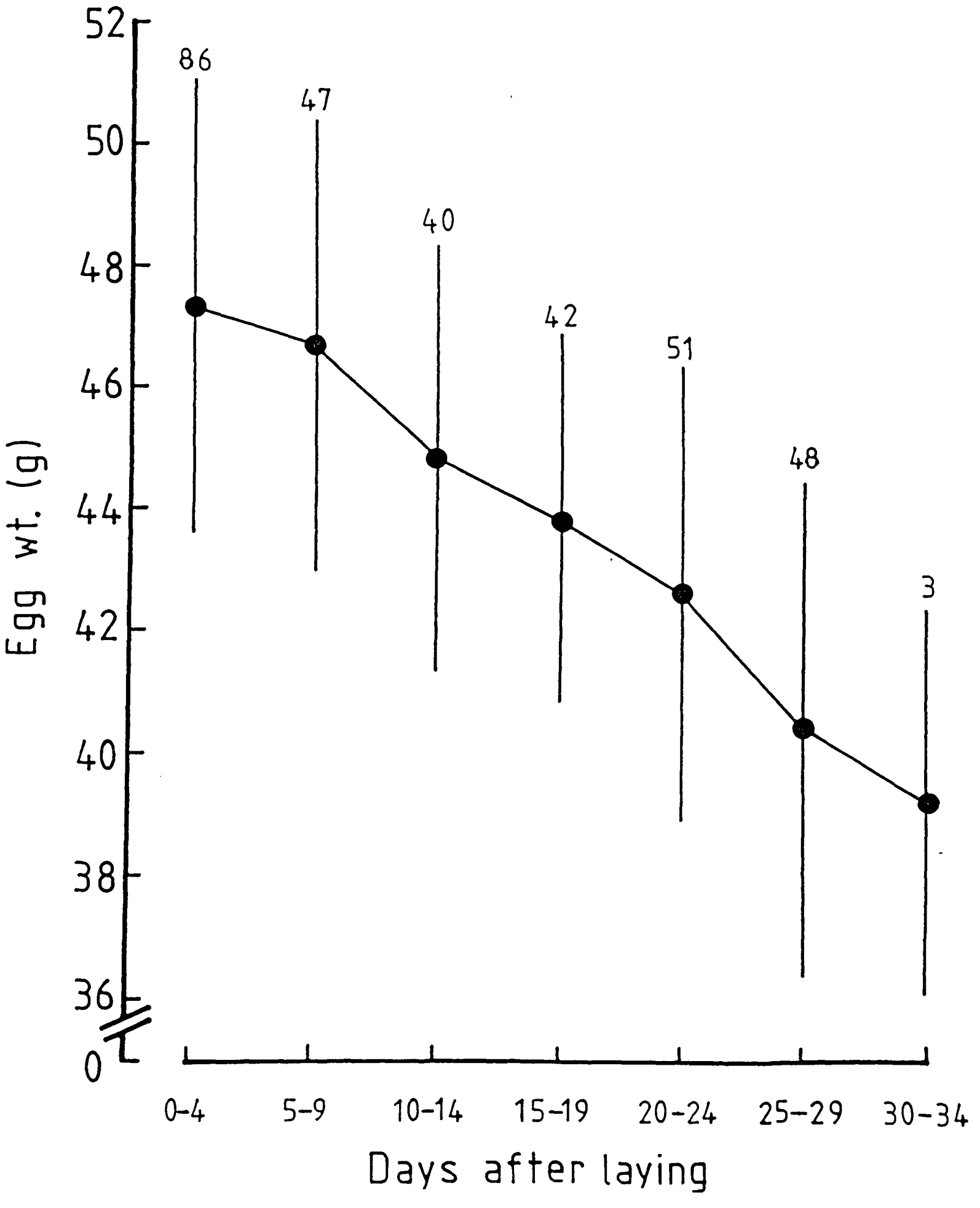
There was no significant relationship between the incubation period and laying date, ambient temperature, or egg volume. There were no significant differences between colonies, despite the much heavier tourist disturbance at colony CGQ.

Although no systematic study was made of incubation shifts, incidental observations suggested that during the day most shifts were 1-3 hours in length, but birds sat for much longer overnight. On 24 occasions during daylight hours and 10 occasions at night the sex of the incubating bird was known. There was no evidence for sex difference in the diurnal pattern of incubation (G = 0.2, 1 df). Overall, males and females took an equal share of incubation duties.

The hatching sequence proceeds from 'starring' (cracking visible towards the blunt egg of the egg), to 'pipping' (shell actually pierced, although internal membranes are not always broken immediately), to hatching (chick completely free of the shell). In a sample of 36 eggs the mean (± sd) interval from first visible starring to pipping was 1.2 ± 0.4 d, and a further 1.3 ± 0.5 d to hatching, ie. a total of 2.5 d on average. The weight of eggs hatching successfully declined steadily during incubation (Figure 6.11). Average weight of 134 eggs at Day 29 (excluding 'pipped' eggs) was only 85.4% of the fresh weight, representing a decline of 14.6% - slightly higher than values obtained in other studies (Dennis 1966; Asbirk 1979c; Petersen 1981). The average weight decline of 15 eggs just 'starring' was only 12.7% however, suggesting that weight loss accelerated once the shell was cracked, possibly due to loss of water vapour. Weight loss greatly accelerated once the shell had pipped; average weight of 10 pipped eggs was 17.3% of fresh weight. This high figure is similar to that given by Belopol'skii (1957), supporting the presumption of Petersen (1981) that Belopol'skii's figure included pipped eggs.

In two-egg clutches the interval between hatching of a and b-eggs could be crucial to the subsequent growth and survival of the b-chick, particularly if food is scarce. Despite being laid usually 3 days earlier, the a-egg hatched on average 0.91 ± 0.58 d (n=93) before the b-egg. For these clutches (both years combined since no significant difference between years), in 18% both eggs hatched on the same day, in 69% the a-egg hatched 1 day earlier, in 12% 2 days earlier, and in 1% the b-egg hatched a day before the a-egg. Although a greater laying interval led to a slighty increased hatching interval, the relationship was not significant (r = 0.11, 91 df). However, incubation of the a-egg prior to laying of the b-egg led to significantly greater hatching asynchrony. Mean hatching

Figure 6.11 Egg weight decline during incubation, for eggs hatching successfully in 1983. Weights of 'pipping' eggs not included. Mean, standard deviation and sample size are given for each 5-day period.



interval (± sd) for clutches in which the a-egg received little or no prior incubation was 0.73 ± 0.57 d (n=33), but significantly longer (1.45 ± 0.52 d, n=11) when the a-egg received moderate or full prior incubation (t = 3.7, 43 df, P<0.001).

6.4.4 Replacement eggs

Only 4 (11%) of 36 pairs whose clutches were abandoned or predated laid replacement eggs. First clutches of those pairs laying replacements had all received some incubation, abandonment occurring between 1-29 June. The 5 replacement eggs were laid after a mean interval (± sd) of 14.6 ± 2.7 d (range 11-18 d). In contrast, at 4 (67%) of 6 nests where clutches were collected within a week of laying (between 29 May and 10 June), replacements were laid. The average replacement interval at these nests was again c.14 days. Replacement clutches on Mousa were always laid in the original site, possibly because suitable alternative sites were not readily available. Asbirk (1979c) and Petersen (1981) both noted that clutches lost or deserted early in the incubation period were more likely to be replaced than those failing later on.

6.5 Discussion

Feeding conditions for Black Guillemots on Mousa appeared to be poorer in 1983 than in 1984, particularly during the early part of the breeding season. In 1983 fresh-egg weight and volume were significantly lower, laying was significantly later, the interval between laying of the a and b egg was longer, and adults were significantly lighter (post-laying) than in 1984. However, average clutch size and breeding success was no different, and the main result appeared to be an increased proportion of breeding attempts by inexperienced birds, tending to lay single-egg clutches, with subsequent poor hatching and breeding success (Chapter 8).

Various factors (such as body size, age, previous breeding experience, and mate change), may contribute to observed variations in laying date, egg size and clutch size between years or between individuals, but environmental conditions in the pre-laying period (usually affecting food availability) are probably of prime importance (Perrins 1970). The physiological drain on females forming eggs is usually considerable, a clutch of two representing 24% of Black Guillemot body weight. Not only must the female acquire sufficient reserves to form the clutch, but her

body condition must be good enough to withstand the additional stress of incubation (Brooke 1978). A number of studies have demonstrated the importance of food supply and female condition in the pre-laying period to clutch and egg-size (Nisbet 1973, 1977; Ankney & MacInnes 1978; Jarvinen & Ylimaunu 1986), the timing of laying (Yom-Tov 1974; Kallander 1974; Drent & Daan 1980), and breeding success (Houston et al. 1983). Although it was impossible to directly assess food availability to Black Guillemots, it is likely that stronger winds and lower temperatures in the 1983 pre-laying period made it more difficult for females to reach breeding condition. Those that did laid on average smaller eggs, and at later dates than in 1984. In other auks, delayed laying has been attributed to rough seas in the pre-laying period of Razorbills (Lloyd 1979), and reduced pre-laying air temperatures for Baltic Guillemots (Hedgren 1979).

The significance of slightly lower sea-surface temperatures in the 1984 pre-laying period, in relation to the timing of breeding, is difficult to assess since so little is known of the activity of the prey species in different oceanographic conditions. Changes in sea temperature could affect different Black Guillemot prey species in different ways. For example a decline in spring sea temperature led to increased survival of young Cod Gadus morrhua (a gadoid) in the North Sea (Dickson et al. 1975), whereas cooler May-June seas caused Eelpout Zoarces viviparus to move to deeper waters in the Baltic, resulting in breeding failure of the Black Guiilemots there, which usually depended on this species (Bergman 1978).

Amongst North Atlantic auks there is a significant negative relationship between median hatching date and mean August sea-surface temperature [Figure 4.1 in Birkhead & Harris (1985)]. The corresponding data points for Mousa (12.2°C in 1983, and 12.7°C in 1984) lie just above the auk regression line.

As Salomonsen (1943) had originally suggested, it is likely that sea temperature exerts an important proximate control on the timing of auk breeding, probably via food availability, whereas factors such as ice conditions, age and previous experience of adults, and local fluctuations of prey populations may also be important in certain circumstances, affecting the timing of breeding of individuals relative to the population mean.

Throughout the nestling period in 1984, chick feeding rate and energy input was much higher than in 1983 (Chapter 9), indicating that food was more readily available through the whole season. However, the reverse

pattern was evident for Arctic Terns breeding on Mousa (and feeding largely on sandeels nearby). A successful, early breeding season in 1983 contrasted with a disastrous, later breeding season in 1984. This difference was attributed to food supply, rather than to adverse weather conditions affecting small chicks (Ewins 1985c). Much more information is required of fish stocks and their responses to fluctuating environmental conditions, before any further understanding of the food supply in relation to the birds' breeding is possible.

The protracted laying period of 5-6 weeks is fairly typical for Atlantic alcids, but the frequency distribution of laying dates is more normal than that of most other auks (which are skewed to the right) (Gochfeld 1980; Birkhead & Harris 1985). Laying tended to be synchronized within colonies on Mousa, the effect being consistent from year to year, indicating some real differences between colonies. The significantly later laying in colony DN appeared to be due to an Otter killing incubating adults there in 1982. In 1983 the number of breeding attempts was reduced there, and later laying in newly-formed pairs probably accounted for much of the delayed laying. However, even omitting this special case, there was still asynchrony between colonies.

Although predation of nests or adults could be a strong selective pressure leading to breeding synchrony in other areas this was unlikely to have been important on Mousa. Rather it may have allowed some swamping of kleptoparasites, since some Arctic Skuas obtained most of their food from food-carrying Black Guillemots (Chapter 10). Although no 'clumping' of deliveries could be demonstrated on Mousa, it is possible that high kleptoparasitic pressure at some colonies confers some selective advantage on Black Guillemots breeding at the same time as their neighbours. The "Fraser-Darling Effect" (Darling 1938) predicts that birds breeding in larger groups receive greater social stimulation than those breeding in a small group. This hypothesis has sometimes been presented to explain greater laying synchrony in denser breeding aggregations, although it is difficult to test rigorously. Although there was some evidence of greater breeding synchrony in larger colonies on Mousa, neither my results nor those of Petersen (1981), in Iceland, lend any concrete support to these ideas.

In many bird species later nesting by young birds is well established (Coulson & White 1956; Coulson 1966; Haartman 1967; Coulson & Horobin 1976; Mills & Shaw 1980; Nisbet *et al.* 1984), and in an expanding Icelandic Black Guillemot colony, Petersen (1981) considered that asynchrony between

nesting areas was primarily the effect of different age structures. The population on that Icelandic study island had been increasing dramatically due to immigration, whereas in Shetland there was no evidence of any such dramatic changes. Clearly, in a stable population it is more likely that first-time breeders just fill in the gaps in colonies, created by deaths. An analysis of egg breadth (commonly used as an indicator of female age) in each year in each colony failed to detect any significant differences between colonies, suggesting that Mousa colonies did not differ markedly in age structure.

Earlier laying in colonies A and CGQ, where nests are beneath flat slabs at some distance from the open sea suggests that the sites may have been occupied by better quality birds. Nests were deeper and their entrances lower than in other colonies, and I suspect that most sites were of higher quality due to their inaccessibility to nest predators such as Hooded Crows and gulls.

CHAPTER 7. BREEDING BIOLOGY: THE CHICK STAGE.

7.1 Introduction

The Alcidae are unusual amongst bird families in having such a wide range of developmental strategies, from the precocial murrelets (Brachyramphus and Synthliboramphus species), leaving the nest at c.14% of adult weight, to the 'intermediate' murres (Uria species) and Razorbill which leave the ledges at 15-30% of adult weight, and the semi-precocial species such as puffins (Fratercula species), Auklets (eg. Aethia species) and Cepphus species, which fledge at 67-91% of adult weight (Sealy 1973; Gaston 1985b). The young of Black Guillemots are completely independent upon leaving the nest, and so one might expect fledging condition and date to be more crucial than for species having some post-fledging parental care.

There is evidence in some birds that post-fledging survival increases with fledging weight (Perrins, Harris & Britton 1973; Jarvis 1974; O'Connor 1976) and earlier fledging (Perrins 1965, 1966; Nisbet & Drury 1972), but studies of auks have so far been unable to demonstrate any such effects (Lloyd 1979; Hedgren 1979, 1981; Harris 1982; Harris & Rothery 1985). Although I was unable to investigate post-fledging survival in this study, I detail events and growth parameters during the chick stage in this chapter, and examine the differences between years in relation to various factors such as egg size, brood size, kleptoparasitism, timing of breeding and weather conditions.

7.2 Methods

Wing lengths were measured to the nearest mm with a stoppered rule, using the maximum flattened chord technique (Svensson 1984). For small chicks the fluffy tips to the remiges were excluded. Wings of freshly dead immatures found on Shetland and Orkney beaches between August and February were measured to assess post-fledging wing growth.

'Fledging' is taken to mean nest leaving, although the young are probably incapable of sustained flight then (Petersen 1981). The fledging period is the total time spent by the chick in the nest. Particularly thorough searches were made when chicks were due to fledge, since some occasionally moved to nearby cavities. The a-chick is taken to be the

first to hatch, and the b-chick the second, in two-chick broods. The day of hatching was taken as the first afternoon a chick appeared, although some could have hatched the previous night.

7.3 Results

7.3.1 Hatching, brooding and chick behaviour

The mean (± sd) interval between hatching of chicks in 93 two-chick broods was 0.91 ± 0.58 d, but 12% hatched 2 days apart (Chapter 6). Adults normally sat very tight during the hatching stage, and continued to brood small chicks, especially in cool and wet weather. Both sexes were recorded on the nest during hatching. During my afternoon nest visits the brooding bird disturbed was a male on 7 occasions and a female on 8 occasions, indicating no significant sex difference in day-time brooding behaviour (G=0.1). Both sexes were noted brooding overnight. Although adults sometimes remained in the nest chamber with large chicks, brooding was only recorded for chicks 0-6 days old. In a sample of 29 chicks being brooded, 62% were 0-1 d old, 28% 2-3 d old, 7% 4-5 d old, and 3% 6 d old; ie. 90% of chicks brooded were 0-3 d old.

Hatched shells usually ended up at the rear of the nest cavity, but on two occasions adults emerged from the nest with the hatched shell in the bill, and deposited it within 1 m of the nest entrance. The only other instances of adults with items other than fish in the bill were 2 cases of 'drawing' small pebbles back across the shoulder/scapulars, in the manner of Lari. This behaviour was also noted only rarely by Asbirk (1979c), and it is unlikely that any carrying of nest material normally occurs in this species.

Chicks were very mobile within nest cavities after 3-4 d old, and usually ran to the darkest recesses upon disturbance. In 2 cases a chick within a week of fledging moved to an adjacent cavity. Food-begging calls of chicks older than c.2 weeks were often loud and occasionally made from the nest entrance. On rare occasions chicks rushed into full view at the nest entrance to receive fish. Wing exercising in the few days prior to fledging was also performed in the nest entrance of smaller cavities; although noted at all times of day, intensity increased at dusk. No chicks were seen to depart from nests during daylight or dusk watches at colony A - their absence the following day infers that they left under cover of darkness. At that time all the breeding adults were roosting communally on

the offshore stacks and it is very unlikely that any adults accompanied fledglings to the sea. Young were never seen to return to the colony after fledging.

7.3.2 The fledging period

In 1983 hatching on Mousa spanned a period of c.5 weeks, from 23 June to 26 July, with the median hatching date 9 July (n=107). In 1984 the range was also c.5 weeks (21 June to 27 July), but the median hatching date fell 2 days earlier, on 7 July (n=135). Hatching dates in 1982 were estimated from wing measurements of chicks on various islands (see Ewins & Perrins 1982) using the Mousa growth data (Figure 7.1). These gave an estimated median hatching date of 6 July for 1982 (n=153, range 23 June - 28 July).

On Mousa the median fledging date was 13 August in 1983 (n=93, range 4½ weeks: 26 July - 25 August), and 12 August in 1984 (n=114, range 5 weeks: 26 July - 29 August). However, a few chicks fledge in early September, since in other parts of Shetland I have seen adults flying to colonies with fish then.

The mean (± sd) fledging period was 36.0 ± 2.4 d (n=83, range 32-43 d) in 1983, and 36.1 ± 2.8 d (n=105, range 32-53 d) in 1984. Although there was a tendency for b-chicks to spend slightly longer in the nest than a-chicks, the difference was not significant for any colony or year. Similarly there was no significant difference between fledging periods of chicks in broods of one or two, nor between 1983 and 1984 for the same brood size. These values are similar to those found in Canada (Cairns 1978), but over 2 days longer than the fledging period in Iceland (Petersen 1981) and 2-3 days shorter than in Denmark (Asbirk 1979c) and Finland (Bergman 1971).

In 63 two-chick broods for which the hatching order was known, the older chick fledged first in 27 (43%), the younger chick in 25 (40%), and in 11 (18%) the chicks fledged on the same day. Siblings fledged within 2 days of each other in 70% of the 52 broods for which departure was not on the same day. The longest interval was 12 days, and involved a runt b-chick in colony CGQ which received little food until its sib fledged.

Few factors seemed to affect the fledging period. Although chick diet and energy intake differed in 1983 and 1984 (Chapter 9), the fledging period did not differ significantly between years. Similarly the mean fledging period in colonies with higher rates of kleptoparasitism was not

significantly extended. However, b-chicks overall had slightly longer fledging periods than a-chicks (36.1 vs. 35.7 d in 1983, and 36.9 vs. 35.7 d in 1984). In colony CGQ the mean fledging period of b-chicks was 1.3 days longer than that of a-chicks in 1983, and 2.3 days longer in 1984 (although none of the differences were significant). The average daily ambient air temperature between the median hatching date and median fledging date (9 July - 13 August in 1983, 7 July - 12 August in 1984) was very similar in 1983 (11.7°C) and 1984 (11.4°C).

Evidence that sibling competition for fish deliveries can affect the fledging period, particularly when food is in short supply (either due to fish scarcity, or as a result of kleptoparasite activities), was provided by two b-chicks in colony CGQ. Although they hatched only 1 day after their sibs, growth was retarded, probably due to the proximity of both nests to Lesser Black-backed Gull territories in which the adult gulls regularly attempted to pirate fish brought in by the Black Guillemots, resulting in reduced provisioning rates. In both instances growth accelerated markedly once the a-chick had fledged. Both chicks fledged at well below the normal b-chick fledging weight, and the fledging periods were extended to 43 and 53 days. In two-chick broods the difference between the fledging period of a- and b-chicks increased with the hatching interval. When chicks hatched on the same day the a-chick fledged on average 1.6 d earlier; when hatched 2 days earlier it fledged on average 3 d before the b-chick. There was considerable variation between nests however, and it is unlikely that any shortening of the fledging period due to size advantage of the older chick confers a major advantage on the chick fledging first.

To investigate the effect of timing of breeding, fledging period was regressed against hatching date. A weak positive, but non-significant, relationship was evident in both 1983 ($r = 0.09$, $n=105$, n.s.), and in 1984 ($r = 0.15$, $n=105$, n.s.), providing no support for the suggestion that young hatched later in the season have shorter fledging periods (Belopol'skii 1957).

7.3.3 Chick growth.

The average wing length and weight of chicks on the day of hatching were both greater in two-chick broods than for single chicks, although none of the differences were significant. Both wing length and weight at hatching were greater in 1984 than in 1983, but the differences were only

significant for wing length (Table 7.I). In both years a-chicks in two-chick broods hatched slightly heavier than b-chicks, but since the differences were non-significant the results were pooled.

The pattern of wing growth differed little between years or in different brood sizes, and the form of the growth curve was characteristically slightly sigmoid (Figure 7.1). Mean wing length (± sd) at fledging was 135.3 ± 4.3 mm (n=73, range 127-147 mm) in 1983, and 134.7 ± 4.7 mm (n=89, range 121-151 mm) in 1984 (results were pooled for all chicks since there were no significant differences with brood size or hatching order). Analysis of wing lengths of freshly dead immatures suggests that wing growth continues post-fledging, until early September (Figure 7.2). The mean (± sd) wing length of 14 immatures found freshly dead between September and June in Shetland, was 154.4 ± 3.3 mm, whereas that of 64 Shetland breeding adults was 161.8 ± 3.4 mm, highly significantly greater ($t = 7.41$, 76 df, $P<0.001$). Thus, although Petersen (1981) considered that "full adult wing length would be gained about 10 days after fledging", these Shetland results indicate that full adult wing lengths are not reached in the first year of life, and that wing growth may continue for 2-3 weeks post-fledging. The average wing length at fledging was 87% of that of fully grown immatures, and 83% of the wing length of breeding adults.

The growth curves for weight were of similar sigmoid form in both 1983 and 1984, with weight increasing slowly at first, then almost linearly in chicks 6-21 days old, followed by a steady reduction in rate of weight increase during the last 2 weeks in the nest. In both years growth rates of chicks more than 21 days old were lower for those in broods of two than in single-chick broods (Figure 7.3). Peak weights were reached on average 3 days prior to fledging, in both years, but the timing for individual chicks varied from 9 to 0 days before fledging. The mean (± sd) maximum weight (N.B. this is not the mean weight 3 days before fledging) attained by chicks in 1984 was significantly greater than in 1983 (432.7 ± 46.3 g, n=90, and 412.5 ± 41.4 g, n=68 respectively; $t = 2.84$, 156 df, $P<0.01$). However, the time taken to reach peak weight did not differ significantly between years (32.8 ± 3.5 d, n=68 in 1983, and 33.2 ± 3.2 d, n=89 in 1984; $t = 0.57$). Since adults post-laying were also significantly heavier in 1984 (Chapter 6), these mean peak weights represented 106% of adult weight in 1983 and 105% in 1984. Over the 3 days prior to fledging chick weight declined on average by 6.8% in 1983 and 6.6% in 1984 (Figure 7.4). For all chicks combined, mean (± sd) weight at fledging was significantly higher in

Table 7.I Chick sizes at hatching (day 0).
Significant differences between years: * P<0.02

		1983		1984	
		b1	b2	b1	b2
Weight	mean	29.5	31.5	32.4	32.7
(g)	sd	3.3	3.9	3.7	4.0
	n	4	18	5	29
	range	27-34	25-39	26-35	24-40
Wing	mean	18.3	18.9	19.3 *	19.6 *
(mm)	sd	0.5	0.9	0.5	0.9
	n	4	19	6	28
	range	18-19	17-20	19-20	18-21

Figure 7.1 Wing growth curves for chicks on Mousa in 1983 and 1984. Sample sizes varied at different chick ages: in 1983, 3-16 for b1, and 10-49 for b2 chicks; in 1984, 5-21 for b1, and 11-69 for b2 chicks.

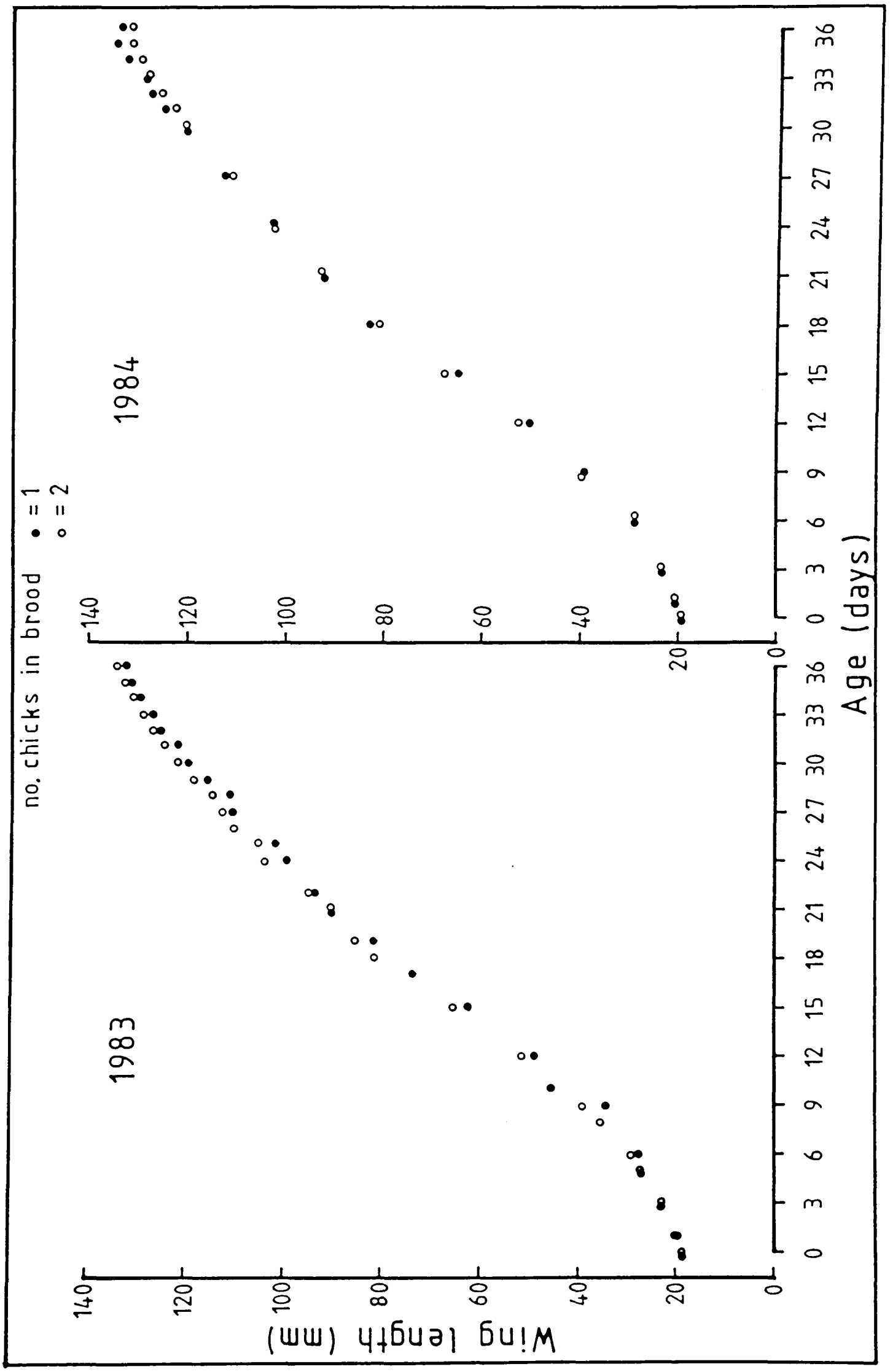


Figure 7.2 Post-fledging wing growth in Black Guillemots, determined from wing lengths of 14 fresh corpses found on Shetland and Orkney beaches.

Key: O median fledging date, 1983-84;
→ mean wing length at fledging;
— — mean wing length of immatures in Shetland between September and June.

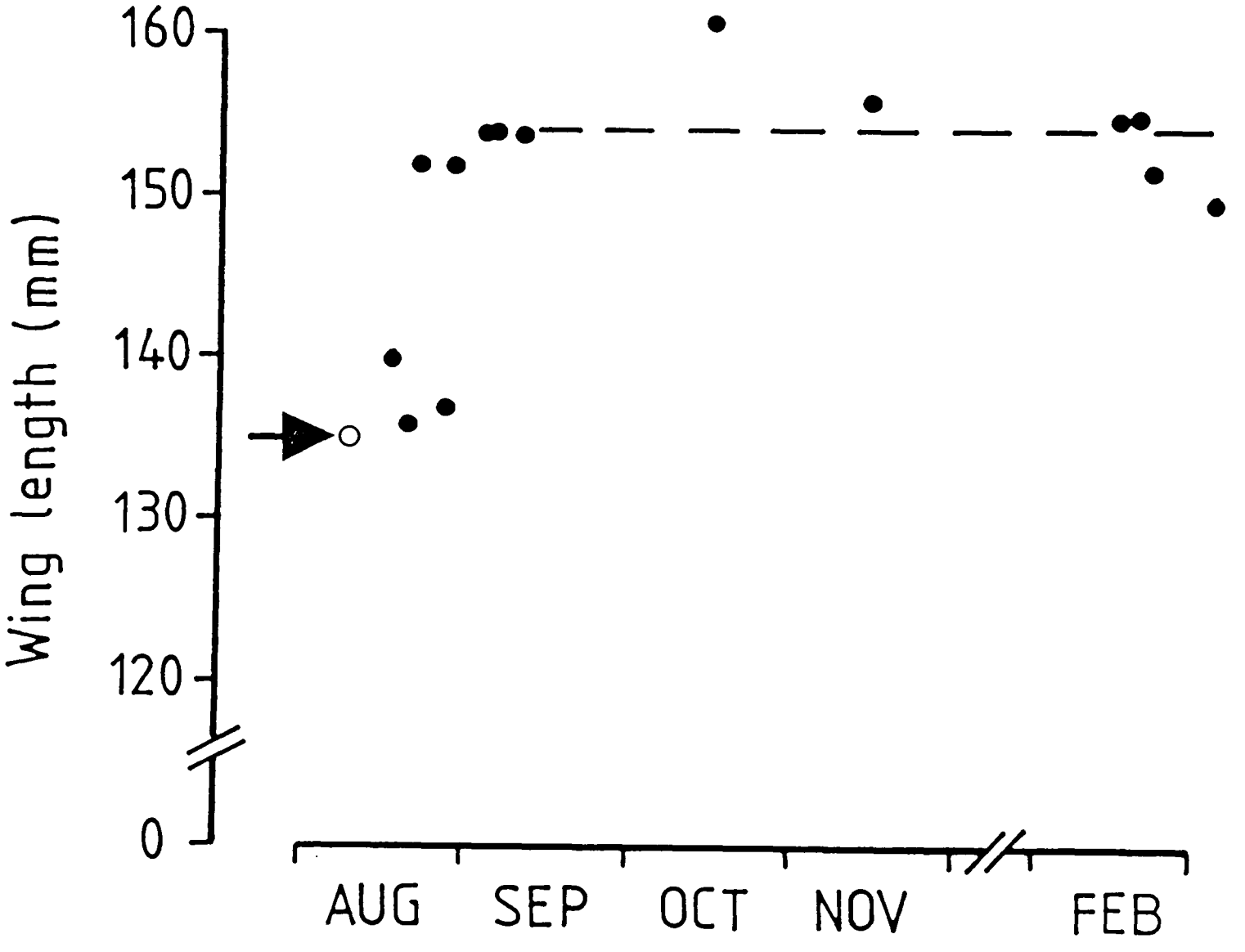


Figure 7.3 Weight growth curves for chicks on Mousa in 1983 and 1984. Sample sizes varied at different chick ages: in 1983, 3-19 for b1 and 6-49 for b2 chicks: in 1984, 5-23 for b1 and 26-28 for b2 chicks.

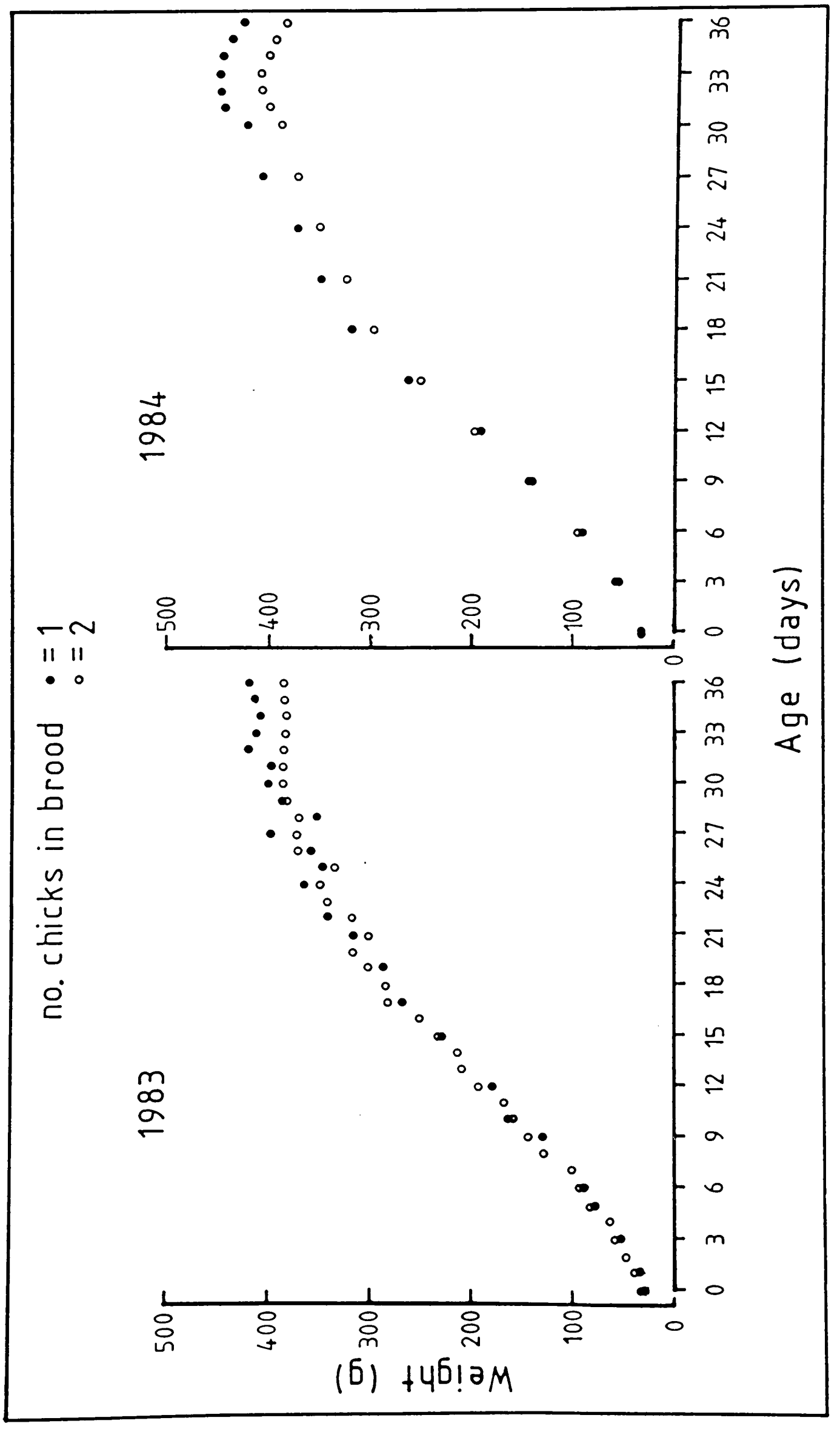
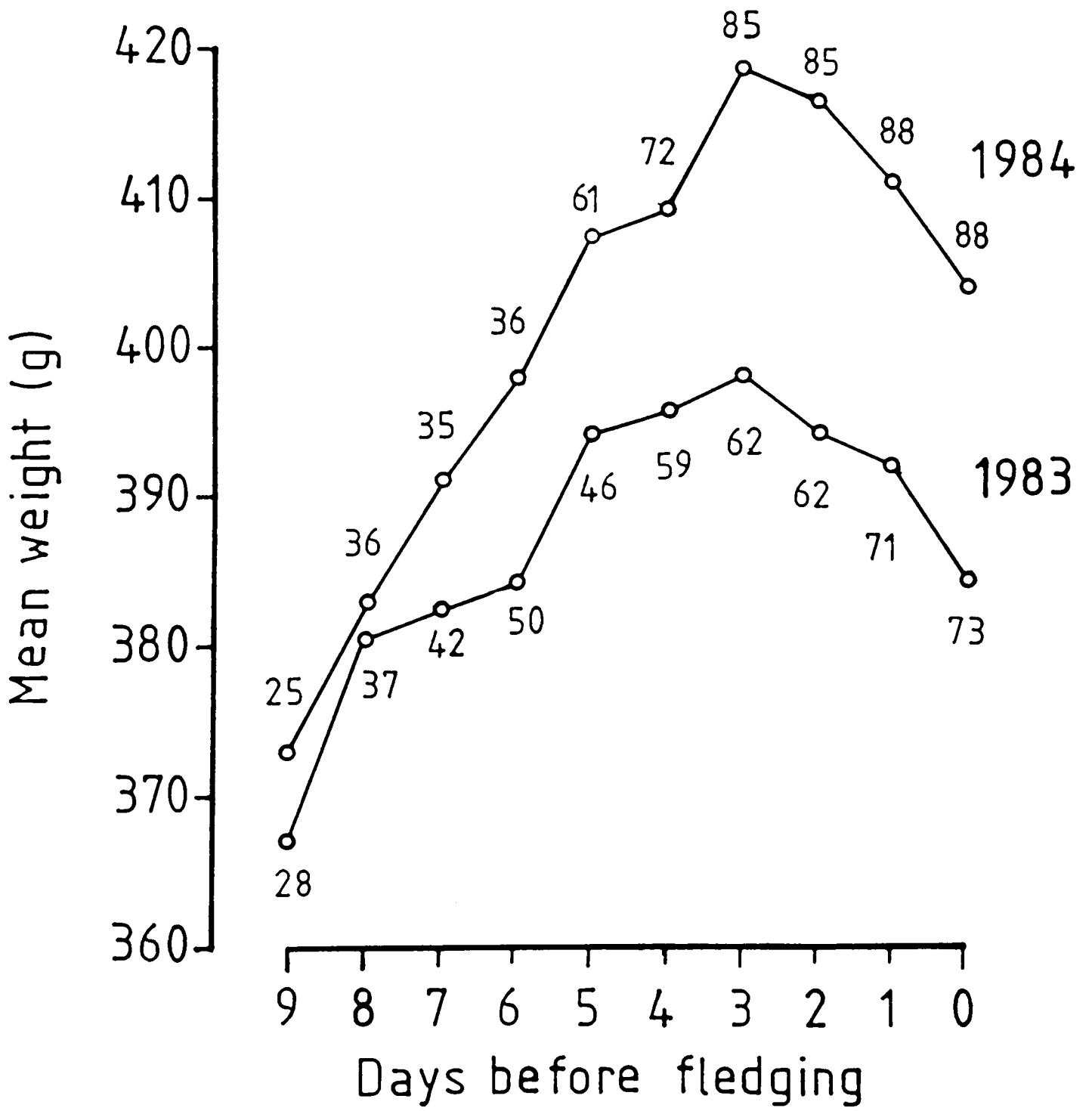


Figure 7.4 Changes in mean chick weights in the 10 days prior to fledging in 1983 and 1984. Data from all nests have been combined; sample sizes are given.



1984 (404.2 ± 43.8 g, n=88) than in 1983 (384.5 ± 34.1 g, n=73) (t = 3.13, 159 df, P<0.01). These fledging weights represented 98% and 99% respectively of adult post-laying (ie. June-August) weight.

Average daily weight increments for chicks in colony A reached a maximum in those 10-14 d old, then declined steadily. In most age categories the increment was markedly higher in 1984 than in 1983 (Table 7.II). For every age category chicks in 1984 gained on average less weight per gram of fish delivered (details of calculation are given in Chapter 9) than in 1983 (Table 7.II). The efficiency of conversion of weight of fish delivered to chick weight (commonly referred to as the Conversion Ratio, CR), decreased progressively with chick age, from 44-63% in chicks 0-4 d old, to 24-28% when 10-14 d old (ie. at the time of maximum daily weight increase), to only 0.3-0.4% at 30-34 d, just prior to fledging. Overall, conversion ratios in 1984 were slightly lower, associated with a greater proportion of fish of lower calorific value in the chick diet, particularly in the later stages of the season (Chapter 9).

To permit comparison with growth rates in other studies the steepest tangent was fitted by eye to the growth curves (also drawn by eye, from Figure 7.3). This maximum growth occured in chicks c.10-11 days old in both years, and was 15.7 g/day in 1983 but 18.0 g/day in 1984. These growth rates are amongst the highest recorded for this species, or any other auk (Sealy 1973; Gaston 1985b).

In the preceding analyses weights of chicks from different brood sizes were combined since there were no significant differences between the two years in the proportion of b1:b2 chicks measured (G-tests, P>0.1). However, on average single chicks were usually significantly heavier at peak weight and at fledging than those in 2-chick broods. These differences were particularly marked in 1984, when within each brood size category chicks reached significantly higher peak weights and fledging weights than in 1983 [though the comparison for b2 chicks was not quite significant (t=1.95, 121 df)] (Table 7.III). There was no significant difference between a- and b-chicks in 2-chick broods for either peak weight or fledging weight, in either year.

Since this species usually occupies the same site in successive years, I compared the fledging weights of chicks in the same nest (and of the same brood size) in the two years. Nests at which a mate or pair change was known to have taken place were omitted. For the sample of 34 chicks in 25 nests, fledging weights were significantly greater in 1984 (paired t-test, t = 5.24, 32 df, P<0.0001).

Table 7.II. Average daily weight increment (Av.DWI) (g) and weight gain per gram of fish delivered, for chicks of different ages in colony A in 1983 and 1984. Sample size (n) given for the number of increments in each age category.

	1983		1984		Mean wt. gain (g) per g fish delivered	
Chick age	Av.DWI	(n)	Av.DWI	(n)	1983	1984
0-4	8.1	(22)	8.3	(19)	.633	.487
5-9	15.3	(20)	16.8	(23)	.495	.438
10-14	17.0	(21)	19.9	(32)	.278	.242
15-19	15.4	(22)	18.0	(21)	.212	.177
20-24	13.6	(27)	10.3	(31)	.167	.076
25-29	6.5	(51)	8.5	(43)	.061	.050
30-34	0.4	(103)	0.5	(87)	.004	.003
35-39	-3.7	(66)	-7.4	(39)	-.049	-.091

Table 7.III Peak weights and fledging weights of chicks in broods of 1 and 2, in 1983 and 1984. Significant differences (t-tests) are denoted by: * P<0.05, ** P<0.02, *** P<0.001

		1983		1984		Sig. differences
		b1	b2	b1	b2	between years
PEAK WEIGHT	Mean	429.7 *	406.0	465.5 ***	422.6	b1:*, b2:*
(g)	sd	45.0	38.6	39.3	45.2	
	n	16	51	19	67	
FLEDGING	Mean	392.3	382.2	428.2 ***	396.0	b1:**
WEIGHT	sd	43.2	30.9	30.5	44.5	
(g)	n	17	56	23	66	
	range	319-493	311-444	378-466	240-484	

Possible factors affecting chick growth.

Fresh egg weight was significantly correlated with day 0 chick weight in 1983 (r = 0.54, 17 df, P<0.02) and 1984 (r = 0.60, 20 df, P<0.01), and with fledging weight in 1984 (r = 0.59, 15 df, P=0.01) (the relationship in 1983 was again positive, but non-significant). Thus heavier eggs usually produced heavier chicks at both hatching and fledging. In Iceland hatching weight was positively correlated with egg volume index (Petersen 1981); this is essentially the same relationship since fresh egg weight and volume index were highly correlated (see section 6.4.1). However, the regression of fledging weight on hatching weight was positive but not significant, as found in this species by Petersen (1981) and in Razorbills by Lloyd (1979). Since average fresh egg weight and volume index were greater in 1984 (Chapter 6) it was not surprising that chicks in 1984 were heavier and had longer wings at hatching than in 1983 (Table 7.I).

