Recruitment to the colony and other aspects of the biology of the kittiwake (rissa tvidactyla (l.))

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How to cite:

Porter, Julie Margaret (1985) *Recruitment to the colony and other aspects of the biology of the kittiwake (rissa tvidactyla (l.))*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/7044/

Recruitment to the colony and other aspects of the biology of the Kittiwake (*Rissa tridactyla* (L.))

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... being a thesis presented in candidature for the degree of Doctor of Philosophy in the University of Durham, 1985.

This is to certify that none of the material contained in this thesis has previously been submitted for a degree in this or any other university.

Julie M. Porter

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ACKNOWLEDGEMENTS

I am extremely appreciative of Dr. J.C. Coulson's wise and patient support and guidance throughout the course of this study. I thank him for his efforts in conducting the continuous study at the unique warehouse Kittiwake colony at North Shields, and for allowing me the privilege of working there.

I am grateful to Professors D. Barker and K. Bowler for permitting me to use the facilities of the Zoology Department at Durham University.

I am indebted to M.G. Brazendale, Dr. J.W. Chardine, Dr. Coulson, Dr. A.F. Hodges, Dr. C.S. Thomas, Dr. E. White and Dr. R.D. Wooller for collecting data at North Shields in past years. I thank Drs. Coulson and Thomas for field assistance during this study. I also thank N.C. Grist for unpublished observations of ringed Kittiwakes at other colonies.

Smiths Shiprepairers North Shields Ltd. and recently Mr. J. Pepper have provided continuous access to and protection of the colony over the past 33 years.

For their assistance during the study, I wish to thank N. Aebischer, Dr. J. Birks, A. Dorin, Dr. R. Elliot, G. MacKinnon, J. Steele, C. Todd and Dr. R. Williams. Particular thanks to E. Henderson and M. Bone for constructing window ledges and making rings; to Susan Coulson for preparing the figures; to P. Carse for typing the manuscript; and to M. Gibson for proofreading.

During this study I was generously supported by a Commonwealth Scholarship (Association of Commonwealth Universities).

I also wish to thank my friends for their companionship, and especially N. Duncan for much needed diversions and support. Finally, thanks to my parents for their understanding and assistance through all stages of my education.

ABSTRACT

This study was initiated to examine the methods and biology of recruitment to the breeding group in the Kittiwake. Long-term changes in the population biology are presented for the history of the colony (1949 to 1984). Mortality rates of adults were particularly high in the early 1970's; concurrently recruitment rates increased, age of first breeding declined, and the body weights of recruits decreased in order to compensate. A model of colony growth is presented which shows that small colonies are proportionately more attractive to recruits in that they have higher rates of increase and recruitment. The North Shields colony followed the expected pattern of growth for 17 years. Evidence presented shows that nest sites at North Shields were then socially limited; there were physically available sites which were not used. In consequence of the social structure of the colony, there was a pool of potential recruits which were temporarily restricted from breeding. Recruits (Kittiwakes breeding for the first time) were at least three years old, were present at the colony as prospectors in at least one year prior to breeding, and arrived by early May in the year of first breeding. The attendance of recruits at the colony in May was more than three times that of prospectors, and recruits had higher body weights. These prerequisites separated recruits from prospectors, but there was further selection at the time of recruitment. Kittiwakes preferred to nest as close as possible to other nesting pairs, but aggression forced a compromise. High quality birds chose sites close to other birds and did better reproductively. Thus individual quality segregated recruits on the basis of their ability to compete for sites in dense areas; some Kittiwakes deliberately waited for aggression from established breeders to decline in order to take up preferred sites. The results are discussed in terms of the importance of the buffering effect of the pool of non-breeders on the size of the breeding group, and individual differences in quality.

CHAPTER 1. INTRODUCTION

Despite extensive research on seabirds, the mechanism of population regulation in these birds is not understood. The classical concept of density-dependent population regulation, originally proposed by Howard & Fiske (1911), modified by Nicholson (1933) and extended to birds by Lack (1954), is not readily interpreted under a dense colony situation, particularly when several workers (e.g. Darling 1938, Birkhead 1977, Harris 1980) have reported the precise converse: higher breeding success under dense conditions.

Krebs (1972) and Ricklefs (1973) have reviewed in detail the theories of animal population regulation. Three general theories of natural regulation of numbers focus on the interactions between the population and the environmental factors of weather, food, shelter and enemies (predators, parasites, diseases). The biotic school (Howard & Fiske 1911, Nicholson 1933, Smith 1935, Lack 1954) proposed that density-dependent factors are most important in preventing population increase. The climatic school (initiated by Bodenheimer 1928) emphasized the role of weather and suggested that it may act as a density-independent control. A comprehensive school stressed the importance of both density-dependent and density-independent controls. In contrast, the self-regulation school concentrated on events going on within a population, in particular on individual differences in behaviour and physiology (e.g. Chitty 1955, Wynne-Edwards 1962). These theories of population regulation are not mutually exclusive which emphasizes the complexity of the problem. Birkhead and Furness (1985) have recently reviewed population regulation of seabirds.

Nearly all studies of population regulation in birds have been concerned with local populations, yet this is often equated with the regulation of numbers over the species' entire range. It is therefore necessary to define the area carefully; while certain factors (e.g. food, nest sites) may limit numbers in one area, some members may move elsewhere, so the total numbers are unaffected. Studies on seabirds have shown that there is often considerable interchange between colonies, particularly of young birds recruiting to the colony to breed for the first time (e.g. Harris 1972, 1983, Coulson & Wooller 1976, Duncan & Monaghan 1977, Brooke 1978, Parsons & Duncan 1978, Coulson 1983). In many instances, a lack of evidence for movement may be due to a lack of observations.

Population size changes, adult survival rates, clutch size and breeding success are well documented for several seabird species (early studies reviewed by Lack 1968, Ashmole 1971; also Carrick & Ingham 1970, Perrins et al. 1973, Lloyd 1974, 1979, Chabrzyk & Coulson 1976, Birkhead 1977, Birkhead & Hudson 1977, Duncan 1978, Dunnet & Ollason 1978a,b, Nelson 1978, 1984, Asbirk 1979, Dunnet et al. 1979, Ainley & DeMaster 1980, Harris 1980, 1983, 1984, Potts et al. 1980, Gaston & Nettleship 1981, Coulson et al. 1982, Ollason & Dunnet 1983, Coulson & Thomas 1985). Certain potentially important aspects of the biology of seabirds remain to be investigated. The least understood aspect of the population dynamics of seabirds appears to be the mechanism whereby young birds are allowed to enter or are prevented from entering a colony to breed for the first time.

Linked with this recruitment to the breeding group is the concept of delayed maturity, which is particularly interesting in birds. Structurally, young birds have grown to adult size in a few weeks or months (cf. mammals) whereas the delay in sexual maturity is measured in years (seabird species reviewed by Wynne-Edwards 1962, Lack 1968, Ashmole 1971, Croxall 1984). In some albatrosses it may be at least 10 years before they breed, while small gulls, turns and storm petrels may first breed at the age of two or three. Theoretically, birds should breed as young as possible (Williams 1966) to maximize their lifetime reproductive output, provided that breeding at a young age does not reduce the number of breeding attempts. The delayed maturity in seabirds is thought to permit young to learn to forage successfully before they themselves attempt to feed offspring (e.g. Dunn 1972, Porter & Sealy 1982, Greig et al. 1983). On the other hand, delayed maturity may also be due to the difficulty of getting into the breeding colony; the annual cull of large numbers of Herring Gulls on the Isle of May has resulted in a lower age of recruitment (Coulson et al. 1982).