It might be expected *a priori* that a longer interval between hatching of chicks in broods of two would give the a-chick greater advantage over the b-chick, particularly when food was scarce. In fact when the b-chick hatched on the same day, or within a day of the a-chick, it fledged on average 1-6 g heavier than the a-chick (though 1-2 days later). With a hatching interval of 2 days the b-chick fledged on average 19 g lighter than the a-chick. Variation between nests was large however, and none of the differences were significant. Thus, in these two years at least, greater hatching interval did not give rise to a-chicks significantly heavier at fledging than b-chicks. However, brood size was important. Single chicks reached significantly higher peak weights, and fledged heavier than chicks in broods of 2 (only significantly so in 1984 however), (Table 7.III; Figure 7.3).

The timing of breeding had a marked influence on chick weight at fledging: fledging weight was negatively correlated with fledging date for single chicks and those in 2-chick broods in both years, although only the 1984 results are shown (Figure 7.5). There was a weak tendency in both years for chicks hatching later to take longer to reach peak weight, but neither relationship approached significance.

Kleptoparasitism of Black Guillemot deliveries appeared to have a significant effect on fledging weights (Figure 7.6). Although data for this plot were from both 1983 and 1984, the effect was similar in each year, ie. higher mean fledging weights in colonies with lower incidences of kleptoparasitism. The two data points for largest colonies are from colony

Figure 7.5 The relationship between fledging weight and fledging date for chicks in broods of 1 and 2 in 1984. Mean, s.e. and sample sizes are given for chicks fledging in each 10-day period.
Linear regressions carried out on the individual data points gave, for b1 chicks: $r = -0.52$, 14 df, $P<0.05$, and for b2 chicks: $r = -0.41$, 57 df, $P<0.01$.

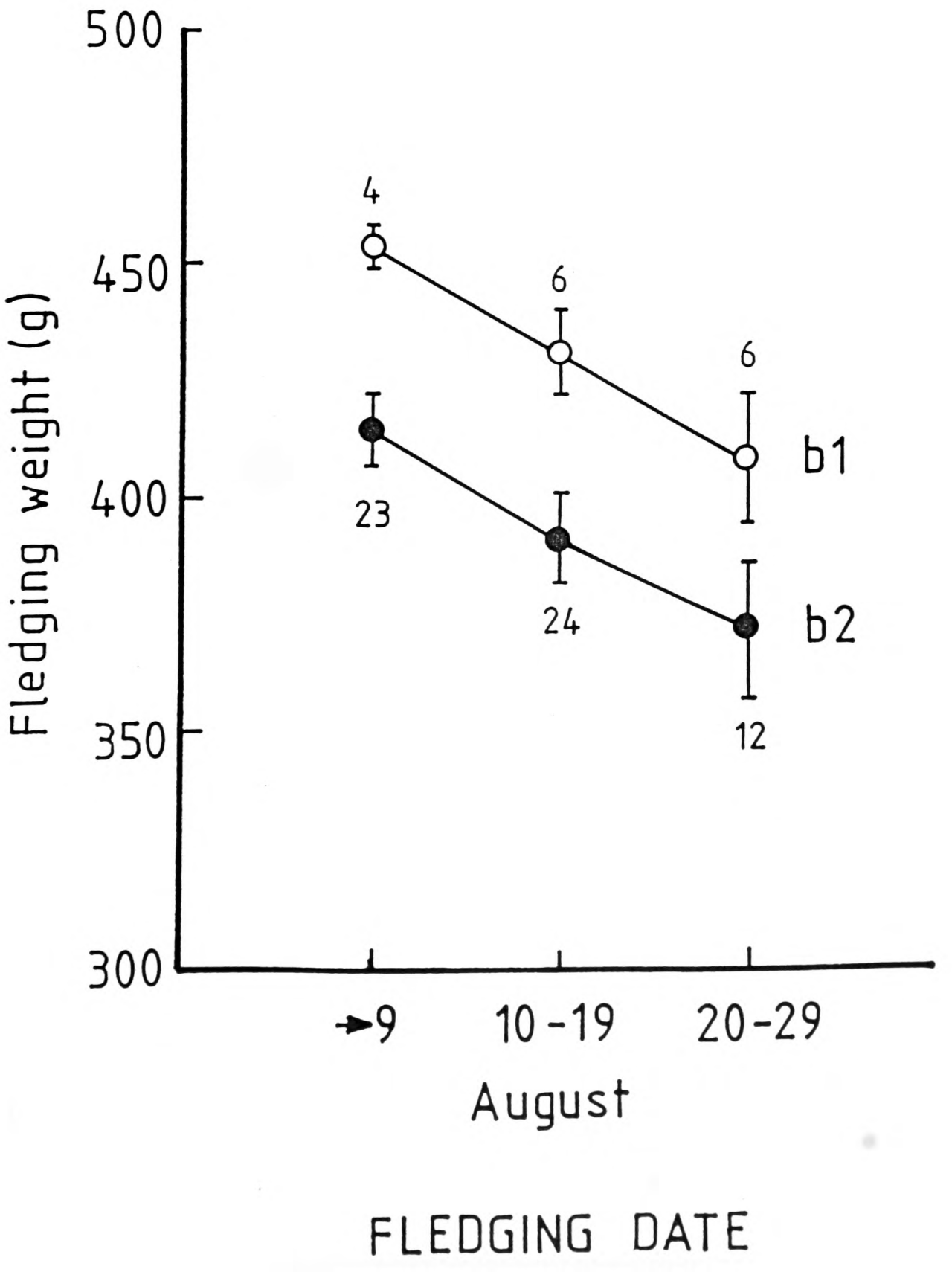
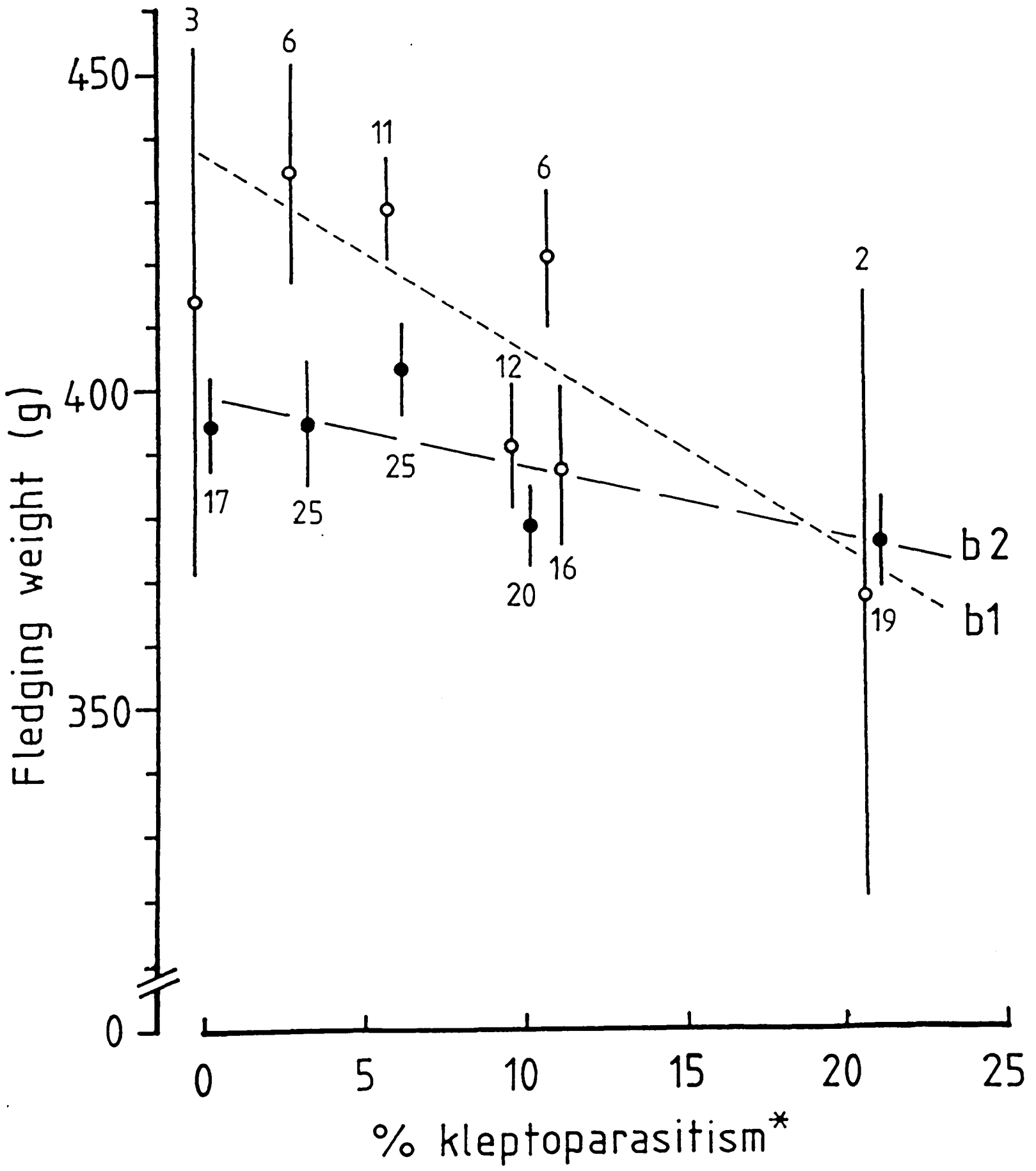


Figure 7.6 Fledging weights of chicks in broods of 1 (open circles) and 2 (closed circles) in relation to the incidence of kleptoparasitism at various colonies in 1983 and 1984. Mean ± se and sample sizes are given.

Note: *The mean % of delivery attempts losing fish as a result of kleptoparasitism, at a colony in a given year. The regressions of actual fledging weight against kleptoparasitism were significant for both b1 ($r = -0.36$, 38 df, $P=0.022$) and b2 ($r = -0.19$, 120 df, $P<0.0001$).



A. Although significantly more nests in this colony had single-egg clutches (Chapter 8) single chicks fledged significantly heavier on average than those with sibs. Therefore differences in mean brood size did not confound the effect of kleptoparasitism on fledging weights - if anything they operated in the opposite direction at colony A.

Chick diet quality has been shown to have significant effects on growth in some bird species (eg. Harris & Hislop 1978; Krebs & Avery 1984; Heath & Randall 1985). Wehle (1980) found that puffin chicks fed a mixed diet of sandeels and Capelin Mallotus villosus grew faster and fledged heavier than those fed just one of these species, suggesting some nutritional deficiency in a highly specialist diet. The effect of chick diet type on various growth parameters was investigated for nests in colony A, and comparisons made between broods whose diet comprised >60% sandeels, and those fed a more mixed diet, comprising a suite of mostly benthic species (see Chapter 9 for further details). The analyses failed to detect significant differences in either year, in peak weight, fledging weight, or fledging period between chicks fed sandeels as opposed to a 'mixed' diet. However, the differences between Black Guillemot chick diets on Mousa were seldom as great as were those in the aforementioned studies.

Weather conditions during the nestling stage were assessed using the daily means of hourly mean wind speeds (knots) and the minimum day-time air temperature (°C). These two parameters were thought to be the best indicators of environmental conditions likely to affect Black Guillemot foraging success and food availability. For the period between median hatching date and median fledging date, the mean daily wind speed ($\pm$ sd) was significantly higher in 1983 than in 1984 (12.2 $\pm$ 5.3 knots, n=36, vs. 9.8 $\pm$ 3.3 knots, n=37; t = 2.26, 71 df, P=0.03). In this period mean daily wind speed exceeded 15 knots on 12 days in 1983, but only on 4 days in 1984. Mean minimum day-time air temperature was significantly lower in 1983 than in 1984 (10.5 $\pm$ 1.7°C, n=36, vs. 11.1 $\pm$ 0.7°C, n=37; t = 2.19, 71 df, P=0.03). The average July sea-surface temperature was unusually high (12.3°C) in 1983, compared to a more normal figure (11.2°C) in 1984 (Appendix III). Therefore reduced chick growth in 1984 was also associated with cooler and windier weather conditions, and a warmer sea-surface, during the chick stage.

Infestation of chicks with ticks (Ixodes sp.) was only noted at two nests, both in cliff-edge crevices on Hascosay. The ticks only occurred on the head and upper neck area, and varied in number from 2-50 per chick. At one nest both chicks were infested in 1982 and 1983, the number of ticks

carried decreasing with chick age. At the other nest the single chick was infested in 1982 only, despite the presence of 2 chicks there the following year. Although severe tick infestation has been documented in other seabirds, sometimes causing impaired chick growth and increased mortality (Feare 1976a; King et al. 1977; Duffy 1983), measurements of these Shetland chicks indicated that growth was little affected by the tick presence. However, Bianki (1967) found that two Black Guillemot chicks, each hosting over 300 ticks, were very weak, and almost certainly under-weight.

7.4 Discussion

Comparison with other studies

Although Black Guillemot chicks are covered with down at hatching they are not homeothermic then, and are brooded until thermoregulatory development is complete (Gaston 1985b). Rol'nik (1948) and Kaftonovski (1951) reported that this development was complete in chicks 3-4 d old, whereas Drent (1965) found that Pigeon Guillemot chicks in the nest cavity were capable of maintaining their own body temperature only 24 hours after hatching. Some of this difference may be explained by the presumably higher ambient temperatures in Drent's study area. Chicks in Shetland are brooded to varying extents up to about 6 days old, much as found in studies elsewhere (eg. Bianki 1967; Asbirk 1979c; Petersen 1981). Variations in timing and duration of brooding behaviour may simply reflect local (and diurnal) fluctuations in ambient temperature. Interestingly Bianki (1967) found that chicks were brooded most overnight and in the early morning, when air temperatures would have been lowest.

The average fledging period of Black Guillemots varies in different areas [data summarized by Harris & Birkhead (1985)]. Much of this variation could be due to different feeding conditions (Petersen 1981). Cramp (1985) gives the average fledging period found by Asbirk (1979c) of 39.5 d as that for the Western Palearctic, but this is probably unusually long since food was very scarce in at least one of Asbirk's study years. Whilst severe food shortage may prolong the time chicks spend in the nest, smaller-scale fluctuations in food supply may have relatively little effect on the fledging period. I suspect that although feeding conditions on Mousa appeared to be poorer in 1983 than in 1984 (see later), food shortage was by no means acute, and chick growth was little affected, with differences reflected in fledging weights rather than duration of the

fledging period. In Iceland lower ambient temperatures were associated with lengthening of the fledging period in that year, possibly via increased energy expenditure by chicks in maintaining body temperature (Petersen 1981). Neither average ambient temperature during the chick stage nor fledging period differed between the two main study years in Shetland. However, it is possible that ambient temperature might account for some of the variation in average fledging periods found in different parts of the species' range, although probably as a factor of secondary importance to food availability.

As with the duration of the fledging period, it is likely that although growth rate and fledging weights may be lowered by reduced ambient temperature (Tuck 1961; Mahoney & Threlfall 1981), food availability is the crucial factor. Sampling of fish populations and assessment of their availability to Black Guillemots would however be a mammoth task, and so food shortages invariably have to be inferred from reductions in growth parameters, provisioning rates, or colony attendance of the birds themselves (eg. Gaston & Nettleship 1982).

Since body size and weight of adult Black Guillemots varies both between sub-species and within the range of each (the general trend being for larger birds at higher latitudes) (Salomonsen 1944; Storer 1952), any comparison of growth parameters must control for adult body size. The average weight at fledging, expressed as a percentage of adult weight (usually for that year), varies considerably in different studies: from 88% in Canada (Cairns 1981) and 89% in Iceland (Petersen 1981), to 83-106% in the Soviet Union (Uspenski 1956; Belopol'skii 1957; Bianki 1967). In two "normal" years in Denmark, the value was 98-102%, but in a year of failing food resources chicks fledged on average at only 90% of adult weight (Asbirk 1979c). A similar picture emerges when peak weights are compared. The Mousa values of 98-99% compare favourably with these figures, and it would be tempting to suggest that higher average chick weights at fledging indicated better feeding conditions during the chick stage. However, the situation is more complex, since breeding success and other growth parameters were normal in study years producing lighter fledglings (eg. Cairns 1981; Petersen 1981).

Caution is necessary when comparing fledging weights in different studies since recent work on Uria species has shown that chicks measured regularly fledged lighter than those just weighed prior to fledging (Harris & Wanless 1984; Gaston 1985b). This effect is not simply a result of disturbance to attendant adults, as it has also been detected in Little

Auks Alle alle, which, like Black Guillemots, leave their chicks unattended between feeds in the nest cavities (Evans 1981).

Although Sealy (1973) stated that no pre-fledging weight decline occurred in Pigeon Guillemots, subsequent studies on Black Guillemot breeding biology have all found an average weight recession of 6-7% of peak weight (Asbirk 1979c; Petersen 1981; this study). A few chicks do however continue putting on weight up to the day of fledging. This decline in weight is not simply due to increased wing exercising and chick activity immediately prior to leaving the nest, since both the feeding rate and average daily energy input to the chick decrease in the few days prior to fledging (Chapter 9). Although chick food-begging calls were found to stimulate adult Puffins to bring back fish, it is still unclear whether it is the chick or the adult which instigates the reduction in feeding rate in the later stages of the fledging period (Harris 1983b).

Weight recession is common in other auks (Gaston 1985b), and Hudson (1979) considered that chicks might have to attain some critical wing loading prior to fledging. This explanation is less plausible for Black Guillemots though, since the young are probably incapable of sustained flight for up to 2 weeks after leaving the nest. Harris (1984) concluded that weight recession was most likely accounted for by loss of fat (excess fat deposits could impair diving ability - an important skill which the independent young must acquire quickly if they are to survive), as well as some water loss as the tissues matured (Ricklefs 1968). These explanations probably apply equally well to Black Guillemots, although it is unclear why chicks should reach a peak weight, followed by a decline, rather than simply growing continuously and then fledging.

Differences between years.

Significant differences between years in growth parameters have been detected in most North Atlantic auks, with the greatest differences occurring at the higher latitudes, where inter-year variations in the marine environment (hence affecting food availability) are often most extreme (Gaston 1985b).

A number of results indicate that conditions were better for breeding Black Guillemots on Mousa in 1984, than in 1983. Eggs were larger and heavier, and breeding earlier in 1984 (Chapter 6) and it is possible that better weather conditions and food supplies in the pre-breeding period enabled adults to start breeding sooner, and in better condition than in

1983. Chick size at hatching and fledging was correlated with egg size and fresh weight, emphasizing that food availability in the pre-laying period may have an important influence on chick growth parameters. In 1984 chicks were significantly heavier at both peak and fledging weights, and on average received a greater weight of fish and energy input per day than in 1983 (Chapter 9).

Breeding adults were significantly heavier (post-laying) in 1984, suggesting that feeding conditions were more favourable then, than at the same stage in 1983, and possibly that they had been in better body condition since the spring. Weather conditions were certainly more favourable in the pre-laying period in 1984. Weight loss by breeders over the course of the breeding season could be adaptive however, in reducing locomotion costs (Norberg 1981). Although adults on Mousa showed no significant seasonal change in post-laying weight, an alternative interpretation of the lower weights in 1983 might be that adults were flying further in search of food, thereby reducing energy expenditure by lowering their own body weight. However, the observations of adults departing for the feeding areas during the chick stage suggest that this was not so. Strangely, in a year of (supposed) food shortage, and significantly lower fledging weights in Denmark, mean adult weight was almost identical to that in more normal years (Asbirk 1979c).

In attempting to account for differences in chick growth between years, it is difficult to disentangle the relative importance of each of the possible contributary factors, since many are inter-related. Improved growth in 1984 was associated with calmer and milder weather at the chick stage, which may have reduced energy expenditure on existence metabolism for both chicks and adults. Although during the chick stage in 1983 there were three times as many days with average wind speeds over 15 knots than in 1984, the sea surface was only infrequently described as "rough" (ie. International Sea State Code 5 or 6). Major water turbulence usually extends only a few metres below the sea surface (Sverdrup et al. 1942; Harris & Wanless 1985; J. Goodmann pers. comm.), and for a species such as Black Guillemot, usually foraging at depths of 10-40 m, excessive turbulence is likely to impede fishing activities only in very rough sea conditions (ie. mainly in the winter months). In fact, in Shetland the species appears to favour feeding in strong tide races whenever possible (pers. obs.).

Rough seas were found to reduce feeding rates of Guillemot chicks in Wales (Birkhead 1976), but not in Scotland (Harris & Wanless 1985), nor for

Brunnich's Guillemot Uria lomvia chicks in Canada (Gaston & Nettleship 1981). No effect of weather conditions on daily feeding rates of chicks was evident on Mousa in either study year. Adverse weather might only influence feeding rates if food is in short supply however, and since food appeared to be plentiful for Black Guillemots on Mousa, this may be one reason why no relationship was found.

I consider that oceanographic factors such as tidal flow, sea-surface temperatures, degree of water mixing, and shifts in plankton distribution and abundance are more likely to exert a stronger influence on chick growth, via changes in prey availability. This might be particularly so in areas like Mousa where significant proportions of the chick diet comprise pelagic fish species (Chapter 9). If young gadoids survived better in 1984 as a result of the cooler sea-surface temperatures (cf. Dickson et al. 1975), this might explain their greater occurrence in the chick diet then (giving rise to improved growth of chicks). However, such direct explanations must only be tentative since there are undoubtedly numerous 'knock-on' effects in the marine food chain resulting from man's intensive harvesting of North Sea fish stocks (Bailey & Hislop 1982).

Chicks fledging from colonies with higher incidences of kleptoparasitism did so at lower weights on average than those from colonies with low rates of piracy. Similarly, Puffins on Great Island, Newfoundland, breeding in burrows on level ground away from the coast lost significantly more fish loads to kleptoparasites than did those nesting in the coastal slopes, and the fledging weights of chicks there were significantly lower as a result (Nettleship 1972). The lower incidence of piracy in 1984 will undoubtedly have contributed to the improved conditions for chick growth, but it is difficult to determine how many of the 'extra' deliveries made by Black Guillemots at colony A for example, were attributable to the reduced brood size of the Arctic Skuas in 1984 (and hence their food requirement) (Chapter 10), as opposed to a real increase in fish availability.

When Puffins on St. Kilda were forced to feed chicks on sub-optimal fish (Whiting), mean fledging weights were lower than when Sprats Sprattus sprattus (the preferred diet, of high calorific value) were readily available (Harris & Hislop 1978). I suspect that the single most important factor accounting for improved chick growth in 1984 was the appearance inshore of large numbers of gadoid fish (probably mostly Norway Pout Trisopterus esmarkii) in the later stages of the 1984 breeding season (Chapter 9). Although the calorific value of these fish was almost

certainly lower than that of sandeels, the greater weight of each gadoid meant that each delivery was much better in energetic terms for both chick and adult. In a study of Pigeon Guillemots in Alaska faster growth rates and greater fledging weights were similarly attributed to increased food availability - in that case gadoids and sandeels (Oakley 1981). However, nutritional quality, and not just quantity of fish in the chick diet may be an important factor controlling growth (Wehle 1980; Oakley 1981; Harris 1984).

CHAPTER 8. BREEDING PERFORMANCE

8.1 Introduction

Reproductive output is affected by many factors, for example: the number, size and quality of eggs laid, parental experience and quality, environmental conditions, food availability, disease and predation. Lack (1954) suggested that natural selection favoured birds which laid that size of clutch which produced the greatest number of surviving young, and this hypothesis was modified later to incorporate the cost to adult survival incurred by breeding, since it is the lifetime reproductive success which is crucial (Williams 1966; Charnov & Krebs 1974). In long-lived birds such as the auks, there must be a trade-off between reproductive effort in any year and costs to adult survival: if conditions are unfavourable it may be better for an adult to adandon the breeding attempt (Stearns 1977), or not to breed at all (Drent & Daan 1980). Support for these modifications to Lack's hypothesis was provided by work on House Martins Delichon urbica which showed that double-brooded adults had a significantly lower survival rate than did those rearing only one brood a year (Bryant 1979). In Black Guillemots the survival rate of adults whose breeding attempt failed was higher than that of those fledging young (Asbirk 1979c).

Although many auks lay only a single egg, Cepphus species usually lay two-egg clutches (Harris & Birkhead 1985; Drent 1965; Kuletz 1983). Therefore, amongst Atlantic or larger auks the Cepphus species have the greatest potential variation in breeding success, and so are suited to investigation of factors affecting breeding performance. In this chapter I present breeding statistics for Shetland and consider differences between years and between clutch sizes in relation to a variety of factors thought likely to affect breeding performance. These results are then discussed alongside those from chapters 6, 7 and 9, to compare breeding and productivity in Shetland with that in studies elsewhere.

8.2 Methods

A nest site was considered to be occupied if a pair were regularly present there during the pre-breeding period, and breeding to have occurred if an egg was seen. Only those sites for which the completed clutch size, number hatching and number fledging were known have been used in the

calculation of breeding statistics. A completed clutch size of 1 egg was scored if no second egg had been laid within 5 days. Occupied nest cavities in which no breeding attempt was made have not been included in these statistics, although these were regarded as zero-egg clutches by Preston (1968). Intact eggs failing to hatch were later broken to assess the stage of embryonic development at failure. It was impossible to distinguish between infertile eggs and those which had failed at an early stage of development. The cause of chick death was determined whenever possible by post-mortem examination or signs left by predator species.

Unused sites were those suitable-looking cavities in which no breeding attempt was made. These comprised: cavities tenanted in the pre-breeding and/or breeding period; cavities regularly inspected by prospecting birds but not regularly tenanted; any other suitable cavities I discovered during thorough searches of breeding areas. For both used and unused sites a number of physical characteristics were measured. For unused cavities which were not tenanted, only those in which all physical characteristics fell within the range of used sites were considered. The distance between the nest entrance of adjacent sites was measured in order to determine the nearest neighbour distance (NND) for each site. Height above sea level (high water mark) was estimated by eye, in conjunction with a 1:10,000 scale OS map. Nest distance from the sea (high water mark) was taken as the shortest direct distance (horizontal) to the open sea excluding tidal pools, and was paced out. For each nest a steel tape measure was used to determine the maximum vertical, and horizontal dimension of the nest entrance. Nest depth was taken as the distance from nest entrance to centre of the scrape, and a record made of whether the scrape was directly visible from the entrance or not. The number of stones in the scrape was estimated and the maximum dimension of the largest measured.

The frequency of agonistic interactions was determined for 3 colonies during the 1984 breeding season by recording the number of separate agonistic interactions observed in a fixed portion of the colony in 10-minute sampling periods, scattered throughout the morning period of colony attendance (0650-1130 h BST). If the number of birds present in the sample area changed during the observation period, the total number of bird-minutes of observation was changed accordingly. Five types of behavioural postures/interactions were regarded as agonistic: Lunge, Threat (wings drooped and tail erect), Twitter-waggle [see Asbirk (1979b)], direct fighting, and aerial chases.

Hatching success was the % of eggs laid that hatched, fledging success the % of eggs hatching which produced a fledged chick, and breeding success the % of eggs laid which produced a fledged chick.

8.3 Results

8.3.1 Breeding parameters

Breeding was not attempted by every pair which tenanted a site in the pre-breeding period (April-May). There was no significant difference between the 3 study years on Mousa in the proportion of tenanted sites at which no breeding attempt was made (10.3% of 68 sites in 1982; 11.8% if 102 sites in 1983; 11.1% of 117 sites in 1984), giving a weighted mean of 11.2% non-breeding. There were consistent (but non-significant) differences between colonies in each year however, with colonies A and L (see Figure 6.2) having the highest incidence of non-breeding (weighted means for all years combined of 11.9% and 15.0% respectively), and colony CGQ the lowest (3.6%).

Clutch size did not vary significantly between years on Mousa nor between Mousa and Hascosay (Table 8.I). Of 292 completed clutches in Shetland 56 (19.2%) had 1 egg, 235 (80.5%) had 2 eggs, and 1 (0.3%) had 3 eggs, giving an overall mean clutch size of 1.81. On Fair Isle however, the mean clutch size in 104 breeding attempts from 1973-77 was only 1.43 (annual variation 1.32-1.63) (R A Broad pers. comm.), and 1.59 in 1966 (Dennis 1966), reflecting a much higher incidence of single-egg clutches than in my study. Since Black Guillemots have only two brood patches, eggs in 3-egg clutches will not receive full incubation (Petersen 1981). Accordingly, although the 3-egg clutch on Hascosay was incubated, no egg hatched: one egg was eventually ejected, another was apparently infertile, whilst the embryo in the third had died, surprisingly within only c.1 week of full development. In addition, at two nests on Mousa 3 eggs were present for only one day in the scrape, but at both it was known that 2 females were involved. All 3 eggs disappeared at one site, whereas at the other one was ejected the day after it was 'dumped' by the extra female, one was infertile, and the other hatched successfully.

Pooling results for all study years on Mousa, and excluding colony DN (at which Otter predation in 1982 affected subsequent performance - see later), there was no significant difference between colonies in the proportion of c1:c2 clutches. However, 22% of 104 pairs at the large

Table 8.I The reproductive performance of Black Guillemots in Shetland, 1982-84.

	HASCOSAY	MOUSA			MOUSA
	1982	1982	1983	1984	1982-84
No. nests [a]	26	56	91	119	266
Mean clutch	1.92	1.75	1.81	1.82	1.80
Mean no. hatching	1.65	1.36	1.43	1.35	1.38
Hatching success [b]	86.0%	77.5%	78.8%	74.1%	76.4%
Mean no. fledging	1.23	1.05	1.34	1.24	1.23
Fledging success [c]	74.4%	77.7%	93.8%	91.8%	89.6%
Breeding success [d]	64.0%	60.2%	74.0%	68.0%	68.5%

Notes: [a] number of sample nests in which breeding was attempted.

[b] % of eggs laid that hatched.

[c] % of eggs hatching which produced a fledged chick.

[d] % of eggs laid which produced a fledged chick.

colony A laid c1, a significantly higher proportion than the 11% of 112 pairs elsewhere on Mousa ($G = 5.2$, 1 df, $P<0.05$), (see also Table 8.VIII).

Overall breeding success did not vary significantly between Mousa and Hascosay in 1982, nor between years on Mousa. Hatching success was better on Hascosay, and fledging success better on Mousa - the lower figures in 1982 being due to Otter predation of some nests (Table 8.I). In the 1974-77 Fair Isle studies fledging success (74%) was comparable with these Shetland values, but the low hatching success (39%) accounted for the very poor overall breeding success of 28.9% (R A Broad pers. comm.).

Further analyses of breeding performance consider the different clutch sizes separately, since the parameters often differed with clutch size (Table 8.II). In 1982 and 1983 there were no significant differences between c1 and c2 clutches in either hatching success, fledging success or breeding success, although most were usually higher for single eggs. However, in 1984 the reverse was true; breeding success for single eggs was highly significantly lower than for eggs in 2-egg clutches (18% vs. 74%, $G = 26.3$, 1 df, $P<0.001$), and although poorer fledging success accounted for some of this, the largest contribution was made by the significantly lower hatching success (32% vs. 79%, $G = 19.6$, 1 df, $P<0.001$). The large sample sizes in 1984, and the magnitude of the significant differences between clutch sizes resulted in the combined years comparisons indicating that c2 nests had better breeding performance (per egg) than c1 nests - significant for hatching success ($G = 135$, 1 df, $P<0.001$) and breeding success ($G = 6.4$, 1 df, $P<0.05$) only. For the three study years on Mousa combined, the average number of fledged young produced by pairs laying 2-egg clutches was nearly 3 times that of pairs laying single-egg clutches (Table 8.II).

There was some suggestion that laying order affected hatching success: in 17 two-egg clutches in which only one egg hatched, it was the b-egg in 12 but the a-egg in only 5 (a non-significant difference, $G = 1.5$, 1 df, $P>0.05$). This slight tendency for better hatching success of b-eggs was unexpected since a-eggs were, on average, larger and heavier than b-eggs (Chapter 6), and so should have been better able to withstand chilling. For chicks however, the trend was in the expected direction. At 11 nests in which one chick died, it was the b-chick in 8 (73%) cases. The b-chick was younger and usually smaller than the a-chick, and so was most likely to suffer from food shortage and/or sibling aggression.

Replacement clutches were laid after loss in 8 nests (Mousa and Brindister study areas - see Chapter 6), giving a mean replacement clutch size of 1.63. Hatching success was 69.2% and fledging success 22.2%,

Table 8.II Reproductive performance in relation to clutch size on Mousa, 1982-84.

	1982		1983		1984		All years	
	c1	c2	c1	c2	c1	c2	c1	c2
No. nests	14	42	17	74	22	97	53	213
No. hatching[a]	0.71	1.57	0.88	1.55	0.32	1.58	0.60	1.57
Hatching success[b] (%)	71.4	78.6	88.2	77.7	31.8	78.9	60.4	78.4
No. fledging[a]	0.64	1.19	0.88	1.45	0.18	1.47	0.53	1.41
Fledging success[c] (%)	90.0	75.8	100.0	93.0	57.1	93.5	87.5	89.8
Breeding success[d] (%)	64.2	59.5	88.2	72.3	18.2	73.7	52.8	70.4

Notes: [a] Mean values per nest

[b] % of eggs laid that hatched

[c] % of eggs hatching which produced a fledged chick

[d] % of eggs laid which produced a fledged chick

giving an overall breeding success of 15.4% - all parameters being lower than for first clutches (Table 8.I). Petersen (1981) similarly found poorer breeding success of eggs in replacement clutches, when compared with first clutches laid in the same laying period. My sample sizes were too small to permit similar comparisons but, overall, replacement clutches fledged proportionately fewer chicks (average of 0.25 per nest) than first clutches (1.23 per nest; $G = 4.6$, 1 df, $P<0.05$).

8.3.2 Causes of breeding failure

The causes of failure of 23 (21%) of the 111 eggs failing to hatch were unknown, the remaining 88 eggs failed due to a variety of suspected or known causes (Table 8.III). Developmental abnormality accounted for 41% of these failures (69% of these eggs failing at early embyonic stages, or due to infertility); adult behaviour for 32% (presumably mostly due to inadequate care by adults whilst turning eggs or moving in and out of the nest cavity; predation (of eggs and/or incubating adult) for 25%, and flooding for 2%. The major differences between years occurred in predation. Although no eggs were taken in 1982, Otter predation of incubating adults in colony DN led to abandonment of the clutch by the mate. In 1984 Hooded Crows Corvus corone cornix took at least 10 eggs from nest cavities, apparently because more pairs laid in open, accessible sites in 1984. At least 2 crow pairs knew the location of virtually all Black Guillemot sites in their territories and systematically checked the sites during the laying period.

Of 49 chicks failing to fledge, the cause of death was unknown for 33 (67%) (Table 8.IV). Most of the 20 chicks vanishing from nests were probably removed by predators, since the normal response of chicks upon disturbance was to scuttle into dark recesses, and I made thorough searches of all cavities. The remains of 4 large chicks were found within 5 m of nests; all smelt strongly of Otter. Corpses carried further away may not have been detected. Observations on Mousa in 1986 suggested that Otter predation of chicks may previously have been underestimated. Empty cavities containing some faeces, with and without chick feathers/down or blood, were unusually common (pers. obs.) and on two separate days an Otter (possibly different individuals) was seen to remove a chick from a nest in colony A and carry it off to the shoreline boulders (P J B Slater pers. comm.). At 11 nests where eggs had hatched, but chicks vanished, chick feathers or remains were found at only 4 (36%). Although crow predation

Table 8.III Causes of Black Guillemot egg failure on Mousa, 1982-84. Figures given are the no. of eggs failing due to each cause.

CAUSE OF FAILURE	1982	1983	1984	1982-84
Developmental				
Infertile/ embryo died during early stages	5	10	10	25
Embryo death mid-development	1	2	1	4
Died in hatching process	1	3	3	7
Adult behaviour				
Egg cracked by adult	-	5	7	12
Egg eaten by adult	-	-	1	1
Egg ejected by adult	1	2	4	7
Desertion due to intra-specific interference	-	-	3	3
Egg never incubated	-	2	3	5
Predation				
Incubating bird killed by Otter	12	-	-	12
Egg predation by Crow	-	-	10	10
Environmental				
Flooded by heavy rain	-	2	-	2
Unknown				
Egg vanished	-	2	5	7
Egg failed to hatch	-	5	3	8
Clutch abandoned	2	2	4	8
Total no. of eggs failing:	22	35	54	111

Table 8.IV Causes of Black Guillemot chick failure and age at death.
Data from Hascosay 1982 and Mousa 1982-84 combined.
Day 0 = the day of hatching.

CAUSE OF FAILURE	No.	Age at death (d) (when known)
Adult behaviour		
Chick exposure	2	0, 1
Chick starvation	3	15, 15, 16
Chick choked on fish	1	18
Chick behaviour		
Fell from nest	2	8
Predation of chick		
by Crow or Gull	4	15, 24, 25, 26
by Otter	4	27, 31, 32, 33
Unknown		
Chick vanished	20	2, 3, 4, 13
Chick dead in nest	13	0, 0, 1, 1, 2, 2, 2, 3, 9, 12, 15
Total	49	

can not be ruled out, the 4 chicks eaten at nests around the tidal pool on Mousa had probably been taken by gulls breeding there. Otters are probably the main predator of chicks in Shetland. Very small chicks found dead in the nest had probably died of exposure. Although weather conditions were never exceptionally bad at hatching, some individuals may not have developed thermoregulatory me chanisms sufficiently by the time adults stopped brooding, at c.3 days old (Chapter 7). One runt chick choked to death with a Butterfish and a cottid species stuck in its gullet.

8.3.3 Possible factors affecting breeding success

I compared various physical parameters of used and unused cavities. Those in which breeding was attempted in either 1983 or 1984 were, on average, significantly further from their nearest neighbouring cavity and at significantly lower altitude than unused sites. There was no significant difference in maximum entrance dimensions, nest depth, horizontal distance from the sea, or maximum scrape stone dimension however (Table 8.V). Significantly more sites in which breeding was attempted had more than one entrance (23% vs. 11%; $G = 4.71$, 1 df, $P<0.05$), but at a significantly higher proportion of unused sites the scrape was visible from a nest entrance (83% vs. 67%; $G = 5.8$, 1 df, $P<0.05$). It might be expected *a priori* that egg breakage would be less likely in sites with a large number of stones in the scrape, and that birds would favour such sites. Although more unused cavities had fewer than 10 scrape stones (24%, as opposed to 14% in used scrapes), the difference was not significant.

Further investigations of nest site quality in relation to breeding parameters were carried out by performing four separate multiple regression analyses. In each the independent variables were those physical characteristics (considered in the previous analysis) of 91 sites in which breeding was attempted in 1983, with dependent variables being: first-egg laying date; clutch size; hatching success, and fledging success. Some independent variables were significantly correlated with dependent variables (Table 8.VI). First-egg laying was significantly later at nests further (in vertical terms) from the sea, but earlier in sites further horizontally from the sea. This was largely due to earlier laying at the large colonies A and CGQ (Chapter 6). Sites with smaller maximum vertical entrance dimension and greater nest depth had larger clutches and significantly better hatching success, but hatching success was also significantly better in sites with larger maximum horizontal entrance

Table 8.V Physical characteristics of cavities on Mousa in which breeding was attempted in 1983-84, compared with tenanted or suitable-looking cavities which were not used. Means and standard deviations are given, although medians were compared statistically.

	USED			UNUSED			
Characteristic	Mean	sd	n	Mean	sd	n	P[a]
NND [b] (m)	14.8	22.4	110	5.4	5.2	28	***
Ht. above sea (m)	7.1	5.4	110	8.2	3.5	28	**
Distance from sea (m)	25.8	21.4	110	27.0	19.9	28	ns
Maximum horizontal entrance dimension (cm)	23.6	13.2	94	26.1	17.8	28	ns
Maximum vertical entrance dimension (cm)	12.1	3.7	94	13.5	7.4	28	ns
Nest depth[c] (cm)	58.5	29.7	97	49.0	20.0	28	ns
Maximum scrape stone dimension (cm)	5.7	2.0	43	6.5	2.1	15	ns

Notes: [a] Significance level, Mann-Whitney U tests, ** P<0.02; *** P<0.001

[b] Nearest neighbour distance

[c] Distance from nest entrance to centre of scrape

Table 8.VI A summary of the regression coefficients determined by multiple linear regression of four separate breeding parameters for 1983 against 10 different physical characteristics of nest sites. Details of characteristics are given in the text. Significance levels are denoted by: * P<0.05, ** P<0.02, *** P<0.01

	Dependent variable			
Independent variable	First-egg Laying date	Clutch size	Hatching success	Fledging success
Ht. above sea level	0.25 **	ns	ns	ns
Distance from sea	- 0.29 ***	ns	ns	ns
Maximum entrance dimension: Horizontal	ns	ns	0.23 *	ns
" : Vertical	ns	- 0.26 **	- 0.28 ***	ns
Nest depth	ns	0.22 *	0.31 ***	ns
# scrape stones	ns	ns	ns	- 0.28 ***

dimensions. This last result was due to the nature of many Mousa nest cavities (under large, flat slabs), where the low ceiling at the entrance (mean max. dimension 12 cm) was usually more critical than the entrance width (mean max. dimension 24 cm), with respect to site accessibility for potential nest predators. Finally, fledging success was negatively correlated with the number of scrape stones. It is difficult to conclude that this relationship was due to anything but chance, or auto-correlation of independent variables, since nestling survival was most likely to be affected by factors such as site vulnerability to predation.

Although there was no significant difference between years in the proportion of sites regularly tenanted in the pre-breeding period at which breeding was later attempted (section 8.3.1), on average 13% more sites were tenanted, and breeding attempted at 16% more sites in 1984 than in 1983. There was no significant difference in pre-breeding counts at Mousa colonies in 1983 and 1984 (Wilcoxon signed rank test, $P>0.1$), indicating that the 'extra' sites tenanted in 1984 were due to a higher proportion of birds associated with colonies that actually occupied sites, rather than remaining at shore rocks and the offshore display areas. Sample sizes were small but many of the sites newly occupied in 1984 were unusually open, with the egg(s) usually visible from outside, through relatively large entrances. It was no surprise to find heavier predation at these sites - of the 11 eggs failing to hatch 7 (64%) were taken by Hooded Crows. At 15 sites newly occupied in 1984 single-egg clutches were significantly commoner than in sites tenanted in 1983 (40% vs. 15%, $G = 4.51$, 1 df, $P<0.05$), and breeding success in 2-egg clutches significantly lower (50% vs. 76%, $G = 5.13$, 1 df, $P<0.05$).

A change of mate, or pair, at a site since the previous breeding season could have a major influence on the breeding output. A breeding attempt was made at significantly more sites at which no change was known to have occurred (98%), than at those where a mate or pair had changed (54%) ($G = 22$, 1 df, $P<0.001$), and was much more likely to be successful (85% vs. 29% respectively) (Table 8.VII). Overall, at 84% of sites breeding was successful in successive years, whereas at only 29% was breeding unsuccessful in consecutive years. This difference was not significant ($G = 1.7$, 1 df), providing no support for the idea that some sites regularly failed whereas others were regularly successful.

Asbirk (1979b) considered that a social hierarchy may exist in this species, and presented evidence for reduced reproductive output of subordinate pairs as a result of intraspecific interference. On Mousa

Table 8.VII Comparison of nest-site occupancy and breeding at sites with, and without a mate or pair change since the previous breeding season.

Mate or pair change known to have occurred since previous season [a]	Total no. sites	Site occupied	Breeding attempted	Breeding successful
NO	143	141 (99%)	138 (98%)	117 (85%)
YES	14	13 (93%)	7 (54%)	2 (29%)

Note: Percentages are of the number in the column to the left, rather than of the total no. of sites in each row.

[a] Based on colour-ring observations, known changes included: a completely new pair, or at least one new parent.

there appeared to be a dominance hierarchy amongst individuals breeding in the densest parts of colonies at least, but there was no suggestion that this affected laying or breeding success. However, very few sites were as close together as the examples quoted by Asbirk. The importance of a social hierarchy was very evident at the communal over-night roost. Up to 60 birds roosted on a small stack off colony A, and there was considerable jostling for positions and agonistic interaction as birds arrived at dusk. The average incidence of agonistic interactions on the ledges at this time (June 1983) was 2.38 x 10^{-2} per bird-minute - almost identical to that at the breeding areas during the mornings. The prime roost sites were at the innermost sheltered parts of ledges and were always occupied by adults. Observations of colour-ringed birds indicated that the same position was occupied nightly.

Some pairs regularly occupied (ie. defended and scraped at) more than one site (maximum of 3 sites) during the pre-breeding period. These sites were on average 7 m apart (range 0.7 - 19 m). At colony A, 12% of pairs occupied more than one site in 1983, and 16% in 1984. There was no evidence in either year that breeding success was affected by tenancy of more than one site however.

Preston (1968) found that aggregate nesters (ie. breeding at high density) exhibited a significantly higher frequency and variety of agonistic interactions than birds nesting in smaller, loose colonies, and suggested that the reduced reproductive output (mostly due to lowered clutch size and proportion of birds actually making a breeding attempt) in aggregate colonies might be due to this agonistic interference. This hypothesis was tested on Mousa in colonies of different size and significantly different nest density (colonies A, CGQ and E). Although breeding density varied significantly between colonies of different sizes on Mousa, neither breeding success nor the frequency of agonistic interactions in June 1984 were significantly different (Table 8.VIII). In fact many of the aggressive encounters involved wandering/prospecting non-breeding pairs and single birds, rather than neighbouring breeders, and thus little support was found for Preston's ideas.

The effect of different levels of human disturbance on breeding performance was assessed by comparing overall breeding success and hatching success on Mousa in 1982 (2-3 checks per nest during the incubation period), with that in 1983 (eggs weighed every 5 days during incubation, and colonies disturbed daily) and 1984 (eggs not removed once laid, but colonies visited daily). No trends were suggested by these analyses.

Table 8.VIII Breeding success in colonies of different size, in relation to breeding density, frequency of single-egg clutches and incidence of agonistic interactions. Data from all years combined.

	Colony size			
	LARGE	MEDIUM	SMALL	Significance level
No. breeding prs.	22+	9-21	1-8	
Number of colonies	1	4	5	
Median NND (m)[a]	6.5	11.7	13.4	P<0.01;P<0.05[d]
Breeding success (%)[b]	68.2	70.5	68.8	n.s.
Mean no. fledging per breeding attempt	1.29	1.34	1.17	
% of breeding prs. laying 1 egg only	22.1	11.2	11.8	P<0.001
Frequency of agonistic interactions[c]	2.38	2.54	2.95	n.s.

Notes: [a] Weighted mean of median nearest neighbour distances for nests in the separate colonies.

[b] Weighted means of breeding success data from more than one year.

[c] Frequency of agonistic interactions (x100) per bird-minute, in June. Sample no. of bird-minutes = 1580, 1010, 360 for the three sizes of colony respectively.

[d] Large:Medium, U=592, n=33,55, P<0.01. Large-Small, U=203, n=33,14 P<0.05. Medium:Small, n.s. (Mann-Whitney U tests).

Although I was unable to control for other factors, a greater difference in disturbance level existed between the 1982 Hascosay figures (nest checks every 7-10 days) and 1983 Mousa figures. However, again there was no significant difference in hatching succes (86% vs. 79% respectively) or breeding success (64% vs. 74%). Hatching and breeding success at Mousa colony CGQ (visited by tourists in addition to my disturbance) were not significantly different from other Mousa colonies. Although it was known that trapping of at least 4 adults on eggs in 1983 (in particularly small cavities) led to desertion, overall there was no significant difference in average hatching, fledging or breeding success between 40 nests at which at least one adult was caught, and 57 nests at which I did not interfere with adults. Modification of the nest entrance stones greatly increased the likelihood of desertion (Appendix II).

Otters were probably the main predator of breeding Black Guillemots and their young, on offshore islands at least. On Mousa in 1982, Otter predation accounted for failure of 10.5% of known nests (Ewins 1985f; Appendix VIII). At 10 sites on Mousa at which Otter predation had definitely occurred, the maximum entrance dimensions were compared with those at other sites, revealing no significant difference. The smallest maxima for predated sites were 10 cm (horizontal) and 9 cm (vertical), only slightly greater than corresponding values for other sites (9 cm and 7 cm respectively). Thus, there was little indication that nests failing due to Otter predation had larger entrance dimensions. Clearly some Otters can get into cavities 9-10 cm across at the entrance. If so, few nests on Mousa would be inaccessible to Otters.

Otter predation of incubating adults at 7 sites in 1982 affected breeding there the following year. In 1983, 6 of the sites were tenanted but breeding was only attempted at one (17%), compared with breeding at 78% of sites at which no predation had occurred (Fisher Exact Probability test, P=0.19). Two years later (1984) all 7 of the original sites were tenanted, and breeding was attempted at 5 (71%).

Much kleptoparasitism occurred at colonies CGQ and A, and this resulted in significantly depressed chick growth in some cases (Chapter 7). In only one instance (a 1983 nest in colony CGQ) was kleptoparasitism thought to have led to starvation and death of a chick (the younger of two). Using data from 1983 and 1984 for colonies A, CGQ and E, a linear regression of % delivery attempts losing fish as a result of kleptoparasite activity, against % breeding success, in fact revealed a positive, but non-significant relationship ($r = 0.56$, 4 df, $P=0.25$). Thus, there was no

evidence that breeding success was affected by kleptoparasitism at the levels experienced on Mousa. Similar conclusions were reached for Puffins nesting close to varying numbers of gulls (Pierotti 1983; Rice 1986), but Nettleship (1972) found lower fledging success in areas where Herring Gulls were common.

There was a seasonal decline in clutch size in both 1983 and 1984 (Figure 8.1). Since breeding statistics were only significantly poorer for single-egg clutches in 1984 (Table 8.II), a marked seasonal decline in breeding success was only expected in 1984. In fact there was little variation for either year in hatching, fledging or breeding success between eggs laid in periods I-IV (even when clutch size was controlled for), but in both years birds laying in periods V-VI generally did worse than earlier nesters, in terms of % success and also overall breeding productivity (Table 8.IX). Fresh egg weight had no significant effect on hatching, fledging or breeding success, either for early or late nesters, or for all nests combined (Table 8.X).

In an effort to disentangle the relative importance of the various breeding parameters to overall breeding success, a multiple regression analysis was carried out on data for Mousa colonies (1983-84), using % breeding success as the dependent variable, and colony size, mean laying date, mean clutch size and mean fresh-egg weight as independent variables. No overall significant correlation was found (r^2 = 0.408, 4,9 df, F = 0.86) and none of the partial correlation coefficients were significant. Thus, when considered by colony, none of these breeding parameters accounted for much of the variations in breeding success.

8.4 Discussion

The breeding success for Mousa and Hascosay were amongst the highest recorded for this species (Tables 8.I & 8.XI). Contrastingly the figures for Fair Isle (50 km south of Mousa) were amongst the lowest recorded anywhere. Petersen (1981: 158) stated that the Fair Isle data were collected only from the latter part of the breeding season - this was in error. The only bias was the possible omission of a few early nests which lost egg(s) within a week or so of laying (R A Broad pers. comm.), which would not explain the large differences in breeding statistics. I suspect that Fair Isle is not a good place for breeding Black Guillemots - as suggested for wintering birds too (Chapters 4 & 5). Fair Isle has relatively little shallow water nearby, although there are some productive

Figure 8.1 The mean clutch size on Mousa in relation to laying period (7-day intervals) in 1983 and 1984. Sample sizes are given for each category.

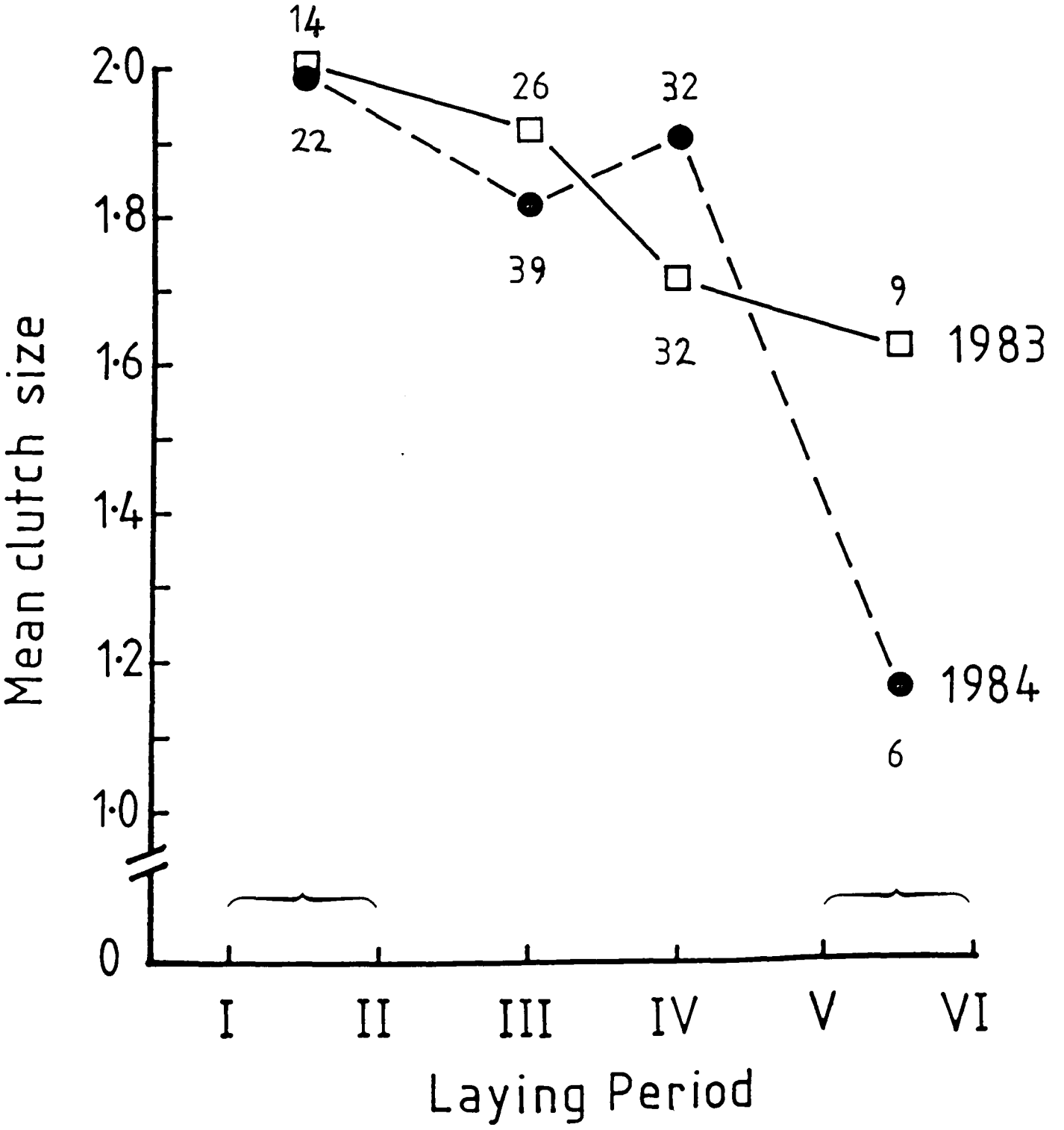


Table 8.IX Reproductive performance in 1983 and 1984 in relation to laying period (see section 6.4.2).

		Laying period			
		I-II	III	IV	V-VI
1983	no. of c2	13	24	24	5
	no. of c1	1	2	8	4
	% Hatching success	89	76	89	71
	% Fledging success	100	90	98	80
	% Breeding success	89	68	88	57
	Mean no. fledging/nest	1.71	1.31	1.53	0.89
1984	no. of c2	21	32	30	1
	no. of c1	1	7	2	5
	% Hatching success	70	73	84	67
	% Fledging success	100	94	89	25
	% Breeding success	70	69	74	17
	Mean no. fledging/nest	1.36	1.26	1.44	0.17

Table 8.X Reproductive success parameters in relation to fresh egg weight and laying date.

		FRESH-EGG WEIGHT (g)			
		39-46	47-50	51-60	Total
EARLY	n	37	45	24	106
(Laying	% Hatching success	68	76	75	73
periods	% Fledging success	96	97	94	96
I-III)	% Breeding success	65	73	71	70
LATE	n	29	31	10	70
(Laying	% Hatching success	83	74	50	74
periods	% Fledging success	83	100	100	92
IV-VI)	% Breeding success	69	74	50	69
Total	n	66	76	34	
	% Hatching success	74	75	68	
	% Fledging success	90	98	96	
	% Breeding success	67	74	65	

tide races around the island. Predation by cats has been noted on Fair Isle (R A Broad pers. comm.) and it is possible that cat predation and disturbance may be an important factor affecting hatching success at the more accessible sites. Mousa and Hascosay however are uninhabited islands lacking ground predators, with extensive shallow foraging grounds nearby, both offering favourable conditions for breeding Black Guillemots.

Petersen (1981: 160) collated all available breeding statistics for Black Guillemots, and suggested that breeding productivity was lower at the edges of the range than towards the centre. When the comparison is restricted to studies with reasonable sample sizes and no biases there is as much variation between years at the same site, or between nearby study colonies, as there is between study sites in different parts of the range (Table 8.XI). Admittedly the Iceland, Norway and Shetland figures are the highest, but I feel that there are too few data from the higher arctic regions (which really should be considered as the centre of the range since the species is far more numerous there) to make realistic comments about geographical variation in breeding output. Looking at clutch size alone one reaches the same conclusion: there is no significant relationship between mean clutch size and latitude ($r = 0.004$, 21 df). The most likely explanations of the differences observed between study sites are variations in food availability and predation pressure. Statistics gathered in only one season should not be regarded as representative of that region since nest predation can be unpredictable and severe (Olsson 1974; Cairns 1985; Ewins 1985f), and atypical environmental conditions can lead to unusually poor breeding productivity (eg. Bergman 1971; Asbirk 1979c).

When results for Mousa were combined for all years, the average reproductive output of pairs laying two-egg clutches was nearly three times that of pairs laying a single egg. Although fledging success was poorer, low hatching success accounted for most of the lower output from single-egg clutches. Very similar results were found by the other main studies (Preston 1968; Cairns 1978; Asbirk 1979c; Petersen 1981), but the reason for the reduced hatching success has not been elucidated. Breeding success in 1984 differed from the previous 2 years in that single-egg clutches fared unusually poorly, particularly at the egg stage. Why was this so ? Better feeding conditions in the pre-breeding period in 1984 (see Chapter 6) probably enabled more birds to reach the condition threshold for breeding (*sensu* Drent & Daan 1980), and so more inexperienced birds were able to make a breeding attempt. These birds tended to lay single eggs, in

Table 8.XI Comparison of breeding statistics in Shetland with those from other studies. Studies/years in which fewer than 20 nests were followed have been ignored, as have studies in which data were probably collected in only part of the breeding season.

Location	Year	No. nests	Mean clutch	% success * HS	FS	BS	
Mousa, Shetland	1982	56	1.75	78	78	60	Present study
	1983	91	1.81	79	94	74	
	1984	119	1.82	74	92	68	
Fair Isle, Shetland	1974	28	1.32	46	94	43	R A Broad, pers. comm.
	1975	22	1.45	38	67	25	
	1976	21	1.57	33	73	24	
	1977	25	1.36	32	64	21	
Denmark	1975	117	1.79	60	55	33	Asbirk 1979c
	1976	127	1.87	54	47	26	
	1977	127	1.86	63	61	39	
Finland	1963-70	31	1.91	100	47	47	Bergman 1971
Norway	1973-75	140	1.94	84	84	70	R Barrett (in Petersen 1981)
Iceland	1975	189	1.93	81	85	68	
	1976	346	1.88	85	89	76	Petersen 1981
	1977	400	1.90	74	83	62	
Bay of Fundy, Canada	1947	49	1.84	52	50	26	Winn 1950
" " "	1962, 1964-67	189	1.78	54	89	48	Preston 1968
St. Lawrence, Canada (a)	1976	90	1.79	62	58	36	Cairns 1978
" " (b)	1977	122	1.95	53	77	41	Cairns 1978
NWT, Canada (c)	1981	20	1.70	56	53	29	Cairns 1984
	1982	52	1.92	51	92	47	
	1983	58	1.72	22	91	20	
" " (d)	1983	26	1.92	62	84	52	Cairns 1984
" " (e)	1977	48	1.94	?	?	51	(e)

Notes: * HS=Hatching success; FS=Fledging success; BS=Breeding success
a Brandypot Island
b St. Mary's
c Pitsulak City
d Piquillit
e Prince Leopold Island. D.N. Nettleship (in Harris & Birkhead 1985).

poorer quality sites, and were inexperienced in breeding duties; as a consequence egg infertility, breakage, desertion and predation were relatively common.

There was considerable evidence in support of these ideas. Although there was no significant difference in pre-breeding attendance counts between years, more sites were tenanted in 1984 and breeding attempted at a greater proportion of sites than in 1983. At the newly occupied sites single-egg clutches were commoner than at previously occupied sites, and hatching success was much lower. This was largely due to egg predation by crows, able to reach the egg(s) since these sites were more open and accessible than normal. Single eggs were laid later than those in two-egg clutches and were lighter and smaller, indicating that they were laid by younger birds [egg breadth increased with adult age in Denmark (Asbirk 1979c), and has been used as a reliable indicator of female age in other seabirds (Richdale 1949, 1955; Coulson et al. 1969)]. Breeding adults were significantly heavier (post-laying) in 1984 than in 1983, again suggesting that they had been in better condition early on.

Most Black Guillemots probably first breed at 4, occasionally 3 years of age (Petersen 1981). Preston (1968) presented some evidence that first-time breeders were more likely to produce single-egg clutches, and in Kittiwakes younger pairs lay smaller clutches (Coulson 1966). Thus, I suspect that the single-egg clutches in 1984 were mostly laid by 3-4-year olds, breeding for the first time, in sub-optimal nest sites, and lacking the experience necessary for successful incubation, brooding and chick rearing.

Seabirds breeding in poor-quality nest sites often experience significantly lower hatching and breeding success [eg. Shag (Potts et al. 1980); Razorbill (Hudson 1982); Puffin (Nettleship 1972)]. Nest site quality also proved to be important for Black Guillemots on Mousa. Cavities in which breeding was attempted were deeper, and a higher proportion had more than one entrance and with the nest scrape not visible from the entrance, than unused sites. Although adult predation was uncommon, birds were at greater risk to kleptoparasitism or any aerial attack when further from the sea, and if cornered by a predator in the nest cavity an alternative exit could be crucial to survival. Larger clutches and greater hatching success in sites with low entrance ceilings and greater nest depth provide further evidence that better quality birds favoured sites inaccessible to nest predators. Cairns (1978) similarly found greater hatching success in darker cavities (his light intensity

measurement was equivalent to my nest depth), but the only other significant physical characteristic was scrape stone size. The largest scrape stones in Mousa nests however, were much smaller than at Cairns' study islands, and greater risk of egg breakage on larger stones may well have contributed to the poorer hatching success on the St. Lawrence islands (see Table 8.XI), in addition to any disturbance effects (Cairns 1978, 1980).

Despite being further from the open sea, occupied nests in colonies A and CGQ were more inaccessible to predators (Chapter 6) and laying was usually earlier in these colonies, suggesting that they may have held better quality birds. Hatching and breeding success in these colonies were no different from elsewhere on Mousa though, perhaps due to the greater availability of sub-optimal sites, at which inexperienced pairs could make a breeding attempt - their poorer productivity counteracting the more successful breeding of the better quality birds.

Evidence for the existence of a social hierarchy was found in the denser breeding aggregations and at the communal over-night roosts, and I interpret the significantly greater nearest neighbour distance between used sites (as opposed to unused sites) as resulting from agonistic behaviour and defence of an area around the nest entrance(s) and nest perches. Dominance at the cliff roosts is of survival value since it enables a bird to occupy a more sheltered site, with a reduced risk of being swept off or eaten, and at which energy requirements for maintenance will be lower than in the peripheral positions. Although Preston (1968) and Cairns (1978) found significantly higher rates of agonistic interaction in denser colonies, no such effect was seen on Mousa. Like Cairns, I found no difference in breeding success with breeding density (ie. colony size), and feel that all other possible factors must first be ruled out (eg. human disturbance, nest site quality, adult age) before any causal link can be established between breeding density and success.

In some studies adverse environmental conditions and high tides caused heavy nest losses (Asbirk 1979c; Petersen 1981), but most nests on Mousa were sufficiently well-drained and far enough from the high tide line to prevent flooding in the breeding season. A wide range of mammalian nest predators has been recorded for Black Guillemots: North American Mink (Olsson 1974; Folkestad 1982), Stoat (Cairns 1985), Otter (Ewins 1985f; P J B Slater pers. comm.), Brown Rat and Hedgehog Erinaceus europaeus (M Gray pers. comm.). Man formerly took substantial numbers of eggs and chicks for food in Shetland (Chapter 3), and in some parts of the range this practice

may still continue (Divoky et al. 1974). The effect of colonisation of offshore islands by Mink can be devastating to ground-nesting birds (Olsson 1974), and even a single Stoat visit caused heavy nest losses and desertion (Cairns 1984, 1985). Although gulls and crows will eat auk chicks their predation on cavity nesting birds is more restricted to eggs. In Razorbills site quality was an important determinant of hatching success - egg predation by Carrion Crows Corvus corone, Jackdaws C. monedula and Herring Gulls was much heavier at ledge sites than in burrows or cavities (Lloyd 1979; Hudson 1982). Site quality was similarly important on Mousa with respect to egg predation by crows and gulls. Although Otter predation of incubating adults was severe in one colony in 1982, Black Guillemots and Otters regularly coexist in boulder areas on Shetland's offshore islands. Most nest cavities would be accessible to Otters and therefore it is unlikely that this predation is widespread. Thus, there appears to be a strong selective advantage for Black Guillemots breeding in a cavity inaccessible to predators, with a good escape route to the sea.

Colonial breeding is generally regarded to be adaptive for bird species which mob predators, such as Black-headed Gulls Larus ridibundus (Kruuk 1964) and Common Gulls L. canus (Gotmark & Andersson 1984), and for species 'swamping' predators by their sheer numbers and synchrony of breeding [eg. Sooty Tern Sterna fuscata (Feare 1976), Guillemot (Birkhead 1977), and Lesser Snow Goose Anser caerulescens caerulescens (Findlay & Cooke 1982)]. Many such studies have found breeding to be more successful in larger and denser colonies, and also as one proceeds towards the colony centre. In my study however, there was no overall difference in breeding success in different colonies, nor was there any suggestion that nest position within a colony affected breeding success. A significantly higher proportion of single-egg clutches was laid in the large colony A, suggesting that more inexperienced and younger birds bred there. This was primarily due to differences in site availability rather than to any greater attraction of larger colonies to young birds. More suitable sites were available at colony A - no breeding attempt was made at 22% of apparently usable cavities there, compared with 0-5% in other colonies. I believe that breeding concentrations of this species result primarily from aggregation of suitable nest sites, rather than from any social or anti-predator function of coloniality. However, in areas where ground predators are common (such as on the Shetland Mainland) potential breeding sites in boulder beaches and low cliffs are not usually used (Chapter 3). First-time breeders may seek a nest site near to conspecifics since their very

presence is an indication of 'safe' breeding conditions. Such behaviour would clearly also lead to aggregation of breeding birds.

Human disturbance of seabird breeding areas has only relatively recently been fully acknowledged as a major factor affecting breeding productivity (Ream 1976; Robert & Ralph 1975; Evans & Nettleship 1985). Amongst the auks, reduced breeding success (largely due to poor hatching success) has been attributed to human disturbance of Common Puffins (Nettleship 1972; Ashcroft 1976; Harris 1984), and in Tufted Puffins Lunda cirrhata the activities of research workers led to increased likelihood of desertion and an extended incubation period (Pierce & Simons 1986). Increased boat and recreational activity was probably responsible for the collapse of Guillemot and Puffin populations in southern Norway (Barrett & Vader 1984). In Shetland there was no evidence that breeding data were adversely affected by human disturbance ranging from weekly to daily nest visits, or even at sites disturbed by tourists for up to 1 hour daily (in fine weather). Petersen (1981) was also unable to demonstrate any harmful effects of his nest inspections, although he suspected that some did exist. Although I was unable to control for other factors possibly affecting breeding success I suspect that merely flushing an incubating Black Guillemot might not constitute an unacceptable level of disturbance [unless the srcape stones were particularly large and sharp-edged, as in Cairns' (1978) study], since a potential predator in the vicinity, such as a crow, gull or Great Skua, usually flushes most birds from the colony. On Mousa such 'natural' flushing probably occurred at least 2-3 times daily in most colonies.

Trapping of adults, particularly in small cavities, or modification of the nest entrance probably constitute much greater disturbance however. Using comparable levels of human disturbance Cairns (1978, 1980) found that hatching success was significantly lower in colonies disturbed daily than in those visited every 4 days, although breeding density effects could not be completely ruled out. Interestingly maximum chick weights were greater on average at Cairns' heavily disturbed colonies, providing support for Petersen's (1981) view that younger, inexperienced birds may be more susceptible to disturbance, since one might expect chicks of experienced parents to reach higher weights. Finally, the frequency of colony visits may not be as crucial as the length of time the birds are kept away from their nests. In Shetland this period rarely exceeded ½ hour, and was shorter in inclement weather, but no comparable times are given by other workers.

Parental quality may be the key factor responsible for variations in Black Guillemot breeding success. It is well known in many seabird species that breeding productivity usually increases with female age (and hence experience), especially during the first few breeding years, reaches a plateau level, and then decreases later in life [eg. Kittiwake Rissa tridactyla (Coulson & Thomas 1985), Herring Gull (Davis 1975), California Gull Larus californicus (Pugesek 1981), Common Tern Sterna hirundo (Nisbet et al. 1984), Arctic Tern (Coulson & Horobin 1976), Gannet Sula bassana (Nelson 1978) and Shag Phalacrocorax aristotelis (Coulson et al. 1969)]. Earlier laying, increased clutch size and egg size usually accompany increased breeding experience (Coulson & Horobin 1976; Coulson & Porter 1985). Not only will parental attentiveness at the nest improve with breeding experience, but older birds will be more proficient at foraging (Orians 1969; Recher & Recher 1969; Dunn E.K. 1972; Searcy 1978), enabling them to devote more time and energy to site defence, courtship, display, maintenance, incubation and chick rearing. These effects will be critical to species with specialized hunting techniques such as the fish-eating auks.

That fresh-egg weight had little effect on breeding statistics, and that only the very latest breeders suffered reduced breeding success, supports the view that feeding conditions were good for Black Guillemots breeding on Mousa. It is likely that in areas of relative food scarcity factors such as egg weight and timing of breeding would have a stronger influence on breeding performance. There was no indication of a seasonal decline in benthic fish availability and adult weights did not decrease significantly during the breeding season (Chapter 9). Although nest site quality is an important determinant of breeding success, the quality of the members of a pair is probably of prime importance. Since good nest sites appear to be in short supply, competition for prime sites is probably intense and high quality birds in good condition will be better able to devote more time and energy to site defence, occupation and breeding duties.

CHAPTER 9. FEEDING ECOLOGY

9.1 Introduction

Throughout most of the range, Cepphus species are benthic, inshore feeders, whose food supplies are generally considered to be more diverse and predictable than in the offshore, pelagic niches of the other auk genera (Lack 1967, 1968; Bedard 1969; Sealy 1972; Gray 1977). Although very little is known of the diet of Black Guillemots in the British Isles (Patten 1906; Oldham 1930; Witherby et al. 1941; Slater & Slater 1972a; Bourne 1982), a considerable volume of data exists for other regions, particularly in the arctic (see Storer 1952; Bradstreet 1980; Cairns 1984; Cramp 1985). Overall the Black Guillemot takes a broader spectrum of prey species than the other Atlantic auks (Pearson 1968; Harris 1970; Harris & Hislop 1978; Blake 1981; Cramp 1985; Harris & Wanless 1985). The general trend is for increasing importance of invertebrates (presumably reflecting overall availability) with latitude in the summer diet of both adults and chicks. The few data on winter food suggest that invertebrates are of greater importance than during the summer (Collett 1877-94; Naumann 1903; Madsden 1957; Kozlova 1961).

Here I describe the diet of full-grown birds during and outside the breeding season, and nestling diet in relation to possible factors accounting for observed variations in composition and delivery rates. The foraging areas of breeding adults are detailed and the adaptive significance of foraging strategies considered in relation to central place foraging theory (Orians & Pearson 1979).

9.2 Methods

9.2.1 Analysis of stomach contents

The stomach (gizzard and proventriculus) was removed from intact corpses found on beaches in Shetland and Orkney (per E. Meek), and stored in 70% alcohol. Additional material came from incubating birds killed by an Otter (Ewins 1985f). I removed the stomachs of 73 deep-frozen corpses of birds killed in spring 1979, after the Esso Bernicia incident at the Sullom Voe oil terminal, and again stored them in 70% alcohol. Stomach contents were examined under a zoom-binocular microscope, after repeated

thorough flushing of the gizzard (this was essential since small items such as otoliths and polychaete jaws frequently lodged between the deep folds of the gizzard wall). Items were identified using reference collections, and the unpublished guides of Watson (1978) and D.A.F.S. (unpubl.) were useful for fish remains. Nomenclature and identification follow Eales (1950), Barrett & Yonge (1958) and Wheeler (1969). "Summer" refers to the breeding season (ie. mid May to mid August), and "winter" to other times of year.

9.2.2 Foraging areas

Most observations outside the breeding season were made in relatively sheltered inshore waters, such as Lerwick and Scalloway harbours (see Figure 2.1). Prey items brought to the surface within c.300 m of the shore were identified to the highest taxon possible. Prey length (or maximum linear dimension in the case of some invertebrates) was estimated in relation to the "head-bill index", since this proved to be a more reliable standard measure than bill length. The mean distance ($\pm$ sd) from the rear of skull to tip of the bill (the "head-bill"index) for 10 breeding adults on Mousa was 85.3 $\pm$ 2.0 mm.

The depth of water in which birds foraged was determined by sampling a range of water depths from a slow-moving boat (less than 6 knots), using an echo-sounder. During surveys in the Hascosay area (winter) and Mousa area (summer), the water depth was recorded for all Black Guillemots seen within 100 m of the boat (distance determined with a rangefinder). In areas where depth changed rapidly the sounding was taken at the spot where the bird had been seen diving. Over relatively level sea beds, the depth reading at the boat was taken to be equivalent to that at the bird's position.
Individuals near breeding or roosting sites were omitted.

During the breeding season observations were made at scattered inshore localities of prey brought to the surface and consumed by full-grown birds. More detailed study of adult foraging behaviour was made at colony A on Mousa (see Figure 6.2), by following departures of breeding adults until they were seen to land on the sea [the "splashdown" - after Cairns (1984)], and commence foraging. A splashdown site was fixed by taking bearings on local landmarks, or with a compass, in conjunction with a distance estimated from the total flight time. Since the average flight speed ($\pm$ sd) was 58.0 $\pm$ 7.7 km h^{-1} (see Appendix IV), and most adults took a direct course between colony and foraging area, this method was thought to provide

a reasonably accurate plot of foraging sites. Water depths at these sites were then obtained from admiralty charts.

9.2.3 Provisioning of chicks

Rates of delivery and details of prey items fed to chicks on Mousa were obtained during hide watches of 2 - 18.5 h duration at colony A, but it was not always possible to determine the identity and size of prey. Other data were collected at a cliff colony of 8 breeding pairs on Hascosay in July 1982. All times are BST.

9.2.4 Fish traps

Benthic fish species were sampled on Mousa between 1 June and 20 August 1984, using un-baited funnel traps of stout plastic mesh (8 mm holes), with an entrance diameter of 5-8 cm at the apex of the funnel (as described by Glimmerveen & Ouwerkerk 1983). Up to 7 traps were set just offshore, the sites varying with sea conditions but always within 20 m of HWM and at depths of up to 6 m. The sea bed was rocky at all sampling sites and vegetated with dense stands of kelp Laminaria spp., conditions favoured by foraging Black Guillemots throughout Shetland. Traps were emptied daily and the length and wet weight recorded for all fish caught. The monthly breakdown of catch numbers (presented in Appendix V) provided an indication of the relative and changing abundance of these inshore, benthic species through the summer months. The few Carcinus maenas trapped have been omitted. Fish specimens were also obtained whilst mist-netting birds carrying fish. Wet weight : length regression equations for the commonest species are given in Table 9.I. The relationship for 'Blennies' was taken to be that for Butterfish Pholis gunnellus, since this was much the commonest blenny caught by Black Guillemots. For the "other fish species", the relationship Wet weight = Length^3 was used as an approximation. The data for sandeels came mainly from undamaged fish caught by a trawler in Mousa Sound.

9.3 Results: Full-grown birds

9.3.1 Diet

Table 9.I. Regression equations for inshore fish species at Mousa in 1984. Wt = wet weight (g), L = length (cm).

Species	No. fish	Regression
Pollachius virens	45	$Wt = 0.00977\ L^{2.96}$
Gaidrosparus vulgaris	41	$Wt = 0.00955\ L^{2.89}$
Ciliata spp.	59	$Wt = 0.00631\ L^{3.02}$
Ammodytes spp.	81	$Wt = 0.00063\ L^{3.57}$
Pholis gunnellus	31	$Wt = 0.00105\ L^{3.39}$
Zoarces viviparus	56	$Wt = 0.00617\ L^{2.90}$
Cottus spp.	61	$Wt = 0.02692\ L^{2.77}$

Winter and summer diets of full-grown birds were compared by the analysis of stomach contents, and observations of prey items brought to the surface on the foraging areas. Both methods probably have inherent biases (see discussion).

There was no significant difference between proportions of the main classes of prey items in the stomachs of oil spill victims ("Esso Bernicia"), and corpses found on beaches in winter (mostly unoiled) ($G = 5.6$, 3 df, $P>0.1$). Although sample sizes in summer were small, stomachs contained more fish and crustaceans, and fewer gastropods than in winter, but a similar spectrum of prey types overall (Table 9.II). At least 30 different prey types were recorded in winter stomachs. Galathea spp. (Squat Lobsters) and gastropod molluscs (probably mostly Littorina and Lacuna species) were particularly frequent, occurring in over 20% and 40% of stomachs respectively. The opercula and shells of gatropods were usually intact (one stomach contained 118 opercula), in contrast to the fragmented crustacean exoskeletons and worn fish vertebrae and otoliths. Many of the Esso Bernicia stomachs not surprisingly contained fuel oil (80%) and Black Guillemot underpart feathers (60%), findings consistent with oiled birds attempting to clean their plumage. Beetles and fragments of terrestrial plants were probably eaten by dying birds. Nematode worms (up to 15 in a stomach, maximum length 12 mm) were probably parasites of the alimentary tract rather than prey items (see Uspenski 1956), and appeared to be rarer in oiled stomachs. Up to 5 small stones (range of maximum dimensions = 0.5 to 7 mm) per stomach were found in 52-75% of the samples and could have been ingested to facilitate grinding up of bones, exoskeletons and shells. The short lengths (up to 6 mm) of coloured, nylon monofilament line, and plastic spheres (<1 mm diameter) may have originated from stomachs of fish prey, as could have algal fragments and small gastropods.

A total of 5 types of invertebrates and 10 fish types were identified when brought to the surface in winter, compared with 2 invertebrate and 8 fish types in summer (Table 9.III). Most unidentified items were probably small invertebrates. Since there was no significant difference between adults and immatures in the proportion of fish brought to the surface in winter (70% and 60% respectively, $G = 2.14$, 1 df, $P>0.05$) the results were pooled. Thus, 67% of prey items observed in winter were fish, compared with 81% in summer (difference not significant however, $G = 0.8$, 1 df, $P>0.1$). Blennies (Pholididae, Stichaeidae, Zoarcidae) accounted for 49% of identified fish in winter and 54% in summer - the difference was not

Table 9.II. The number and frequency of occurrence of prey items in stomachs of full-grown Black Guillemots.
N.B. Table continued overleaf.

	WINTER				SUMMER	
	Esso Bernicia 1979		Shet. & Orkney 1982-84		Shet. & Orkney 1982-84	
Total no. stomachs	73		16		7	
No. with prey remains	58	(79%)	14	(88%)	4	(57%)
Total no. (minimum) of identified items	391		99		13	
Taxon/species	No.[a]	% Freq.[b]	No.[a]	% Freq.[b]	No.[a]	% Freq.[b]
POLYCHAETA						
Aphrodite aculeata	4	5	-	-	-	-
Nereis spp.	19	17	10	14	1	25
Spirorbis sp.	1	2	-	-	-	-
CRUSTACEA						
unident. Amphipoda	-	-	1	7	1	25
Pandalus montagui	1	2	-	-	-	-
Pandalus spp.	2	2	2	14	-	-
Galathea strigosa	1	2	2	7	-	-
G. squamifera	3	3	-	-	-	-
G. dispersa	2	2	-	-	-	-
G. intermedia	12	9	3	14	-	-
Galathea spp.	20	19	2	14	1	25
Eupagurus spp.	1	2	-	-	2	50
Porcellana longicornis	1	2	-	-	-	-
Portunus depurator	-	-	-	-	1	25
Eurynome aspera	-	-	1	7	-	-
unident. crabs	3	3	1	7	4	25
unident. Reptantia	12	14	7	43	-	-
GASTROPODA						
Calliostoma zizyphinum	-	-	1	7	-	-
Gibbula cineraria	-	-	13	7	-	-
Littorina saxatilis	12	2	-	-	-	-
L. littoralis	19	5	4	14	-	-
Lacuna spp.[c]	36	7	37	21	-	-
unident. Gastropoda	212	38	4	14	-	-

Notes: [a] Minimum no. of individuals identified
[b] Frequency of occurrence in stomachs containing prey
[c] Probably mostly Lacuna pallidula

Table 9.II. (continued)

Taxon/species	WINTER *Esso Bernicia* 1979 No.[a]	WINTER *Esso Bernicia* 1979 % Freq.[b]	WINTER Shet. & Orkney 1982-84 No.[a]	WINTER Shet. & Orkney 1982-84 % Freq.[b]	SUMMER Shet. & Orkney 1982-84 No.[a]	SUMMER Shet. & Orkney 1982-84 % Freq.[b]
PISCES						
Sprattus sprattus	1	2	-	-	-	-
unident. Gadidae	4	7	-	-	-	-
Ammodytes spp.	3	5	-	-	-	-
Gobius sp.	-	-	1	7	-	-
unident. Pleuronectidae	1	2	-	-	-	-
Agonus cataphractus	-	-	1	7	-	-
Zoarces viviparus	1	2	1	7	-	-
Pholis gunnellus	1	2	1	7	1	25
unident. fish	17	26	7	29	2	25
MISCELLANEOUS						
Algae	+	19	+	21	-	-
Porifera	+	2	-	-	-	-
Coelenterata	+	2	-	-	+	25
Nematoda	+	2	+	36	+	100
Echinoidea	2	2	-	-	-	-
Coleoptera	-	-	+	14	+	25
Terrestrial plants	+	12	-	-	-	-
Grit	+	52	+	64	+	75
Feathers	+	76	-	-	-	-
Man-made artefacts	+	7	+	14	+	25

Notes: + Material present
[a] Minimum no. of individuals identified
[b] Frequency of occurrence in stomachs containing prey

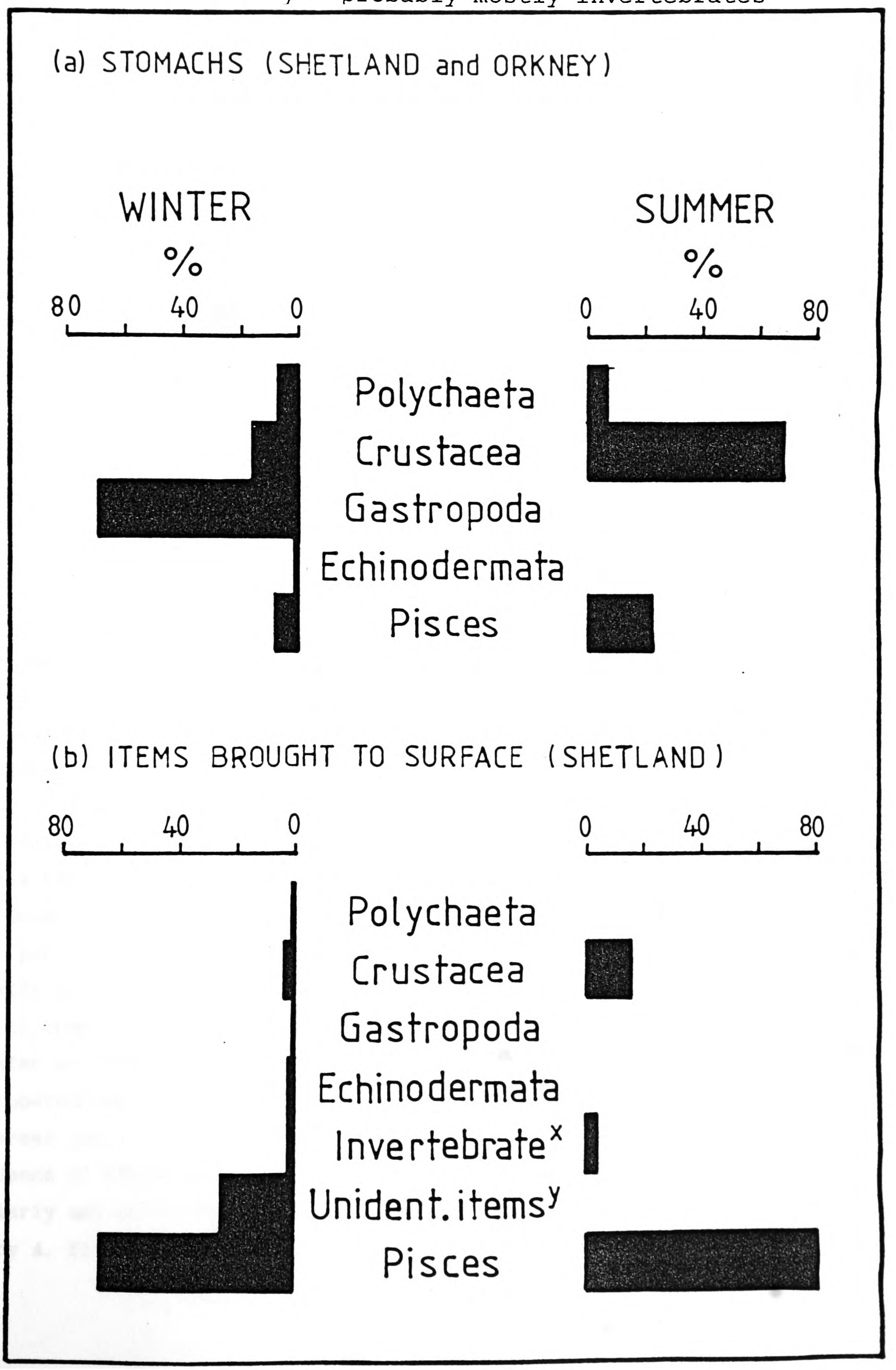
Table 9.III. Prey items brought to the surface by full-grown Black Guillemots on feeding areas, 1982-85 (excluding those prey delivered to chicks).
Total no. of items in winter = 312; in summer = 32.

	WINTER		SUMMER	
Prey type/species	No.	% of total	No.	% of total
POLYCHAETA				
Nereis spp.	4	1.3	-	-
CRUSTACEA				
unident. Natantia	1	0.3	-	-
Galathea spp.	3	1.0	-	-
Eupagurus spp.	-	-	3	9.4
Carcinus maenas	-	-	1	3.1
unident. crabs	4	1.3	1	3.1
unident. crustacea	2	0.6	-	-
GASTROPODA				
unidentified	1	0.3	-	-
ECHINODERMATA				
unident. Asteroidea	6	1.9	-	-
unident. invertebrates	6	1.9	1	3.1
unident. items[a]	77	24.7	-	-
PISCES				
Pollachius virens	2	0.6	-	-
Ciliata spp.	2	0.6	-	-
unident. Gadidae	1	0.3	-	-
Ammodytes spp.	5	1.6	3	9.4
Gobius spp.	-	-	1	3.1
Pholis gunnellus	30	9.6	9	28.1
Chirolophis ascanii	-	-	1	3.1
Zoarces viviparus	1	0.3	2	6.3
unident. blenny	6	1.9	2	6.3
unident. Cottidae	8	2.6	6	18.8
Cyclopterus lumpus	1	0.3	-	-
Liparis sp.	-	-	1	3.1
Spinachia spinachia	13	4.2	-	-
unident. Pleuronectidae	6	1.9	1	3.1
unident. fish	133	42.6	-	-

Note: [a] Probably mostly invertebrates

Figure 9.1 The frequency of prey types (as % of total no. of items), taken in winter and summer by full-grown birds, as determined by: a) Stomach analyses, b) Items brought to the surface and consumed.

Note: x = unidentified invertebrates
y = probably mostly invertebrates



significant (G = 0.2, 1 df, P>0.1) - but few observations were made in areas where sandeels would have been expected, so these results relate only to sheltered inshore waters lacking large areas of sandy seabed. A bulge in the throat, accompanied by discernible swallowing actions was occasionally noted at surfacing, suggesting that prey had already been ingested (see later). Despite the differences and biases in these two methods of diet determination, there appears to have been a greater diversity of food taken in winter than in summer (Figure 9.1).

9.3.2 Provisioning of chicks

Black Guillemots only carried one prey item at a time to the nest. Once suitable prey (almost always a fish) had been caught and manipulated, adults returned to the colony. Occasionally birds carrying a particularly long or heavy fish (larger blennies and gadoids weighed up to 16 g, c.4% of adult body weight) would rest on the water at intervals. Long, 'floppy' sandeels and blennies may have caused considerable drag in flight. When no predators or kleptoparasites were present birds usually flew straight to the nest. However, any disturbance caused a delivering bird to make large arc(s) out over the sea, or to land in the offshore gathering area (see Chapter 10). Disturbed adults with a fish regularly dipped their heads beneath the water surface. Although this *will* have kept the fish moist (Petersen 1981), I consider that in most instances this was primarily the "bill dipping" behaviour characteristic of birds on the water in states of alertness (Asbirk 1979b). Twice in July 1984 a bird in adult plumage, but with heavily abraded remiges (typical of 2-3-year-olds, Asbirk 1980), came to colony A with a fish. It made no attempt to enter a nest cavity and both fish were eventually stolen by Arctic Skuas. No individuals with such abraded feathers bred on Mousa.