Many seabird studies have documented the presence of immature birds at the colony in one or more years before they breed, as well as the presence of birds of breeding age which have apparently never bred (e.g. Kittiwakes, Coulson & White 1956, 1958, Wooller & Coulson 1977; McCormick's Skuas, Burton 1968; Gannets, Nelson 1966; Adelie Penguins, Carrick & Ingham 1970, Ainley 1978; Royal Penguins, Carrick & Ingham 1970; Wandering Albatross, Carrick & Ingham 1970; Manx Shearwaters, Perrins et al. 1973; Cassin's Auklets, Manuwal 1974; Herring Gulls, Chabryzk & Coulson 1976, Duncan 1978, Coulson et al. 1982; Common Guillemots, Birkhead & Hudson 1977; Puffins, Petersen 1976, Harris 1983, 1984; Lesser Sheathbills, Burger 1979; Shags, Potts et al. 1980; Brunnich's Guillemots, Gaston & Nettleship 1981). Very few workers have considered in detail the reason for this phenomenon, where birds with the apparent capacity to breed do not.

Recruitment to the breeding colony is difficult to study without an extensive ringing programme or the ability to identify these potential breeders in the field (e.g. Herring Gulls, Coulson et al. 1982; Fulmars, Ollason & Dunnet 1983; Kittiwakes, Coulson & Thomas 1985). Some workers have demonstrated that there is competition and selection at the time of recruitment (e.g. Nelson 1966, Coulson 1968, Wooller & Coulson 1977, Lewis & Zwickel 1980, Petrinovich & Patterson 1982) and some have used recruitment to the breeding group as a measure of fitness of the recruits' parents (e.g. van Noordwijk et al. 1980, Cooke et al. 1984); but the process by which recruitment occurs is rarely examined.

This study was initiated to examine the methods and biology of recruitment to the breeding group (subsequently referred to as "recruitment") in the Kittiwake, and to consider whether or not this aspect of the population dynamics is an important factor in colony or population regulation.

Although the North Shields colony has been studied since 1952, prior to this study little attention had been given to the biology of Kittiwakes before breeding for the first time. However, the presence of non-breeding Kittiwakes in adult plumage has been recorded at the North Shields and neighbouring colonies (Coulson & White 1956, 1958, Coulson 1959, Coulson & Wooller 1976, Wooller & Coulson 1977). Wooller & Coulson (1977) demonstrated that no Kittiwake under the age of three years has bred, although Coulson (1959) showed that two year olds were present at the colony. Coulson & White (1956) recorded more non-breeding Kittiwakes at younger (and therefore smaller) colonies; these prospectors arrived later in the season than breeders (Coulson & White 1958, Coulson 1959), had their peak numbers in July when adults were feeding young (Coulson 1959), and were seen both within the colony and on the periphery (Coulson 1959). Coulson & White (1958) and Coulson & Wooller (1976) found that no Kittiwakes which had bred at North Shields were seen at another colony. In contrast, Kittiwakes ringed as prospectors were seen at more than one colony.

Coulson (1968, 1971) showed that there was considerable competition for sites in the centre of the colony where density was the highest. The quality of the recruits in the centre was higher in terms of body weight, survival and reproductive output. Wooller & Coulson (1977) found no evidence to suggest that differences in the quality of birds nesting in the centre or the edge were inherited or that older birds competed better. They concluded that recruits were segregated by quality at the time of recruitment.

CHAPTER 2. METHODS

2.1 The study site

The study colony is located on a warehouse on the north side of the River Tyne in North Shields, Tyne and Wear, England (55° 00'N, 01° 27'W; Fig. 2.01). The warehouse was formerly a brewery, but during the history of the colony it has been used for storage of dockyard materials and since 1979 for small boat construction on the ground and first floors.

Kittiwakes have nested on the window ledges of all four sides of the building, even though one side (north) is not in sight of the river. They have nested on all five floors of the building, but most nests are on the top three floors of the south and west sides. The window ledges are about 0.75m long and 0.30m deep. The immediate physical characteristics of each ledge are identical. In 1962 and in 1983 additional ledges were attached to the existing window frames. In 1962, one ledge was added to each window on the third and fourth floors of the south side and to the four windows closest to the river on the third floor of the west side. In 1983, a third ledge was added to each of those windows, a second ledge was added to the six windows closest to the river on the fourth floor of the west side, and two extra ledges were added to the door on the fourth floor of the south side. All new ledges were identical in size to the existing ledges. The addition of the new ledges increased the density of possible nest sites in the apparently favoured centre of the colony (Coulson 1968).

Coulson & Thomas (1985) have most recently described the history of the colony. The warehouse was first colonized in 1949 when four pairs nested on the south side. The peak in numbers occurred in 1965 (104 pairs) and since then there have been about 80 nesting pairs.

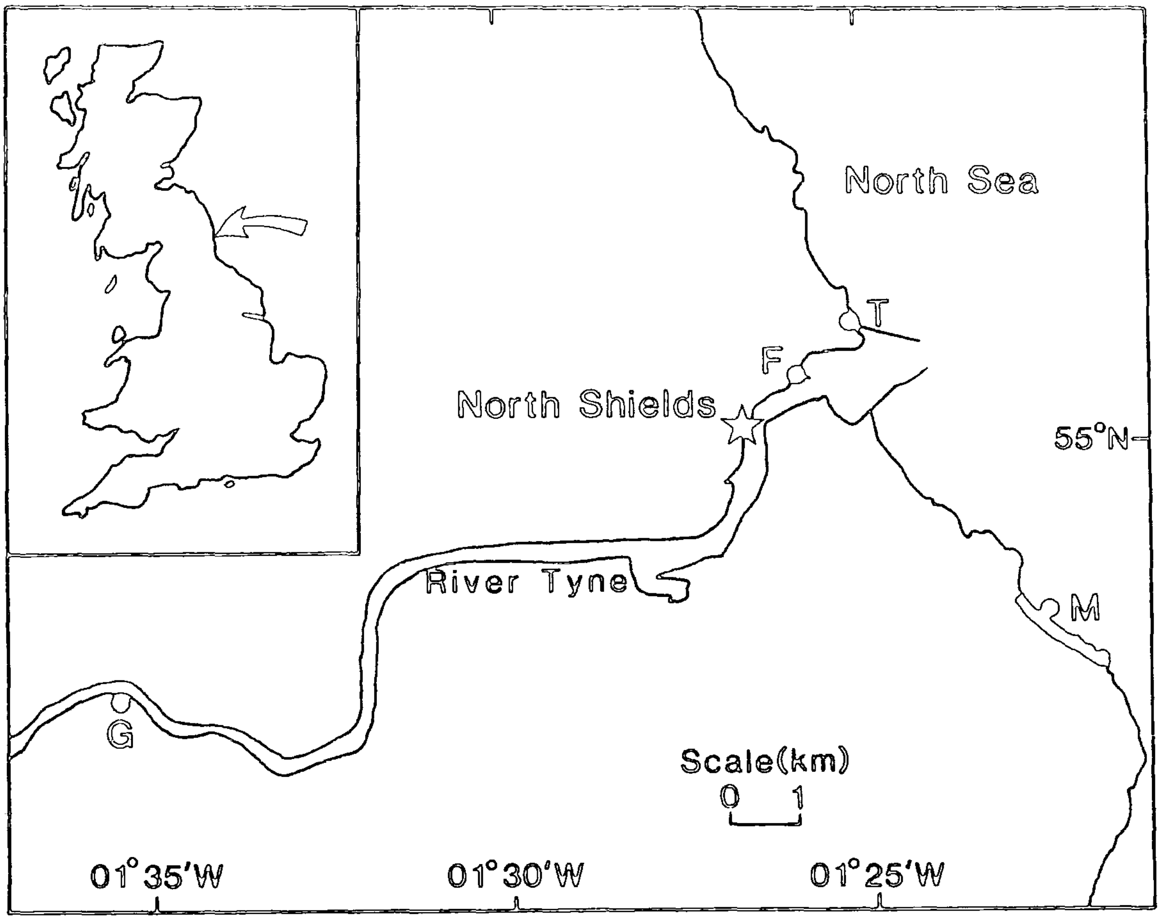

FIGURE 2.01: Location of the study colony in North Shields, Tyne and Wear, England. The location of nearby Kittiwake colonies at Marsden (M), Tynemouth (T) and Gateshead (G), and a loafing area at the North Shields Fish Quay (F) are also shown.