Occasionally fish were delivered through small gaps in the nest cavity roof, particularly when chicks were large and mobile. Delivering birds normally scuttled rapidly into the cavity upon landing and I only once saw a chick come to the entrance to receive fish in full view from outside. Transfer of fish at the nest entrance might be risky in the presence of kleptoparasites. This would explain why at study colonies in Iceland (Petersen 1981) and Greenland (P G H Evans pers. comm.) (where the incidence of kleptoparasitism was much lower than on Mousa), chicks regularly met deliveries at the nest entrance. At 5 different nests in colony A, fish were delivered by the mate of the individual which had

caught the fish. In all 8 instances the mate was already standing at the nest perch, grabbing the fish in 2 cases, and being passed the fish in 6 cases. On 4 occasions at other nests the mate made unsuccessful attempts to snatch a fish from the delivering partner. A colour-ringed pair were once watched exchanging a sandeel at least 6 times during a 5-minute period at a cliff perch 20 m away from their nest containing 2 small chicks. This was reminiscent of Guillemots with display fish (Birkhead 1974b; pers. obs.)

Fish were usually dead by the time chicks received them, but blennies (especially Butterfish) were sometimes still wriggling when delivered. Despite regular nest checks only 9 "rejected" fish were found lying in and around the nest cavities in the 3 study years on Mousa. However, at a nest on Hascosay, which hatched one chick in each year, a total of 49 fish were found at and below the site. Of the 58 rejected fish, 62% were Butterfish, 33% sandeels, 3% cottids and 2% Yarrell's Blenny Chirolophis ascanii. The fish tended to be longer than those fed to chicks at that age (see Figure 9.17), but there was no significant difference in length for either Butterfish or sandeels. Although cottid species have sharp spines a few were eaten by chicks (Table 9.VII): post-mortem examination of 14 dead chicks identified choking as a cause of death in only one case. Although some of the rejected fish at the Hascosay nest may have been too large for the chick to swallow, most were suitable. Perhaps (at least) one parent failed to regulate the rate of delivery, since the chick was always above average weight for its age, and so was unlikely to be hungry.

Weighing of chicks indicated that some received food within 24 hours of hatching. Although no systematic watches were made for this, 11 feeds to day 0 chicks were recorded, with a maximum of 3 feeds to a chick on the first day. These fish were always less than 9 cm long (mean 6.0 cm) and included sandeels, blennies and gadoids. Most adults stopped bringing in fish once the last chick had fledged, but 3 deliveries were noted the day after, and one delivery 2 days after the chick(s) had gone. All of these fish were subsequently swallowed by the adult.

With the exception of one sandeel held by the tail and two held with the head pointing down the gullet and only the tail protruding (in the manner of Guillemot deliveries), adults held fish cross-wise in the bill, usually just behind the gills. Slater & Slater (1972a) suggested that individuals showed strong directional preferences for orientation of fish held in the beak ... "about half of them prefer the left side and half of them the right", although only 9 of the 15 individuals showed significant

fish orientation preference (Slater 1974). To investigate this, the direction in which the fish head pointed (relative to the delivering bird flying forwards) was recorded at colony A. There was no evidence for significant directional preference on different days in relation to wind speed or direction, although in 1983 significantly more fish were held facing to the right than to the left ($G = 13.3$, 1 df, $P<0.001$). The results for recognizable individuals, for which prey orientation was scored for 10 or more deliveries in a season, indicated significant directional preference in 7 of the 35 bird-years (20%) - 2 being "left-handed" and 5 "right-handed" - and there was significant heterogeneity between individuals in both years (Table 9.IV). Only one out of a possible 13 individuals (A6♀) showed a consistent significant directional preference in both years. Although the pooled G-statistic was significant in 1983 this was mainly due to the large number of deliveries recorded for A5♀. When this individual was excluded there was no significant directional preference in either year.

9.3.3 Individual and sex differences

Fish delivered by individuals for which at least 20 items were identified were classified as "pelagic" (sandeels and gadoids - excluding rocklings), or "benthic" (blennies, flatfish, cottids, rocklings and others). Since there was no evidence of variation in chick diet composition between colonies on Mousa, the proportion of pelagic and benthic species brought in by marked individuals was compared with the overall proportion for Mousa in that year (overall nestling diet is summarized in Table 9.VII). Analysis with G-tests revealed that of 15 individuals in 1983 and 17 in 1984, in both years six delivered significantly more pelagic species, and four significantly more benthic species than the average for the island. In other words 67% of marked birds in 1983, and 59% in 1984 specialized in either pelagic or benthic fish (Table 9.V). There was significant heterogeneity between individuals in both years ($P<0.001$). Overall, males predominated amongst benthic specialists (8♂♂ vs. 4♀♀), and females amongst pelagic specialists (6♀♀ vs. 2♂♂). A general consistency was apparent for individuals sampled in both years: 80% of males, but only 57% of females were in the same category in the two years (Table 9.V). No evidence was found to suggest that mates complemented each other's suite of delivered fish types; some mates were specialists on the same types, whereas others overlapped very little.

Table 9.IV. The orientation of fish delivered by individuals at colony A in 1983 and 1984. Significance of departures from expected 1:1 frequencies were determined using G tests.
(* P<0.05, ** P<0.01, *** P<0.001)

	1983			1984		
	No. fish facing			No. fish facing		
Individual	Left	Right	G	Left	Right	G
A1♂	13	14	.04	26	19	1.07
A1♀	14	13	.04	20	18	.10
A5♂	20	32	2.80	22	12	2.90
A5♀	11	83	62.45 ***	8	12	.77
A6♂	4	10	2.66	11	15	.60
A6♀	7	22	8.15 **	23	42	5.55 *
A12♂	14	13	.04	17	22	.63
A12♀	19	16	.26	9	10	.05
A17♀	13	17	.53	9	9	0.00
A21♂	26	20	.78	11	8	.46
A21♀	15	6	3.90 *	14	15	.03
A27♂	13	5	3.58	24	12	4.02 *
A27♀	17	11	1.25	19	38	6.40 **
A17♂	12	11	.04			
A20♂	11	9	.20			
A20♀	21	33	2.69			
A3♂				17	12	.84
A3♀				23	49	9.47 **
A11♂				18	18	0.00
A11♀				17	12	.84
A19♂				5	5	0.00
A19♀				13	6	2.57
TOTAL:			89.40 ***			36.31 **
POOLED:	230	315	13.31 ***	306	343	2.11
HETEROGENEITY:			76.09 ***			34.20 *

Table 9.V. Specialisation on prey types by adults delivering at colony A. Significance of departures from the overall ratio of benthic: pelagic species was determined with G tests. (ns = non-significant).

Individual	Direction of significant specialisation 1983	1984
A1♂	Benthic	Benthic
A3♂	-	ns
A5♂	Benthic	Benthic
A11♂	-	Pelagic
A12♂	Pelagic	ns
A17♂	Benthic	-
A20♂	Benthic	-
A21♂	Benthic	Benthic
A27♂	ns	ns
A1 ♀	ns	ns
A3 ♀	-	ns
A5 ♀	Benthic	Benthic
A6 ♀	Pelagic	Pelagic
A11 ♀	-	ns
A12 ♀	Pelagic	ns
A17 ♀	ns	Benthic
A19 ♀	-	Pelagic
A20 ♀	ns	-
A21 ♀	ns	Benthic
A27 ♀	Pelagic	Pelagic

The diversity of fish types delivered by individuals was investigated using the Shannon-Wiener index of diversity, given by the formula: $H = -\sum_{i=1}^{n} p_i \log_e p_i$, where p_i is the proportion of species i in a sample of n species. Fish were grouped into families (see Table 9.VII), but blennies were considered as one group since it was sometimes difficult to differentiate between species. The mean diversity index was significantly lower for pelagic specialists than for benthic specialists in 1983 (H = 0.458 : 1.385 respectively, t = 4.73, 8 df, P<0.002) and in 1984 (H = 0.681 : 1.329, t = 4.2, 8 df, P<0.01). Thus, individuals specializing on sandeels and/or gadoids delivered fewer other species, whereas benthic specialists brought in a significantly wider variety of fish types. There was no significant difference in the overall diversity index (H) between years (0.980 : 1.055, t = 0.9, 33 df, P>0.1), based on 7 males and 8 females in 1983 and 10 pairs in 1984. Although there was no significant difference overall for diversity index of individuals in successive years (r = 0.54, 11 df, P>0.05), the diversity of fish types delivered by individual males showed greater consistency between years than was the case for females (Figure 9.2). Despite the impression from this figure that females delivered a wider range of fish types in 1984, there was no significant difference for either sex in the mean diversity index between years (P>0.1). Combining data for both years, males delivered a significantly greater diversity of fish than did females (for males mean H = 1.200; for females mean H = 0.856, t = 2.92, 33 df, P<0.01).

There were significant differences within pairs in the total number of deliveries made, when compared to an expected 1:1 ratio. In 1983 (8 pairs sampled), a significant difference was found in 3 pairs - in two cases it was the female which delivered most. In 1984 (10 pairs sampled), a significant difference was revealed in 6 pairs - in five of these the female provided most deliveries. In both years females made more deliveries overall (significant only in 1984, P<0.001), but there was considerable heterogeneity between pairs (G = 33.9, 7 df, P<0.001 in 1983; G = 58.0, 9 df, P<0.001 in 1984). Sampling bias due to the temporal distribution of observation periods was ruled out as an explanation for the predominance of female deliveries, since hide-watches were made at regular intervals throughout the nestling periods. There was no significant diurnal variation in deliveries (grouped into 5 h periods) for females or males (G = 5.8, 1.9 respectively, 3 df, P>0.05 in both cases). One further factor which must be considered is the possibility that handling (for colour-ringing and weighing) subsequently made an adult more timid about

Figure 9.2 The relationship between the Shannon-Wiener index of diversity (H) of fish types delivered by 13 adults in 1983 and 1984. Based only on individuals for which 20 or more deliveries were identified in each year.
The dotted line represents y = x.

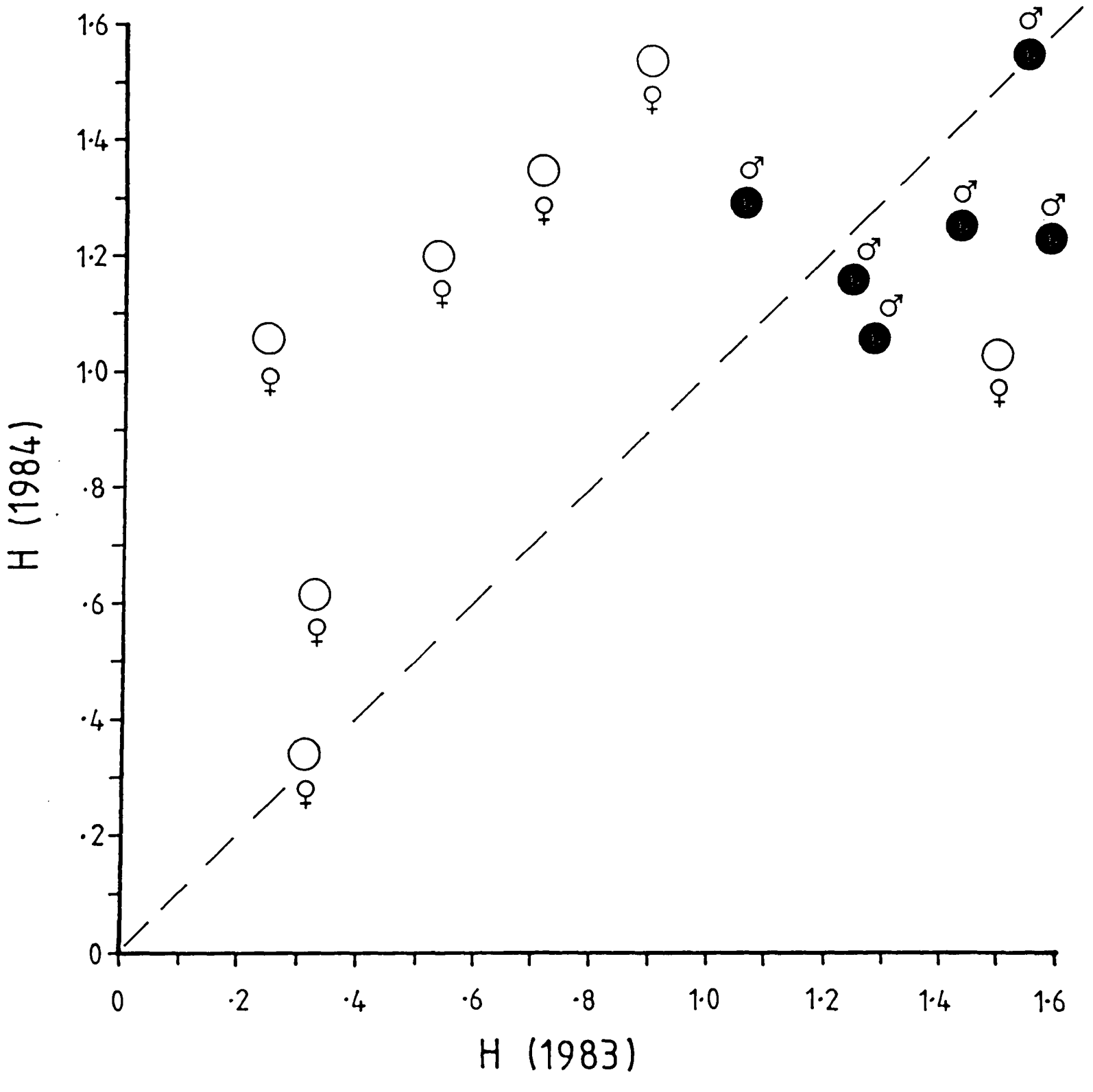
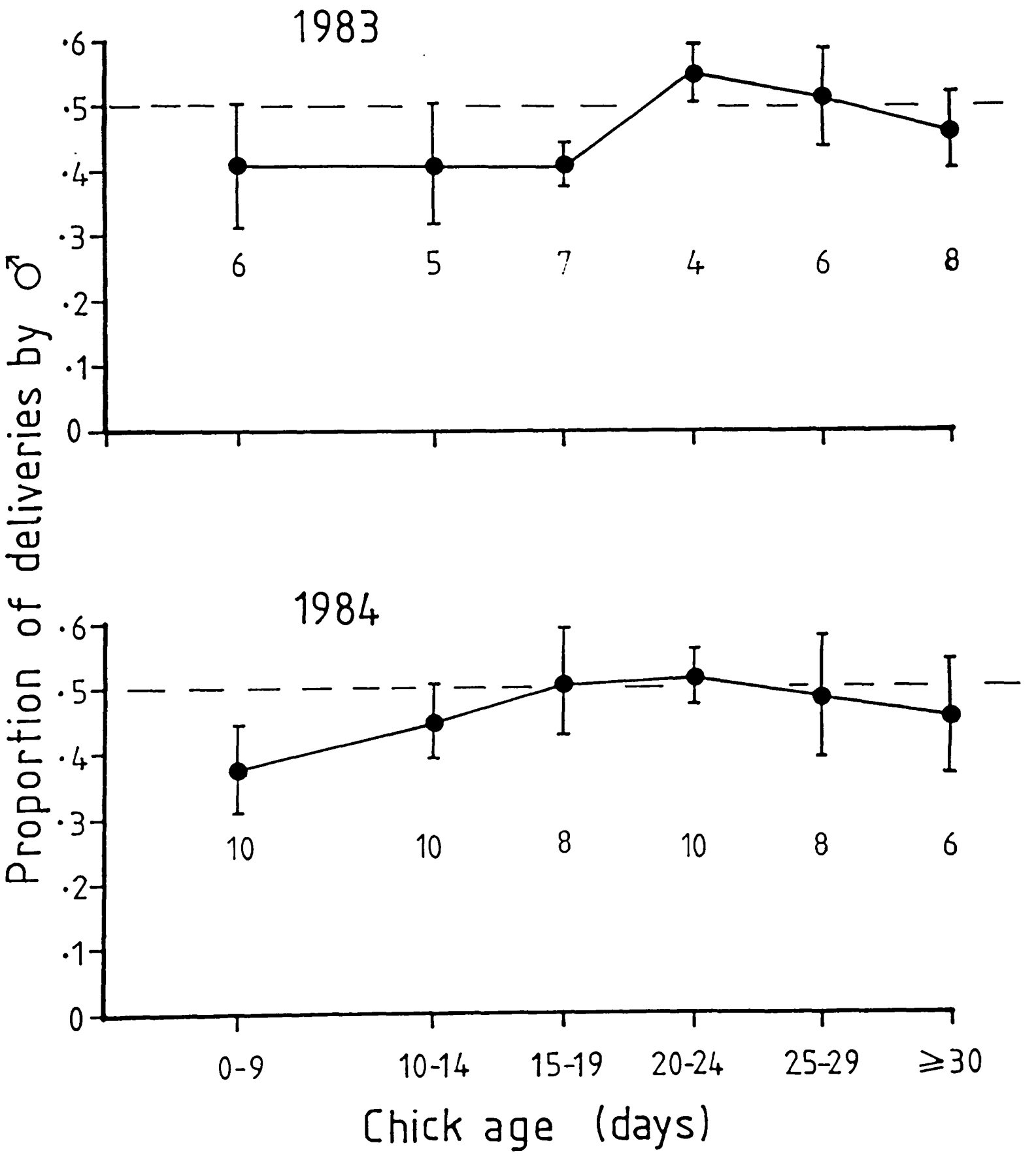


Figure 9.3 The proportion of deliveries made by the male, at different chick ages in 1983 and 1984. Mean ± se and sample number of nests is given for each age category.



approaching the area. For a total of 16 pairings in which only one mate had been handled, only two (13%) of the handled birds made significantly fewer deliveries than the mate, and one made significantly more deliveries. Therefore, there was little evidence that adult delivery behaviour was affected by earlier handling at the nest area.

During the earlier stages of the nestling period in both years, females made more deliveries than males (Figure 9.3). Combining the data for all nests of marked pairs, chicks up to 2 weeks old received significantly more feeds from females than from males (1983; $G = 6.84$, 1 df, $P<0.01$): 1984; $G = 13.95$, 1 df, $P<0.001$). However, there was no significant sex difference in either year for deliveries to older chicks.

9.3.4 Foraging areas

Comparison of water depths in which Black Guillemots foraged with the 'availability' of different depths revealed significant preferences for foraging in shallow waters, and avoidance of areas of water deeper than 40-50 m (Figure 9.4). Although the winter and summer surveys were conducted in different regions, the frequency distributions of depth classes surveyed were similar (Figure 9.4a,b), and there was a suggestion that proportionately more birds foraged in water 30-50 m deep in summer. This was borne out by casual observations from boats in other parts of Shetland. Over 40% of splashdowns of Mousa colony A breeders within 1.5 km of the colony were in water 30-50 m deep - a much higher figure than was found during the boat transects in the Mousa area during the 1984 summer. This difference was largely due to some colony A birds regularly feeding in tide races off the south-eastern corner of Mousa, which occurred in water 30-50 m deep. There was a highly significant sex difference in foraging depths in summer - colony A females diving in deeper water than males ($G = 26.7$, 2 df, $P<0.001$) (Figure 9.5).

In July 1984 I followed 73 departures of breeding adults from colony A to splashdown sites at which diving began. The mean travel time ($\pm$ se) was 40.8 ± 3.1 s, with a range of 8-118 s. The distance travelled was estimated using the mean speed of direct flight (given in Appendix IV). Since there was no significant sex difference in travel distance the data were pooled for the various distance categories (Table 9.VI), revealing that 97% of breeders fed chicks with fish caught within 1.5 km of the colony (total range 0.1 - 1.9 km). I compared the depths in which different fish were caught by following recognizable birds to splashdown,

Figure 9.4 Frequency distributions of depths of water in which Black Guillemots foraged (shaded) in relation to water depths sampled (unshaded): a) Winter - Hascosay area
b) Summer - Mousa area
c) Summer - Mousa colony A adults feeding young; splashdowns and water depths within 1.5 km of the colony.

Total no. of birds in the sample (n) and area surveyed (km^2) are given.

Distributions differed significantly in all cases: a) $G = 6.20$, 2 df, $P<0.05$.
b) $G = 17.35$, 3 df, $P<0.001$.
c) $G = 25.29$, 3 df, $P<0.001$.

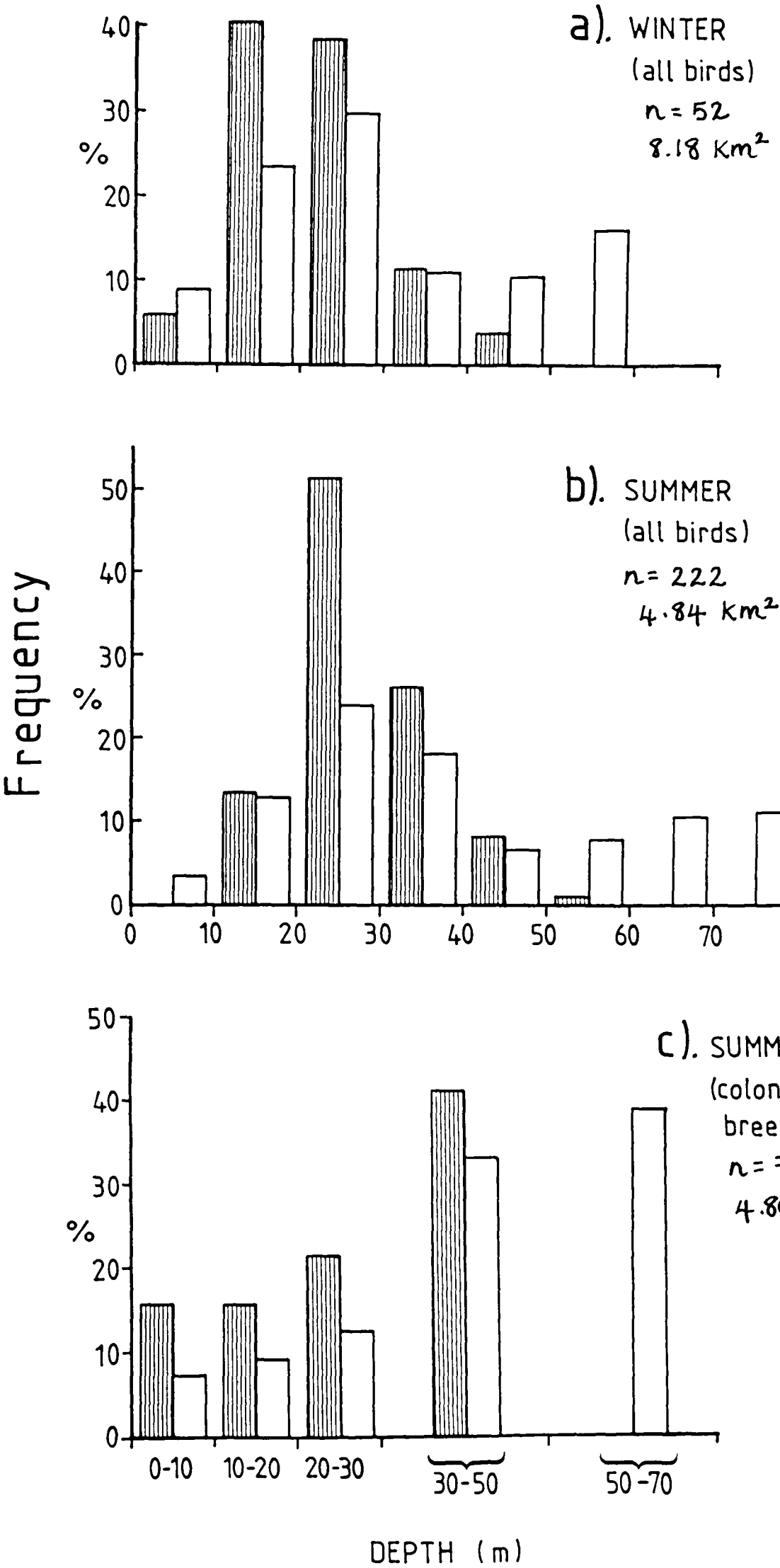

a). WINTER
(all birds)
n = 52
8.18 Km²
%
40
30
20
10
0
b). SUMMER
(all birds)
n = 222
4.84 km²
Frequency
%
50
40
30
20
10
0
0 10 20 30 40 50 60 70 80 90
c). SUMMER
(colony A
breeders)
n = 71
4.80 Km²
%
50
40
30
20
10
0
0-10
10-20
20-30
30-50
50-70
DEPTH (m)

Figure 9.5 Water depth at splashdown sites of breeding males and females from colony A in July 1984. Data pooled for different individuals - 6 males (25 splashdowns), and 8 females (46 splashdowns).

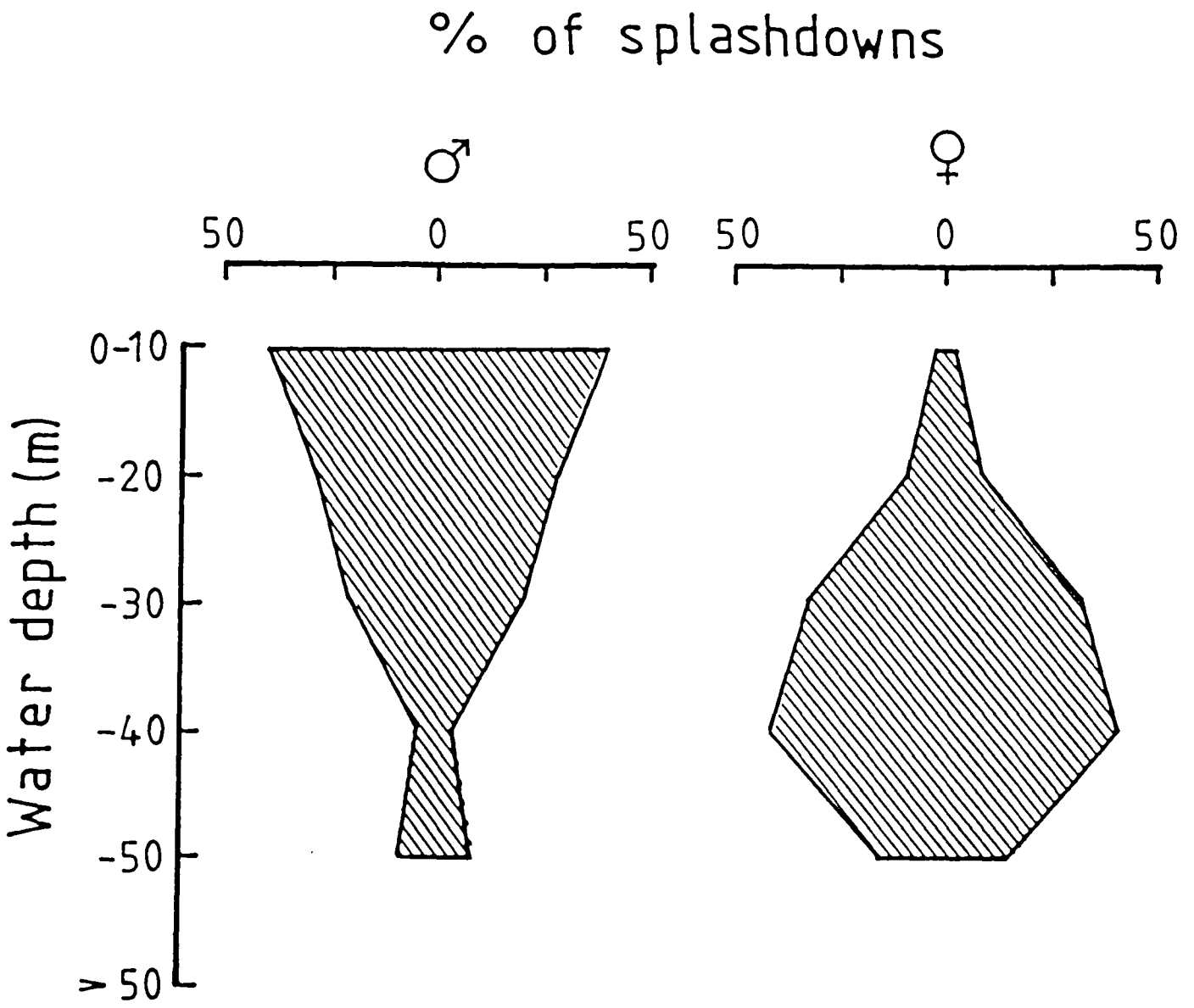


Table 9.VI. The estimated distances travelled to feeding areas by adults provisioning chicks at colony A in July 1984. Based on 73 departures, of at least 24 different individuals.

Distance travelled (km)	%
0 - 0.10	0
0.10 - 0.25	16.4
0.25 - 0.50	30.1
0.50 - 0.75	15.1
0.75 - 1.00	17.8
1.00 - 1.25	6.8
1.25 - 1.50	11.0
1.50 - 1.75	0
1.75 - 2.00	2.7
> 2.00	0

and assuming that the next fish they brought back had been caught in that depth of water (Figure 9.6). Sandeels and gadoids were rarely caught in water shallower than 10 m, whereas blennies were caught in water of all depths, and other species (almost all having benthic lifestyles) mostly in water less than 30 m deep. Overall, pelagic fish were taken in signficantly deeper water than benthic species ($G = 40.6$, 2 df, $P<0.001$), but it was impossible to determine whereabouts in the water column they were captured. At the individual level, there was a significant positive correlation between the proportion of pelagic species delivered and mean water depth at the splashdown sites (Kendall coefficient of rank correlation, $\tau = 0.286$, $n=8$, $P<0.02$).

A more precise indication of foraging areas during the chick period was provided by following departures of colony A adults feeding young, in July and early August 1983 ($n=160$) and July 1984 ($n=224$). Data were analysed by dividing departures into three directions: north, east-south, and south-west. There was no overall significant difference in departure directions between years ($G = 4.6$, 2 df, $P>0.05$); only the results for 1984 are depicted (Figure 9.7). In both years there was a seasonal shift - the proportion of birds departing in a south-westerly direction decreased after mid July, with a corresponding increase in the proportion going northwards. This shift was only significant in 1984 ($G = 19.1$, 6 df, $P<0.01$). Although some individuals consistently returned to the same resticted area to forage on a number of separate observation days in July 1984, others regularly switched foraging sites, both within and between days. The data have been pooled for the month for two individuals exhibiting these two types of strategy (Figure 9.8). Individuals could be broadly classified, with respect to foraging area, as "specialist" (the A3♀ type) - more than 75% of splashdowns in one area - or "generalist" (the A1♂ type) - visiting a number of different areas. Although sample sizes were small for some individuals, it appeared that roughly half the breeders were generalists and half specialists. I found no evidence of departing birds actively following others to foraging areas. Ashcroft (1976) noted this phenomenon in Puffins however, and interpreted it as supporting the idea of coloniality facilitating transfer of information about feeding sites (Ward & Zahavi 1973). When two Black Guillemots did depart together in the same direction they rarely landed within 50 m of each other.

An unusual source of food was exploited by Black Guillemots around Mousa in the summer months, particularly in April. When boats trawling for sandeels stopped at the end of a trawl, to begin winching-in the net, up to

Figure 9.6 The percentage of fish types delivered by individually recognizable colony A adults feeding in different water depths in July 1984. Total number of each type given in brackets.

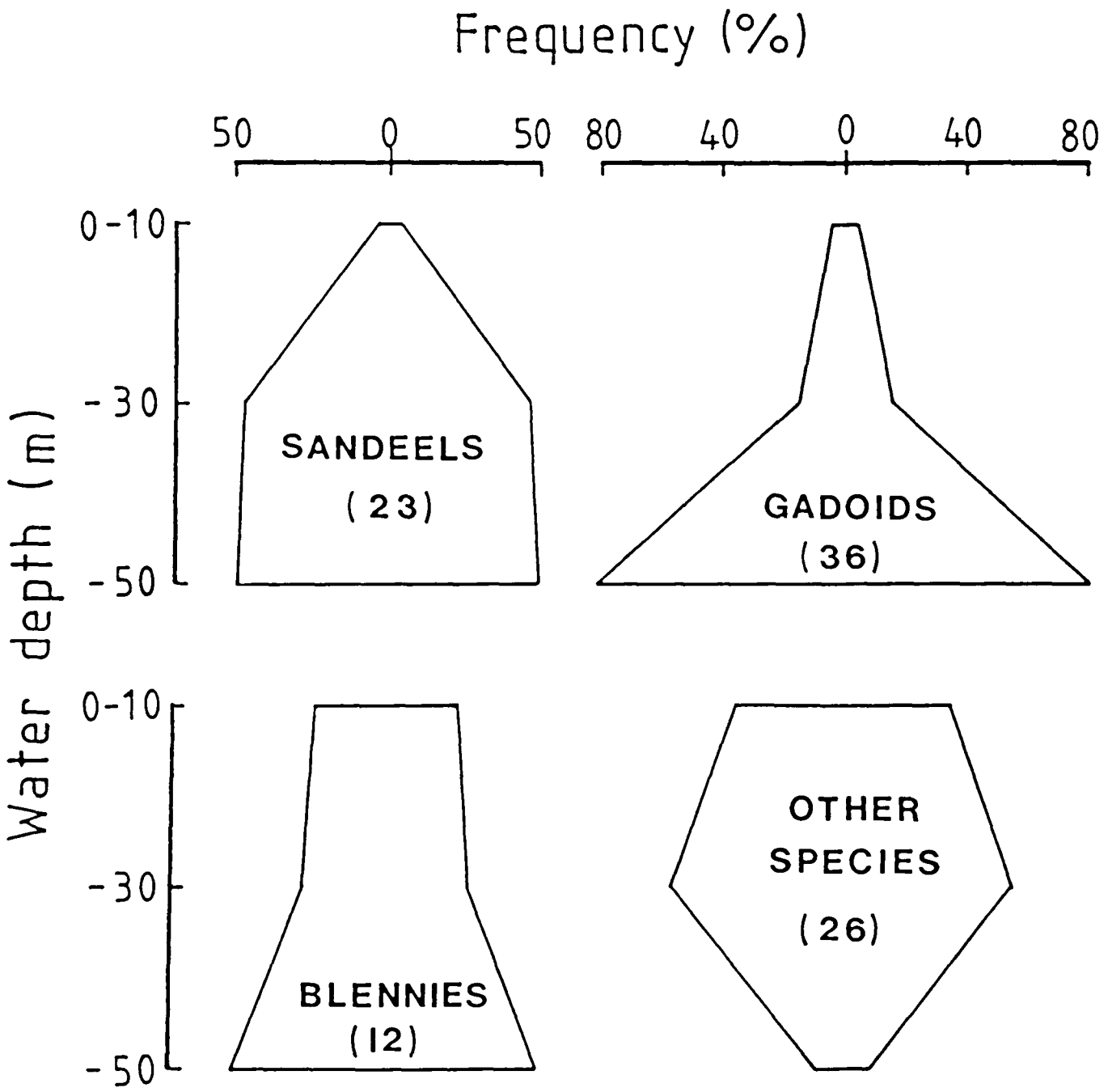


Figure 9.7 Departure directions to foraging areas of adults feeding chicks at colony A in July 1984 (expressed as percentages of the 224 departures). Small arrows refer to birds foraging within 500 m of the colony.

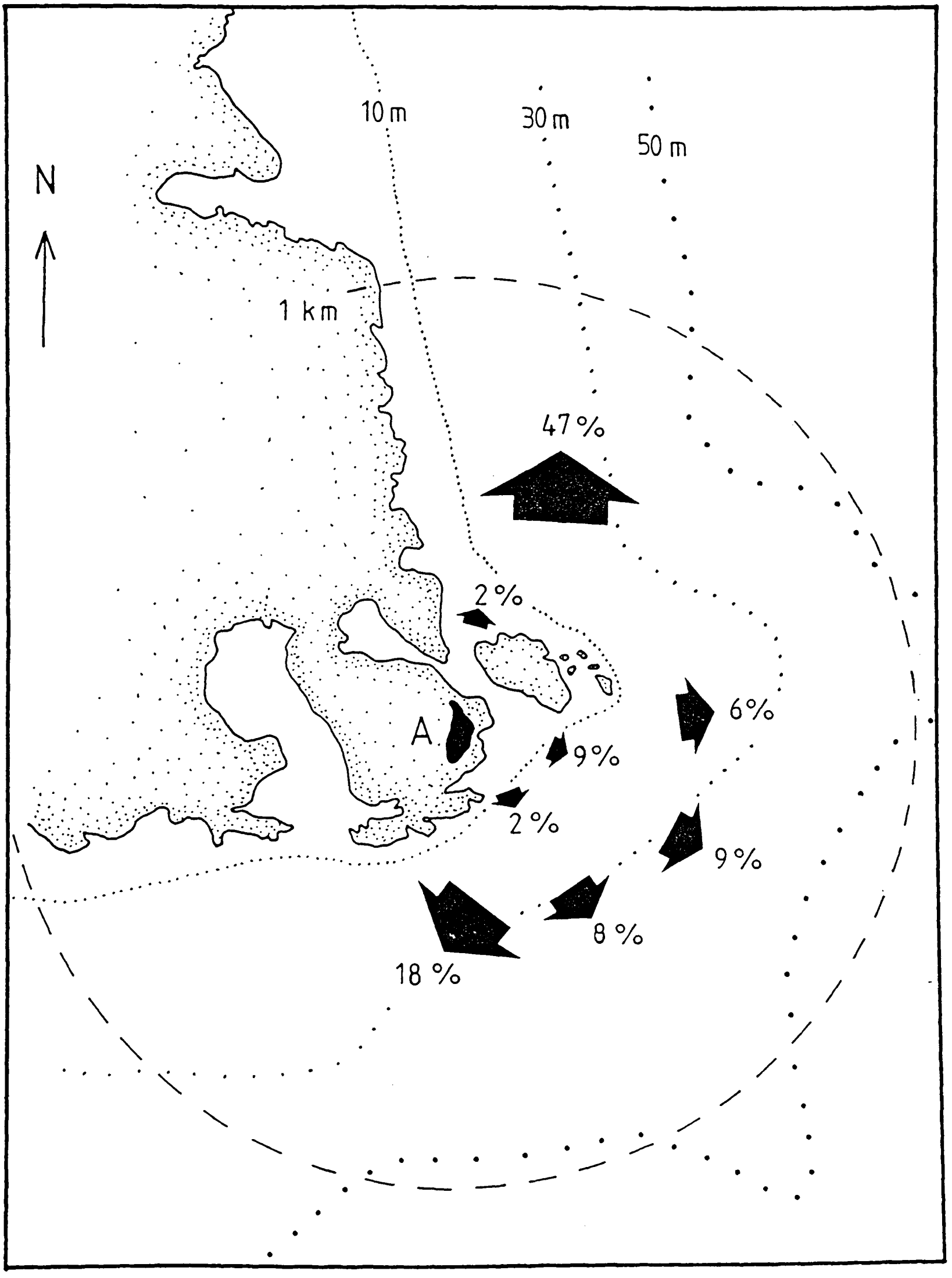


Figure 9.8 Departure directions and splashdown sites (indicated by asterisks) for two individuals from colony A in July 1984 (sample sizes in brackets).

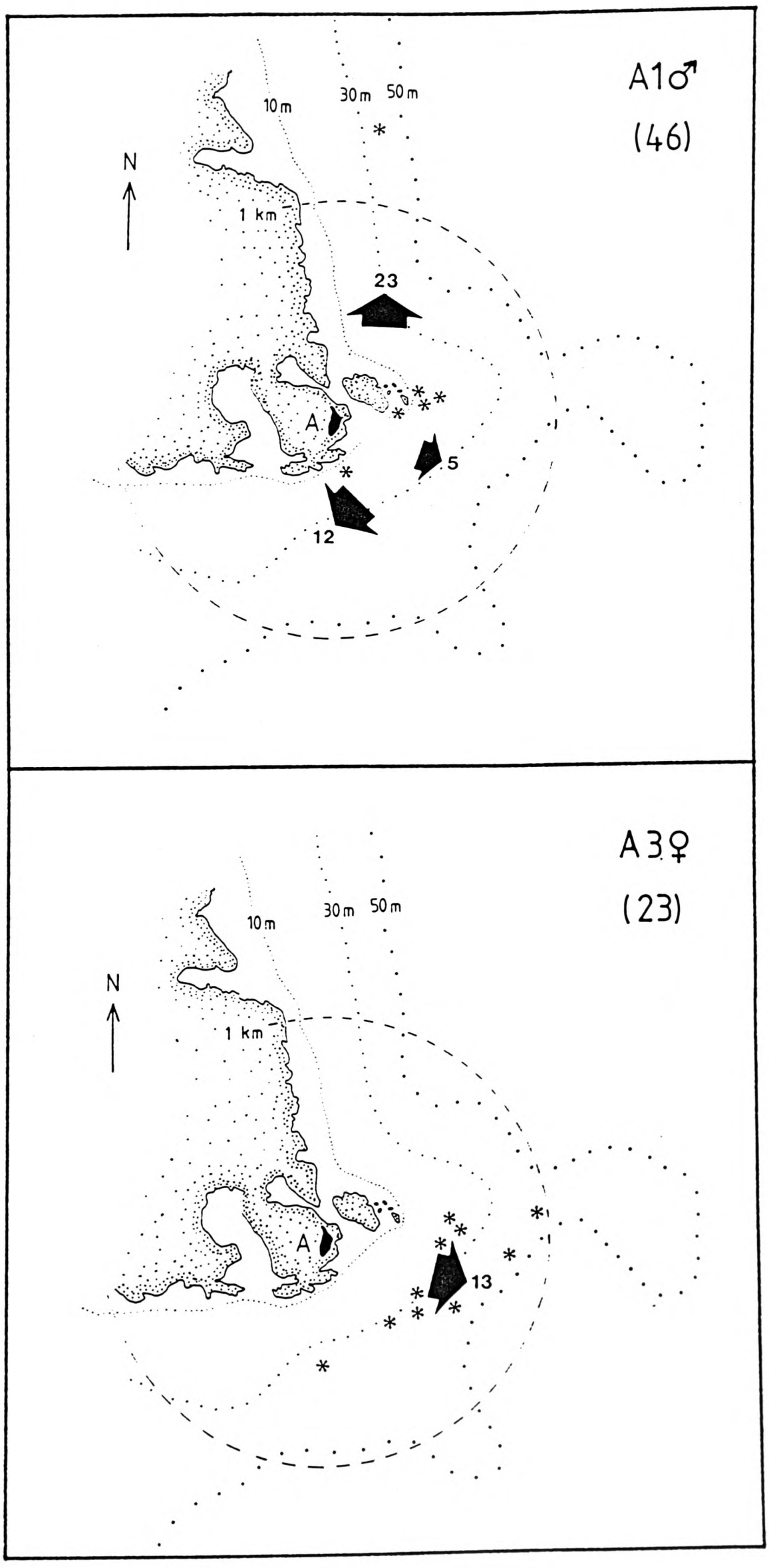
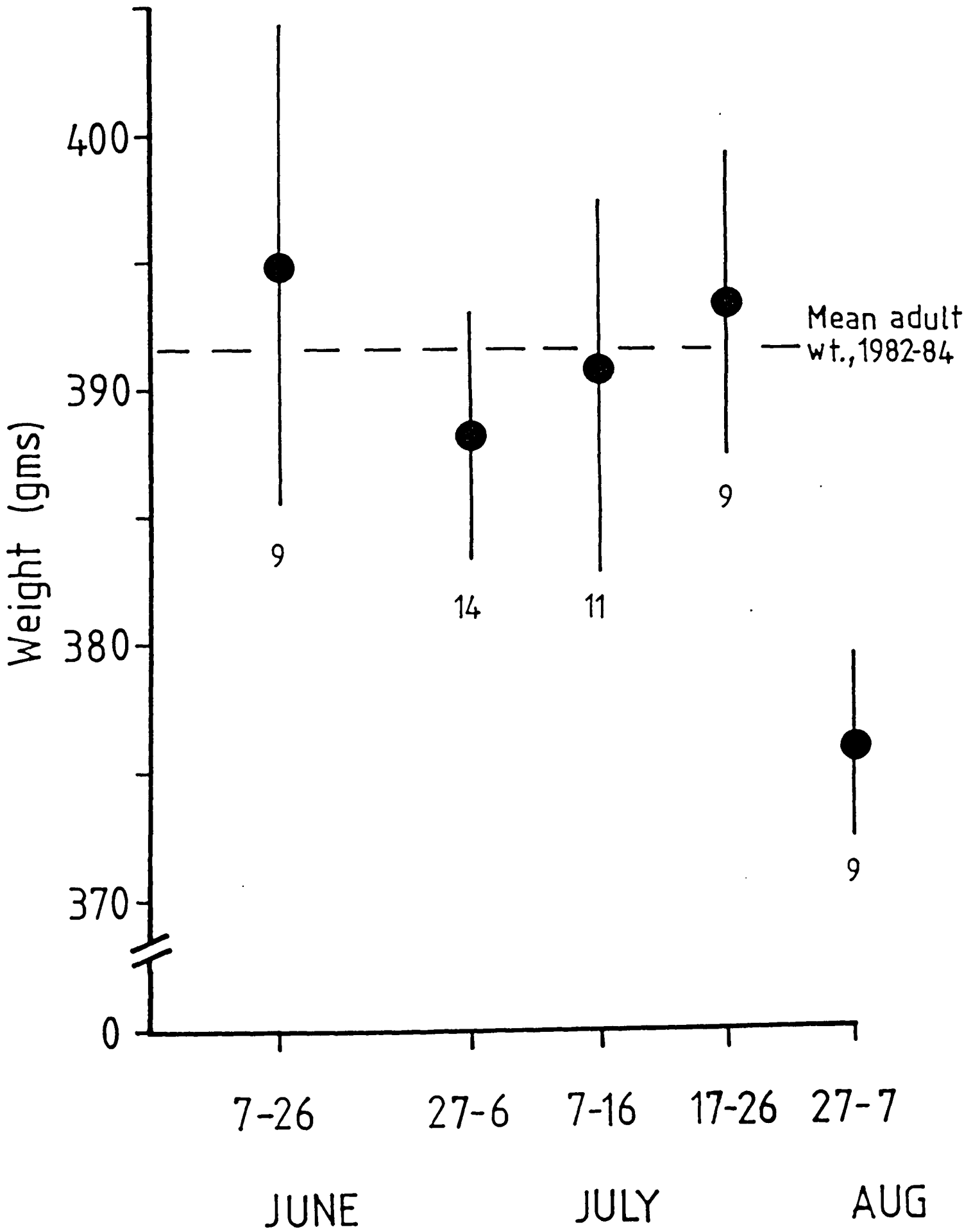


Figure 9.9 The weights of breeding adults on Mousa at different stages of the summer in 1983. Mean ± se and sample size are given for each period.



20 Black Guillemots could be seen flying or swimming into the area behind the boat (usually 30-200 m aft), and commencing diving on the moving net. As the net was hauled closer to the boat, dives became shorter and were often made right up to the stern. Sandeels were often seen in the bill at resurfacing and had presumably been taken from the mouth of the net or when trapped in the side meshing. Smaller numbers were also reported to dive on scallop dredges whilst they were hauled-in from small boats (R Cowie pers. comm.).

If the demands of reproductive activities were stressful to adults, one might expect adult weights to decline over the course of the breeding season. Although this was the case for breeders on Mousa (Figure 9.9), there was no significant difference between mean weights ($F = 1.18$; 4,47 df, $P>0.05$), and the linear regression of adult weight on date, though negative, was non-significant ($r = -0.69$, 3 df, $P>0.1$). However, weight loss during the breeding season could be adaptive, in reducing locomotion costs, since considerable energy must be expended by adults bringing fish back to the nest (Norberg 1981; Barrett 1984).

9.4 Results: Chicks

9.4.1 Diet

When the results of hide-watches of chick feeds made throughout the chick period at a number of colonies in Shetland were pooled, and compared with prey delivered to chicks on Mousa in 1983-84, no significant difference in overall diet composition was found (groupings were: sandeels, blennies, gadoids, and other species) ($G = 6.32$, 6 df, $P>0.1$). Fish accounted for 99% of items delivered, the most important types being sandeels (49-64%) and blennies - probably mostly Butterfish - (21-27%). Gadoids (excluding the small number of rocklings taken, which were readily distinguished by their very different shape), made up only 1% of prey in other parts of Shetland, but c.15% on Mousa in both years (Table 9.VII). Certain species, notably rocklings (Ciliata spp. and Gaidrosparus vulgaris), Zoarces viviparus and cottid species, were surprisingly rare in the chick diet, considering their commonness in benthic funnel traps set in the sub-littoral zone (Appendix V; Glimmerveen & Ouwerkerk 1983). The significance of these results are discussed later in relation to the size and activity of different fish species.

Table 9.VII. The percentage composition of chick diet on Mousa, and elsewhere in Shetland, based on observations of adult deliveries.

Taxon/species	% of total identified items SHETLAND 1982-84	MOUSA 1983	MOUSA 1984
CRUSTACEA			
unidentified[a]	1.4	0	0
CEPHALOPODA			
Eledone cirrhosa	0	0	0.1
Unident. Invertebrate	0	0	0.1
CLUPEIDAE			
unidentified	0.5	0.3	0.1
GADIDAE			
Trisopterus esmarkii	0.5	1.0	3.5
Pollachius virens	0.2	11.1	0.7
Ciliata spp.[b]	0.7	1.9	2.3
unidentified[c]	0.2	3.4	10.5
AMMODYTIDAE			
unidentified[d]	63.7	55.3	49.1
GOBIIDAE			
unidentified	0.7	0.4	0.1
CALLIONYMIDAE			
Callionymus sp.	0	0	0.1
PHOLIDIDAE			
Pholis gunnellus[e]	24.1	16.5	15.2
STICHAEIDAE			
Chirolophis ascanii[e]	0	0.2	0.7
ZOARCIDAE			
Zoarces viviparus[e]	0.7	0.6	1.8
Unidentified blennies	2.1	3.3	7.5
TRIGLIDAE			
Eutrigla gurnardus	0	0	0.1
COTTIDAE			
unidentified[f]	1.8	1.8	1.2
AGONIDAE			
Agonus cataphractus	0	0.1	0.1
CYCLOPTERIDAE			
Cyclopterus lumpus	0	0	0.1
LIPARIDAE			
Liparis spp.	0	0.4	1.6
GASTEROSTEIDAE			
Spinachia spinachia	0	0.1	0.4
PLEURONECTIDAE			
unidentified	3.4	3.6	4.9
Total no. of prey items	435	1815	2228

Notes:
[a] probably crabs, or *Galathea* spp.
[b] probably mostly *C. mustela*
[c] mostly *Pollachius virens* or *Trisopterus esmarkii*
[d] almost certainly mostly *A. marinus*
[e] grouped as 'blennies'
[f] probably *Myoxocephalus scorpius* or *Taurulus bubalis*

Further analysis is based largely on the results from intensive study at colony A in 1983 and 1984. The composition of chick diet varied significantly with date in both years (Figure 9.10). Gadoids were delivered more often after late July, particularly in 1984 when sandeels decreased in importance during the season - gadoids and blennies showing a corresponding increase in frequency. In recent years, industrial fishing for sandeels has occurred around Mousa from April to September, as well as at other suitable areas of sandy sea bed in Shetland (Bailey 1982; Ewins 1983a; Warburton 1983). In 1984 a daily record was kept of the number of individual boats trawling for sandeels around Mousa. After late July many boats moved away from the area, as the catch per unit effort decreased (information provided by the trawler crews). At this time the proportion of sandeels in the chick diet was declining rapidly (Figure 9.11). Kuletz (1983) attributed a reduction in the proportion of sandeels brought to Pigeon Guillemot chicks in Alaska to stronger winds causing water turbulence, and so reducing the availability to the birds. On Mousa no significant relationship was found between the proportion of sandeels in the chick diet and mean daily winds speed, in either 1983 ($r = -0.16$, 26 df, $P>0.05$) or 1984 ($r = 0.33$, 21 df, $P>0.05$).

The composition of chick diet showed significant variation with chick age (groupings as for analysis of variation with date) (Figure 9.12). As chicks grew they received proportionately fewer sandeels and more blennies and gadoids, this trend being more obvious in 1984. Date effects were controlled for by comparing diet composition of small (0-9 days old), medium (10-19 days old) and large (20-34 days old) chicks within each of two 10-day periods for which there were sufficient sample sizes for each age category. No significant variation was found in either year (G tests, $P>0.05$ in all cases), indicating that the observed variation in diet composition with chick age was largely a date effect, rather than due to chick age *per se*.

Deliveries recorded during an all-day watch on 17 July 1984 were grouped into sandeels, blennies, and other fish, and analysed by 3-hour periods. Although the proportion of sandeels was highest in the early morning (62-76%, as opposed to 46-54% later in the day), there was no significant diurnal variation in chick diet composition ($G = 3.56$, 12 df, $P>0.1$). When the groupings were analysed in relation to tidal state (4-hour periods being: High tide $\pm$ 2 h; Low tide $\pm$ 2 h; Mid tide - 2 h falling and 2 h rising), no significant tidal variation was evident ($G = 3.08$, 4 df, $P>0.1$). However, more blennies were caught around high tide (42%) than

Figure 9.10 Nestling diet composition on Mousa in 10-day periods in 1983 and 1984. Variation with date was significant in both 1983 ($G = 83.70$, 12 df, $P<0.001$) and 1984 ($G = 27.57$, 12 df, $P<0.01$); n = total number of identified deliveries.

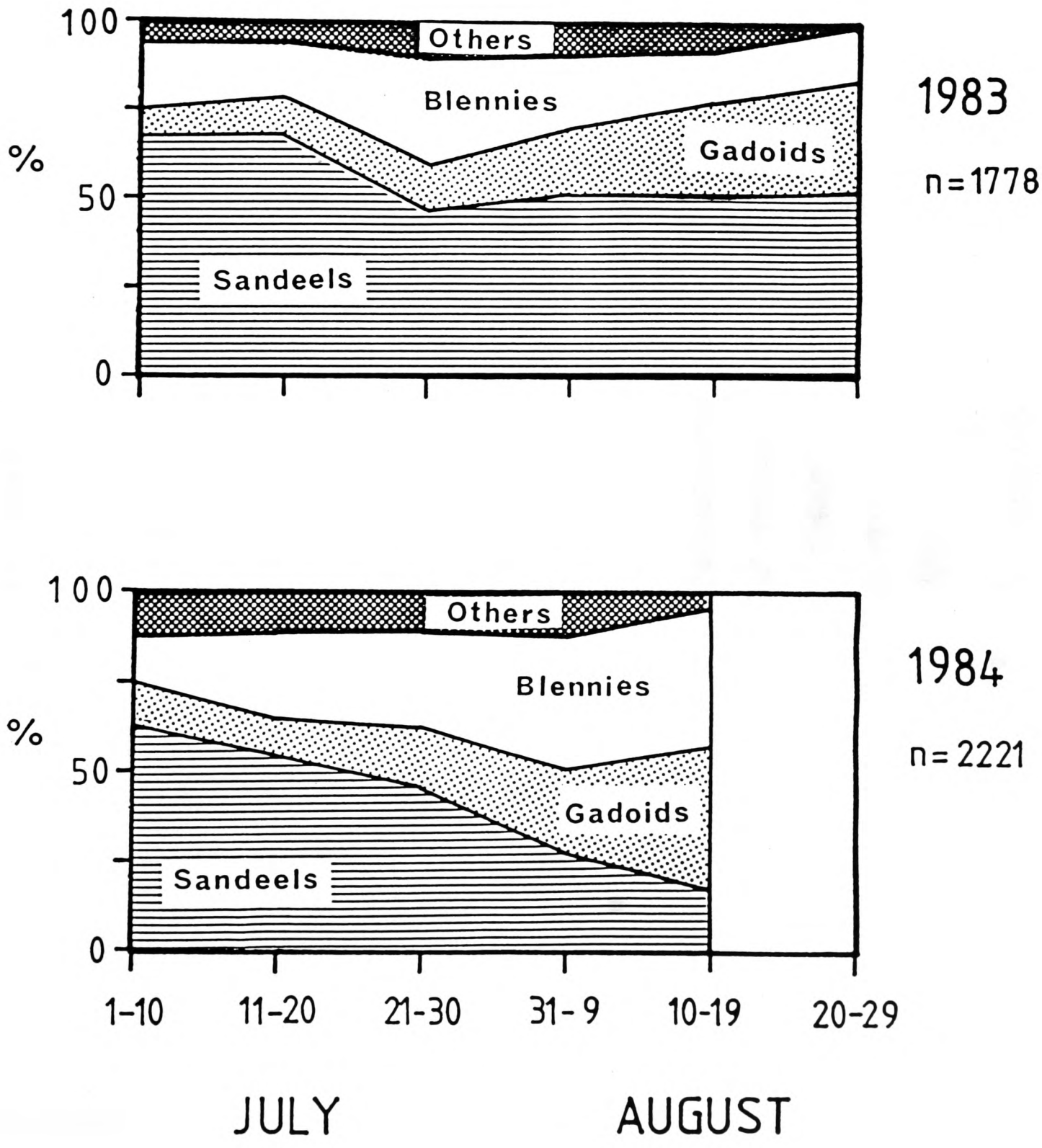


Figure 9.11 The number of boats fishing for sandeels around Mousa in 1984 in relation to the percentage of sandeels in the diet of Black Guillemot chicks.
Circles = boats; bars = sandeels.

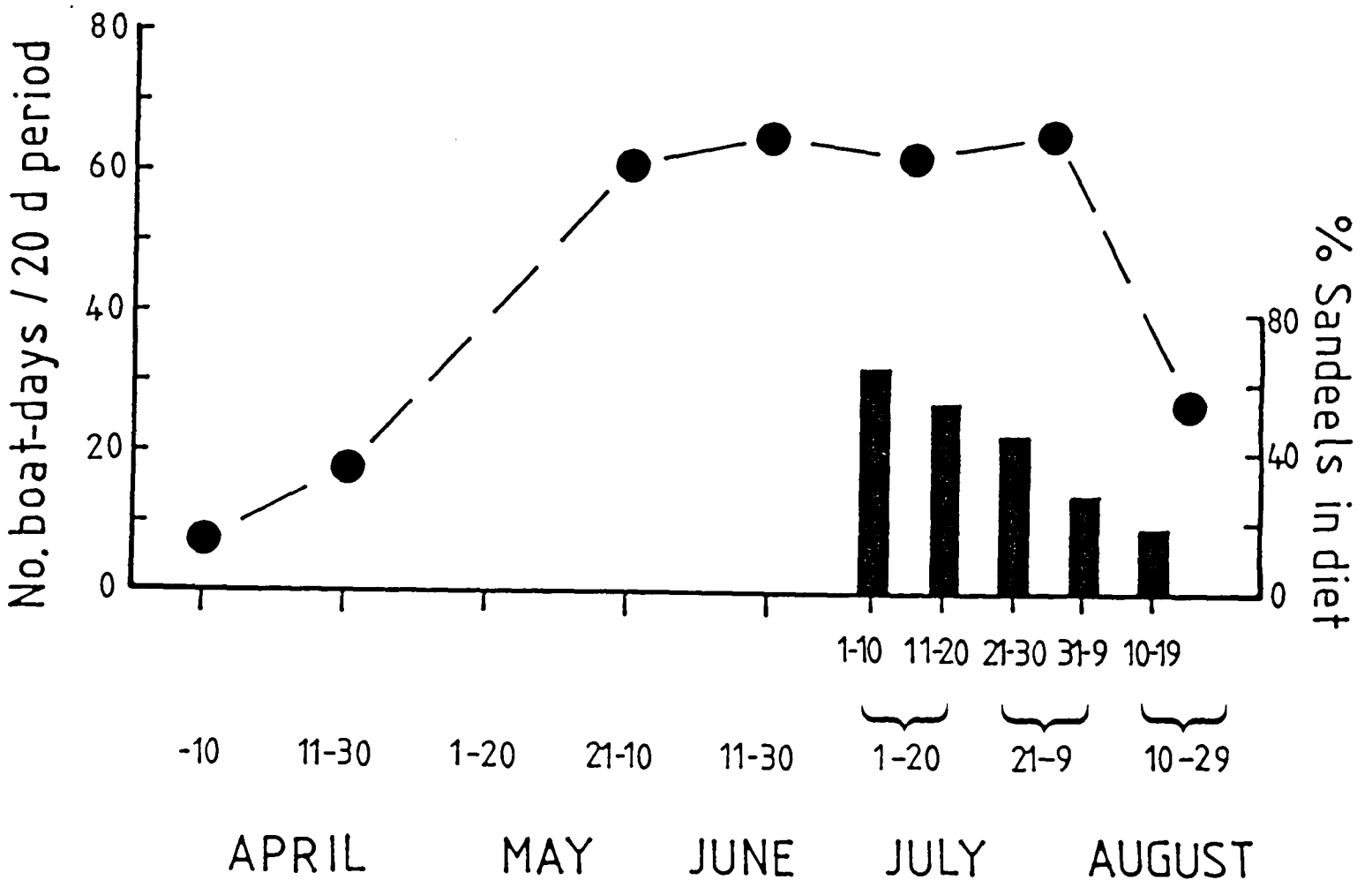
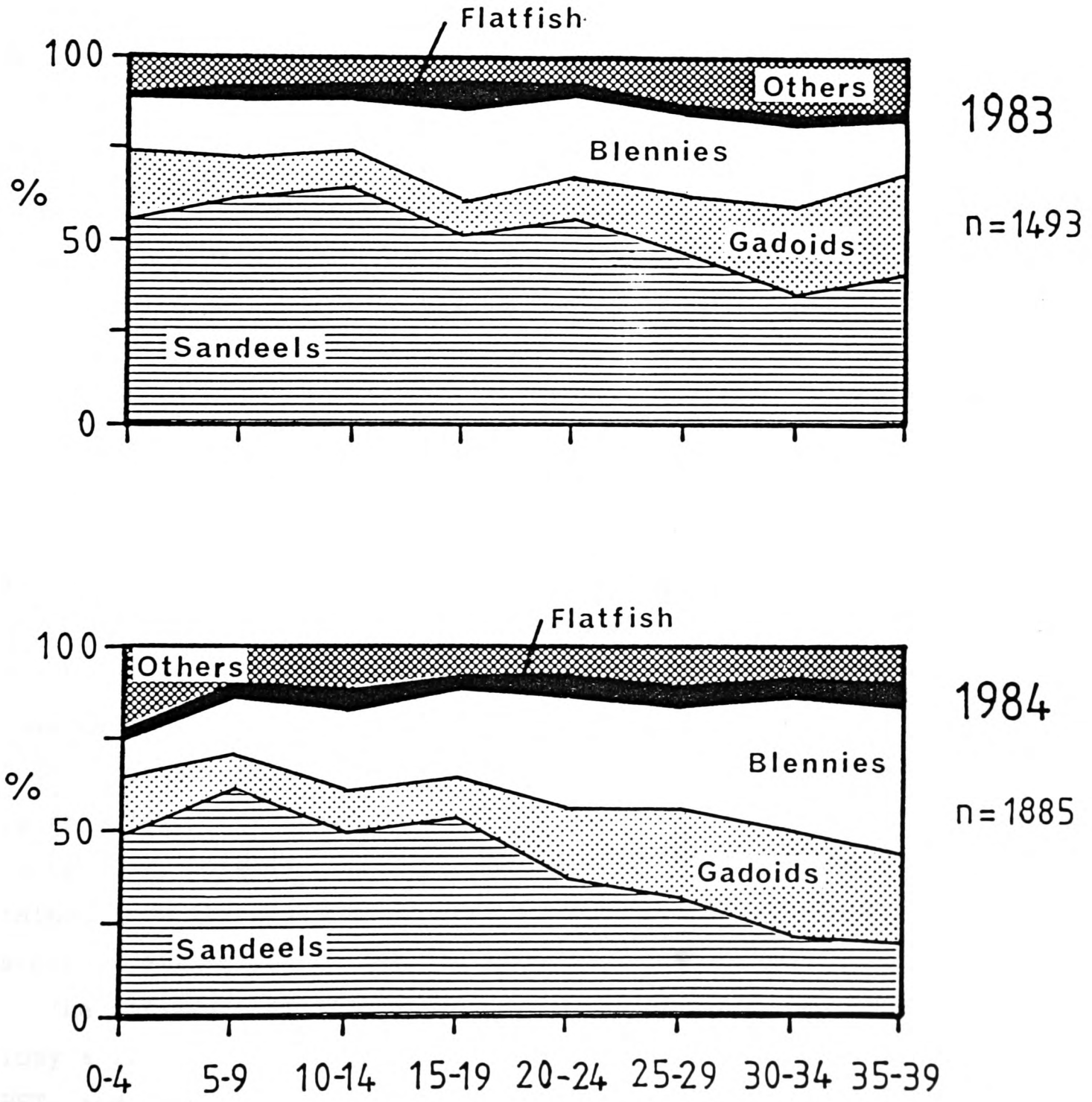


Figure 9.12 Diet composition at different chick ages at colony A in 1983 and 1984. Variation with age was significant in both 1983 ($G = 414.2$, 21 df, $P<0.001$) and 1984 ($G = 163.4$, 21 df, $P<0.001$). n = total number of identified deliveries.



around low tide (34%), or at mid tide (25%), although none of these differences were significant. The same analyses, when performed on a 24-hour watch on 6-7 July 1984, also failed to detect significant tidal or diurnal influence on chick diet composition.

9.4.2 Delivery rates

At a sample of over 20 nests in colony A at which all deliveries were recorded, at regular stages in the nestling period of 1983 (total of 1647 chick-hours observation) and 1984 (2024 chick-hours of observation), average hourly delivery rates increased rapidly to a peak in the 04-05 h BST period. However, when the data were pooled for the whole season it appeared that deliveries were made at a rather uniform level throughout the day, with some fluctuation about a mean rate of 0.6/hour/chick, and a suggestion of an evening peak in 1983 but not in 1984 (Figure 9.13). The morning peak was more apparent when 24 h watches at Mousa colony A were analysed separately, and the day-time average delivery rate rose from approximately 0.3 to 0.8/hour/chick between 7 and 17 July, as chicks grew older (see Figure 9.15). Since the incidence of kleptoparasitism at some Mousa colonies may have been higher than elsewhere (Chapter 10), comparative data are presented for 24 h watches at the Hascosay colony, where kleptoparasitism was rare. A similar increase in the average delivery rate was noted from 11 to 25 July, and although there were considerable fluctuations, delivery rates appeared to be consistently higher on the latter date, though lacking a morning peak (Figure 9.13). These results are discussed later in relation to studies elsewhere, and to the problems of interpreting pooled data gathered throughout the season.

There was significant diurnal variation in mean hourly delivery rates of sandeels ($F = 2.8$; 9,82 df, $P<0.01$) and gadoids ($F = 2.13$; 9,82 df, $P<0.05$), but not for blennies or other fish at colony A in July 1984 (Figure 9.14). For these data, total deliveries showed a morning and evening peak, largely accounted for by sandeels. Similar results were obtained from the analysis of data for July 1983, but gadoids were even scarcer at either end of the day than in 1984.

The influence of tidal state on delivery rates was investigated at colony A in July by excluding deliveries made before 0700 h and after 1900 h BST, and calculating average delivery rates at three stages of tide for the major fish types. Neither total delivery rate nor sandeel delivery rate showed significant variation with tidal state (Table 9.VIII).

Figure 9.13 Diurnal variation in mean delivery rates at Mousa (colony A) and Hascosay during selected 24-hour watches, and pooled for the entire season on Mousa.

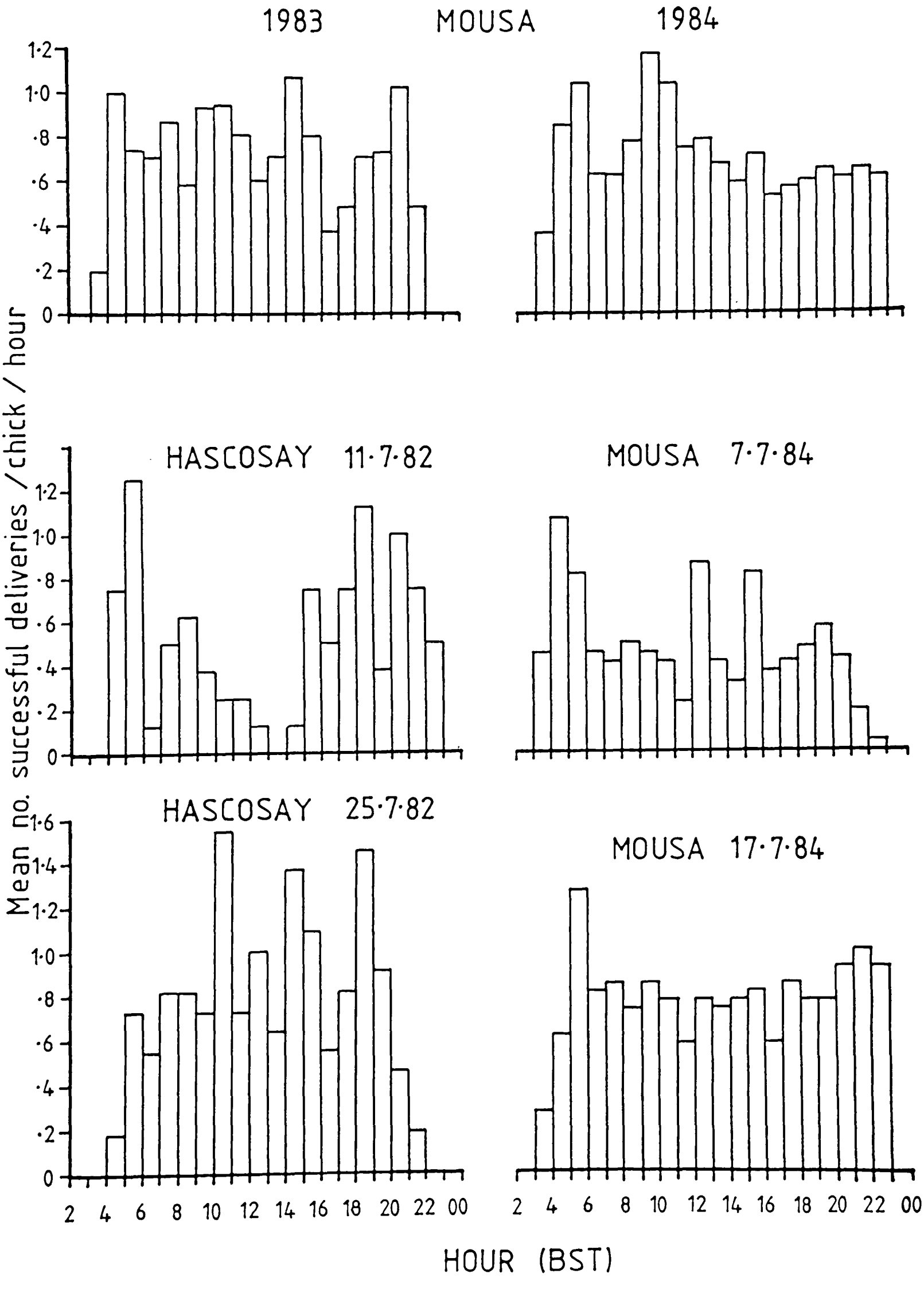


Figure 9.14 Diurnal variation in mean delivery rates for the main fish types at colony A in July 1984. Times are BST. Based on 75 hours of observation on 17 different days. N = number of separate days sampled in each 2-hour period.

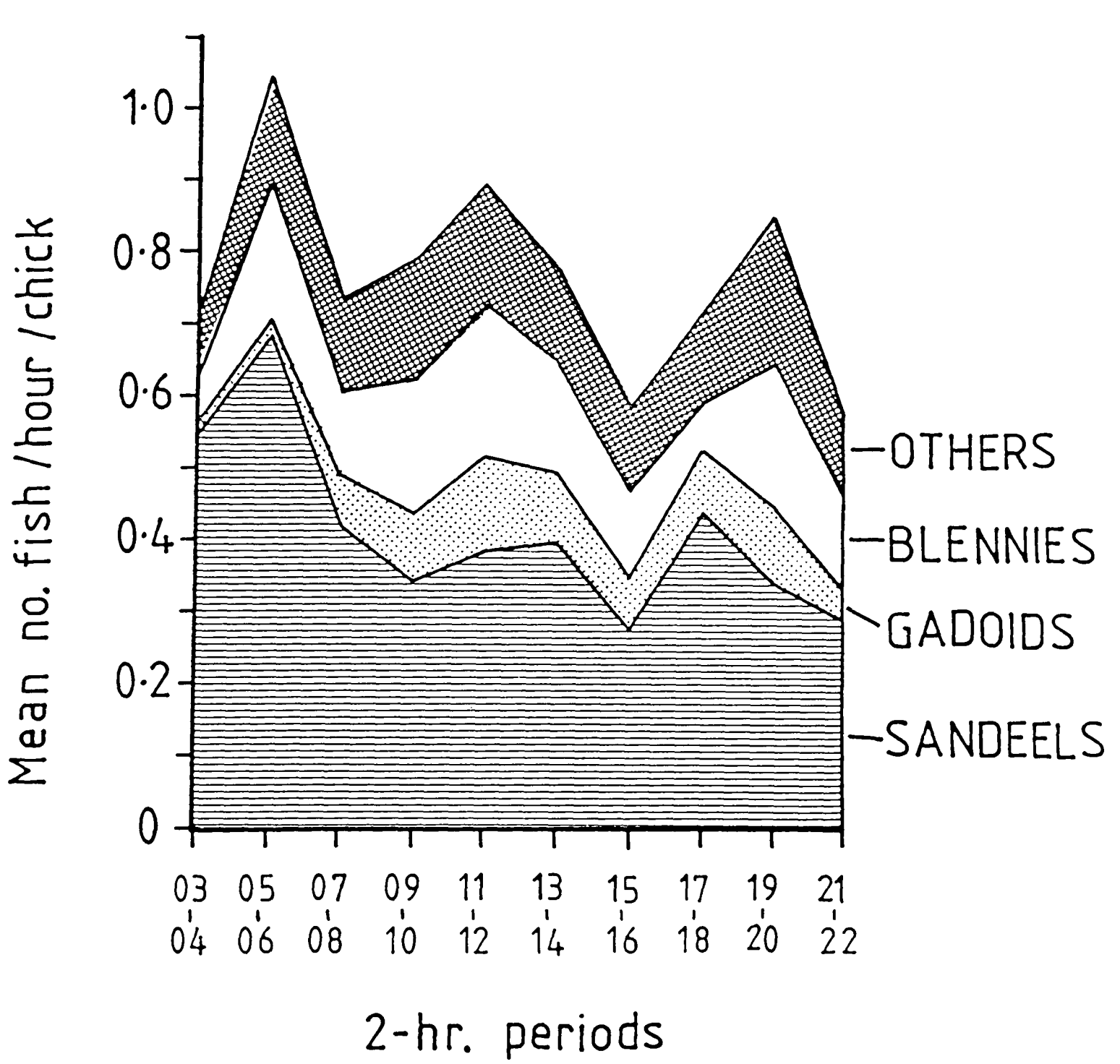


Table 9.VIII. Average rates of delivery of major fish types at colony A in July 1983 and 1984, at different tidal states, for deliveries between 0700 and 1900 h BST only.

		Average no. fish delivered per hour			
FISH TYPE	YEAR	HT[a]	MT[b]	LT[c]	G (2 df)
Sandeels	1983	10.0	13.2	13.2	0.5 ns
"	1984	9.1	8.8	10.3	0.1 ns
Blennies	1983	5.6	3.4	4.8	
"	1984	4.8	3.3	3.6	
Gadoids	1983	2.6	2.8	2.6	
"	1984	2.4	2.4	2.3	
Other species	1983	3.7	2.0	2.9	
" "	1984	4.0	3.3	2.8	
Total deliveries	1983	21.9	21.4	23.5	0.1 ns
" "	1984	20.3	17.8	19.0	0.2 ns
Total no. hours	1983	7	12	13	
observation	1984	29	28	16	

Notes: [a] HT = High tide ± 2 h

[b] MT = Mid tide (2 h flooding, and 2 h ebbing)

[c] LT = Low tide ± 2 h

Although mean values for other categories were too small to permit statistical treatment, delivery rates for blennies and other species (mostly benthic) were highest around high tide in both years. Little tidal variation was evident for gadoids in either year. The same trends were found when 24 h watches were analysed separately.

Delivery rates increased steadily with chick age to a peak at 25-29 days old, then decreased at a similar rate until fledging (Figure 9.15). In all chick age categories mean delivery rates were higher in 1984 than in 1983, although the difference was only significant in the 25-29 d age group ($t = 3.04$, 15 df, $P<0.01$). This lack of significance emphasizes the often considerable differences between pairs: inter-delivery intervals ranged from 10 seconds to nearly 2 hours during daylight hours. An adult once made 3 deliveries in 5 minutes, but this was exceptional. Although previous studies of Cepphus species have compared average provisioning rates for chicks with and without sibs (eg. Aitchison 1972; Asbirk 1979c; Petersen 1981), only Cairns (1984) took chick age into account. Since peak rates of provisioning may be three times those for small chicks, it would be misleading to quote an 'average' figure without detailing the proportion of chicks of different ages on the observation days. By combining delivery data from two 24 h watches in July 1984, it appeared that single chicks received more feeds on average than did those with a sib, and that the difference was greater for older chicks. Overall, single chicks received 15% more feeds than those in broods of two (Table 9.IX).

9.4.3 Prey size and energetics

The estimated lengths of sandeels delivered at colony A were very similar in 1983 and 1984, but with fewer 2-5-year-old fish and more younger fish in August 1984 (Figure 9.16). Observations were made at regular intervals during the nestling period in both years, with no biases towards deliveries to chicks of any particular age, which might also have explained differences in fish lengths (Figure 9.17). Therefore I conclude that large sandeels were not so readily available to Black Guillemots in August 1984. A sample of sandeels from a trawler in Mousa Sound in July 1984 showed an almost identical distribution of lengths to that shown by Warburton (1983) for catches in Shetland during July 1980. Thus, it appears from Figure 9.16 that Black Guillemots were selecting older (ie. larger) sandeels to feed to chicks, and that very few 0-class fish were delivered. Measurements of fish dropped in mist-nets, and by birds chased by

Figure 9.15 Mean hourly delivery rates to chicks of different ages at colony A in 1983 and 1984. Means ± se and number of separate observation periods (not less than 2 h long) are shown for each age class.

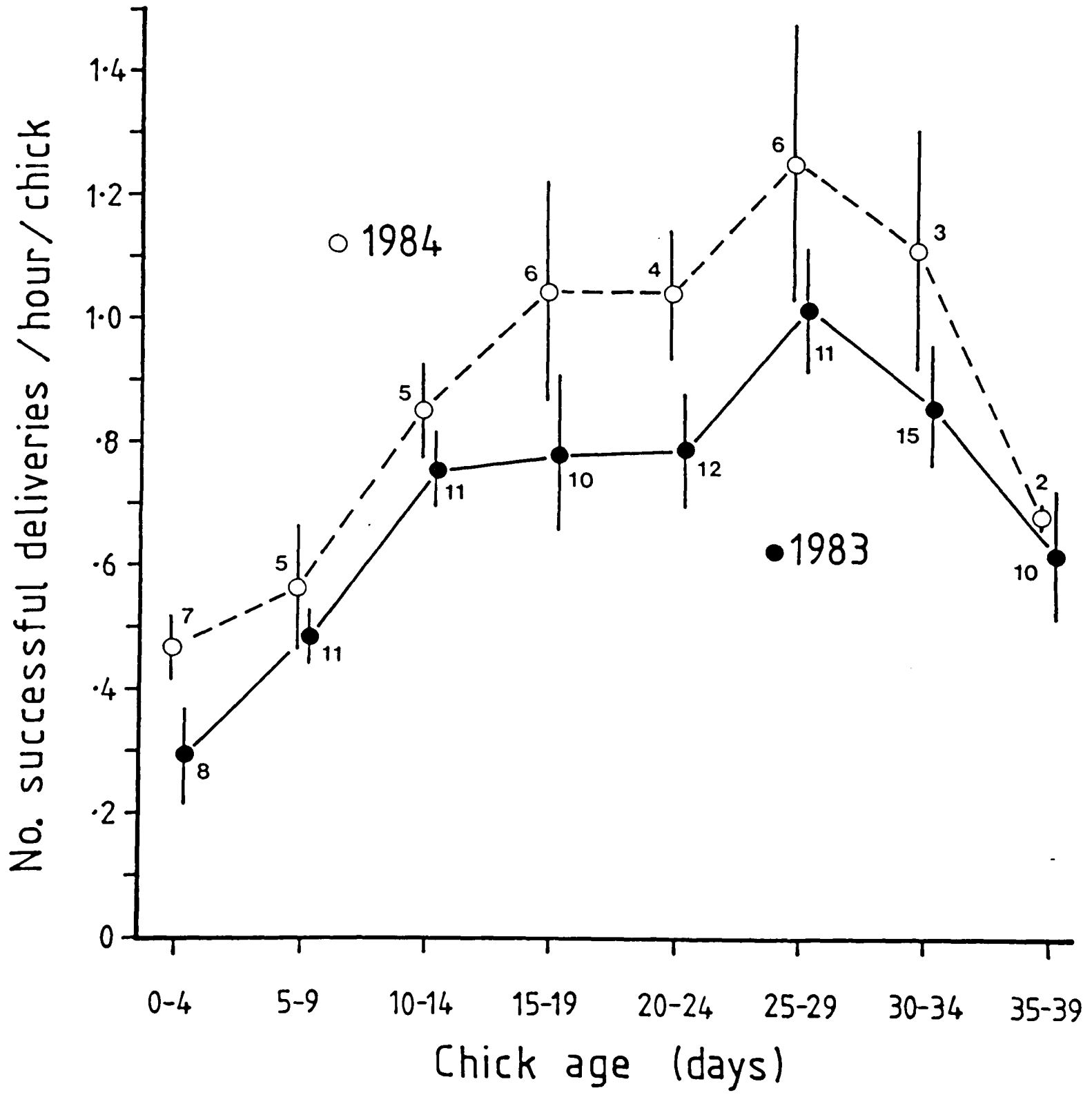
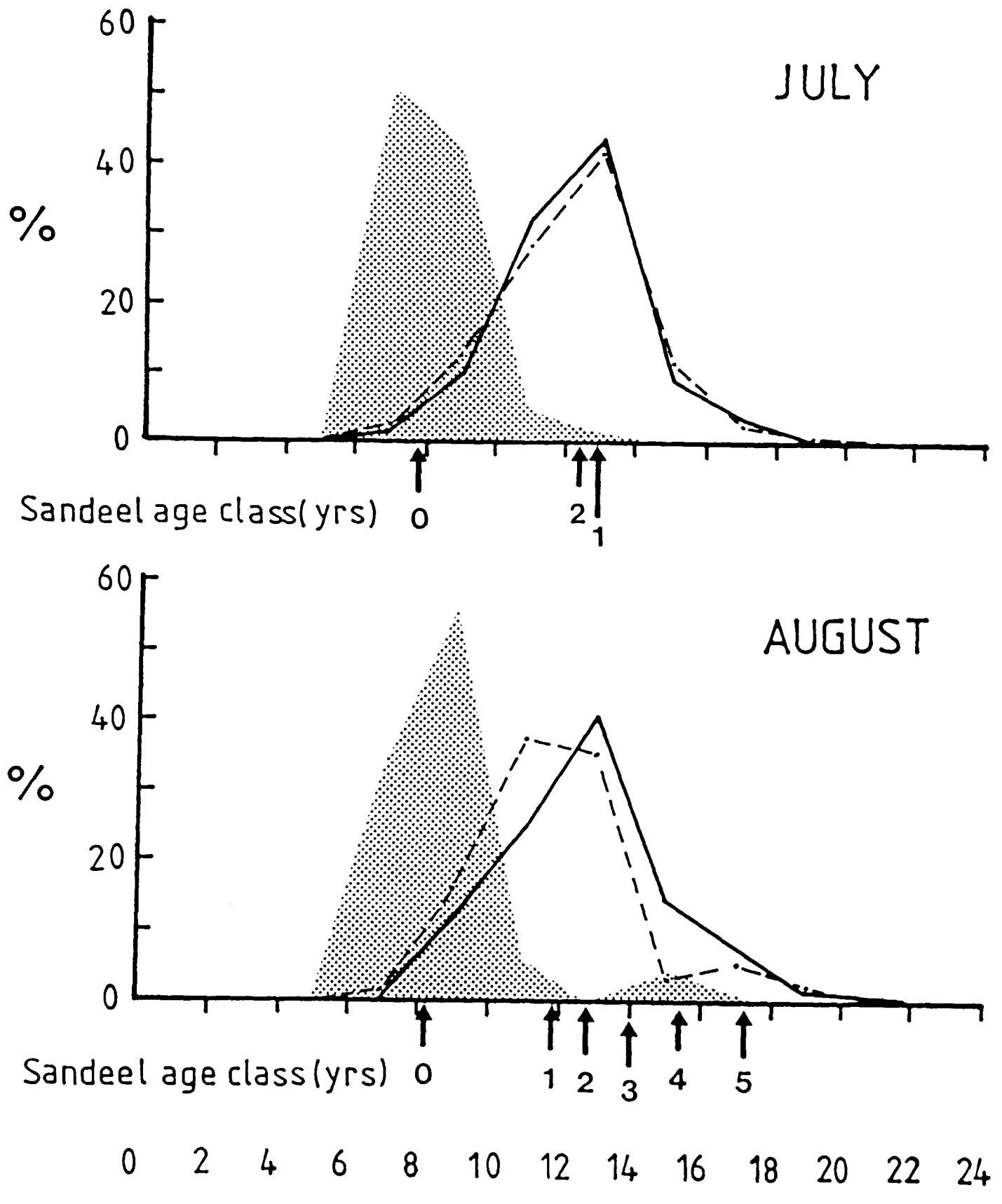


Table 9.IX. Average delivery rates per chick varying with brood size, for different chick ages. Data combined from two 24-hour watches at colony A in July 1984.

Chick age (days)	Average no. deliveries / day / chick b1	b2	Difference (%), chicks in b1-b2
0 - 4	7.80	7.75	+ 0.6 %
5 - 9	10.00	9.50	+ 5.3 %
10 - 14	15.50	8.00	+ 93.8 %
15 - 19	16.25	12.50	+ 30.0 %
TOTAL	12.12	10.54	+ 15.0 %

Figure 9.16 Frequency distributions of lengths of sandeels caught by trawlers in 1980 (stippled), and by Black Guillemots in July and August (1983-84). Arrowed numbers represent mean lengths of sandeel age classes (redrawn from Warburton 1983). Deliveries to chicks in 1983 are represented by the solid line; in 1984 by the dashed line.



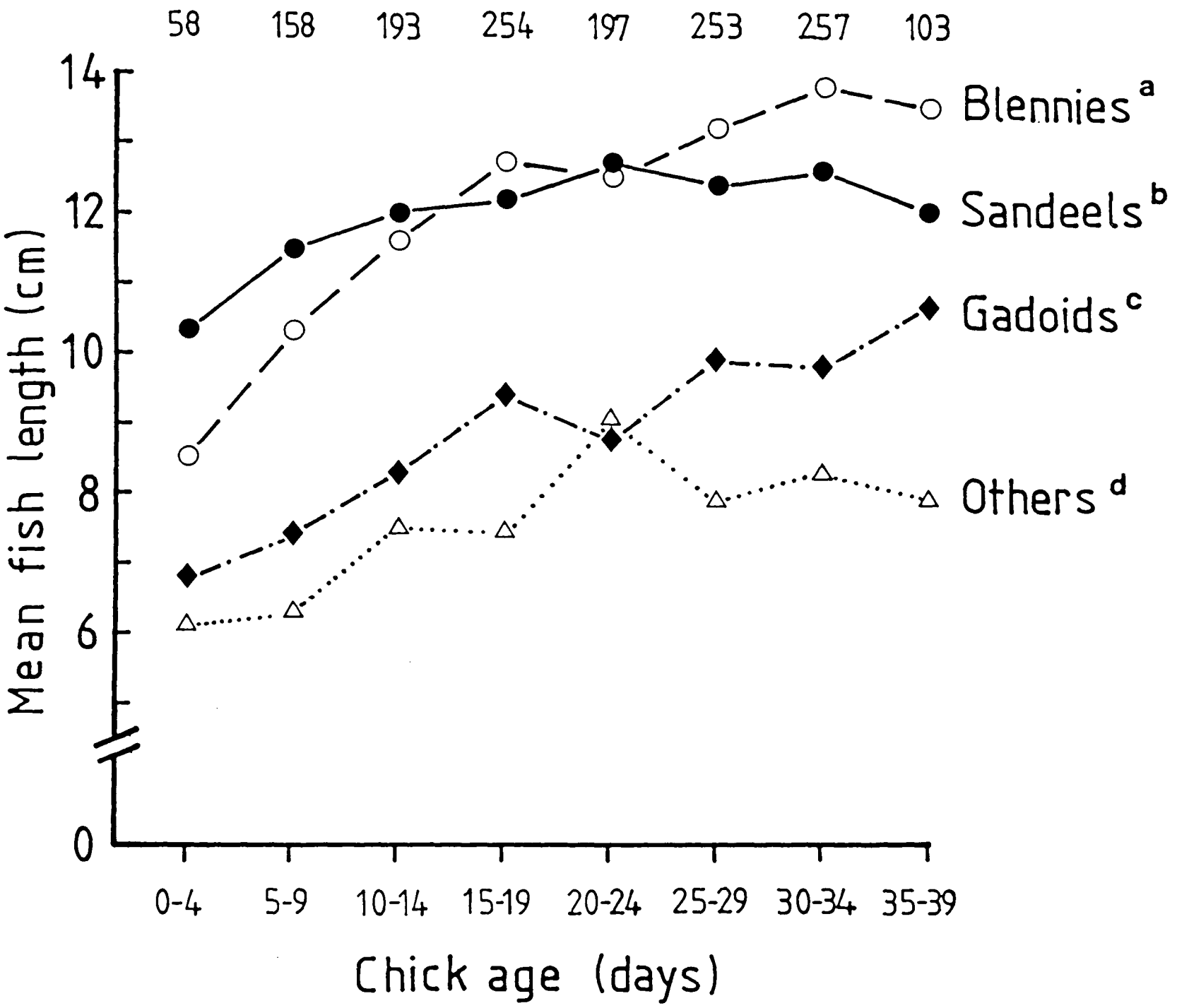
kleptoparasites confirmed that fish lengths were not over-estimated. In contrast, there was no evidence for selection of large Butterfish: there was no significant difference in mean length of Butterfish caught in funnel traps, and those delivered to chicks (14.5 vs. 14.2 cm respectively, $t = 0.3$, 460 df, $P>0.7$). Similar lengths were recorded for Butterfish caught in traps in slightly deeper water elsewhere in Shetland (Glimmerveen & Ouwerkerk 1983).