2.2 Data collection

2.2.1 Long-term investigation

Coulson & Thomas (1985) have described in detail the methods for the collection of data for the long-term investigation. Additional information on ringing is presented here.

In every year since 1954 all breeders on the North Shields warehouse colony have been individually marked with a unique combination of colour rings and a BTO monel ring (Coulson & White 1958). Once incubation commenced, all unringed breeding Kittiwakes were caught from inside the warehouse, weighed (from 1959 to 1984 using a Mettler balance accurate to the nearest gram), wing-length measured (Spencer 1972) and colour ringed. The age of the bird was determined from its plumage, as outlined in Coulson (1959), and sexed from a combination of its size (Coulson et al. 1983) and its behaviour (Coulson & Wooller 1976). Non-breeders visiting on ledges were also caught and processed in the same manner.

In each year since 1952, all chicks which fledged from the warehouse colony were ringed prior to fledging. From 1952 to 1965 a BTO metal ring only was used. From 1966 to 1971 chicks were given a BTO monel ring and a single darvic ring (each year had a different colour). If these birds returned to the colony in a subsequent year, they were caught and given a unique colour combination as above. From 1972 to 1984, chicks have been ringed with a BTO monel ring and a single laminated darvic colour ring. A different colour was used for each year and each ring was engraved with a unique combination of one letter and one number. The engraving, which was carried out on two parts around the ring, allowed the fledged chicks to be individually recognized through a spotting scope. These laminated darvic rings were not normally replaced; two birds which fledged in 1972 were breeding in 1984 and their rings remained legible.

Searches of colonies on the east coast of Britain revealed that once a Kittiwake breeds at North Shields, it rarely, if ever, moves to another colony (Coulson & White 1958, Coulson & Wooller 1976). This enables estimates of survival rates of breeding males and females for each year to be determined; those birds which disappeared from the colony could be assumed to be dead. Similarly, all unringed breeding birds could be assumed to be recruits, breeding for the first time. Thus annual recruitment rates (proportion of recruits in the breeding colony) could be calculated.

2.2.2 The present study

The colony was visited at least twice weekly from 1 January to 25 September 1982, from 10 January to 6 September 1983, and from 6 January to 28 August 1984. During that time, data were collected for the long-term investigation as outlined in Coulson & Thomas (1985). The colony was visited at least five times per week from 28 May to 31 July 1982 and from 14 April to 15 June 1983 in order to make detailed observations of behaviour and attendance of Kittiwakes on the west side of the warehouse (less frequent observations continued to 24 August 1982 and 30 August 1983). These observations were made from a point about 25m from the base of the warehouse and observation bouts ranged from three to 12 hours and most were about seven hours in duration. The west side of the colony was observed for 373 hours in 1982 and 288 hours in 1983. Observations were spread between 0530 GMT and 2100 GMT. Visits after dark in 1983 showed that there was virtually no nocturnal activity at the colony (see also Chardine 1983). The weather conditions were recorded during each visit.

Spot observations were used to document the number and location (roof, ledges with nests, ledges unoccupied by breeders) of Kittiwakes present on the west side of the warehouse. At the beginning of each observation bout and at half hourly intervals thereafter, the identity and location of all

Kittiwakes were noted on prepared recording sheets. A zoom 15 to 60x spotting scope aided identification. In addition, in 1983, all arrivals of Kittiwakes, which had not bred prior to 1983, on ledges and any subsequent aggression were recorded.

Terms that describe the status of the Kittiwakes at North Shields are as follows: established breeders had bred at North Shields in a previous year, recruits bred for the first time in the current year, prospectors had not bred before and did not breed in the current year, and potential recruits were prospectors at least three years old (the minimum age of first breeding, Wooller & Coulson 1977). Kittiwakes were experienced if they were present at the colony in a previous year. Prospectors and breeders which fledged from North Shields (natal Kittiwakes) were of known age, and referred to as follows: juveniles (in their first calendar year of life), one year olds (in their second calendar year of life), two year olds (in their third calendar year of life), etc.

The timing of reproductive events for breeders was determined from inside and outside the warehouse. The arrival date of an individual was considered to be the first date it was seen in the calendar year. The departure date was the last date an individual was seen. The date of pair formation was the first date in each calendar year on which the two birds of a subsequent breeding pair were seen together at the colony. The laying date was the day the first egg of a clutch was laid.

In addition to these observations at North Shields, the neighbouring Kittiwake colonies at Marsden, Tynemouth and Gateshead (Fig. 2.01) were searched for ringed birds. Visits were made several times in each season and the status of ringed Kittiwakes recorded. In 1982 records were obtained from N.C. Grist. In 1983, the North Shields Fish Quay was visited two to eight times per month. This is the closest loafing area (a site where birds engaged in non-feeding and non-nesting activities) to the North Shields colony. All loafing Kittiwakes were counted, and ringed individuals were recorded.

2.3 Analyses of data

The long-term data set used by Coulson & Thomas (1985) is computerized and was updated to include 1984. Most other data were also put onto computer files and SPSS (Statistical Package for the Social Sciences; Nie et al. 1975) and SPSS Update 7-9 (Hull & Nie 1981) were used for statistical analyses.

There is considerable year to year variation in population measures at North Shields (Coulson & Thomas 1985). Descriptions of long-term trends are presented as five year running means to smooth out these irregularities. In all cases, a five year weighted average was used with binomial coefficients (1, 4, 6, 4, 1). The use of a weighted rather than a simple average tends to produce a smoother curve while preserving the main features of the time series (Kenney & Keeping 1954). Statistical analyses were carried out on the original, annual means.

The spot observation data on attendance are presented as the mean number per scan, which gives a relative quantity which can be used to make seasonal or diurnal comparisons. When calculating the attendance of individuals, the proportion of spot observations the individual was recorded, represented the proportion of daylight hours those individuals were present at the colony.

Unless otherwise stated, Student's t-tests were used in hypothesis testing. Throughout, the null hypothesis was rejected if $P < 0.05$. If $P > 0.05$ the result was noted as not significant (ns). Means ± one standard error are presented. For details of statistical tests used see Appendix D.

Common and scientific names of species mentioned in the text appear in Appendix A. Additional methods are presented where appropriate.

CHAPTER 3. POPULATION DYNAMICS OF THE NORTH SHIELDS COLONY

3.1 Introduction

Coulson & Thomas (1985) have described the long-term changes from 1952 to 1982 in the population dynamics and breeding biology of the Kittiwakes in the North Shields colony. The aim of this chapter is to update the Coulson & Thomas study as well as to present long-term trends on other aspects of population biology in order to provide the ground work for a detailed consideration of the process of colony growth and recruitment. This investigation examines the biological implications and the relative importance of mortality rates, birth rates and dispersal to the number and quality of breeders at North Shields. A model of colony growth is presented and compared to the situation at North Shields. The limits of colony size are considered.