The mean length of fish delivered showed a significant increase with chick age for all major types in 1983 (Figure 9.17). Similar significant increases were found in 1984, but mean lengths of all groups decreased during the last two chick age categories, and this was offset by gadoid lengths increasing at a steeper rate than in 1983 [gadoid length = 0.138 (chick age) + 7.54, $r = 0.79$, $P<0.02$]. There was little evidence to suggest that any of these increases were due to corresponding increases in mean lengths of fish populations over the summer months. Mean lengths of 0, 1 and 2-year-old sandeels increased only fractionally from July to August (Warburton 1983), and Pholis gunnellus, Zoarces viviparus and Ciliata spp. caught in funnel traps around Mousa showed no significant increase in mean lengths between July and August ($P>0.1$ in each case).

Although even small chicks sometimes took fish which were initially too long for complete ingestion (the tail protruded from the bill until the head had been digested), these were usually sandeels or small blennies - relatively narrow-bodied species which were unlikely to constrict the gullet, lacking potentially hazardous spines or armouring. Gadoids and flatfish have considerably deeper or wider bodies than other species taken and are not normally delivered in significant numbers until the chick's gape is of sufficient width to accomodate fish with such girths. Thus, only a few small individuals were fed to chicks less than 2 weeks old (see Figure 9.12). Cottid species have sharp, backward-projecting spines behind the gills and a large girth; they were only rarely delivered to chicks less than 2 weeks old. However, although this group comprised many of the rejected fish found in other studies (Petersen 1981; Cairns 1984), only a few were found in Mousa nests, and few chicks in colony A were regularly fed small cottids.

The estimated daily weight of fish delivered to colony A chicks increased with chick age in both years, approximately in the manner shown for energy input in Figure 9.19. The average total daily weight of fish delivered to small (0-9 days old) chicks represented c.27-35% of chick body weight in both years, whilst that to chicks over 35 days old represented

Figure 9.17 The mean length of major fish types delivered to Black Guillemot chicks of different ages in 1983. Total number of fish in each age category is given.



Linear regressions, for 6 df:

a Length = .045 chick age + 11.08, r = .711 P<0.05

b Length = .136 chick age + 9.37, r = .919 P<0.01

c Length = .104 chick age + 6.87, r = .956 P<0.01

d Length = .060 chick age + 6.37, r = .763 P<0.05

only 19-21%. Chicks 10-34 days old received on average 25-32% of body weight daily in fish in 1983, but 35-44% in 1984. The corresponding mean % weight increase for 0-9 d chicks was 19-21%, 3-4% for 10-34 d old chicks, and -1% for chicks over 35 days old, indicating a progressive decline with chick age in the rate of conversion of food to body mass.

The energy contents of average fish delivered at various chick ages were calculated from the mean lengths, the length:wet weight relationships given in Table 9.I, and published energy equivalents. Equivalents used (kJ per gm wet weight) were: sandeels = 6.5 (Harris & Hislop 1978); blennies = 5.87 [value for Butterfish given by Dunn E.H. (1975)]; gadoids = 4.52 [mean of values for Saithe Pollachius virens, Pollack P. pollachius and Whiting (Dunn E.H. 1975; Harris & Hislop 1978)]; other species = 5.83 (mean of values for rocklings, cottids and flatfish species given by the same authors). The energy contents of sandeel, blenny and gadoid deliveries in 1983 were similar for chicks up to 25 days old, but thereafter sandeels provided rather lower energy returns per average load. In 1984 there was little difference in average energy content between sandeel and blenny deliveries, but after chicks were 10 days old an average gadoid delivery provided roughly twice the energy of deliveries of any other species (Figure 9.18). The overall increase with chick age in average energy content per delivery largely reflects the increasing size of fish delivered (see Figure 9.17). By incorporating average delivery rates of the main fish types, I determined average energy inputs by different fish types to the diet at varying chick ages (Figure 9.19). Total daily energy intake per chick was higher at all ages in 1984 than in 1983, partly due to higher delivery rates (see Figure 9.15), but the inflated peak for chicks 15-34 days old in 1984 (when on the basis of these calculations average daily energy intake by chicks was 36-55% higher than in 1983), was mainly due to the greater size, and hence energy content of gadoids delivered at this stage.

9.5 Discussion

Diet

The wide range of prey items taken by full-grown Black Guillemots in Shetland broadly reflects the diversity of inshore benthic communities (Barrett & Yonge 1958; Earll 1975; Gray 1977). The available literature indicates dietary differences between regions, largely accounted for by

Figure 9.18 The energy content of mean fish lengths for sandeels, blennies and gadoids delivered to chicks of different ages at colony A in 1983 & 84.

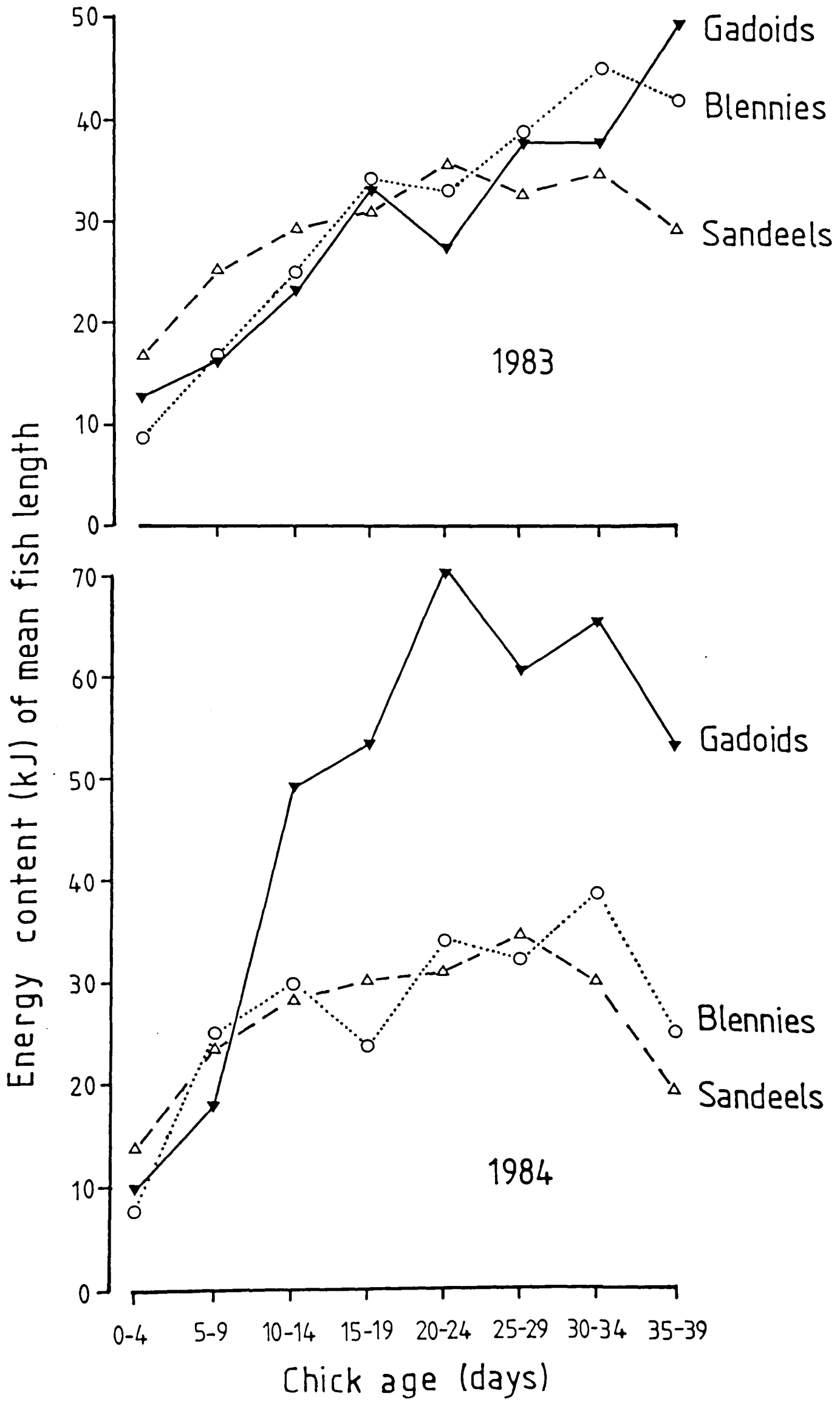
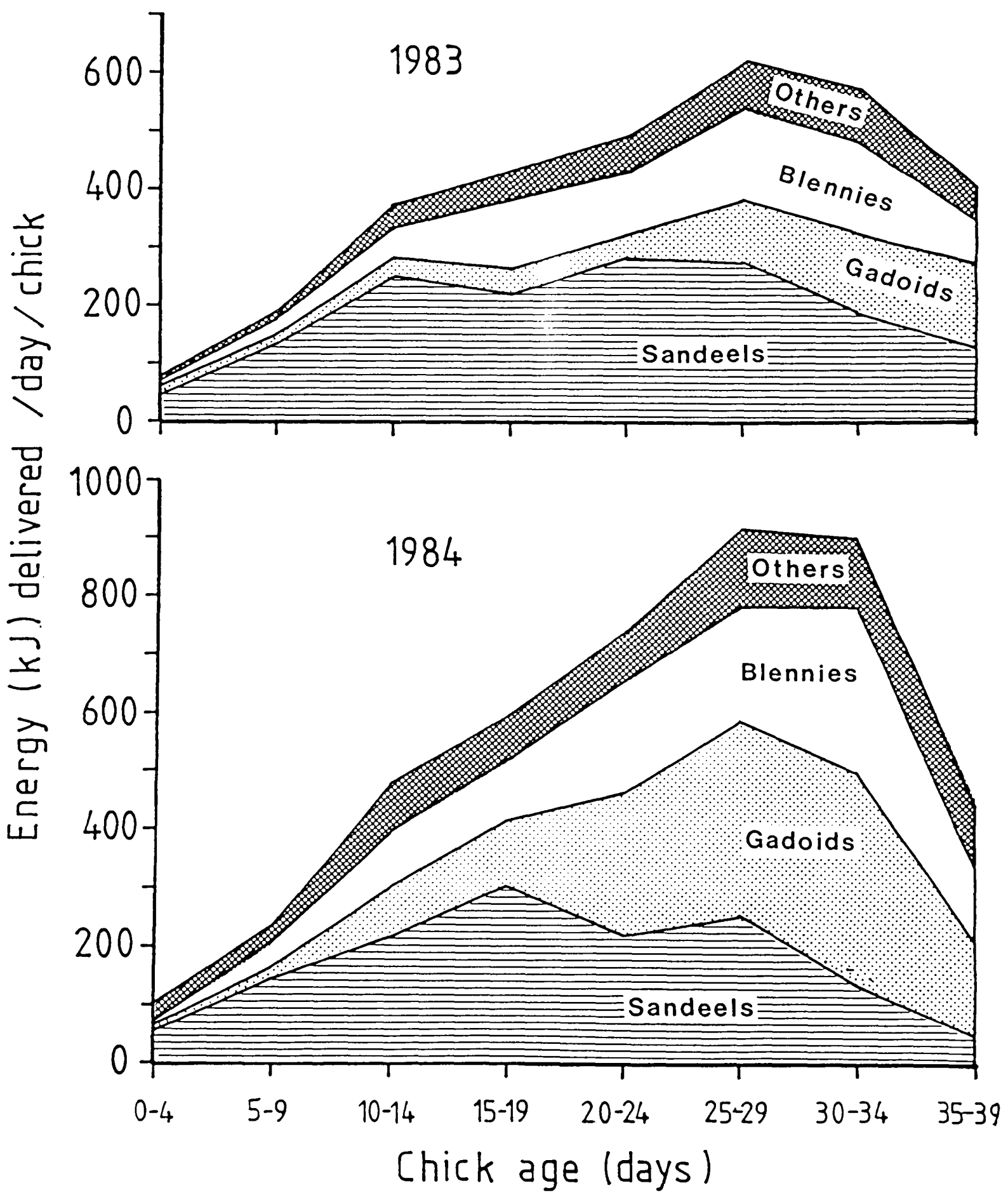


Figure 9.19 The energy input of major fish types to the diet of chicks of different ages at colony A in 1983 and 1984. Energy contributions of fish types varied significantly between chick age categories in 1983 ($G = 334.3$, 21 df, $P<0.001$) and 1984 ($G = 620.9$, 21 df, $P<0.001$).



differences in abundance and availability of the species concerned (Cramp 1985). For example, Madsden (1957) found gobies to be the predominant prey in Black Guillemot stomachs in winter in Denmark, as was the case for other auk species killed in the Skaggerak oil incident (Blake 1983), reflecting the abundance of gobies in this area. Gobies and Lumpenidae, but rarely sandeels or blennies, were taken by Black Guillemots in the White Sea, again reflecting species abundance (Bianki 1967). In arctic regions invertebrates are often more numerous and comprise larger portions of the diet of both full-grown and nestling Black Guillemots in summer (Hartley & Fisher 1936; Uspenski 1956; Belopol'skii 1967; Bradstreet 1980; Cairns 1984), than in more temperate parts of the breeding range (Winn 1950; Preston 1968; Slater & Slater 1972b; Asbirk 1978c, 1979c; Cairns 1981; Cramp 1985; pers. obs.). Overall, Black Guillemots are flexible and opportunistic in diet preference, feeding on whatever suitable species are locally available (Kaftanovski 1951). The association with boats trawling for sandeels in Shetland is a good illustration of such adaptability and opportunism.

Since the benthic fauna (in particular benthic vertebrates) undergoes seasonal changes in response to changes in sea temperature and light intensities (see Winslade 1974b,c; Cushing & Walsh 1976; Keegan et al. 1976), it is not surprising that a predator foraging in this environment throughout the year should show seasonal changes in diet composition. Many of the fish species taken by Black Guillemots during the summer are not readily available in winter. Adult Ammodytes marinus, probably the main sandeel species in Shetland coastal waters (Warburton 1983), remain buried in the sand from August to April, emerging for only a brief period to spawn in December-January (Winslade 1974c; R S Bailey pers. comm.); blennies and other small benthic fish migrate to deeper water in winter and show reduced activity due to lower water temperatures (Gibson 1969; R N Gibson in litt.). Hence a greater proportion of invertebrates are consumed in winter in Shetland. Although gastropod molluscs and crustaceans are the most numerous prey types in winter stomachs, fish are probably most important in energetic terms since the weight of digestible tissue per item is far greater. The importance of Galathea species in particular was unexpected, although Collett (1877-94) and Patten (1906) found remains in small samples of stomachs. However, Pearson & Eleftheriou (1981) regularly noted G. intermedia during benthic surveys in Sullom Voe, and Fowler (1981) found G. strigosa "in large numbers in rock holes" in Yell Sound during July, suggesting that the genus occurs quite commonly (at least in that area) in

habitats utilised by foraging Black Guillemots. The only other study of seasonal differences in diet in a particular area is that of Belopol'skii (1957) in the Barents Sea, in which the importance of fish in the diet increased from April to August, presumably at the same time as fish numbers and activity also increased.

Determination of diet composition from analysis of stomach contents is complicated by differential rates of digestion of prey remains; hard parts such as mollusc shells, crustacean exoskeletons and polychaete mandibles will remain intact longer than bones of small fish species, and so under-emphasize the importance of fish. Further, the energetic importance of fish and other larger prey is under-stressed by analysis of % abundance in total sample or frequency of occurrence in stomachs. Another source of bias is the likelihood that items such as small gastropods, crustaceans and polychaetes were present in the stomachs of larger crustacea or fish when ingested [these are common prey species of blennies for example (Qasim 1957; Vikingsson et al. 1978)]. It is also possible that conclusions drawn from analysis of oiled or beached birds refer only to the diet of weak and dying individuals: if a bird becomes progressively weaker, it may be unable to catch fish, and may attempt to fill its stomach with relatively poor quality food items such as molluscs and crustacea. Blake (1983) noted that significantly fewer stomachs of heavily oiled auks contained identifiable food remains in one area, but not in another area. A final caution is necessary when considering items brought to the surface for manipulation. The evidence from my own work, and that from captive auks and penguins diving (Swennen & Duiven 1977; P J Butler in litt.), indicates that small items may be ingested underwater - the body depth of a fish being more critical than the length - whilst larger items are brought to the surface. Comparison of Figures 9.1a and b emphasizes this point, but there appears to be no way of quantifying in the field the proportion of items ingested sub-surface, other than by shooting a bird after recording all surfacings during the preceeding hour. This was not attempted in these studies.

Inter-specific competition for food is not usually considered for Cepphus species, perhaps because the niche and diet are usually so dissimilar from other auks. However, Scott (1973) compared resource allocation and overlap of foraging depths and prey types in Pigeon Guillemots, with Common Murres Uria aalge and two Cormorant species. Shags often forage in similar areas and water depths to Black Guillemots in Shetland, and in some parts of Scotland, the diet is very similar (Lumsden & Haddow 1946; Rae 1969). In summer in areas such as Mousa Sound and

stronger tide races, Black Guillemots often feed alongside large numbers of Shags and other auks, where there may be some competition for sandeels, although prey size probably segregates the other auk species (Harris 1970). At other times of year any competition is probably much reduced since other auks are uncommon in coastal waters, and Shags tend to congregate near tide races, leaving Black Guillemots alone to exploit inshore waters in most areas. Although Otters also take similar benthic species to Black Guillemots, items tend to be larger and caught closer to the shore, rarely in water deeper than 10 m (Watson 1978; Glimmerveen & Ouwerkerk 1983). Since average densities of Otters in Shetland are one per 1.1 - 2 km of coastline (Watson 1978; Glimmerveen & Ouwerkerk 1983), significant competition for food resources with Black Guillemots is unlikely.

Many bird species raise their young on a diet different from that of full-grown individuals (Marshall 1951). This was the case for Black Guillemots in Shetland, with 99% of the chick diet comprising fish, but full-grown birds consuming invertebrates as well. The predominance of sandeel and Butterfish deliveries in Shetland has also been noted on Fair Isle (Slater & Slater 1972a) and Foula (Furness 1983), and in Orkney - although there Butterfish comprised over half the chick diet (M Gray pers. comm.). At higher latitudes invertebrates may occur in such abundance during the summer that despite the smaller size and lower calorific value compared with fish, they may be brought to chicks in moderate numbers (Belopol'skii 1957; Petersen 1981; P G H Evans pers. comm.).

Cottids, although common in the macrobenthic epifauna, are scarce in the chick diet, probably on account of their sharp spines and the defensive distension of gill covers when alarmed. The Viviparous Blenny Zoarces viviparus is one of the commonest inshore fishes in summer in Shetland, with numbers increasing in August (Appendix IV; Glimmerveen & Ouwerkerk 1983), yet it is rarely caught by Black Guillemots. The nocturnal habits of this blenny, as for all rockling species (R N Gibson in litt.; H Kruuk in litt.) could explain their scarcity in the diet. However, in the Gulf of Finland 95% of fish fed to chicks were Z. viviparus in one year (Bergman 1971). At present so little is known of the basic ecology of these inshore fish that no further comments can be made on changes in availability to Black Guillemots.

The composition of chick diet showed significant variation with chick age, but this was primarily a date effect, probably reflecting changes in the availability of fish types. Various environmental factors have been considered to cause changes in fish activity (this has often been inferred

from changes in seabird diets and feeding rates): wind speed and sea state (Gibson 1969; Potts 1969; Dunn E K 1975; Birkhead 1976; Kuletz 1983); tidal state (Slater 1976); current strength (Warburton 1983), and sea temperature (Bergman 1971, 1978). That no significant effect of wind speed on the proportion of sandeels in the chick diet was found on Mousa is perhaps not unexpected, since Black Guillemots typically forage along the sea bed in inshore waters (Uspenski 1956; pers. obs.). Sandeels normally feed just off the bottom during the day (Winslade 1974a), and thus their activity might only be affected by wind-induced turbulence of surface layers in very shallow waters. Concentrations of feeding Black Guillemots and other seabirds regularly occur in tide races in Shetland. Birds complete a series of dives in the area, being continuously swept downstream, then fly back to repeat the sequence. Presumably water mixing and flushing of nutrients leads to increased feeding activity of invertebrates, and so current strength is probably the most important determinant of fish activity.

Chick diet composition showed no significant diurnal or tidal variation. Nevertheless, rates of delivery of sandeels were significantly higher in the early morning, coincident with a peak in sandeel feeding activity following the hours of darkness spent buried in the sand (Winslade 1974a). In the absence of food (copepods, larval crustacea and annelids), swimming activity of sandeels is very low (Winslade loc. cit.); thus it is possible that variations in sandeel deliveries to chicks reflect local fluctuations in zooplankton abundance. Although Penny & Newton (1982) found Butterfish delivered more often around low tide, this result was based on only a small number of sample days. My results indicate that more blennies (ie. Butterfish in the Shetland case) were caught around high water, as found by Preston (1968) and Petersen (1981). Tidal influence on movements up and down shores, general activity etc. has been established for some benthic fish (Gibson 1969), but the activity rhythms of Butterfish are confusing - varying from arhythmic to active around high water (R N Gibson in litt.) - and could show regional variation. There was no evidence of significant variation in sea temperatures between years in Shetland (Appendix III).

Foraging areas

Outside the breeding season Black Guillemots in Shetland foraged up to 7 km away from the overnight communal roost areas (Ewins 1985b). However,

the foraging range in summer is constrained by breeding commitments at the colony, and the majority of adults on Mousa fed chicks with fish caught within 1.5 km of the colony. Foraging birds were often found at greater distances from nesting areas in summer, and many were immatures, non-breeding or failed adults. Breeding adults might also range further when feeding for themselves, thereby reducing the risk of depleting food resources near the colony, but limited observations from Mousa lend no support to this idea since most adults regularly fed less than 1 km from their colony. Although foraging ranges in winter have not been previously documented, distances from breeding colonies to feeding areas in other studies vary from 0.1 - 7 km, mostly up to 4 km (eg. Kartaschew 1960; Preston 1968; Bergman 1971; Asbirk 1979c; Cairns 1980, 1984; Petersen 1981; P G H Evans pers. comm.). These distances are similar to those for Cepphus columba and C. carbo (Drent 1965; Kuletz 1983; Nazarov & Labzyuk 1972; Thoresen 1984), but considerably shorter than maximum foraging ranges for other diving seabirds in the North Sea (Pearson 1968; Cramp & Simmons 1977; Cramp 1985).

Black Guillemots in Shetland rarely foraged in water deeper than 40-50 m at any time of year; similar foraging depths have been found elsewhere (Petersen 1981; Nilsson 1982; Cairns 1984; Cramp 1985; Piatt & Nettleship 1985). Although overall benthic productivity decreases with depth and distance from the shore (Mann 1976), the major factor restricting foraging depths may be an energetic one. In agreement with the basic theories of optimal foraging (Krebs et al. 1983), it appears that Black Guillemots return to the surface only with large prey items, consuming small items (requiring no surface handling) whilst foraging underwater. Direct observations in Shetland confirmed this; birds descended steeply to the sea bed then moved quickly between areas of rocky, vegetated benthos, investigating dark recesses and probing beneath Laminaria fronds in the manner described by Uspenski (1956). Although Kozlova (1961) gave the distance travelled underwater in a 60 s dive as 40-50 m, in Shetland the net displacement was rarely over 30 m and maximum dive times were usually c.100 s. The speed of direct underwater swimming is 1.5-2 m s^{-1} (Uspenski 1956), and of direct descent to the sea bed 1.6 m s-1 (pers. obs.). Travel time to and from benthic foraging habitats would be at least 50 s for a dive in 50 m of water. Thus, with reduced benthic productivity and effective search times at greater depths, energetic returns may not balance the additional energy and time costs associated with deeper dives.

Sandeels and gadoids are usually regarded as pelagic species, in comparison with blennies and other benthic fish which spend much of their time inhabiting holes and crevices (Gibson 1969), rather than in dense shoals. However, this distinction may be misleading since both Ammodytes marinus and 0-class Trisopterus esmarkii (Norway Pout, a gadoid) normally occur just off the sea bed during daylight hours (Winslade 1974a; Bailey 1975). Adults specialising in these fish sometimes brought in flatfish from the same area, suggesting that they were catching the "pelagic" species close to the bottom. Dive times also supported this idea. I believe that the observed differences in water depths between pelagic and benthic captures (Figure 9.6) reflect differences in substrate type and variations in water movements between foraging areas, factors which are known to affect benthic community structure (Erwin 1976). Although the precise distribution of sand patches around Mousa is not known, fishing boats can only trawl for sandeels over sand; areas trawled regularly coincide with those used by pelagic specialists (eg. A3 female, shown in Figure 9.8).

Individual specialisation on particular fish types has previously been documented for Black Guillemots by Slater & Slater (1972b), and for Pigeon Guillemots by Drent (1965), Koelink (1972), Eldridge & Kuletz (1979) and Kuletz (1983). Although benthic fish are usually considered to have more restricted ranges than schooling species, and hence to be more predictable in time and space, both sandeels and Butterfish (together accounting for 70-80% of fish delivered to chicks in Shetland) are rather mobile species whose populations often show temporal and spatial fluctuations, at least on a local scale (Qasim 1957; Winslade 1974a,b,c; Warburton 1983; R N Gibson in litt.). The skippers of boats trawling around Mousa reported that sandeels sometimes vanished from some areas, and appeared at others. The significant shift in foraging areas of colony A breeders in 1984 probably reflected local movement of sandeel stocks since fishing boats moved to other areas at the same time. Thus it appears that in summer at least, Black Guillemots forage in an environment which is predictable, at least in the short term, yet patchy, although on a finer scale than for offshore habitats (Erwin 1976; Steele 1976). Regular use of restricted productive foraging areas and the switching between areas are phenomena consistent with the idea of varying patch quality, and further emphasize the plasticity of the foraging behaviour. However, it is difficult to determine whether individuals regularly feeding in an area did so because of an intimate knowledge of the physical characteristics of the benthic

environment there, and so were better able to catch fish; or whether they acquired a search image for particular fish types (or were adept at particular capture techniques) and so returned to areas frequented by large numbers of the preferred prey.

The tendency for females to specialize in sandeel and gadoid deliveries, and males in deliveries of benthic fish, is closely connected with the foraging sites used, and probably the nature of the benthos there. Belopol'skii (1957) also found that females took more gadoids than males. Since there is no significant sexual dimorphism in this species (Cramp 1985), this difference is difficult to explain other than by chance. The higher diversity of deliveries made by males could be due to their foraging in shallower water over vegetated sea beds, where benthic fish communities are more diverse than in sandy areas (Wheeler 1969). In areas with rocks and seaweed cover, many of the fish species are poor swimmers and rarely stray from cover (Gibson 1969), in contrast to the fewer species frequenting sandy bottoms, which avoid predation by schooling, rapid swimming, or burying into the sand.

Provisioning and energetics

Although an equal share of provisioning was found between the sexes in Pigeon Guillemots (Drent 1965), both Preston (1968) and Asbirk (1979c) found that male Black Guillemots made more deliveries than females. Chick age effects were not considered however, and the results of Cairns (1984) and myself confirm that Petersen (1981) was right in proposing that the role of the sexes changes with the age of chicks. Cairns (1984) suggested that males did more brooding during the day. Chicks are brooded regularly during the first 3-6 days of life, until thermoregulatory mechanisms are fully developed (Kartaschew 1960; Shilov 1968). On Mousa however, the sexes brooded small chicks to an equal extent during the day (Chapter 7), and the reason for the preponderance of female deliveries to small chicks remains unclear.

Some chicks were fed small fish within a few hours of hatching, and the rate of delivery increased steadily thereafter to a peak at 25-29 days old, before declining prior to fledging. A similar pattern was found by Petersen (1981) in Iceland, but Cairns (1984) detected no significant variation with chick age, although his data, with smaller sample sizes, were analysed in a different manner. Average delivery rates were higher for all chick ages in 1984 at colony A, at least partly due to the

significantly lower incidence and success of kleptoparasitism by the resident pair of Arctic Skuas there - having two chicks to feed in 1983, but only one in 1984. However, feeding conditions were probably better in 1984, particularly in the latter stages of the chick period, when large gadoid prey became available, providing more energy per delivery for the chicks. The overall consequence was that both single chicks and those with sibs were on average heavier in 1984 at peak and fledging weights, than in 1983 (Chapter 7).

Overall, single chicks received more feeds than did those with siblings, as noted by Asbirk (1979c) and Petersen (1981). However, Cairns (1984) found that individual rates were comparable between broods with one or two chicks. As already mentioned, comparison of pooled delivery rates for chicks of different ages is meaningless unless appropriate weightings are given to age catgories, since there can be 3-fold differences in rates simply due to chick age.

Fagerstrom et al. (1983) proposed a gradual change with chick age in the factors limiting rates of energy uptake by the brood; initially the energy needs and digestive capacity of chicks are limiting, but later on parents may be unable to meet the energy requirements of chicks at all times. My results support this hypothesis. As chicks grow, the effect on average delivery rate per chick of having a sibling becomes greater (Table 9.IX). Further evidence is provided by differences in growth parameters, and form of the weight growth curves for single versus two-chick broods (Figure 7.3; Table 7.III). Chicks in artificial broods of 3 in Iceland had reduced growth rates after 3 weeks of age, took longer to fledge and fledged at lower weights than those in smaller brood sizes (Petersen 1981), indicating that adults were unable to provide sufficient food. Similarly, Keolink (1972) noted that adult Pigeon Guillemots never delivered more than 200 g of fish per day, resulting in depressed growth rates in broods of 2 and 3 chicks, and that parents doubled their rate of fishing when feeding nestlings. These findings for Cepphus adults feeding young support the idea of an 'optimal working capacity' (Royama 1966), and a ceiling to parental performance (Drent & Daan 1980), above which any extra costs to parental fitness would not be matched by a corresponding increase in offspring survival.

This hypothesis may account for the considerable confusion over diurnal patterns of delivery in Cepphus species. Peaks of chick provisioning at either end of the hours of darkness are understandable in terms of increased activities of many prey species then, together with

greater energy demands of chicks. As the broods' energy requirements increase, so parents are unable to satiate chicks so easily, and food-begging calls continue through the day, stimulating parents to provide more food [this role of food-begging calls has been demonstrated for Puffins by Harris (1983b)]. Thus a bimodal peak of deliveries in the early chick period becomes obscured at later stages since adults are required to provide food all day (as suggested in Figure 9.13). Clearly the stage of the chick period at which observations are made may determine to a large extent the diurnal pattern of deliveries obtained.

Adults can increase the energy input to the nestling diet in three ways: (i) increase rates of delivery (ii) increase prey size, and (iii) select prey of higher energy value. Although (i) is constrained by adult foraging and flight efficiency, there are a number of possible restrictions on prey size: gape size of chicks, increased risk of detection by kleptoparasites when transporting large fish (Chapter 10), and weight of fish an adult is capable of carrying from the capture site to the nest. Since the mean size of most fish species in the area showed no marked change over the Black Guillemot nestling period [as concluded by Petersen (1981)], adults are selecting progressively larger fish as chicks grow, although deep-bodied and broad species are usually much shorter than sandeels and blennies. The evidence for sandeels supports the ideas of central place foraging theory (Orians & Pearson 1979); in this case the central place is the nest site, and adults only return with larger than average sandeels. However, for species such as the Black Guillemot, which carry only one prey item, Lessells & Stephens (1983) considered that individuals should be unselective about prey size up to a certain critical travel time. Cairns (1984) has calculated this critical time (ie. range) to be approx. 2 km, and invoked this argument in explaining lack of significant load weight increase with travel distance, since most breeders caught fish within this range of the colony. Although based on sufficient data for only 5 individuals on Mousa, the correlation of mean load weight with travel distance was positive, but non-significant (Kendall rank correlation, $\tau = 0.8$, $P=0.08$).

Finally, adults could provide prey of higher energy value. During the late nestling period in 1984 the evidence points to a shortage of large sandeels, at the same time as large gadoids became available. Not only did gadoids appear to be more numerous, but the average lengths of those delivered were greater than in 1983. Thus, a gadoid delivery to large chicks in 1984 provided up to twice the energy value of a sandeel or

blenny. Although no information is available on fluctuations in gadoid populations in the area (other than by inference from seabird diet), they are a highly mobile, pelagic group, and I would expect Black Guillemots to exploit such a profitable food source whenever possible. A comparable situation occurs in the Canadian arctic: when ice bodies were present Black Guillemots exploited the associated rich food supplies, taking largely Boreogadus saida (Arctic Cod, another gadoid) from beneath the ice surface. In the absence of ice, birds fed opportunistically on a wide range of prey in shallower water (Bradstreet 1980; Cairns 1984).

Demands on adults are further increased when provisioning large chicks since the efficiency of conversion of food to body weight decreases markedly after day 20, as more energy is channelled into plumage development, exercise and other functions - up to 3 times more food is required per gram increase in body weight then (Koelink 1972). In these terms, the greater total energy input to the chick diet in 1984, and the increased contribution of the most profitable prey type (gadoids) can be understood in the light of adults foraging in an optimal manner, attempting to maximize chick growth rates and their reproductive output. That chicks in 1984 were significantly heavier at peak weight and at fledging (Chapter 7) lends further support to these ideas.

CHAPTER 10. KLEPTOPARASITISM

10.1 Introduction

Kleptoparasitism, or piracy, usually refers to the stealing of food obtained by another species (Rothschild & Clay 1952; Meinertzhagen 1959). I have used these terms interchangeably here, taking them to include both inter- and intra-specific attempts at food stealing. This feeding behaviour is widespread amongst birds (Brockmann & Barnard 1979) and is particularly common amongst the Laridae and Stercorariidae (Ingolfsson 1969; Hatch 1970; Dunn 1973; Taylor 1975; Furness 1977; Cramp & Simmons 1983; O'Donald 1983). Many members of the auk family are suitable hosts for kleptoparasitism since their prey are normally very conspicuous when brought in to the often large breeding colonies, and it is not surprising that at least 13 species have been recording pirating fish from Puffins for example (Harris 1984). Most of the detailed investigations of kleptoparasitism of auks have focussed on larger Puffin colonies (Grant 1971; Nettleship 1972; Andersson 1976; Ashcroft 1976; Arnason & Grant 1978; Pierotti 1983; Hudson 1985).

Although Black Guillemots typically breed in much smaller colonies than other auks (Chapter 3), kleptoparasitism is well-known in this species, by: gulls (Bent 1921; Winn 1950; Bergman 1960, 1971; Slater & Slater 1972a,b; Cairns 1978), terns (Bardarson 1975; Petersen 1981) and Arctic Skuas (Montague 1926; Lovenskiold 1964; Petersen 1981; Penny & Newton 1983). However, most of these accounts comprise only descriptions of a small number of incidents, and only Cairns (1978) and Friesen & Cairns (in prep.) have attempted any detailed investigations. On Mousa some Arctic Skuas and a few Herring, Lesser Black-backed and Common Gulls Larus canus regularly kleptoparasitized Black Guillemots during the nestling period, providing an excellent opportunity for study of the dynamics of these interactions.

In this chapter I describe and quantify kleptoparasitism at the breeding colonies, but also in the foraging areas outside the breeding season. Variability in, and factors affecting, the incidence and success of kleptoparasitism are analysed in relation to their effects on Black Guillemots and the relative profitability of different foraging strategies of the pirates.

10.2 Study areas

As part of studies of foraging activities outside the breeding season, details were kept of all instances of kleptoparasitism observed between September and May (1982-84). Much of this work was carried out in relatively sheltered inshore waters such as Lerwick and Scalloway harbours (see Figure 2.1) where potential pirate species regularly occurred in large numbers.

Detailed observations during the breeding season were made on Mousa in 1983 and 1984, but some data were also collected in 1982. Three colonies were chosen for study - varying in the number of breeding pairs, proximity to, and mean elevation above sea level, and proximity to breeding territories of potential kleptoparasites (Figure 10.1). Unrestricted observations of kleptoparasitism was only possible for nests in the northern section of colony A. This area usually held c.28 nests with young, and, for the purposes of this chapter only, will be referred to as colony A (for full extent of colony A see Figure 6.2). Nests were located in a boulder area, overlapping partly with the breeding territory of a pair of Arctic Skuas which regularly pirated deliveries here. No gulls bred within 200 m of this colony. Colonies C,G, and Q were considered as one unit (total c.19 nests with young) since the normal approach for all adults delivering fish was via the entrance to the tidal pool (Figure 10.2). Nests were located under boulders around the tidal pool, scattered amongst territories of c.100 pairs of Lesser Black-backed Gulls and c.25 pairs of Herring Gulls. At low tide a large expanse of rock was exposed at the seaward end of the pool. Nests at colony E (c.18 held young) were mostly in crevices on the steep slopes and cliffs (max. height 25 m); no skuas, and only 1 pair of Herring Gulls bred within 200 m of the colony area.

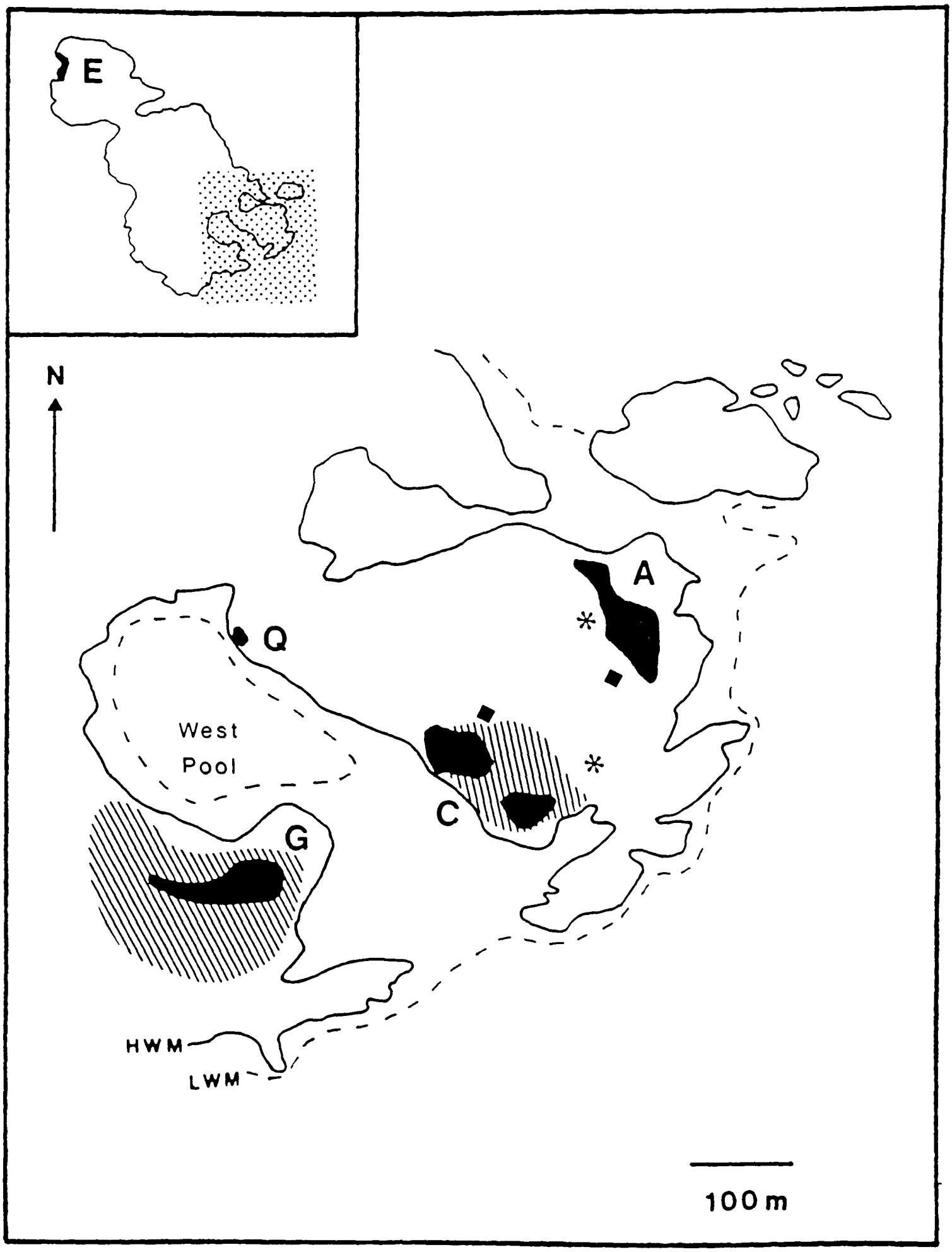
Common Gulls did not breed on Mousa, but up to 10 adults frequented the island in July and August in each year. The island held 16-17 breeding pairs of Arctic Skua, a small colony of Kittiwakes, 1000+ pairs of Arctic Tern and less than 10 pairs of Puffin (Ewins 1983a, 1984a).

10.3 Methods

10.3.1 Pirate - Black Guillemot interactions

All observations were made from hides in positions enabling unrestricted views over a wide area. Even so, the outcome of a small

Figure 10.1 The location of Black Guillemot study colonies, Arctic Skua nests and Gull colonies.



Black Guillemot nesting areas

* Arctic Skua nests

Gull colonies

position of hides

Note: High (HWM) and Low (LWM) water marks are for spring tides.

number of chases was unknown, and these have been omitted from some analyses. Due to the alarm caused by my entering hides, observation periods were started 10 minutes after entry (preliminary work had shown that colony activity reverted to normal after this interval). Observation periods were at least 1 hour long - usually 2 hours or more - and were scattered throughout the nestling period at each colony. The bulk of this work was completed at colony A (over 180 h of timed watches), but comparative data were gathered from colonies CGQ (over 31 h) and E (14.5 h). All delivery attempts were recorded during the sample watches (as described in Chapter 9 methods), and details noted of approach path, height, and kleptoparasitic attacks. During hectic bouts of delivery and/or piracy, a dictaphone was used. This greatly improved the efficiency of observation and recording. As a result it was thought that very few attacks or deliveries were overlooked.

An attack was scored when a pirate attempted to obtain the fish held in a Black Guillemot's bill. The encounter time (t_e) was recorded on a stopwatch, taken from the moment the Black Guillemot detected the attack (some form of evasive action was usually taken immediately), to the time the pirate stopped pursuing. Details were noted of pirate species, age and number, type of attack, response, the number and species of birds following the pirate (the so-called "attendants"), and final outcome. However, despite the standardized recording sheets and dictaphone it was sometimes impossible to gather all information pertaining to an attack.

In pursuits involving 2 Arctic Skuas the lead often changed, and so it was impossible to score one individual as an attendant: such attacks were scored as made by 2 pirates. In 1984 investigations were made using focal animal sampling (Altmann 1974) on random samples of birds flying into view off colony A, into the effect of differing kleptoparasitic pressure on the total delay time (t_w) spent waiting offshore, prior to making the final delivery attempt. Rates of delivery and piracy were measured during 1-hour watches, alternating with 1-hour periods of focal sampling.

10.3.2 Arctic Skua - Arctic Tern interactions

During the latter stages of the Arctic Tern nestling period in 1983 (between late June and early August), I monitored a random sample of kleptoparasitic attacks by Arctic Skuas. At a number of sites on Mousa (but not at sea) between 0900-1400 h BST, an adult skua was followed for at least 15 mins. and standard details noted for each attack made. Arctic

Terns on Mousa rarely carried more than a single fish in the bill. Although fish length could not always be estimated during chases of terns, there was no suggestion that the size distribution of fish 'chased' differed markedly from that of fish brought in by Arctic Terns during the nestling period.

10.4 Results: Kleptoparasitism outside the breeding season

From a total of 358 Black Guillemots seen to bring prey items to the surface, only 24 (6.7%) were attacked by kleptoparasites. Most of the birds attacked were dealing with large or awkward prey, with longer than average surface handling times (eg. Blennies, a Starfish, a Sea Stickleback and a Cottid species). Twenty-nine separate attacks were recorded; 25 by one individual, 3 by two and 1 by four pirates. When more than one bird was involved in an attack it was not possible to distinguish between pirate and attendants since all appeared to participate to an equal extent. All these attacks were by gulls, 63% by Herring Gulls (Table 10.I). Although a Black Guillemot would occasionally swim towards a conspecific surfacing with prey, such cases were not regarded as constituting kleptoparasitism since social interactions of this kind occurred regularly between bouts of foraging at all times of year.

Only two types of attack were recorded:

(a) "Swoop down" - gull(s) would swoop down on a bird with prey, the normal response being either to swallow prey rapidly or to dive. Evasive dives were usually deep (presumably to prevent gulls from following underwater movements from above), and the bird usually resurfaced at least 10 m from the attack site. 26 (90%) attacks were of this type.

(b) "Swim towards" - if a gull was already on the water within c.20 m, it might swim rapidly towards a bird surfacing with prey. In the 3 cases observed the dive response was sufficient to cause the pirate to abort the attack.

Of the 29 attacks, 2 (7%) resulted in prey definitely being lost to the pirate (one involving an extremely large Butterfish - the adult Herring Gull persistently swooped down, for over 2 mins., whenever the bird resurfaced, and eventually the fish was released). In 17 cases (59%) prey

Table 10.I The number of kleptoparasitic attacks made by various gull species on Black Guillemots outside the breeding season.

Species	ATTACKS No.	%
Black-headed Gull **a**	1	2.9
Common Gull	3	8.6
Kittiwake	4	11.4
Herring Gull	22	62.9
Gt. Black-backed Gull **b**	4	11.4
Glaucous Gull **c**	1	2.9

Notes: a *Larus ridibundus*

b *L. marinus*

c *L. hyperboreus*

was retained by the Black Guillemot. In 10 cases (35%) the bird resurfaced without prey. Small and medium-sized items can probably be ingested underwater (P Butler pers. comm.) - a bulge is sometimes visible in the throat as the bird surfaces - and so it remains uncertain just how many items were abandoned underwater.

10.5 Results: Kleptoparasitism at breeding colonies

10.5.1 General characteristics of pirate - host interactions

Most Black Guillemots flew in with fish to the colonies, over the nearest seaward shore, and only a small number used other approaches. Birds waiting on the water usually did so in a restricted area off the colony (Figure 10.2). Occasionally, during periods of heavy kleptoparasite activity, some birds walked/ran with fish to the nest, attempting to avoid detection.

Attacks were of 3 types:

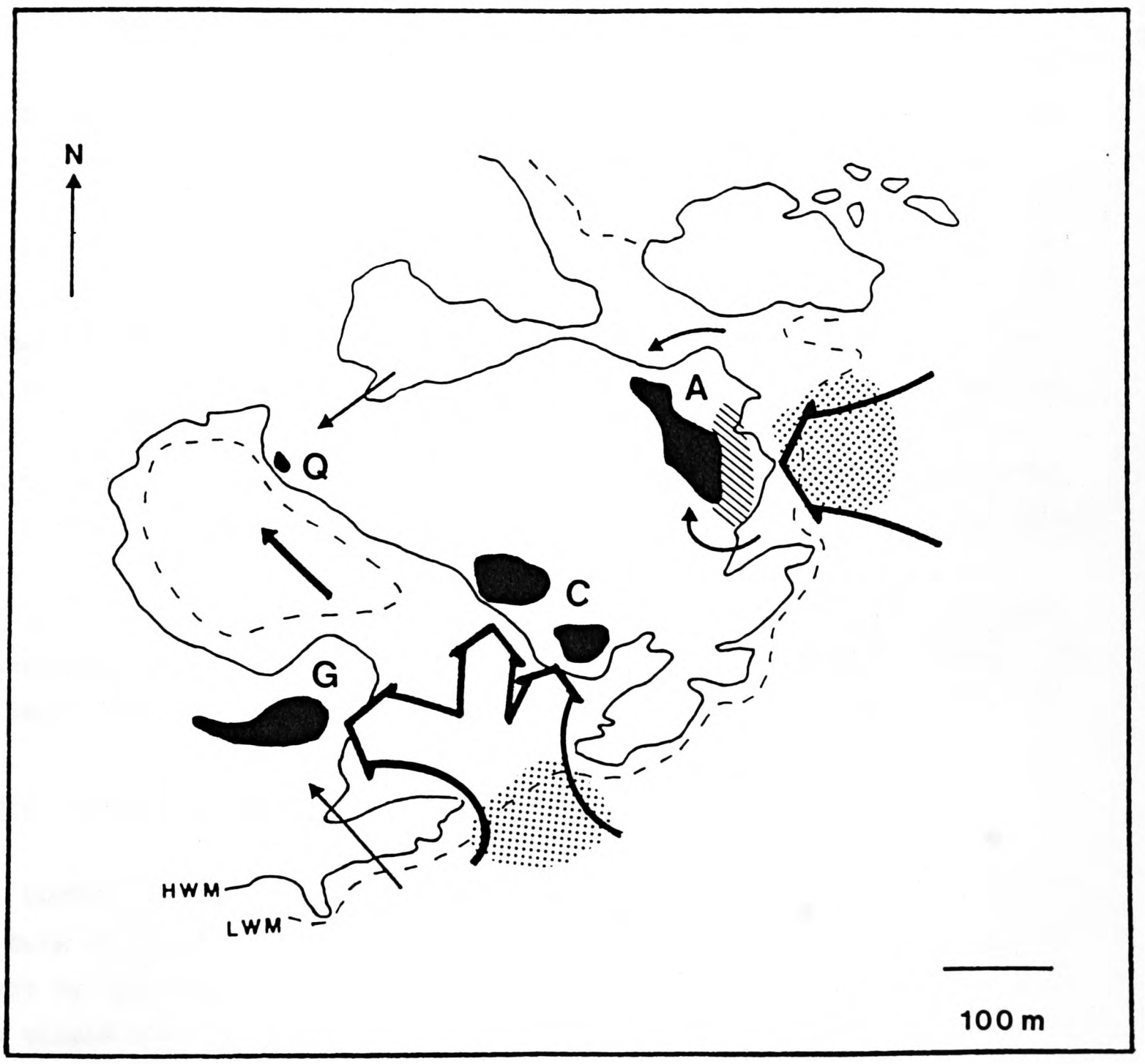
I **Aerial pursuit** - either over sea or land.
II **Swoop down** - usually on the sea, but sometimes on perched birds.
III **Rush towards** - in the immediate vicinity of the nest.

Response of the fish-carrying bird was of 3 types:

A **Dive** - host dives underwater with fish, usually for 10+ secs.
B **Aerial** - attempts to out-fly or out-manoeuvre pirate.
C **Dash under boulders** - usually the nest, but occasionally the bird hid under nearby rocks for a few minutes.

By far the commonest attack type was aerial pursuit. The colony A pair of Arctic Skuas specialized in this method and either patrolled the approach paths by slow flight over the shore rocks (the 'patrol zone') or spotted incoming birds from elevated perches in this area (Figure 10.2). Pursuits were either initiated as soon as the target bird was spotted (at times as much as 300 m from the shore), or the skua would attempt an ambush by remaining perched until the incoming bird was over the patrol zone, and then attacking. The element of surprise often resulted in fish being dropped immediately. At times, individual Herring, Lesser Black-backed and Common Gulls frequented the seaward edge of the patrol zone at colony A and

Figure 10.2 The location of Black Guillemot approach routes and offshore waiting areas at colonies A and CGQ.



Black Guillemot nesting areas

offshore waiting areas

Arctic Skua patrol zone

Approach routes of delivering birds
(width approx. proportional to frequency of use)

attended skua attacks, being quite successful in preempting the skua in retrieving released fish (see below).

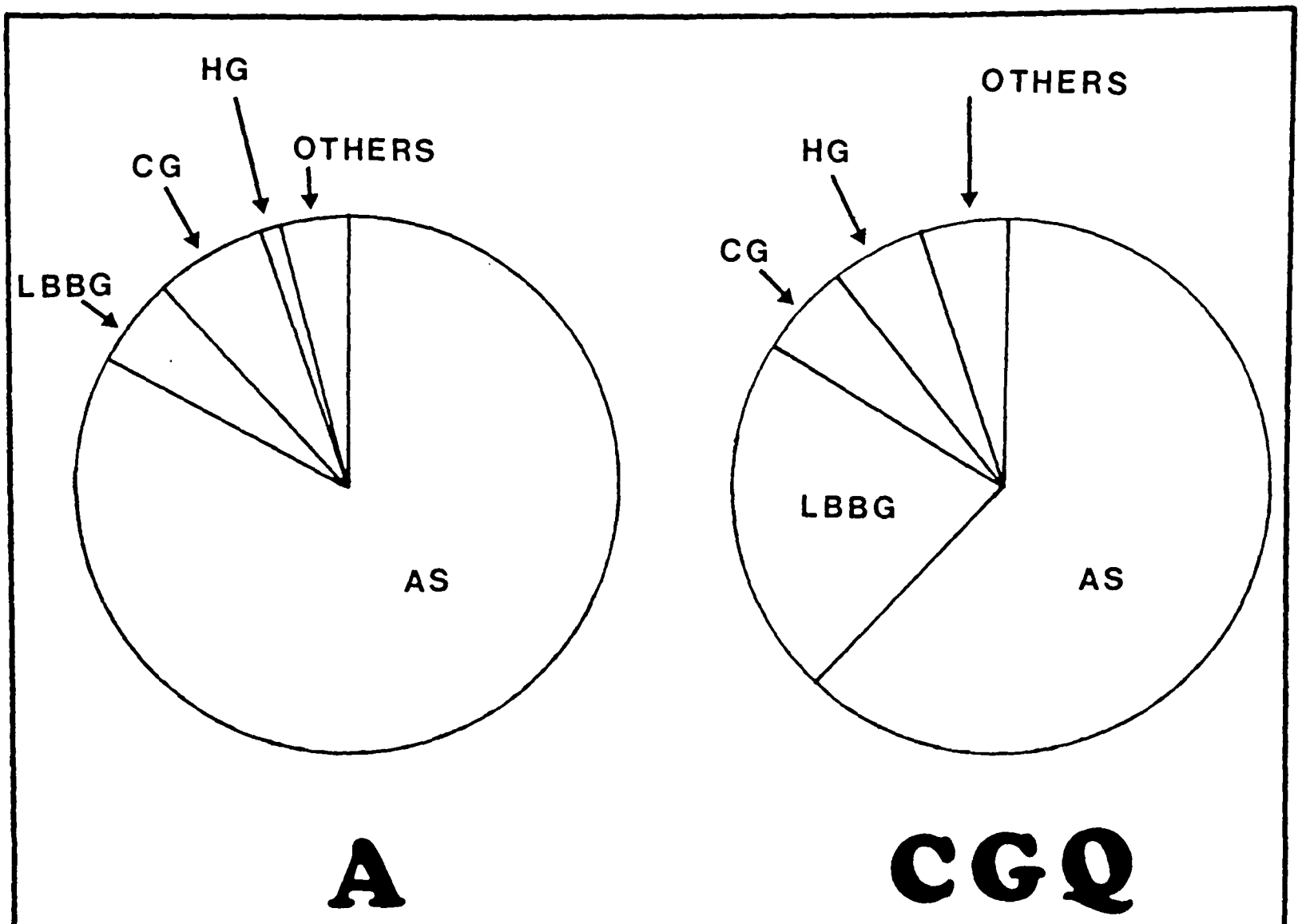
Most of the attacks made at colony CGQ were aerial pursuits by the Arctic Skua pair nesting on the slopes above colony C (Figure 10.1). At high water delivering birds could splash-down and dive in the West Pool when attacked. However, since the water there was so shallow (1-3 m), their movements underwater were easily tracked by gulls hovering above. The white upperwing patch of diving Black Guillemots is very obvious down to at least 8 m when seen from above, provided the water surface is not too choppy (pers. obs.). The persistent swoops on a Black Guillemot every time it resurfaced often resulted in the fish being released or abandoned underwater. At mid and low water much of the area between the open sea and CGQ colonies was exposed rock and incoming birds were vulnerable to piracy for a longer period than at colony A. This may not have been of direct importance for gulls however, since Black Guillemots could out-fly all gull species present in level flight (pers. obs.). Since gull territories were interspersed with Black Guillemot nests around the West Pool, attack type III was regularly practiced - a gull on territory rushing towards a bird with fish just before it reached the nest entrance (in the manner seen in Puffin colonies). The skua patrol zone was ill-defined at colony CGQ, possibly due to restrictions imposed by harassment from territorial gulls, but it often included much of the outer reaches of the West Pool, and shore rocks.

At colony E, delivering birds would simply fly straight to the nest. If attacked they veered out to sea in a large arc, or descended rapidly to the water and dived, then waited before repeating the attempt.

10.5.2 Analysis of attacks and responses

Combining the results for 1983 and 1984, Arctic Skuas accounted for the bulk of attacks at colony A (83%) and CGQ (62%), and the frequency of piracy by the other 10 bird pirate species varied between sites. Pursuit by a single Common Seal was the only record of a non-avian pirate (Figure 10.3). Attacks by gulls were commoner at colony CGQ than at A, accounting for much of the significant difference between colonies in the proportion of attacks made by the four main pirate species (X^2 = 63.8, 3 df, $P<0.001$). A total of 25 attacks was recorded at colony E, 15 (60%) by Common Gulls, 7 (28%) by Arctic Skuas, 2 (8%) by Herring Gulls and 1 (4%) by a Hooded Crow.

Figure 10.3 Pirate species in 1983-84 at colonies A and CGQ.



	% of attacks: A	CGQ
AS = ARCTIC SKUA	83.0	62.2
LBBG = LESSER BLACK-BACKED GULL	5.2	21.7
CG = COMMON GULL	6.6	5.6
HG = HERRING GULL	1.2	5.6
BLACK GUILLEMOT	0.2	4.2
ARCTIC TERN	2.1	0
KITTIWAKE	0.9	0
GREAT SKUA	0.1	0
FULMAR	0.2	0
SHAG	0.1	0
HOODED CROW	0.5	0
COMMON SEAL	0	0.7
n =	1016	143

The percentage of delivery attempts attacked was significantly higher in 1983 than in 1984 at both colonies A and CGQ, but not at E (Table 10.II). The overall success rate of attacks (an attack was regarded as successful whether the pirate retrieved the released prey or not), was significantly lower in 1984 at colony A (34% vs. 42%), but there was no significant difference between years in pirate success at CGQ. The percentage of fish lost by Black Guillemots as a result of pirate activity was significantly lower in 1984 than in 1983 at both colony A and CGQ. In 1983 a significantly greater proportion of delivery attempts was attacked at colony CGQ than at A (47%:25%, X^2 = 29.0, 1 df, P<0.001), and significantly more birds lost fish (21%:10%, X^2 = 13.1, 1 df, P<0.001). In 1984 the percentage of deliveries losing fish was significantly higher at colony CGQ than at A (11%:6% respectively, X^2 = 5.7, 1 df, P<0.05) (Table 10.II).

Analysis of pirate number and attendant species is confined to attacks by Arctic Skuas and Lesser Black-backed Gulls (together they accounted for 84-88% of attacks) and data have been pooled for all colonies and years. For skua attacks without attendants, 93% involved a single attacker, and no more than 2 skuas were ever recorded in a chase (Table 10.III). Attendants followed single skuas in 66 attacks, and 2 skuas in four. Of the 103 attacks made by Lesser Black-backed Gulls without attendants, 98 (95%) involved a single bird, and only 5 (5%) were by two birds. On average pirates were accompanied by attendants once every 13-14 attacks (Table 10.IV).

The number of skuas in an attack had no significant effect on the outcome (Table 10.III), nor on whether the fish was released or not by the Black Guillemot (X^2 = 2.1, 1 df, P>0.05). Although the percentage of chases in which a fish was obtained was higher with 2 skuas than with 1 (37% vs. 28%), each individual skua obtained fish in only 18% of the attacks (Table 10.III). Attacks by Arctic Skuas accompanied by attendants were significantly more likely to result in the Black Guillemot releasing fish than if no attendants were present (66% vs. 35%, X^2 = 27.2, 1 df, P<0.001), but with attendants following, skuas obtained fish in significantly fewer instances (7% vs. 28%, X^2 = 103.4, 1 df, P<0.001). There was no significant difference in the proportion of fish released but not recovered, between skua attacks with and without attendants (Table 10.IV). Sample sizes were too small for Lesser Black-backed Gull attacks to permit similar analyses.

Table 10.II Comparison of overall incidence and success of kleptoparasitism at study colonies in 1983 and 1984. Significance of differences between years (all with X^2 tests, 1 df): * P<0.05, *** P<0.001.

	Colony/Year					
	A		CGQ		E	
	1983	1984	1983	1984	1983	1984
No. delivery attempts	1569	1743	124	149	51	108
Attacked: No.	387	325	58	32	4	12
%	24.7	18.6	46.8	21.5	7.8	11.1
	***		***		ns	
SUCCESSFUL ATTACKS						
No.	162	110	26	17	0	3
% of those attacked	41.9	33.9	44.8	53.1	0	25
	***		ns			
% of delivery attempts	10.3	6.3	21.0	11.4	0	2.8
	*		*			

Table 10.III The outcome of kleptoparasitic attacks by 1 and 2 Arctic Skuas. Data for attacks without attendants, and pooled for all years and colonies.

			Final outcome [a]					
	Total attacks		X		✓		✓o	
No. skuas	No.	%	No.	%	No.	%	No.	%
1	851	92.6	563	66.2	235	27.6	53	6.2
2	68	7.4	39	57.4	25	36.8	4	5.9
	919							

Notes: [a] X Black Guillemot retains fish

✓ Pirate gets fish

✓o Fish released by Black Guillemot, but not retrieved

[b] $X^2 = 2.63$, 2 df, $P>0.05$.

Table 10.IV The outcome of kleptoparasitic attacks by Arctic Skuas and Lesser Black-backed Gulls, with and without attendant species. (Data combined for all years, colonies and number of pirates).

		ARCTIC SKUA		LESSER BLACK-BACKED GULL	
Attendants [a]		-	+	-	+
Total attacks	No.	919	70	103	9
	%	92.9	7.1	92.0	8.0
FINAL OUTCOME [b]					
X	No.	602	24	91	7
	%	25.5	34.3	88.4	77.8
√	No.	260	5	10	0
	%	28.3	7.1	9.7	
$√_o$	No.	57	3	2	0
	%	6.2	4.3	1.9	
$√_o$(att)	No.	-	38	-	2
	%	-	54.3	-	22.2

Notes: [a] attacks with (+) or without (-) attendants

[b] X Black Guillemot retains fish

√ Pirate gets fish

$√_o$ Fish released, but not retrieved

$√_o$(att) Fish released, and retrieved by an attendant

The majority (87.3%) of the 79 attacks (by either Arctic Skuas or Lesser Black-backed Gulls) accompanied by attendants involved only one attendant, but 10.1% involved 2, 1.3% had 4, and 1.3% had 5 individuals following the pirate. A total of 94 individuals were recorded attending kleptoparasitic attacks: Lesser Black-backed (37), Herring (33) and Common (20) Gulls were the most regular, but singles of Gt. Black-backed Gull, Kittiwake, Arctic Skua and Hooded Crow were also recorded. As attendants, gulls were very successful in retrieving fish released by the Black Guillemot. The percentage success (number of chases in brackets) for the regular attendant species were: Herring Gull 91% (21), Lesser Black-backed Gull 71% (17), and Common Gull 75% (8). Although 15% of the Black Guillemots attacked were attacked more than once during a delivery attempt, there was no significant increase in the proprtion of birds releasing fish with increasing number of successive attacks on the one individual (X^2 =1.1, 1 df, P>0.05) (Table 10.V).

The data concerning response type and outcome of the different attack types by Arctic Skuas and Lesser Black-backed Gulls are pooled for 1983 and 1984, and are presented separately for colonies A and CGQ (Table 10.VI). There was no significant difference in the frequency of aerial as opposed to other types of attack by Arctic Skuas between the two colonies (X^2 = 0.1, 1 df, P>0.05), but non-aerial attacks were significantly more frequent at colony CGQ than at A (59% vs. 30%, X^2 = 7.0, 1 df, P<0.01). At both colonies skuas engaged in more aerial, but fewer rush-towards and swoop-down attacks than did Lesser Black-backed Gulls (Table 10.VI). A comparison between species of the overall success rates (data pooled for the two colonies) revealed that Arctic Skuas were significantly more successful than Lesser Black-backed Gulls in aerial attacks (38% vs. 12% respectively, X^2 = 14.0, 1 df, P<0.001), but did not differ significantly for either swoop-down (15% vs. 4%) or rush-towards (23% vs. 30%) attacks.

Sample sizes were too small for many of the response type categories to permit statistical analyses, but since there were no obvious differences between colonies, the results were combined. Of aerial attacks by Arctic Skuas, 42-48% were successful when the Black Guillemot's response was aerial, but only 5-17% when the target bird dashed under boulders, and 0% when it dived underwater. Aerial attacks by Lesser Black-backed Gulls resulted in success rates of 12-18% if the response was aerial, but 0% if the Black Guillemot dived or rushed under boulders (Table 10.VI). For swoop-down and rush-towards attacks, both pirate species had the greatest chances of success when the response was aerial.

Table 10.V The frequency and outcome of different numbers of kleptoparasitic attacks on individual delivery attempts. Data for all colonies in 1983-84 combined.

		NUMBER OF SEPARATE ATTACKS										
		1	2	3	4	5	6	7	8	9	10	Total
Attack frequency	No.	821	108	22	7	4	0	0	0	1	1	964
	%	85	11	2	1	<1	0	0	0	<1	<1	
% of Black Guillemots releasing fish		40	36	55	29	25	-	-	-	0	0	

Table 10.VI Attack types, responses and outcomes of kleptoparasitic pursuits by Arctic Skuas and Lesser Black-backed Gulls at colonies A and CGQ in 1983-84.

Species	a	% of attacks A	% of attacks CGQ	b	Responses A No.	Responses A %	Responses CGQ No.	Responses CGQ %	Birds releasing fish A No.	Birds releasing fish A %	Birds releasing fish CGQ No.	Birds releasing fish CGQ %
ARCTIC SKUA	I	93	94	A	19	3	4	5	0	0	0	0
				B	597	77	71	87	288	48	30	42
				C	156	20	7	9	7	9	7	5
					772		82					
	II	5	6	A	6	16	4	80	0	0	0	0
				B	6	16	1	20	5	83	0	0
				C	25	68	0	0	1	4	-	-
					37		5					
	III	3	0	B	4	18	-	-	2	50	-	-
				C	18	82	-	-	3	17	-	-
					22							
				Total	831		87					
LESSER BLACK-BACKED GULL	I	70	41	A	2	5	1	8	0	0	0	0
				B	33	89	11	85	4	12	2	18
				C	2	5	1	8	0	0	0	0
					37		13					
	II	19	47	A	9	90	14	93	0	0	1	7
				B	0	0	0	0	-	-	-	-
				C	1	10	1	7	0	0	0	0
					10		15					
	III	11	13	B	4	67	1	25	2	50	1	100
				C	2	33	3	75	0	0	0	0
					6		4					
				Total	53		32					

Notes: **a** Attack type: I = Aerial, II = Swoop-down, III = Rush towards

b Response type: A = Dive, B = Aerial, C = Dash under boulders

Kleptoparasitic attacks made by other species (see Figure 10.3) were swoop-down attacks at birds waiting offshore with fish. All but one (by a Herring Gull) were unsuccessful. An adult Hooded Crow occasionally scavenged in colony A, and rarely managed to surprise a bird arriving with fish (normally all colony activity ceased when a crow was in the vicinity; birds sat offshore alarm-calling until the crow departed). Of 6 direct attacks by the Hooded Crow, 3 were successful. Of 8 attacks by Black Guillemots, 3 were aerial - resulting in the delivering bird dropping to the water and diving - and 5 were swim-towards attacks, the response being to dive or swim away then fly. No intra-specific attack was successful.

Encounter times (t_e) for attacks at colonies A and CGQ were pooled since there were no significant differences for any pirate species between colonies. For aerial attacks by Arctic Skuas, followed by an aerial response, successful attacks were significantly longer than unsuccessful ones (medians 4.0:3.0 s, n=156, 203 respectively; Mann-Whitney U test, P=0.014).

10.5.3 Effects on Black Guillemots

Adult behaviour was affected in various ways by kleptoparasite activites. Direct bodily contact during attacks was rare, being recorded on only 8 occasions (ie. less than 1% of all attacks) in the 3 study years. All these cases involved Arctic Skuas - in 5 the fish was snatched directly from the bill in flight. Direct attacks by Black Guillemots on pirates were seen on only 4 occasions, all occurring after the host had been harassed at the nest entrance, by an Arctic Skua or Lesser Black-backed Gull.

Although a few delivering birds approached by alternative low routes, most approaches were from the nearest seaward shore in all years (Figure 10.2). Birds normally flew in with fish at less than 30 m above sea/ground level, but 2 alternative strategies were also adopted: "High" (approach at >30 m altitude, then a rapid, steep descent at the last minute), and "Walk" (walk or run from shore rocks to the nest). The walk approach was mostly used by birds nesting within 10 m of the HWM, but a bird once walked 35 m to deliver a fish. Approach category was recorded in July 1984 for most deliveries at colonies A and CGQ, revealing that a significantly greater percentage of approaches at A were "low", than at CGQ (97% vs. 55% respectively, X^2 = 378, 1 df, P<0.001). At colony A only 2% of delivering birds made high approaches, but they were attacked significantly more often

than high approaches at colony CGQ. Significantly fewer birds making low deliveries lost fish as a result of pirate attacks at colony A, than at CGQ (Table 10.VII).

Adoption of alternative approach methods appeared to be an attempt by Black Guillemots to increase the chances of making a successful delivery. At colony CGQ on a sample of 7 days in July 1984, the proportion of birds using approaches other than "low" (ie. high or walk) increased significantly with the proportion of deliveries attacked ($r = 0.91$, 5 df, $P<0.01$). Although no such relationship existed for colony A, some individuals there made extremely low, ground-hugging approaches when kleptoparasitic pressure was high.

The total time spent waiting offshore (t_w) with fish at colony A increased logarithmically with increasing proportion of deliveries attacked - the regression being significant at the 1% level. There was a marked rise in t_w once kleptoparasites attacked in excess of 30-35% of delivery attempts (Figure 10.4). The longest recorded delay was nearly 40 minutes. To investigate the hypothesis that Black Guillemots swamp kleptoparasites by "clumping" deliveries, in time, I have only used data collected at colony A from 0600-1900 h BST, since delivery rates peaked at either end of the day (see Figure 9.13). Variation in numbers of chicks in the colony has been controlled for by restricting the analysis to the period during which chick numbers levelled off, ie. 20 July - 4 August in 1983, and 17-31 July in 1984. If deliveries were temporally clumped, Morisita's Index of Dispersion (I_δ: Southwood 1966) of the number of delivery attempts per 15-minute period should be significantly greater than 1, and one would expect clumping to be greater with increased incidence of kleptoparasitic attacks. In fact, no such trends were apparent in either year, and the temporal dispersion of deliveries did not normally deviate significantly from random (Table 10.VIII).

10.5.4 Factors affecting the incidence of kleptoparasitism

There was usually considerable fluctuation over one day in the hourly rate of attacks by Arctic Skuas. The pattern shown for 17 July 1984 (Figure 10.5) was typical, with peaks of deliveries at either end of the day, broadly matched by peaks of skua piracy. However, periodic 'bursts' of intensive piracy occurred at various times of day (1300-1400 h BST in this example) and their timing was often unpredictable. However, omitting the early afternoon peak, there was a significant positive correlation for

Table 10.VII The incidence and success of piracy of Black Guillemots using different approach strategies, in 1984.

			Frequency (%)		
	Colony	N	LOW	HIGH	WALK
Total deliveries	A	1408	97.4	1.8	0.7
	CGQ	138	55.1	42.0	2.9 [a]
Deliveries attacked	A	252	17.7	34.6	0
	CGQ	25	21.1 [b]	15.5 [c]	0
Attacks where fish released	A	80	32.5	11.1	-
	CGQ	13	62.5 [d]	33.3	-

Notes:
[a] Low:rest, comparison between colonies, $X^2 = 379$, 1 df, $P<0.001$
[b] Comparison between colonies, $X^2 = 0.54$, 1 df, ns.
[c] " " " , $X^2 = 3.89$, 1 df, $P<0.05$
[d] " " " , $X^2 = 5.98$, 1 df, $P<0.05$

Figure 10.4 The relationship between offshore waiting time (t_w) and incidence of kleptoparasitism at colony A. (Mean ± s.e. given for 9 days, based on a sample of 178 birds).

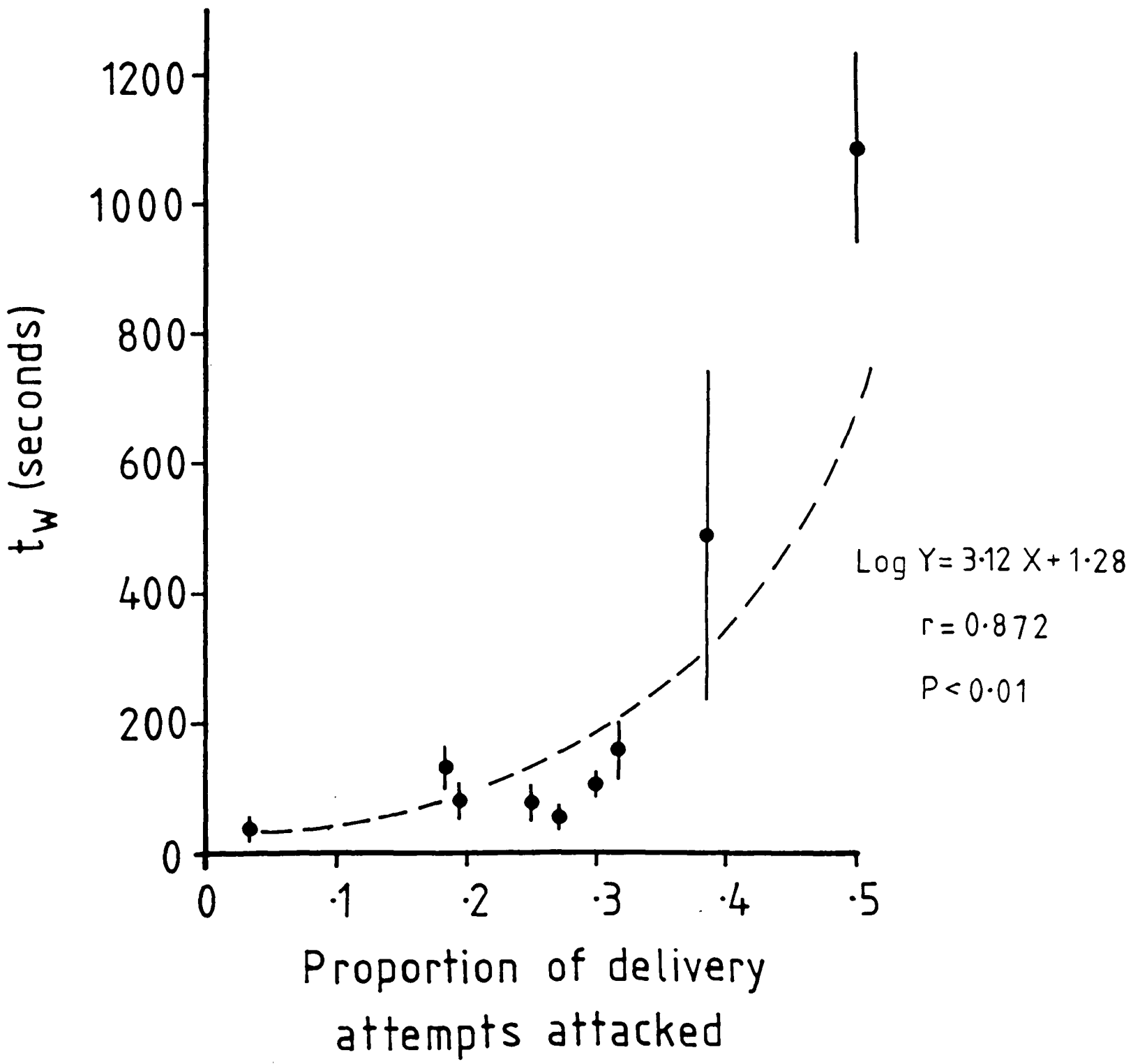


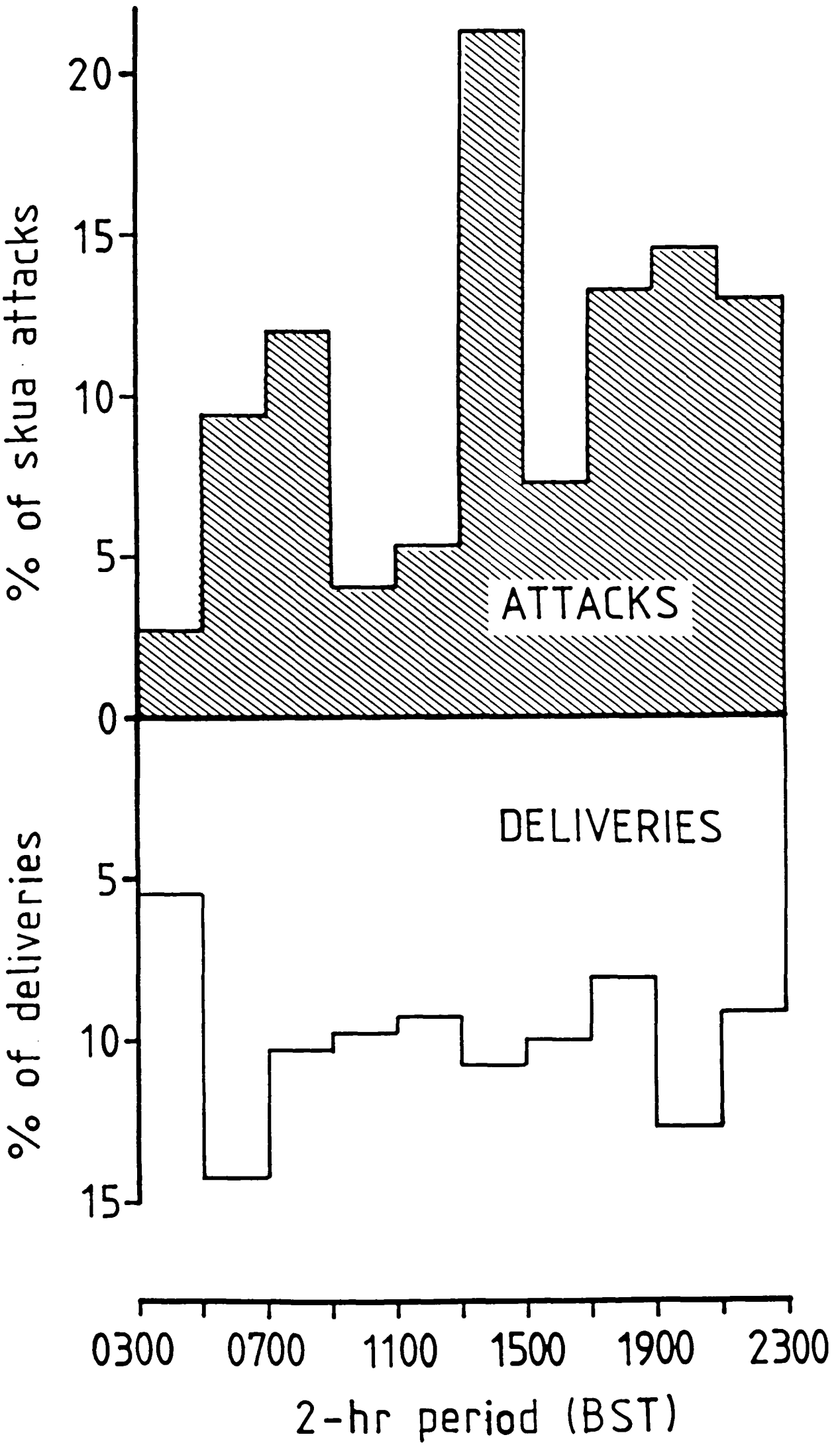
Table 10.VIII The variation in number of delivery attempts per 15-min. period in relation to incidence of kleptoparasitism at colony A.

Year	No. attacks /15 mins.	No. periods	Delivery attempts /15 mins. Mean	sd	I_δ [a]	Signif.[b]	Dispersion
1983	0	16	6.31	1.78	0.925	ns	Random
	1	20	6.95	4.01	1.180	*	Clumped
	2	13	8.85	2.23	0.954	ns	Random
	3-8	32	8.56	2.74	0.986	ns	Random
1984	0	31	5.97	7.30	1.036	ns	Random
	1	24	6.71	4.56	0.948	ns	Random
	2	15	6.93	3.07	0.915	*	Regular
	3-8	24	7.79	5.91	0.965	ns	Random

Notes: [a] I_δ = Morisita's Index of Dispersion

[b] Significance level, * = $P<0.05$

Figure 10.5 The diurnal variation in rates of delivery, and Arctic Skua kleptoparasitism on Black Guillemots at colony A on 17 July 1984.



17 July between hourly delivery rate and skua attack rate ($r = 0.44$, 19 df, $P<0.05$).

The daily average number of delivery attempts attacked per hour was significantly correlated with average delivery rate at colony A, in both 1983 ($r = 0.49$, 27 df, $P<0.01$) and 1984 ($r = 0.63$, 25 df, $P<0.001$). A summary of average hourly rates of delivery attempts and piracy rate and success is presented for 1984 only (Figure 10.6), although the pattern was very similar in 1983. In both years observations were usually made between 0600-1900 h BST, reducing variability in delivery rates due to diurnal effects. No significant correlation was found between the proportion of deliveries attacked and attempted delivery rates in 1984 or 1983, but Black Guillemots were only rarely pirated during the early nestling period. Therefore the nestling period was divided into 3 stages for further analysis, corresponding to rising, stable, and falling average delivery rates (Figure 10.6). There was a significant trend in both years for an increase in the proportion of deliveries attacked as the season progressed, but no significant difference in the % success of attacks between periods (Table 10.IX). Similar results were obtained when only attacks by Arctic Skuas were analysed.

Although there was no significant correlation in either year between daily mean wind speed (at Lerwick, 15 km north of Mousa) and either the incidence or success of piracy by Arctic Skuas at colony A, it was clear that during very calm spells Black Guillemots were less effective in aerial evasion of skua attacks. Calm conditions were often accompanied by sea fog and reduced visibility, which facilitated ambushing of birds appearing out of the mist at the shore rocks.

Both Arctic Skuas and other pirate species at colony A attacked a higher proportion of Black Guillemots delivering sandeels than other fish types, but the difference was significant only for skuas ($X^2 = 17.3$, 1 df, $P<0.001$) (Table 10.X). For the 3 main fish types, and all items combined, comparisons of the frequency of attacks made by Arctic Skuas on birds carrying fish of different lengths, with the frequency of these size classes in overall delivery attempts, revealed that Arctic Skuas attacked significantly larger fish on average (for sandeels $X^2 = 79.9$, 4 df, $P<0.001$; blennies $X^2 = 17.5$, 4 df, $P<0.01$; gadoids $X^2 = 12.9$, 4 df, $P<0.05$; all prey $X^2 = 104.2$, 6 df, $P<0.001$). No significant differences were found for attacks made by other species.

A comparison between the 3 study colonies (data pooled for 1983-84) indicated that both the proportion of deliveries attacked and the % success

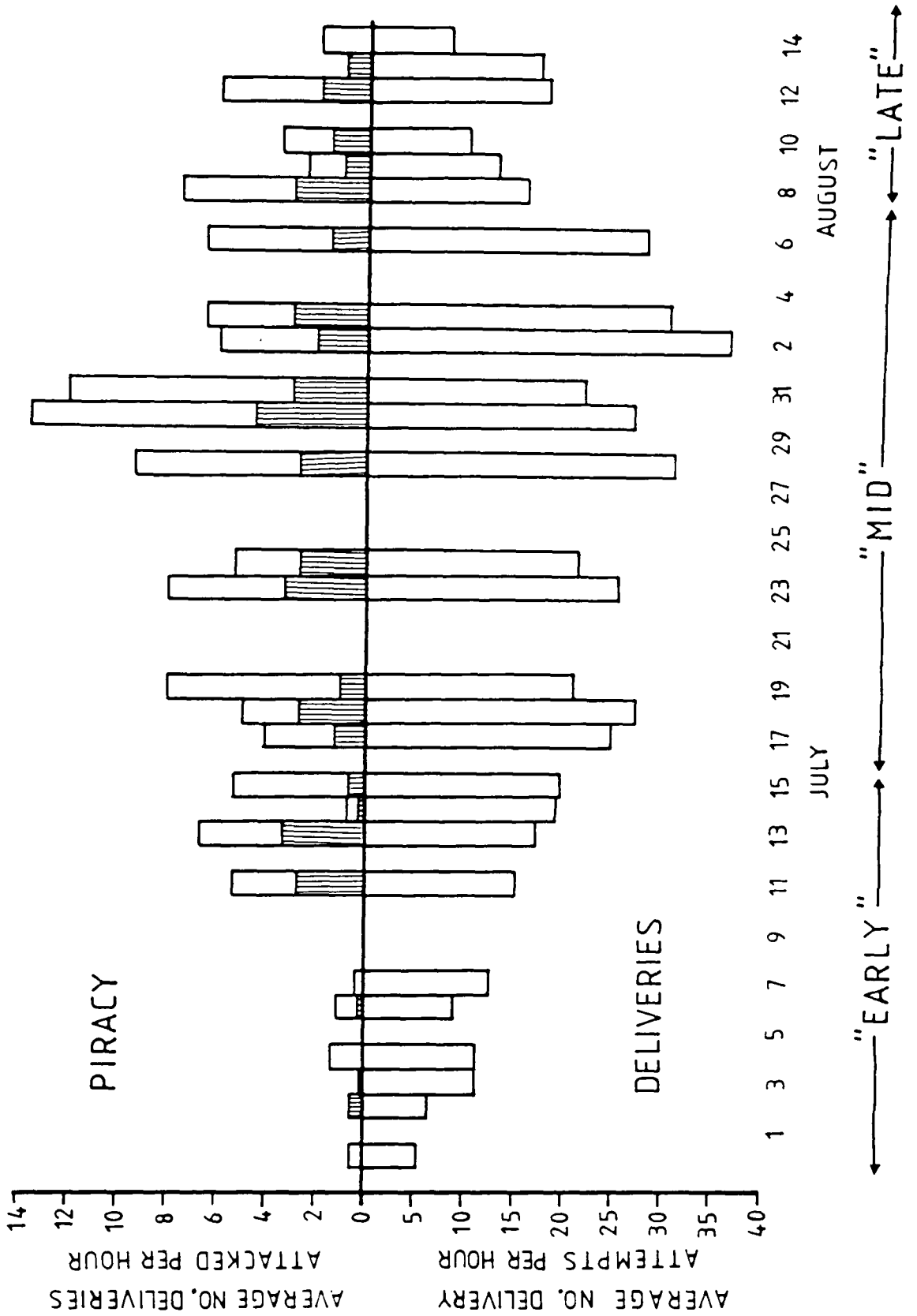


Figure 10.6 Variation in average hourly rates of delivery attempts and kleptoparasitism at colony A in 1984. (shaded sections represent fish released by Black Guillemots).

Table 10.IX The incidence and success of kleptoparasitism at colony A for different stages of the nestling period in 1983 and 1984.

	No. delivery attempts		Deliveries attacked				Fish released (%)	
			1983		1984			
Period	1983	1984	No.	%	No.	%	1983	1984
EARLY	314	547	27	8.6	51	9.3	40.7	27.5
MID	896	1082	247	27.6	231	21.3	38.5	34.2
LATE	359	114	113	31.5	43	37.7	49.6	39.5
		X^2	56.6		63.8		3.9	1.6
		df	2		2		2	2
		P	<0.001		<0.001		ns	ns

Table 10.X Comparison of the frequency of fish types brought in by Black Guillemots with those attacked by kleptoparasites, at colony A in 1983-84.

	Number and frequency (%) of fish type				
	SANDEELS	BLENNIES	GADOIDS	OTHERS	Total
Total fish brought in	2097 (51.9)	936 (23.2)	611 (15.1)	399 (9.9)	4043
Attacked by Arctic Skuas	438 (58.6)	160 (21.4)	90 (12.0)	60 (8.0)	748[a]
Attacked by other species	91 (58.7)	31 (20.0)	17 (11.0)	16 (10.3)	155[b]

Notes: [a] $X^2 = 17.3$, 1 df, $P<0.001$

[b] $X^2 = 2.79$, 1 df, $P>0.05$

of piracy increased with distance of Black Guillemot nests from the sea, and also with decreasing height of nests above sea level (Table 10.XI). However, the number and proximity of kleptoparasite breeding territories also increased with incidence and success rate of attacks.

The Arctic Skua pair at colony A hatched 2 chicks in both years, but in late June 1984 one died when c.2 weeks old. Therefore, during the Black Guillemot nestling period, the skuas here had 2 chicks to feed in 1983, but only 1 in 1984. In a random sample of 65 skua attacks on species other than Black Guillemots in July 1983, Arctic Terns (92%) and Kittiwakes (8%) were the only hosts. The colony A skuas had significantly greater success in attacks on terns, than skuas elsewhere on Mousa (79% vs. 55%, n=40, 20; X^2 =4.1, 1 df, P<0.05). All terns attacked were carrying sandeels. Encounter times (t_e) for attacks on Arctic Terns did not differ significantly between the colony A area and the rest of the island, nor did the median t_e for successful and unsuccessful pursuits (7.0:7.5 s respectively, Mann-Whitney U test, P>0.05). Using the relationships given in Chapter 9, the mean energy content of a fish pirated from an Arctic Tern in July 1983 was 5.135 kJ. The average lengths of sandeels brought in by Arctic Terns were not significantly different in July 1984 (Ewins 1985c), and the mean energy content of fish carried then was 5.365 kJ. The mean energy content of a sandeel pirated from a Black Guillemot in 1983 was 41.1 kJ, and 38.1 kJ in 1984.