3.2 Colony size and density, reproductive output and adult survival rates: long-term trends to 1984

Many of the results presented in this section are an update from Coulson & Thomas (1985). They are included in order to discuss concurrent changes in other aspects of population dynamics. Data which are presented as five year running means are tabulated in Appendix B.

3.2.1 Colony size and density

Fig. 3.01 shows the number of breeding Kittiwakes at North Shields throughout the history of the colony, from 1949 to 1984. Numbers increased steadily from 1949 to 1965 at a mean rate of about 23% per annum to a peak colony size of 104 pairs. Following 1967, there was a progressive decline to 1977 when there were 67 breeding pairs. From that time, until 1981 (and again in 1983), there was an increase in numbers to approximately 90 pairs, although in 1982 and 1984 there were only about 70 pairs. Coulson (1983)

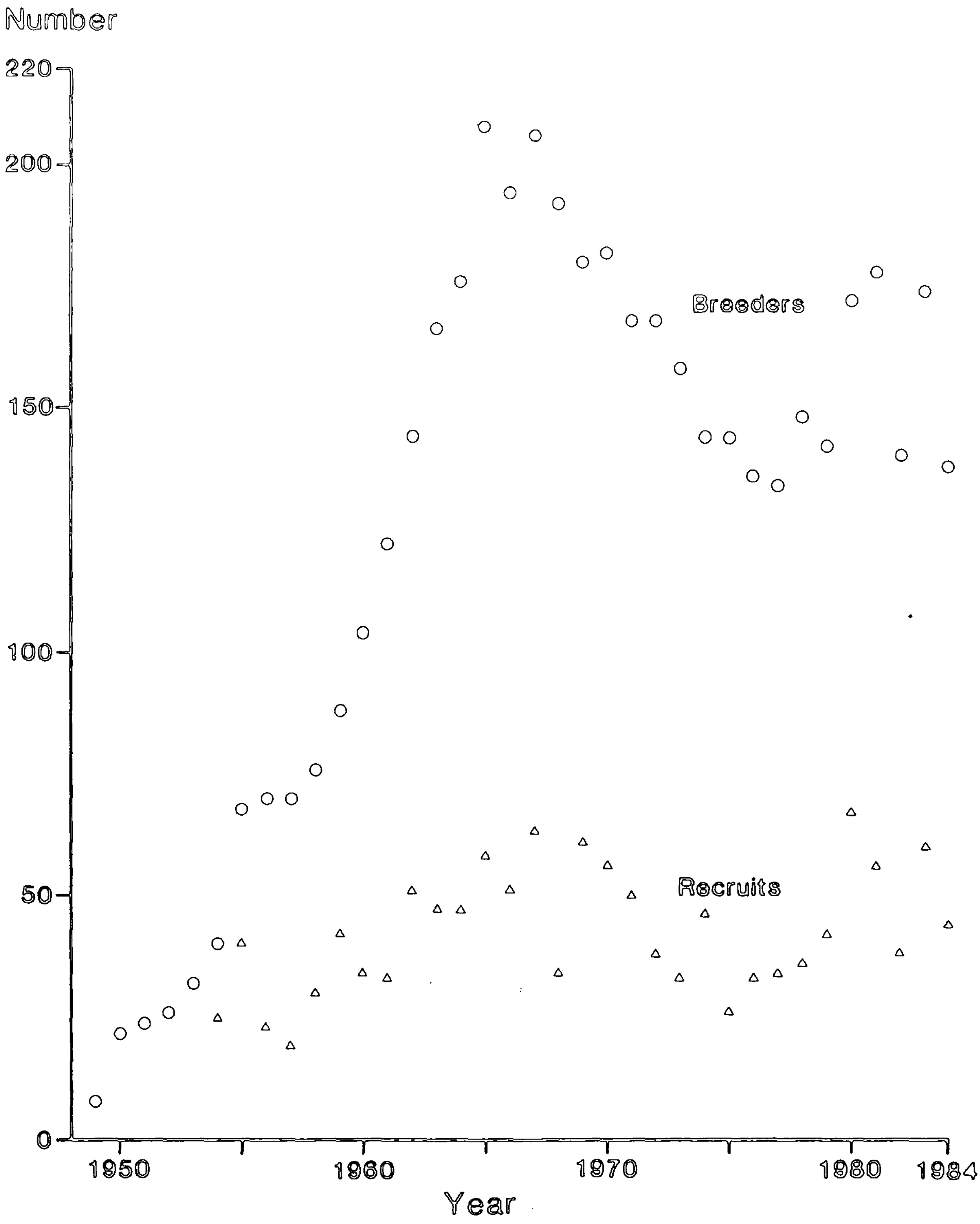

FIGURE 3.01: The number of Kittiwakes breeding at the North Shields colony in each year between 1949 and 1984. Also shown is the number of recruits in each year between 1954 and 1984.

showed that the changes at North Shields after the growth phase (1949 to 1965) were representative of those which have taken place in many colonies, which points to a common cause for the decline in numbers.

Density at North Shields is readily measured by the proportion of window ledges which contain two nesting pairs. Fig. 3.02(a) shows the relationship between colony size and the number of ledges with two pairs at North Shields in each year. This relationship during the growth years (to 1967) appeared to follow a sine curve (which would be expected). When numbers were low, no pairs doubled up. In 1954, although all ledges on the warehouse were not occupied, pairs began to nest on ledges which already contained one nest. Since there are a finite number of window ledges at North Shields, as colony size increased, there were fewer empty ledges available. The top of the curve would represent the saturation point at North Shields (there are ledges for a maximum of 186 pairs). The points after the peak in colony numbers (open circles in Fig. 3.02(a)) followed the pre-peak pattern closely, although there was a suggestion that density was slightly higher than expected. In 1983, new ledges were added to the warehouse (see Section 2.1) which considerably increased the number of available sites in the centre of the colony. As the proximity of the new ledges was closer, the measure of density in Fig. 3.02(a) is not strictly comparable; 1983 and 1984 fall well below the other points.

Fig. 3.02(b) shows that as colony size increased, so did the proportion of ledges with two pairs, that is the density of nests. The linear correlation for the points from 1954 to 1967 is significant ($r_{12} = +0.97$). If the linear regression line ($y = -0.549x - 3.078$) for the years of colony growth is extrapolated to the point where 100% of the ledges were occupied by two pairs, the maximum colony size would be 188 pairs. In fact, the North Shields warehouse has 186 potential nest sites. While colony size and the

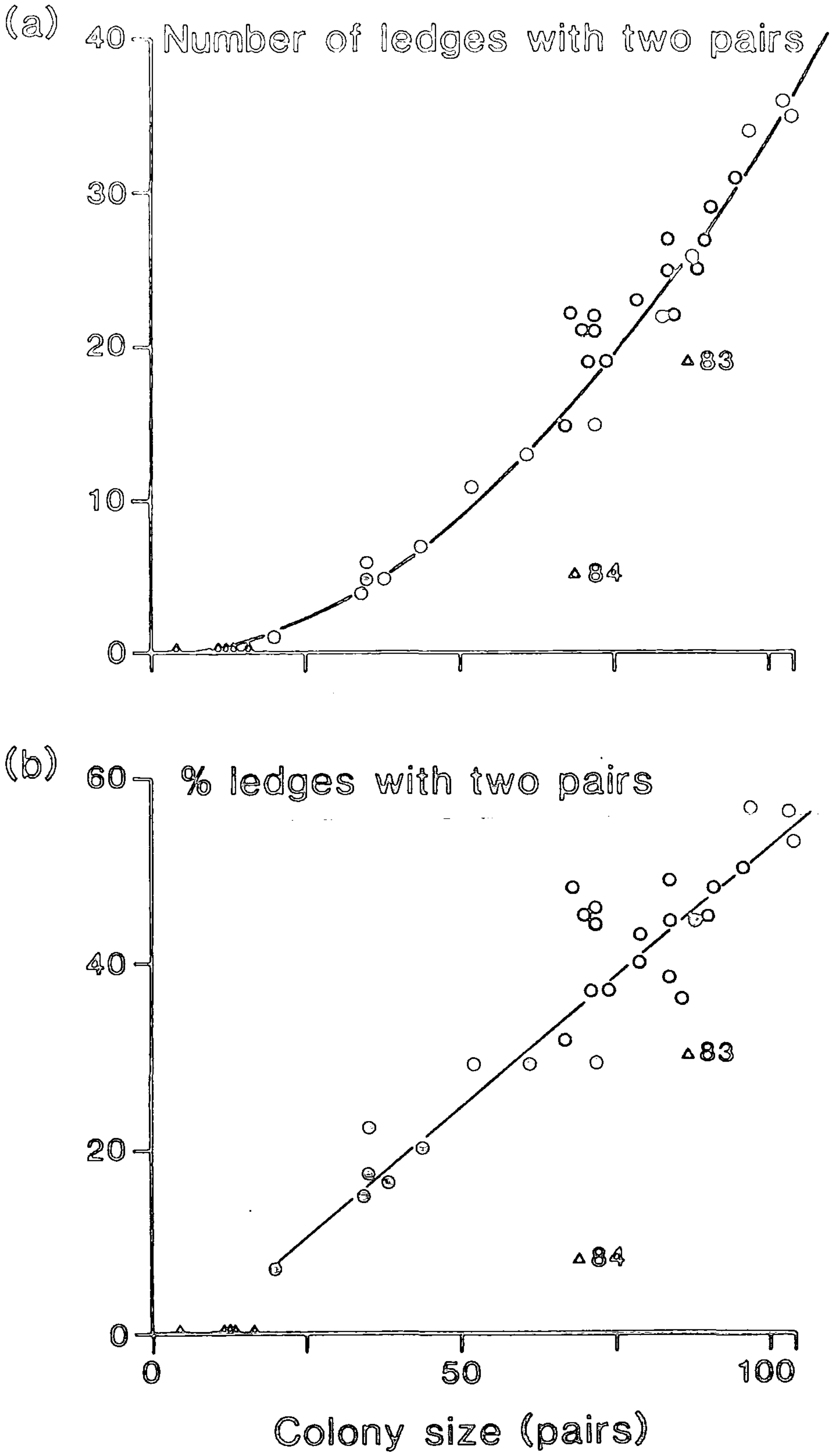

FIGURE 3.02: The relationship between colony size and density ((a) the number and (b) the percentage of ledges occupied by breeders with two pairs) at the North Shields colony in each year between 1949 and 1984. Solid circles are 1954 to 1967, open circles are 1968 to 1982, open triangles are 1949 to 1953, and 1983 and 1984 are indicated. Curve (a) fitted by eye; linear regression line (b) through solid circles.

density of nests increased, presumably competition for nest sites also increased.

3.2.2 Reproductive output

The number of chicks fledged per pair represents the annual reproductive output of each pair. As previously described by Coulson & Thomas (1985), the five year running mean of the number of chicks fledged per pair (Fig. 3.03) showed an increase until about 1960 when adult survival rates were also at a peak and the age structure of the colony had stabilized. A slight drop in the number of chicks fledged per pair in the next two years was followed by a recovery until 1965. Subsequently, there was a progressive decline until 1969, followed by an arrest, and then a further decline from 1972 to 1977. Since 1978 there has been a relatively stable level of annual chick production of about 1.05 per pair.

What happened to breeding performance during changes in density? In Fig. 3.04 density (% ledges with two pairs) is plotted against the mean number of chicks fledged per pair in each year. The points fall into two distinct categories: years of colony growth (1954 to 1965) and years during the decline in numbers (1968 to 1982). For each group there is a significant correlation between density and the number of young fledged per pair (1954 to 1965, $r_{10} = +0.66$, $y = 0.0098x + 1.03$; 1968 to 1982, $r_{13} = +0.70$, $y = 0.0079x + 0.75$). Data for 1966 and 1967 were not included in this analysis as they fell after the peak and before the rapid decline (represented by open symbols in Fig. 3.04). This finding implies a reproductive advantage due to the dense nesting which will be examined further in Section 5.3.4. The two slopes were not significantly different, while the intercepts were. This change in intercept would occur if some form of "stress" affected chick production equally in all breeding Kittiwakes in the colony.

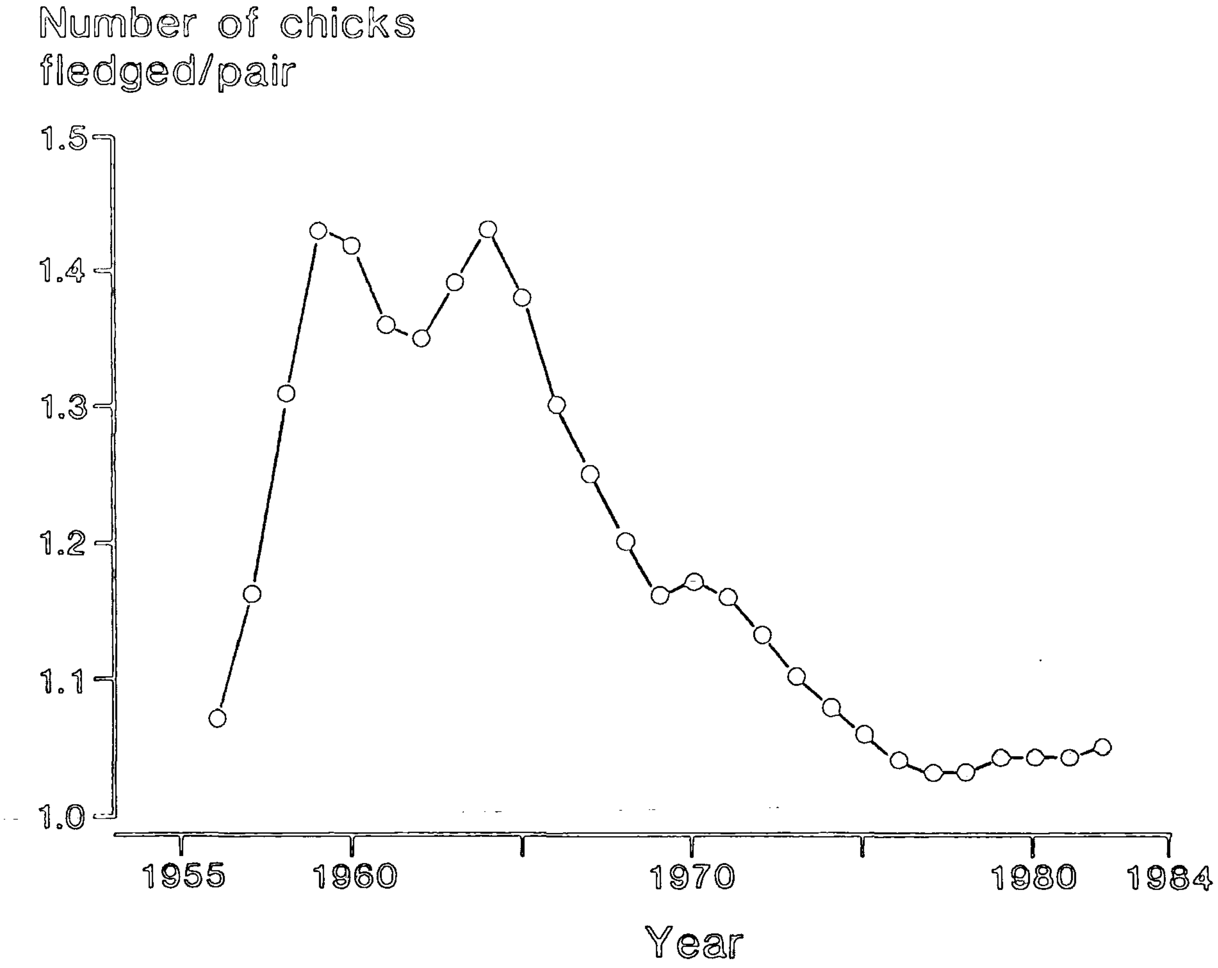

FIGURE 3.03: The five year running mean of the number of chicks fledged per pair at the North Shields colony over the period 1954 to 1984.