10.6 Discussion

Outside the breeding season Black Guillemots only bring to the surface those prey items that require further manipulation prior to ingestion. Although the surface handling time varies considerably (pers. obs.) it is always much less than the total time fish are carried in the bill when provisioning chicks during the breeding season - kleptoparasites then have longer in which to detect and pursue the host. Thus it is not surprising that only 7% of birds with prey were attacked outside the breeding season, compared with 10-33% at the breeding colonies. Since most of the feeding observations were made in harbours (supporting large numbers of gulls in winter), it is likely that the observed incidence of kleptoparasitism was higher than in other parts of Shetland outside the breeding season. Although probably insignificant to Black Guillemots in energetic terms outside the breeding season, kleptoparasitism by gulls may be locally

Table 10.XI Overall incidence and success of kleptoparasitism in relation to distance of nests from the sea.

		Colony		
		E	A	CGQ
Total no. of delivery attempts		159	3312	273
No. attacked (%)		16 (10%)	712 (22%)	90 (33%)
No. releasing fish (% of those attacked)		3 (19%)	272 (38%)	43 (48%)
Approx. no. nests with young		18	28	19
Distance from sea (m) [a]	Mean:	10.32	41.53	228.97
	se:	2.17	1.75	14.59
	range:	1-25	25-65	168-401
Height above sea level (m) [b]	Mean:	12.21	3.85	1.17
	se:	0.82	0.06	0.10
	range:	7-20	3-4	0.45-2

Notes: [a] distance from high water mark at open sea (ie. excluding the shores of tidal pools)

[b] height above high water mark

important in maintaining a selective pressure against bringing large or awkward prey items, with long handling times, to the surface.

The available data from elsewhere in the range suggest that the incidence and success rates of kleptoparasitism observed on Mousa during the breeding season were not exceptional. In North America, Friesen & Cairns (in prep.) found that 7-21% of attacks by Arctic Skuas resulted in the Black Guillemot dropping fish, and Winn (1950) witnessed a Herring Gull robbing one pair "two out of every three times they tried to approach the nest"; whilst Penny & Newton (1983) found that fish were dropped in 4 of 19 chases (21%) by Arctic Skuas in northern Norway.

On Mousa, kleptoparasitism was most frequent at colonies in the south-eastern part of the island. Although the greater proportion of attacks made by Lesser Black-backed and Herring Gulls at colony CGQ, than at A, can largely be explained by the closer proximity of Black Guillemot nests to gull territories, piracy was not confined to the immediate vicinity of Larid nests. Common Gulls, for example, did not breed on Mousa, yet regularly practiced kleptoparasitism at Black Guillemot colonies there. Intra-specific 'attacks' were either made in flight, or by swimming towards a bird with fish on the water; none was successful. Thoresen & Booth (1958), Slater & Slater (1972a) and Petersen (1981) have also recorded intra-specific piracy by Cepphus species. However, on 8 occasions I saw adults arriving at the nest entrance with a fish, which was then either passed to the mate, or the mate snatched the fish and then made the delivery. It is possible that some recorded instances of intra-specific piracy actually involved mates.

Arctic Skuas, Herring and Lesser Black-backed Gulls were the most regular pirates of Black Guillemot deliveries, as was the case for most studies of Atlantic Puffins (Harris 1984). Although attacks by 2 skuas resulted in Black Guillemots losing fish more often than those by a single skua, the difference was not significant. For Arctic Skua - Puffin piracy in Iceland, Grant (1981) obtained a similar non-significant result, but Arnason & Grant (1978) found group attacks to be significantly more successful. Taylor (1979) found groups of skuas to be much more successful than singles in chasing terns in north-east Scotland. However, their results do not concern skuas on breeding territories, and the average return per individual pirate was obviously reduced with increasing pirate number. All attacks by 2 skuas on Mousa involved mates. Thus, although each parent obtained fish on only 18% of pursuits on average (compared to

28% in pursuits by single skuas), the net food input to the skua brood was greater when both parents participated in a chase.

When attendants accompanied skua chases, Black Guillemots were significantly more likely to lose their fish, but the initiating skua was significantly less likely to recover the fish - an attendant doing so on 83% of occasions when the fish was released. For a gull the highest returns are when following an Arctic Skua - Lesser Black-backed Gulls for example had 71% success when they took the role of attendants, but only 0-10% when pirates. That no more than 7-8% of pursuits were accompanied by attendants suggests that gulls are mostly unable to follow pirates (or that alternative food supplies are more profitable). Since skuas with attendants suffer significantly reduced chances of securing a fish, one would expect them to adopt strategies minimizing the likelihood of acquiring attendants. The superior acceleration of Arctic Skuas may largely account for these results, since in most instances, from a standing start, Herring or Lesser Black-backed Gulls would be too far behind the skua when the Black Guillemot released the fish to have a realistic chance of retrieving it before the skua.

At cliff nest sites delivering birds harassed by kleptoparasites were quickly able to descend to the sea and dive with the fish (the most effective escape response). Contrastingly, at boulder colonies inland (such as A and CGQ) birds were more prone to kleptoparasitism since they had less air space in which to manoeuvre and had further to fly to reach the sea if attacked. The greater than normal speed on impact with the water often resulted in fish being lost then. Accordingly the incidence and success of kleptoparasitism was highest at nests furthest from the sea, and on flat, low ground. Similarly, Andersson (1976) thought that the significantly lower success of Arctic Skua attacks on Puffins at Hermaness, Shetland (Puffin colonies on vegetated cliffs), compared with attacks at an Icelandic colony 1 km inland (Grant 1971) was due to the ability of Puffins to make a quick escape by descent to the sea at Hermaness.

It was shown earlier (Chapter 7) that a higher incidence of kleptoparasitism at colonies depressed the mean weight of chicks at fledging, the effect being most obvious when more than 10% of deliveries on average were lost to pirates (Figure 7.6). Further, at colony CGQ (the highest incidence of piracy) the difference in duration of the fledging period between a- and b-chicks was greater than at other colonies, and particularly heavy kleptoparasitism at two nests resulted in the b-chicks receiving little food - their growth rate improved once the a-chick had

fledged, but both fledged well below the normal weight, and 7-16 days beyond the normal b-chick fledging period. Therefore, kleptoparasitism of Black Guillemot deliveries on Mousa did significantly affect chick growth, at colonies where nest position rendered the delivering bird more vulnerable to piracy. Breeding success, however, was apparently unaffected by piracy of deliveries (Chapter 8), even at nests experiencing kleptoparasitic pressure higher than for the colony as a whole (eg. those nests closest to the centre of a gull or skua territory).

On Great Island, Newfoundland, Nettleship (1972) showed that Puffins nesting on level ground lost significantly more fish loads to gull pirates than did those on slope habitats (13.5% vs. 4.4%). This was reflected in significantly depressed chick growth. He attributed this to greater vulnerability to gull attack on level habitats, further from the coast, since Puffins took longer to get airborne, and had reduced control during landings there. To my knowledge this is the only other demonstration amongst auks of kleptoparasitism affecting chick growth.

The most crucial factors determining the outcome of an attack are probably the distance of the Black Guillemot from the sea at initiation of the attack, and the separation of pirate and host when the pirate is first detected. Although Black Guillemots carry only a single fish, losing "all or nothing", whereas Puffins usually carry 5-20 fish (Harris 1984) and may only release part of the load, the effect of a successful attack may be greater on Puffins since their feeding grounds are normally further from the colony, and chicks receive only 4-10 feeds per day (Harris 1984).

Black Guillemots delivering large sandeels are more likely to be attacked by skuas than those carrying small fish: not only are the returns greater for the skua, but a long shiny fish dangling from the bill is usually very obvious, and flight is often noticeably laboured, facilitating early detection by pirates. At colonies experiencing heavy kleptoparasitism this could be an important factor affecting the optimum fish size for an adult feeding chicks.

Adults modified approach paths and strategies in response to kleptoparasitic pressure, with varying success. Although overall skuas attacked more often at either end of the day (mirroring peaks of deliveries), intensive bouts of attacks occurred at various times of day. No reason was apparent for their timing, other than the fluctuating demands made by the skua brood: persistent food-begging by skua chicks was often followed by a series of attacks, regardless of delivery rate at the time. Once more than about 1 in 3 deliveries were attacked, Black Guillemots

spent considerably longer periods waiting offshore. This suggests some form of 'critical level' of piracy, above which it pays to delay a delivery.

During the focal animal sampling periods it became apparent that birds waiting offshore at colony A were monitoring skua activity in the patrol zone. Whenever the skua's attention was diverted (such as when chasing other skuas, gulls or sheep out of the territory), Black Guillemots took the opportunity to 'sneak in' a delivery, undetected. There was no suggestion that delivering birds took off en masse at these, or any other times, or that they were more likely to deliver whilst another Black Guillemot was being chased. The usual response of a bird flying in with fish, upon seeing a skua chasing another Black Guillemot, was to veer away and return to the offshore gathering area. In the absence of any distractions of this kind, deliveries were apparently made at random, and the overall analysis of temporal dispersion of deliveries provided little evidence for active "clumping" of deliveries as a means of swamping the kleptoparasites. Although Ashcroft (1976) recorded temporal clumping of Puffin deliveries, Harris (1984) more cautiously considered that it should be advantageous for Puffins to come ashore with others, to reduce the chances of losing fish to kleptoparasites, but concluded that swamping "is difficult to establish". Similarly, Slater & Slater (1972b) and Cairns (1978) failed to find any evidence for temporal clumping of Black Guillemot deliveries.

In accounting for the significantly lower proportion of delivery attempts losing fish as a result of kleptoparasitic attack in 1984, the breeding and foraging strategies of Arctic Skuas (the main pirate species) must be considered. I focus here on the pair at colony A. Firstly, the effective brood size was 2 in 1983, but only 1 in 1984, and so the energy demands on the adults were considerably reduced. Breeding success of the 1000+ pairs of Arctic Terns (the main alternative host species here) on Mousa was much higher in 1983 (c.1 young fledged per pair) than in 1984 (less than 0.1 young fledged per pair) (Ewins 1985c). Some skua broods in other parts of the island were also reduced to 1 chick in 1984 - presumably food shortage led to starvation of the younger sib - and this difference in food requirement of skua pairs is thought to be the main factor accounting for the lower incidence of piracy of Black Guillemots in 1984. Although the heaviest mortality of tern chicks in 1984 occurred in late June, some fish were still available to skuas until mid July, since failed terns and young non-breeding birds, pairing for the next year, regularly carried

display fish for protracted periods. In 1983 the majority of tern chicks had fledged by 20 July, and moved to shores close to the colonies. Thus, in 1984 the availability of fish from terns decreased from early July onwards, whereas in 1983 fish were brought in until late July in good numbers. By mid July the average delivery rate of Black Guillemots at colony A was increasing rapidly, and the skuas switched from terns to Black Guillemots at this time in both years (Figure 10.6).

The average duration of chases of Arctic Terns was significantly longer than for those on Black Guillemots, both for successful (medians 7.0:4.0 s) and unsuccessful chases (medians 7.5:3.0 s) (Mann-Whitney U test, $P<0.001$ in both cases). Furness (1980) estimated that an average Arctic Skua chasing an Arctic Tern (mean chase duration 10 s) required 0.04 kJ, whereas chases of Puffins (mean duration 3 s) - the same type as for Black Guillemots - required only 0.01 kJ. Although the success rate of attacks by the colony A skua pair on Arctic Terns was double that of attacks on Black Guillemots (79% vs. 35%), the energetic cost of pursuit was 4 times greater and the net energy return only 1/8 that of successful chases of Black Guillemots. Piracy of Black Guillemots should therefore be attempted by skuas, at least at this site, whenever possible. The change to piracy of Black Guillemots occurred in both years when availability of fish from terns was decreasing, but the prime determinant of this switch was probably the increased delivery rate of the Black Guillemots (rate of piracy was significantly correlated with delivery rate), since terns were still bringing in fish in good numbers in late July 1983, when most skua attacks were directed at Black Guillemots. Similar conclusions were drawn by Furness (1980) for Arctic Skuas on Foula, Shetland - maximizing their net rate of energy intake by switching to Puffins (from Arctic Terns) as soon as they began to bring fish loads to the island.

In conclusion, although some Black Guillemot chicks experienced reduced growth rates, and adult deliveries were often delayed by pirate activity, I suspect that on the whole the species does not suffer too badly as a result of kleptoparasitism on Mousa. At larger inland boulder colonies the benefits to Arctic Skua pairs pirating Black Guillemots must be considerable however, particularly in years when Arctic Terns experience low breeding success.

CHAPTER 11. GENERAL DISCUSSION

Although Black Guillemots were dispersed fairly evenly in coastal waters in Shetland, there were sizeable concentrations in certain areas and at certain times of year (Ewins 1985a; Ewins & Kirk 1985). The effect of oil pollution on the population would be most severe at these "hot spots". The autumn moult, when adults are concentrated in large moult flocks and are flightless for 4-5 weeks, is the most vulnerable time. Despite rich feeding grounds in Yell Sound the breeding density there in 1983-84 was the lowest in Shetland, largely due to the slow rate of recolonisation following losses there 6 years earlier during the Esso Bernicia oil spill in Sullom Voe. Also, the age structure was still biased towards young birds, since adult Black Guillemots in Shetland seldom move more than 10 km from their breeding colony, so it would have been immatures which subsequently moved into the area.

There was no evidence for any sub-lethal effects of pollution on Shetland Black Guillemots. The concentrations of organochlorine and heavy metal contaminants in eggs were very low and these chemicals were unlikely to have had any damaging effects, and the breeding productivity figures were among the highest recorded for the species.

Black Guillemots require a suitable breeding site and sufficient food supplies nearby with which to raise young. Outside the breeding season food is presumably of the highest importance, since the constraint of nesting duties is removed (although birds first visit the breeding sites 2-3 months prior to egg laying). The use by Black Guillemots of Shetland's coastal waters accorded with these main requirements. In mid winter birds spent most of the 6-7 hours of daylight foraging. At first light birds flew up to 7 km to foraging areas, then returned at dusk to roost in groups on the sea in sheltered locations. As day length increased so did the birds' attachment to the breeding colonies. During the breeding period adults rarely moved further than 3 km from the colonies, but once the young have departed most went to traditional moulting areas (probably mostly within 10 km of the breeding areas), where they underwent the complete post-nuptial moult. By early October most adults have dispersed to nearby wintering areas.

Black Guillemots normally dive in water shallower than 40-50 m. At greater depths, the effective search time on the sea bed is very short due to the time taken to travel to and from the surface. The availability of

such suitable shallow foraging areas is a key determinant of the observed distributions. Chicks were fed only fish, mostly caught on, or close to, the sea bed. Adults supplemented their diet with a variety of invertebrates, especially in winter when fish were scarcer. Overall, the species is a generalist, taking a wide range of the diverse benthic fauna, although particularly rich localised food sources, such as sandeels, are exploited opportunistically.

In the breeding season, regional numbers correlated well with the area of shallow water nearby, but in winter there was a marked tendency for birds to move to sheltered, inshore waters. Heavy winter seas probably cause many benthic organisms to seek deeper water and/or more sheltered environments, thereby reducing their availability to diving birds along more exposed coasts. The energetic costs of maintenance and risk of death will presumably both be higher for Black Guillemots in very rough seas. In addition, most suitable nest sites in Shetland are concentrated along more exposed coasts, rather than along the lower, sheltered coasts. The inshore feeding habits of the birds resulted in the breeding distribution being fairly regular overall, reflecting local availability of nesting areas (ie. relatively low numbers in inshore regions far from suitable breeding areas), whereas the winter distribution was more irregular, with marked concentrations in inshore areas. Overall, winter densities of birds on the foraging areas were higher than recorded elsewhere, emphasizing Shetland's suitability for Black Guillemots.

Recently fledged young dispersed fairly evenly around the coasts. However, the dispersion of adults during the post-breeding complete moult was rather irregular. Moulting adults require sheltered conditions and adequate food supplies during the period of flightlessness. Although strong tidal races are good feeding areas for Black Guillemots and other seabirds at most times of year, they are less suitable during the flightless period since birds would be swept down-current and spend much energy swimming back to the original position. Thus, the autumn moult flocks are usually found amongst groups of offshore islands or at the entrances to bays or sheltered waters between larger islands - locations which afford protection from heavy seas, from any direction. In Shetland at least, predation is probably not the main reason for these aggregations. I believe they are simply concentrations of adults in areas which traditionally have provided suitable conditions for moulting.

Availability of suitable nest sites and proximity to good feeding grounds are the most important factors accounting for the observed breeding

distribution, colony sizes and numbers overall. Shetland is very suitable for Black Guillemots as breeding sites occur close to shallow feeding grounds along all but a few stretches of coast. The lack of ringing recoveries away from Shetland of birds ringed in the main island group further indicates that conditions in Shetland were particularly suited to Black Guillemots. However, birds from Fair Isle and Foula, both small, very exposed islands, often move considerable distances outside the breeding season. Elsewhere Black Guillemots move south in winter, in response to ice, temperature and darkness in the breeding areas, all of which reduce food availability.

On islands with mammalian predators Black Guillemots normally bred in crevices on higher cliffs only, whereas on predator-free offshore islands accessible sites in boulder beaches and walls were also used. Otters were the main predator but their predation appeared not to be significant since Otters and Black Guillemots coexisted on most offshore islands.

The more favourable weather and sea conditions between April and August in 1984, compared with 1983, had a strong influence on various aspects of breeding on Mousa. Although prey availability could usually not be assessed other than by inference from the birds themselves, feeding conditions appeared to be far better in 1984. Adults were heavier, eggs were larger and heavier and were laid earlier, and a higher proportion of young, inexperienced birds were able to attempt breeding in 1984 than in 1983. Chicks fledged heavier in 1984, partly due to the appearance of large numbers of gadoid fish inshore during the later stages of the chick period. The high weight and energy content of a gadoid meant that chicks were provided with more energy per feed at a time when their demands on parents were greatest.

Adults of long-lived species such as Black Guillemots are faced with a trade-off when breeding, between costs to their own fitness and that of their offspring. The factors limiting the rate of energy uptake by the brood change with chick age, initially from the digestive capacity of small chicks, to the provisioning potential of the parents when the chicks are large (Fagerstrom et al. 1983). It is not just that chicks require more food in proportion to their body size - large chicks require up to three times more food per gram increase in body weight than do smaller chicks (Koelink 1972). The 'ceiling' to parental performance will vary between years and between areas, depending on food availability, environmental conditions and adult condition. Since adults were in better condition, and feeding conditions appeared to be better in 1984, this ceiling level was

probably higher. Parents were thus able to devote more time and energy to raising young than in 1983.

Breeding success and output, however, were actually lower overall in 1984. This was due to the very poor success of single-egg clutches. The greater availability of food in the 1984 pre-breeding period enabled more inexperienced females to reach the condition threshold for breeding (Drent & Daan 1980), and they tended to lay single eggs, slightly later than older birds. Black Guillemots probably take a few years to develop their specialised hunting skills sufficiently to enable them to withstand the extra burdens imposed by breeding. Having attained the condition threshold in 1984, inexperienced pairs were forced to occupy sub-optimal nest sites, since the prime sites were held by older, established breeders. These poorer-quality sites were more open and accessible to nest predators. In many areas the availability of suitable nest sites appears to limit breeding numbers.

Although breeding success was not affected by kleptoparasitism of adult deliveries, chicks in colonies at which more than 10% of deliveries were lost as a result of piracy fledged lighter. This may have been due in part to the extra time adults spent waiting offshore with fish, as well as any reduction in actual provisioning rate due to fish loss. At all times of year kleptoparasitism is clearly an important constraint on prey size selection by Black Guillemots - large, awkward and readily visible items brought to the surface are more likely to be detected and attacked by pirates. However, there was no significant clumping of delivery attempts at the breeding colonies, as an anti-pirate strategy. Overall, Black Guillemots suffered little from piracy, although specialist pairs of Arctic Skua clearly benefitted considerably from this food source, particularly when other sources of fish were not available.

Whilst breeding success and adult survival could be affected by a wide variety of factors (eg. adverse weather, human disturbance, disease) I consider that oil pollution and island colonisation by predators such as mink are the two most serious threats to the well-being of Black Guillemots in Shetland. Changes in oceanographic factors, and the confounding effects of man's over-fishing of North Sea fish stocks undoubtedly have serious implications for Shetland seabirds, but the generalist inshore feeding niche of Black Guillemots renders them the least sensitive of our diving seabirds to any such effects. Shetland's Black Guillemot population is healthy, but the Esso Bernicia incident showed that the species is vulnerable. Regular and reliable monitoring is essential if we wish to

detect and quantify changes in the species' status or ecology, seek explanations for such changes, and take appropriate action where necessary.

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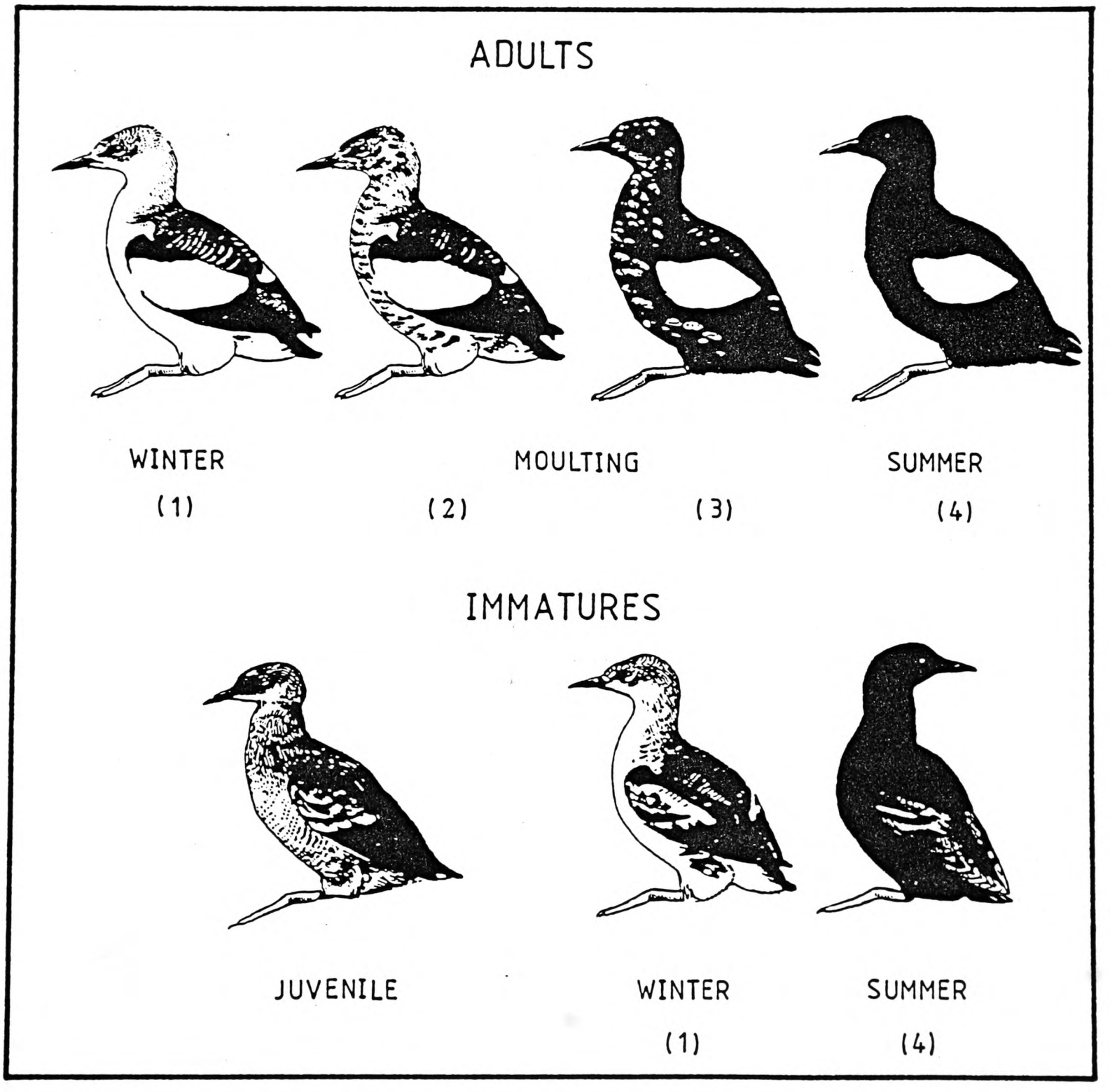
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Appendix I. Plumage categories for adult and immature Black Guillemots (adapted from drawings by Jon Fjeldsa (in Asbirk 1979b, 1980)).
Moulting plumage categories for immatures are as for adults. Most juveniles have attained winter plumage by November. 1 = winter plumage; 2 = white with some black; 3 = black with some white; 4 = summer plumage.



Appendix II. A published note concerning trapping methods and caution necessary when ringing Black Guillemots. Ringers' Bulletin 6: 46 (Ewins 1983b).

ON RINGING TYSTIES

Intensive studies on Tysties (Black Guillemots) in Shetland during the past two years have highlighted some important points regarding ringing of nestlings and adults at breeding sites. Some suggestions and cautionary notes are presented here.

General points

1. Ringing at nests which require rope-work is not recommended. Apart from danger to the ringer, chicks have a stronger tendency to take 'premature leaps' at such sites.
2. Where possible, ringing activities should be concentrated in the early to mid afternoon, when adult attendance at breeding areas is lowest and disturbance is thus minimized.
3. Visits should be restricted to 30 minutes, especially on cooler days. Due to the large spread of laying dates some birds may still be incubating when others have ringable chicks.
4. Rearrangement of nest-cavity stones is to be avoided, particularly in the region of the entrance. Adults are prone to desert after even slight modifications, especially during incubation.

Chicks

These can first be ringed at 1 week old. A torch and small hand-mirror are often invaluable in locating chicks which have run into dark corners of the nest-chamber following disturbance. A standard seabird wire 'Snitcher'/hook around the tarsus is usually the best means of catching them.

Adults

From a total of 50 breeding adults caught, only two were thought to have deserted as a result of trapping. Adherence to the following guide-lines should minimize disturbance due to ringing activities. In general though, trapping of incubating adults is not recommended unless vital to a specific study.

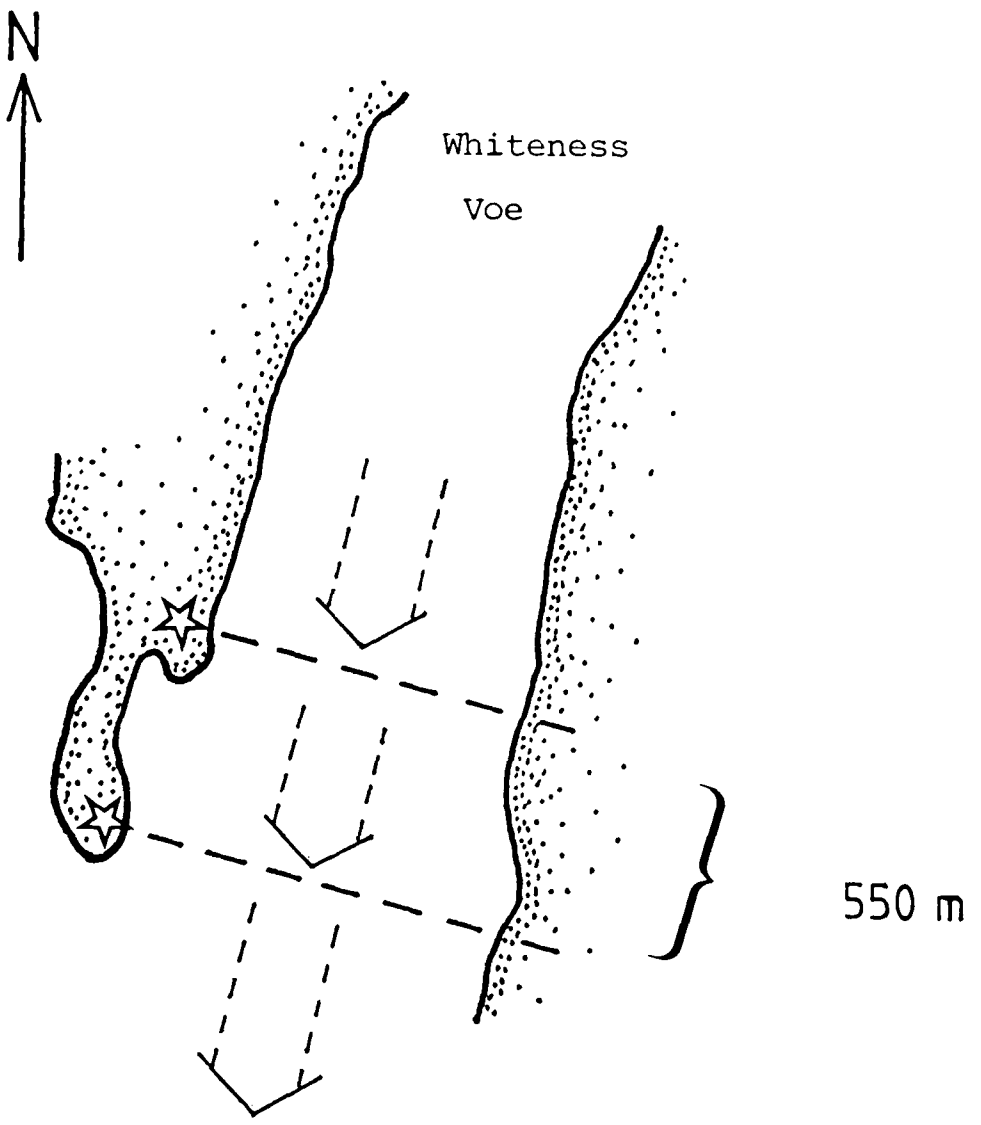
1. No attempt should be made to remove adults from the more open nests, lacking rear chambers and dark recesses.
2. If possible birds should not be disturbed in the first 10 days of incubation, at hatching, or during the first few days after hatching (when chicks are vulnerable to chilling and are brooded).
3. In Shetland, late June to early July appears to be the safest time to catch incubating adults. Disturbance can be kept to a minimum by quickly placing the bird into a large bird-bag; it can be ringed, wing-measured and weighed with the bird's head still well within the bag (taking other biometrics just increases the handling-time unnecessarily). Then replace the bird in the nest-chamber and move quickly away from the area.
4. A more preferable trapping technique is interception of adults flying in with fish. Either standing mist-nets or flick-netting can be very effective in suitable sites, birds tending to come in sooner if the operators are hidden to view from the sea. A nice bonus from this method is a fish-sample in the bottom shelf of the net!

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APPENDIX III. Average monthly sea-surface temperatures (°C) for January-August, 1980-85. Temperatures were recorded 4-6 times monthly at Fair Isle, by D. Wheeler.

Month	1980	1981	1982	1983	1984	1985
Jan	6.9	6.2	6.1	6.7	6.5	7.0
Feb	6.1	5.7	6.4	6.1	-	6.7
Mar	6.4	6.7	6.6	6.8	6.7	6.7
Apr	7.5	7.5	7.8	7.5	6.9	7.4
May	9.0	8.5	8.7	8.8	8.8	8.6
Jun	12.2	9.8	10.2	10.2	10.3	10.4
Jul	11.4	11.3	11.3	12.3	11.2	11.0
Aug	11.4	11.9	12.9	12.2	12.7	11.7

APPENDIX IV. The determination of mean speed of direct flight



Flight direction

A total of 31 birds flying out of the voe towards roosting areas in the late afternoon, were timed over a fixed distance of 550 m on 20 March and 30 November 1983. One observer gave a flag signal when a flying bird crossed the 'starting line'. On both dates winds were force 3-4 southerly, and only birds covering the distance by direct flight were considered.

Mean speed of direct flight = 58.0 km h^{-1}

sd = 7.7

range = 46.6 - 74.2 km h^{-1}

APPENDIX V. Average monthly catches of fish species in benthic funnel traps set in water up to 6 m deep, around Mousa in summer 1984 In July and August 7 traps were set, but in June only 5.

Species	Average no. fish /trap/month June	July	August	Total	(%)	
Gadus morrhua	-	0.3	0.4	0.7	1.9	14%
Trisopterus esmarkii	0.4	0.6	0.1	1.1	3.0	Gadoids
Pollachius virens	0.4	1.7	1.3	3.4	9.3	
Gaidrosparus vulgaris	1.0	2.6	2.7	6.3	17.2	36%
Ciliata mustela	1.2	2.3	3.4	6.9	18.9	Rocklings
Gasterosteus aculeatus	-	0.1	-	0.1	0.3	
Spinachia spinachia	0.6	0.6	-	1.2	3.3	
Liparis montagui	-	0.1	-	0.1	0.3	
Cottus sp.	2.6	3.7	2.7	9.0	24.6	
Chirolophis ascanii	0.4	0.7	0.3	1.4	3.8	32%
Zoarces viviparus	2.0	1.0	5.3	8.3	22.7	Blennies
Pholis gunnellus	1.4	0.6	0.1	2.1	5.7	
TOTAL	6.0	14.3	16.3			

Appendix VI. A paper concerning post-mortem shrinkage of Black Guillemot wings (Ewins 1985e).

Ringing & Migration 6: 115-117, October 1985

Variation of Black Guillemot wing lengths post-mortem and between measurers

Peter J. Ewins

Ewins, P. J. 1985. Variation of Black Guillemot wing lengths post-mortem and between measurers. *Ring. & Migr.* 6: 115-117.

This note details post-mortem shrinkage in 23 Black Guillemot wings. Most shrinkage occurred within 2 months and there was no further significant change in wing length after 12 months, when wings were an average of 1.5% shorter than their original lengths. No significant differences in variance or mean wing lengths were found between measurers using the maximum flattened chord technique.

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INTRODUCTION

In order to make meaningful comparisons between wing length measurements from live birds, freshly dead specimens and museum skins it is essential to know (i) the extent of post-mortem wing shrinkage for the species, (ii) the measuring technique used, and (iii) the order of variation between measurers. This note presents information concerning these aspects for wings of Black Guillemots *Cepphus grylle*.

METHODS

During 1982-83, 23 wings were collected from freshly dead adult and immature Black Guillemots in Shetland. All wing lengths were measured using the maximum flattened chord technique described by Svensson (1984), accurate to 1 mm, using a 300 mm stoppered rule. After the fresh measurement had been made the muscle tissue was removed, the exposed skin and bones treated with alum preservative, and the wings then left to dry at room temperature in the closed position. Each was measured again 2, 12 and 20 months later. Variation between measurers was determined in March 1985 by asking nine people with previous experience of measuring bird wings (most were ringers) to measure the maximum flattened chord of a sample of 15 of the wings. In addition I measured these 15 wings on 7 independent occasions on one day to determine within measurer consistency. For a comparison of techniques I also measured the wings by the flattened chord method (Svensson 1984).

RESULTS

Although most of the shrinkage occurred within the first 2 months, significant decreases in wing length were still found from 2 to 12 months, but not thereafter (Table I). The decline in mean wing length of the sample after 20 months was 2.52mm (±S.E. 0.45) but there was considerable variation between wings — one decreased by 6mm whereas another apparently increased by 1mm (Fig. 1).

The mean wing lengths obtained by different measurers are presented in Table II. Although there was less variation between measurements by one person than between 10 different people, there was no evidence in either case for any significant heterogeneity of variance (Bartlett's test, $\chi^2 = 0.0628$, d.f. = 6; $\chi^2 = 1.4136$, d.f. = 9 respectively). Similarly an analysis of variance revealed no significant differences between the means, either within or between measurers ($F = 0.05$, d.f. = 6,98; $F = 0.09$, d.f. = 7,112 respectively). Nevertheless, the spread of measurements for any given wing was greater between measurers: the author was consistent to within ± 1mm, but the range was ±2mm for the other 9 measurers.

A randomly selected set of measurements made by the author were compared with those of the other measurers by ranking the lengths obtained for each wing and calculating Kendall's coefficient of concordance. There was a significant tendency for individuals to consistently measure 'long' or 'short' relative to the mean

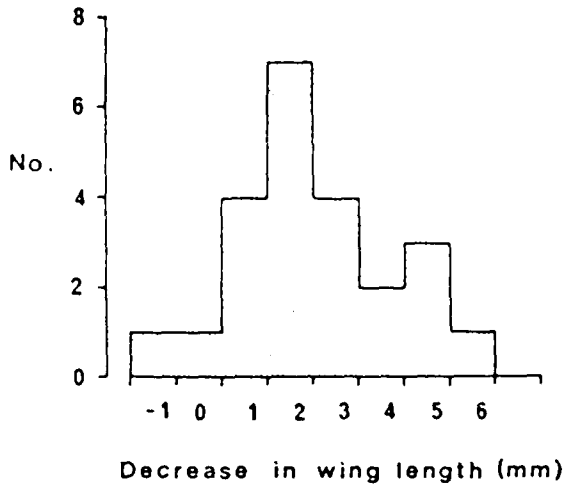


Figure 1. Frequency distribution of total change in length of 23 Black Guillemot wings at 20 months after death.

TABLE 2. Variation in mean wing lengths obtained by different measurers for 23 Black Guillemot wings.

Independent repeated measurements by author		*Measurements by different people*	
MEAN	S.E	MEAN	S.E
159.6	1.4	159.1	1.4
160.4	1.3	159.7	1.4
160.1	1.3	159.7	1.4
160.1	1.3	160.0	1.4
159.9	1.4	159.3	1.4
159.9	1.4	159.1	1.3
159.5	1.3	158.7	1.3
-	-	157.5	1.3
-	-	158.6	1.4

wing length ($\chi^2 = 66.69$, d.f. $= 9$, $p<0.001$), and deviations were largest for the last three measurers in Table 2, whose technique involved much less straightening of the primaries. The mean wing length determined by the flattened chord method was 154.73mm (±S.E.1.36), which was highly significantly smaller than the means of all sets of maximum chord measurements.

DISCUSSION

In a study of post-mortem shrinkage of Puffin *Fratercula arctica* wings Harris (1980) found that mean wing length had declined by 1.1% at 2 months after death but remained stable thereafter. Although Puffin and Black Guillemot wing lengths are almost identical, the present study revealed certain differences, with Black Guillemot wings continuing to shrink slightly up to 12 months post-mortem, with an overall decrease of 1.6% after 20 months. Data are scant for other seabirds; Barth (1967) recorded 1.2% shrinkage for wings of Lesser Black-backed Gulls *Larus fuscus* and Herring Gulls *Larus argentatus*. Post-mortem wing shrinkage in waders has been more thoroughly investigated, varying between 1.0-2.7% (Vepsalainen 1968; Greenwood 1979; Green 1980).

TABLE 1. Changes in mean wing lengths after death of 23 Black Guillemot wings.

Wing (mm)	*At death*	*+2 months*	*+12 months*	*+20 months*
Mean length	162.1	160.3	159.7	159.6
S.E.	1.0	1.1	1.1	1.1
Mean total decline	-	1.87	2.39	2.52
Total % shrinkage	-	1.2%	1.5%	1.6%
Paired-sample t-test 't'	-	5.405	3.755	1.368
P	-	<0.001	<0.01	NS

The importance of stating the measuring technique is stressed by the significantly lower mean wing length obtained with the flattened chord technique — 4.8mm (3%) less than the mean maximum chord. Asbirk (1979) did the same comparison on 57 Black Guillemot skins and found a mean difference of only 2.4mm. This difference between comparisons may be largely due to the greater variability associated with the flattened chord method — the main reason that this method is not in popular use today. The variance of wing length measurements were greater, but not significantly so, between measurers than for repeat measurements made by one person. Although the degree to which some individuals straightened the flattened wing varied, the means of the sample of 15 wings were not significantly different. However, since some people consistently measured short or long, significant differences between means obtained by different measurers might be found with a much larger sample of wings.

In conclusion, comparison of museum skins and wings of live or freshly dead Black Guillemots can be made with the application of a correction factor for shrinkage to the sample means of dry wings. If the maximum flattened chord method is used by people with some previous experience of measuring wings, variability due to differences between measurers' techniques is unlikely to lead to significant differences between mean wing lengths of samples.

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Appendix VII. A published note of a melanic Black Guillemot in Shetland.
Scottish Birds 13: 26 (Ewins 1984b).

Melanic Black Guillemot in Shetland

A Black Guillemot (Tystie) in summer plumage but lacking any white on the wings, regularly fed in Lerwick harbour, Shetland, during spring 1982. The plumage lacked the metallic sheen of typical summer adults, being a matt chocolate-brown colour. Upper and under wing coverts were dark brown, with the only paler area being the greyish-brown shade to the under-side of the remiges. The legs and gape were bright red, suggesting that this individual was an adult rather than a first-year bird.

Following encounters with other Tysties on the feeding areas, the melanic bird was usually driven-off or directly attacked. The white wing patches of Tysties probably have an important signalling function during communal displays, pairing, and in determination of social status (Asbirk 1979). It is likely that the absence of these patches rendered this bird a subordinate individual, and may well have precluded it from any breeding activities, as extensive surveys failed to locate it at any breeding site.

There appear to be only two previous records of melanic Tysties in Britain : an all-dark bird with dark-greyish head (moulting ?) seen near Fetlar, Shetland on 20th August 1975 (R. J. Tulloch, *pers. comm.*), and a sighting in the Sound of Harris. Outer Hebrides in summer 1894 (in Salomonsen 1944). Salomonsen (1941, 1944) gives details of 28 records of melanics known to him, the bulk, 17 individuals, coming from West Greenland.

The studies of Tysties in Shetland are commissioned and funded by the Shetland Oil Terminal Environmental Advisory Group.

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P. J. EWINS

Appendix VIII. A published note about Otter predation on Black Guillemots. British Birds 78: 663-664. (Ewins 1985f).

Otter predation on Black Guillemots During visits to many of Shetland's offshore islands in summer 1982, it became clear that otters *Lutra lutra* were an important predator on Black Guillemots *Cepphus grylle*. Many accounts of the otter's diet include birds, although in small numbers compared with the fish component (Erlinge 1967; Jenkins & Harper 1980); the species taken are usually those commonly associated with freshwater study areas.

In Shetland, otters are the only mammalian ground predator on most smaller islands, and frequent similar boulder areas to many breeding Black Guillemots (one occupied nest was within 15cm of an old otter corpse trapped under the boulders). Of 18 nest failures at which otter predation (see evidence below) or scavenging had occurred, seven resulted from direct predation of incubating adults, eight from predation on nestlings, while at three remains only of adults were found. In one study area, six adults and two nestlings had been taken from a total of eight different nests, representing a 10.5% failure rate of occupied nests. Although all the nestlings showed signs of having been eaten by otters, the possibility that they had initially been killed by large gulls *Larus* or Great Skuas *Stercorarius skua* cannot be ruled out. A complete Black Guillemot foot was found in one otter spraint, and remains of Puffins *Fratercula arctica* and Storm Petrels *Hydrobates pelagicus* were also recorded at several places frequented by otters.

Adult Black Guillemots taken on the nest had usually been decapitated, and in a series of adjacent nests in one colony the uneaten bodies were found still on the eggs. Nestling remains were normally found less than 2m from the nest entrance, decapitated, neatly skinned, and with the sternum crushed. In all cases, relatively few feathers had been ingested and many skins and carcases smelled strongly of otter, some having been urinated upon. Weldon (1881) described an otter catching a Cormorant *Phalacrocorax carbo* on the water and then decapitating it once ashore, and Stephens (1957) found that two pigeons *Columba* presented to captive otters were decapitated, with feathers strewn about, but none of the flesh eaten. These accounts of otters handling avian prey are similar to findings in Shetland, but the reasons for leaving a carcase uneaten are unclear, although food-storing may be involved.

Olsson (1974) in Sweden and Folkestad (1982) in Norway found that many Black Guillemots and other seabirds were killed by minks *Mustela vison*, particularly in boulder areas where minks make their lairs. Although otters are probably less numerous than minks, their predation could influence nesting dispersion or regulate the size or formation of accessible seabird colonies in such areas as Shetland.

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Appendix IX. A summary of recommendations made to the Shetland Oil Terminal Environmental Advisory Group on future monitoring of Black Guillemot breeding numbers in Shetland [from Ewins (1985a)].

With weather conditions being suitable for Black Guillemot census work on average for 35 days in the pre-breeding period in Shetland, various combinations and frequencies of the monitoring alternatives could be completed, depending largely on SOTEAG priorities and availability of funds. The various alternative regimes vary from detailed counts at small monitoring sites, to a complete Shetland survey. The location of the selected monitoring sites and regional sample stretches of coastline are shown on the map overleaf.

In addition to the recommendation that regular boat counts in Sullom Voe be continued, the following two programmes are suggested for monitoring of pre-breeding numbers (between 27 March and 15 May, in Shetland):

Programme A (every 2 years).

The entire Yell Sound area should be surveyed twice and two counts made at each of the selected monitoring sites. If weather conditions were unusually poor, one count would suffice at some monitoring sites. This work could be completed in 34 man-days (ie. one person for one season).

Programme B (every 4 years). (or in the next pre-breeding season should there be good reason to suspect significant change over a wider area).

All regional sample areas and selected monitoring sites should be surveyed twice. This could be completed in 68 days of fieldwork (ie. 2 people for one season).

Since programme B covers that work detailed in programme A, the proposed 2-yearly scheme would alternate, ie. A-B-A-B- etc. Should oil, pollution affect any stretches of coastline, the results of pre-breeding surveys there the following season could be compared with the base-line data presented in this report and impact on breeding numbers assessed.

The location and boundaries of potential monitoring areas.