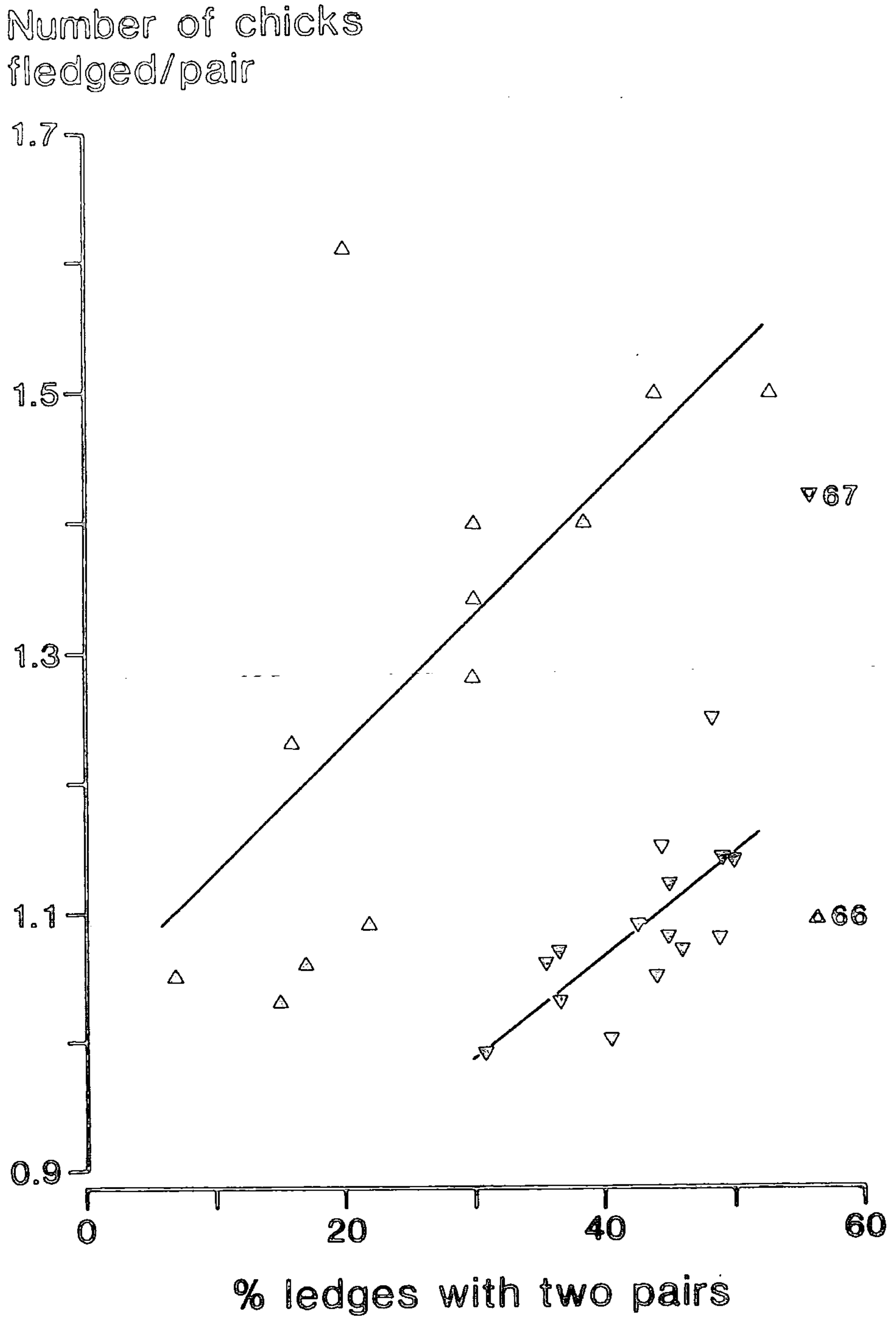

FIGURE 3.04: The relationship between the density of nests (% ledges with two pairs) and the number of chicks fledged per pair at the North Shields colony in each year between 1954 and 1982. Linear regression lines are through two groups of years: 1954 to 1965 (triangles) and 1968 to 1982 (inverted triangles).

3.2.3 Adult survival rates

Fig. 3.05 shows the five year running means of adult annual survival rates of male and female Kittiwakes from 1954 to 1984. These were discussed in detail by Coulson & Thomas (1985). Table 3.01 shows the annual survival rates by year and sex, and age (updated from Coulson & Wooller 1976). As found by Coulson & Wooller (1976), females had a higher annual survival rate than males, and this was age-related. There are three peaks of adult survival rates in Fig. 3.05 (1961-2, 1970-1, 1977-8) and three subsequent declines. The study by Coulson & Wooller showed that in years when survival dropped, the differences in survival rate between the sexes increased markedly. Coulson and Wooller attributed this to the earlier arrival date of males and their need to defend territories for longer. On the other hand, the current reduction in adult survival rates has affected both males and females. Coulson & Thomas (1985) have shown that arrival dates of Kittiwakes are becoming later each year and suggest this is due to environmental stress prior to their reoccupation of the colony, causing them to take longer to attain the physiological state to return. This stress may also account for the increased mortality rates. The adult female survival rate reached the lowest level in 1983-84 (0.61) and was approximately the same as that of males (0.66). While the decline in adult male survival rate in the early 1970's was due primarily to low survival in adults with one, two and three years of breeding experience (Table 3.01, column 3), the recent high mortality rate has affected all age classes (Table 3.01, column 5).

3.3 Recruitment rates

Coulson & Thomas (1985) concluded that the decrease in adult survival rates was the most important factor accounting for the depletion in the number of breeding adults. The decline in almost every aspect of Kittiwake

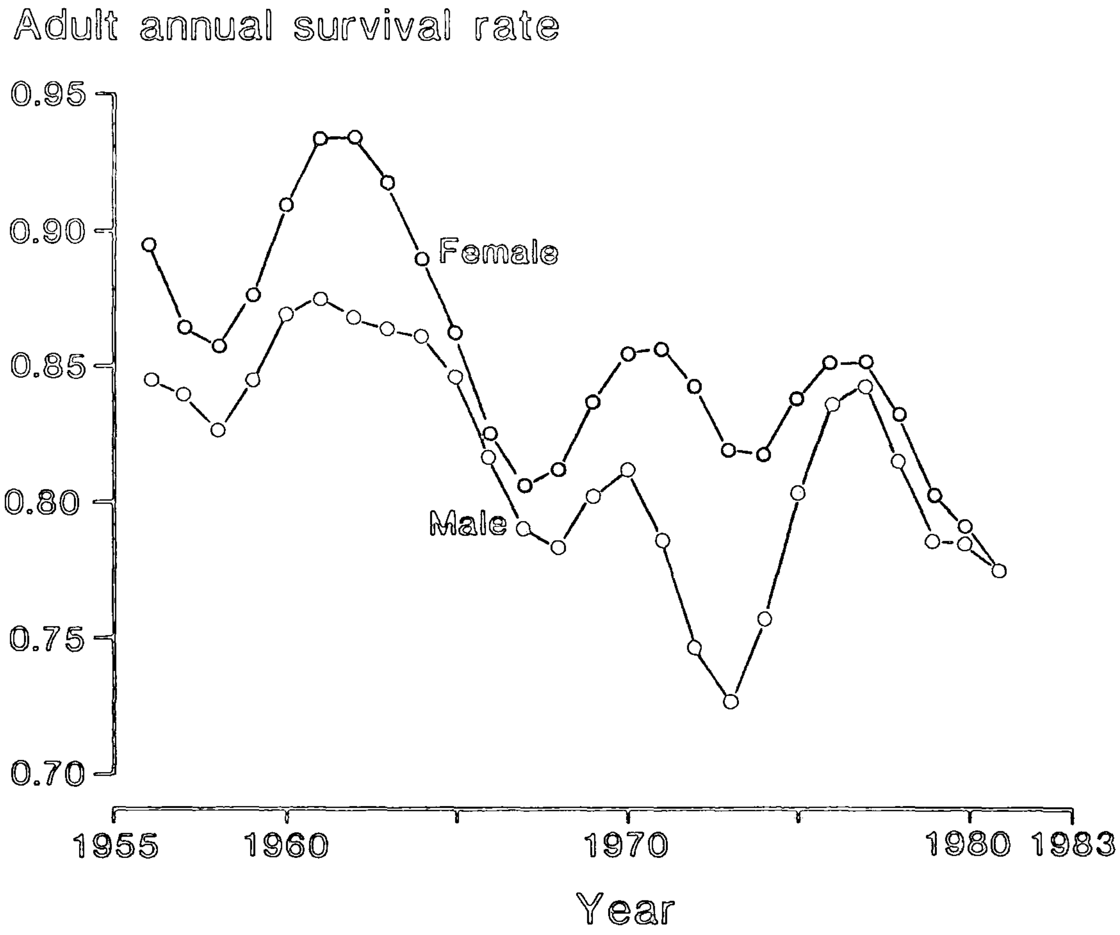

FIGURE 3.05: The five year running mean of the annual survival rates of male and female breeding Kittiwakes at the North Shields colony over the period 1954 to 1983.

TABLE 3.01: The adult annual survival rates of male and female Kittiwakes according to their breeding experience during five stages in the development of the colony. Numbers at risk are in parentheses. Data from 1954 to 1974 are from Coulson & Wooller (1976).

Previous breeding experience (years)		(1)	(2)	(3)	(4)	(5)
		Annual survival rates				
		1954-64	1964-69	1969-74	1974-79	1979-84
Males	1	0.90	0.83	0.77	0.87	0.86
		(148)	(80)	(75)	(67)	(114)
	2- 3	0.86	0.82	0.76	0.81	0.71
		(174)	(160)	(108)	(100)	(144)
	4- 5	0.79	0.83	0.83	0.83	0.76
		(85)	(107)	(72)	(83)	(68)
	6-10	0.83	0.78	0.74	0.82	0.59
		(52)	(122)	(113)	(73)	(61)
	11-17	-	0.67	0.66	0.81	0.72
			(15)	(35)	(36)	(39)
Females	1	0.94	0.85	0.85	0.93	0.78
		(123)	(93)	(77)	(58)	(112)
	2- 3	0.93	0.89	0.84	0.83	0.81
		(179)	(148)	(139)	(89)	(133)
	4- 5	0.91	0.85	0.85	0.85	0.62
		(101)	(109)	(90)	(71)	(73)
	6-10	0.89	0.76	0.75	0.86	0.72
		(90)	(128)	(87)	(120)	(74)
	11-17	-	0.78	0.66	0.79	0.73
			(54)	(48)	(52)	(60)

breeding biology, coupled with the reduced expectation of life, resulted in a shortage of recruits to the colony and a decline in colony size. This section considers the concurrent patterns of recruitment. Fig. 3.01 shows the number of recruits per year from 1954 to 1984. Fig. 3.06 shows the five year running means of annual recruitment rates (proportion of recruits in the breeding colony each year) for males and females. Males had higher recruitment rates than females, reflecting their lower survival rates and the fact that the Kittiwake is monogamous. At the present time, both survival and recruitment rates are nearly the same for males and females.

Recruitment rates decreased steadily from the early years of the colony until about 1964 to 1966 (Fig. 3.06), although the absolute number of recruits increased until 1967 (Fig. 3.01). When colony growth was occurring, recruitment was high and immigration also must have been high (see below; Harris 1983, Perrins & Birkhead 1983). In general, when survival rates were lowest (1969, 1974, 1981, 1982), recruitment rates were high, suggesting a compensatory effect. In the early 1970's, when male mortality was particularly high, male recruitment rates stayed high; this was the time when there was the greatest difference between males and females for both recruitment and survival rates. Fig. 3.07 shows a plot of the number of deaths in each year and the subsequent number of recruits. Each point represents one year (open circles are years of growth, 1954-1965). The relationship is positive and significant ($r_{27} = +0.49$, $y = 0.356x + 33.16$). In order for this form of compensation to operate, there must be a pool of potential recruits from which new recruits can be drawn (see further discussion of this in Sections 4.2 and 4.3).

3.4 Characteristics of recruits

The decline in colony size after 1965 was due primarily to increased adult mortality rates and a subsequent reduction in breeding success

FIGURE 3.06: The five year running mean of the annual recruitment rates for male and female Kittiwakes at the North Shields colony over the period 1954 to 1984.

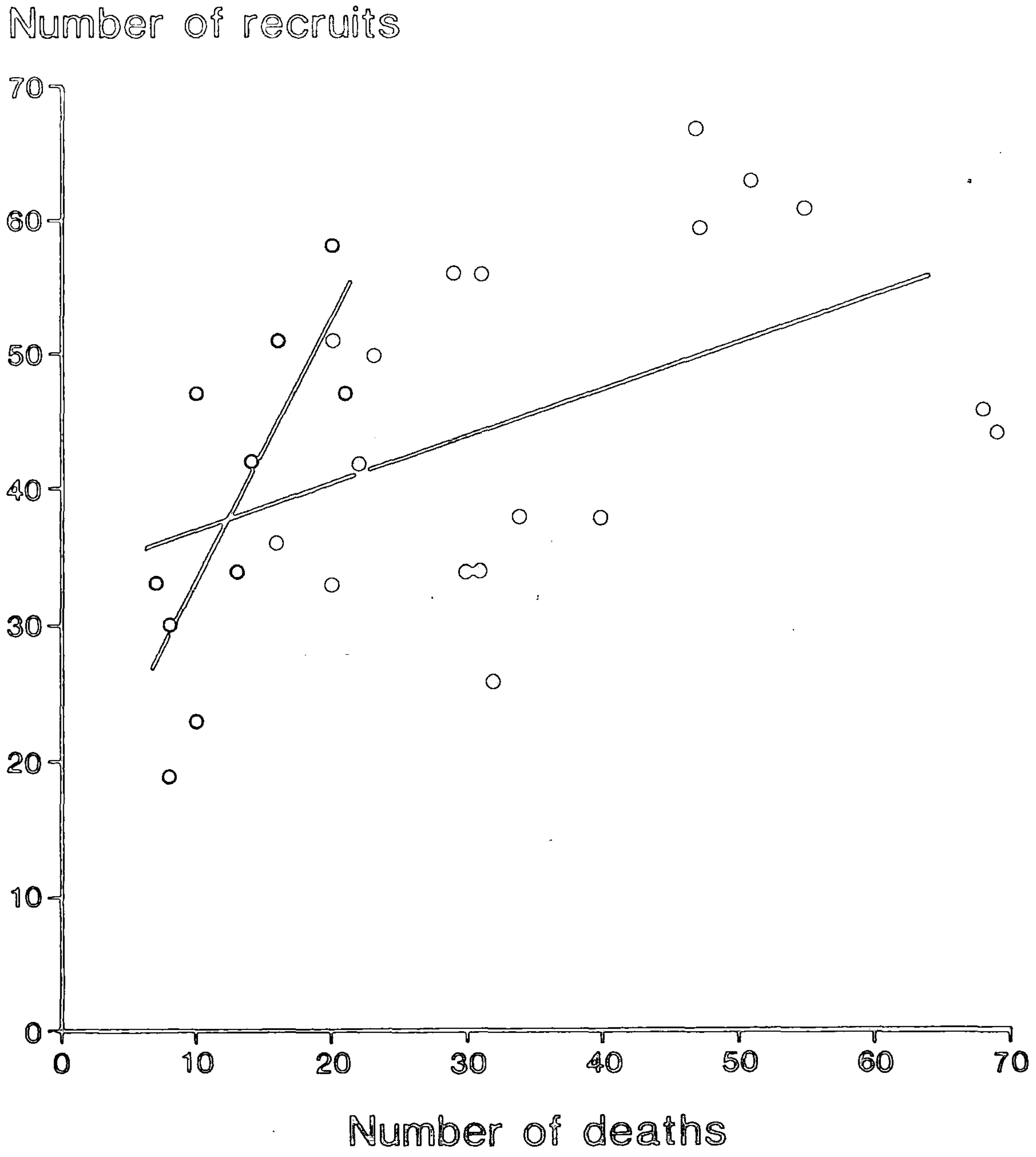

FIGURE 3.07: Relationship between the number of deaths in one year and the number of recruits in the following year at the North Shields colony between 1954 and 1984. Open circles are 1954 to 1965, solid circles are 1966 to 1984. Linear regression lines through open circles and through all points.

(Coulson & Thomas 1985). Although Fig. 3.07 showed a compensatory effect for mortality by recruitment, this was sometimes only partial compensation. It is necessary to examine the implications this had on the characteristics of the recruits in terms of their dispersal (immigration and emigration), age of first breeding and body size over the long-term.

3.4.1 Proportion of natal recruits

Fig. 3.08 shows the five year running mean of the proportion of male and female recruits which were fledged from North Shields. No North Shields fledged chick returned to North Shields until 1956, when one male bred. No female returned and bred until 1964. Wooller & Coulson (1977) have reported the stronger tendency for male Kittiwakes to return. The proportion of natal recruits increased progressively until the early 1970's (about 50% for males, 15% for females) and has tended to decline since. By 1965, the parental breeding group was of a reasonable size and colony growth had slowed. There is a significant linear correlation between the number of chicks fledged in a year and the number from that cohort which subsequently returned to breed (Fig. 3.09; $r_{25} = +0.72$, $y = 0.112x - 1.78$). Thus changes in the proportion of natal (North Shields fledged) birds which recruited can be accounted for by changes in chick production at North Shields. The proportion of chicks which fledged from North Shields and subsequently returned to their natal colony was approximately 11%. Given the annual adult survival rates in Fig. 3.05, it would be necessary for about 30% of the chicks produced to return and breed in order to make up for adult mortality in a closed system. Hence the North Shields colony is not a closed population; it is not self-sustaining, although this is partially due to young reared at North Shields moving into other colonies (Wooller & Coulson 1977).

In Fig. 3.10 the percent of each cohort (chicks fledged from North

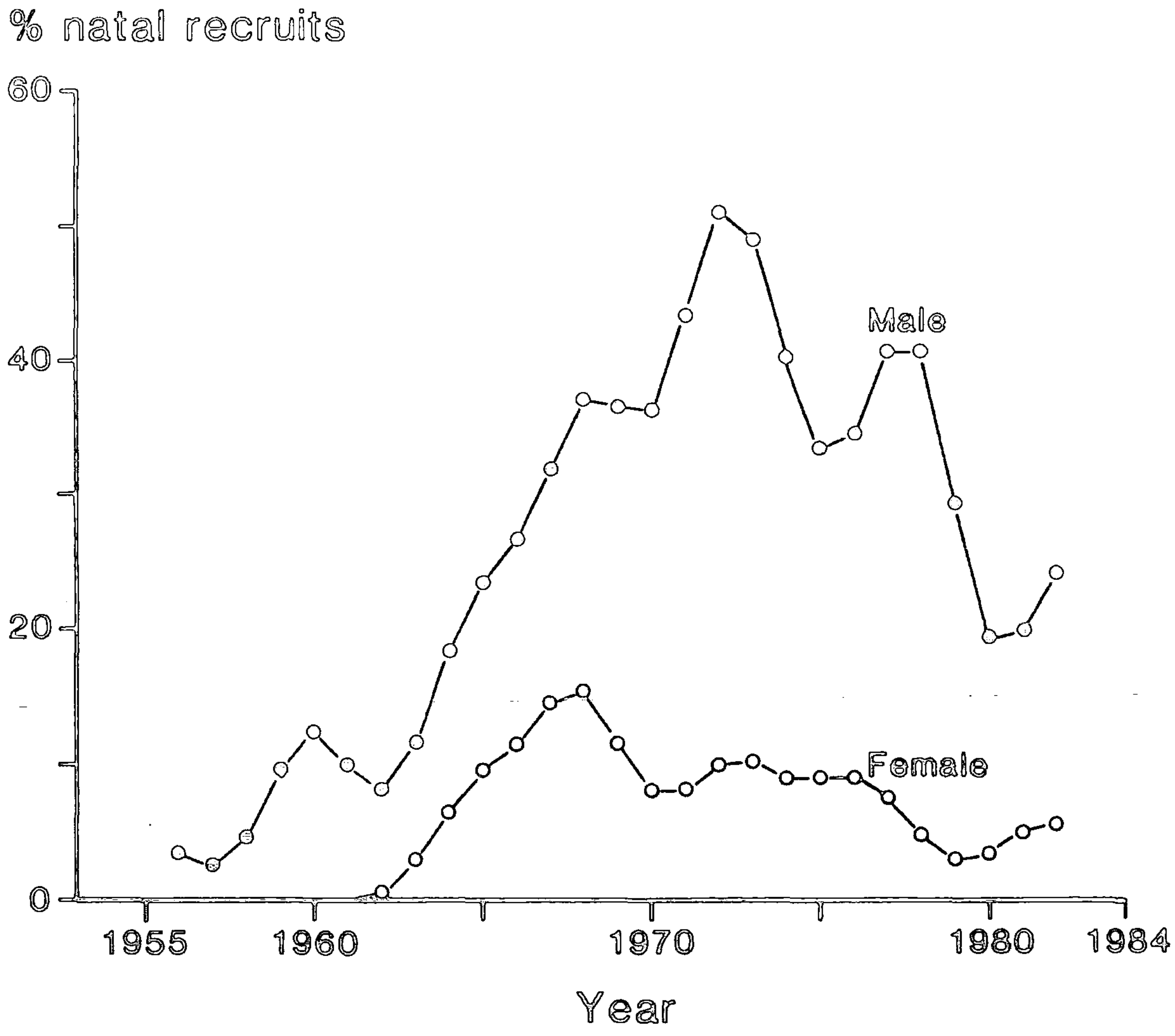

FIGURE 3.08: The five year running mean of the percent of male and female recruits which were natal (fledged from North Shields) at the North Shields colony over the period 1954 to 1984.

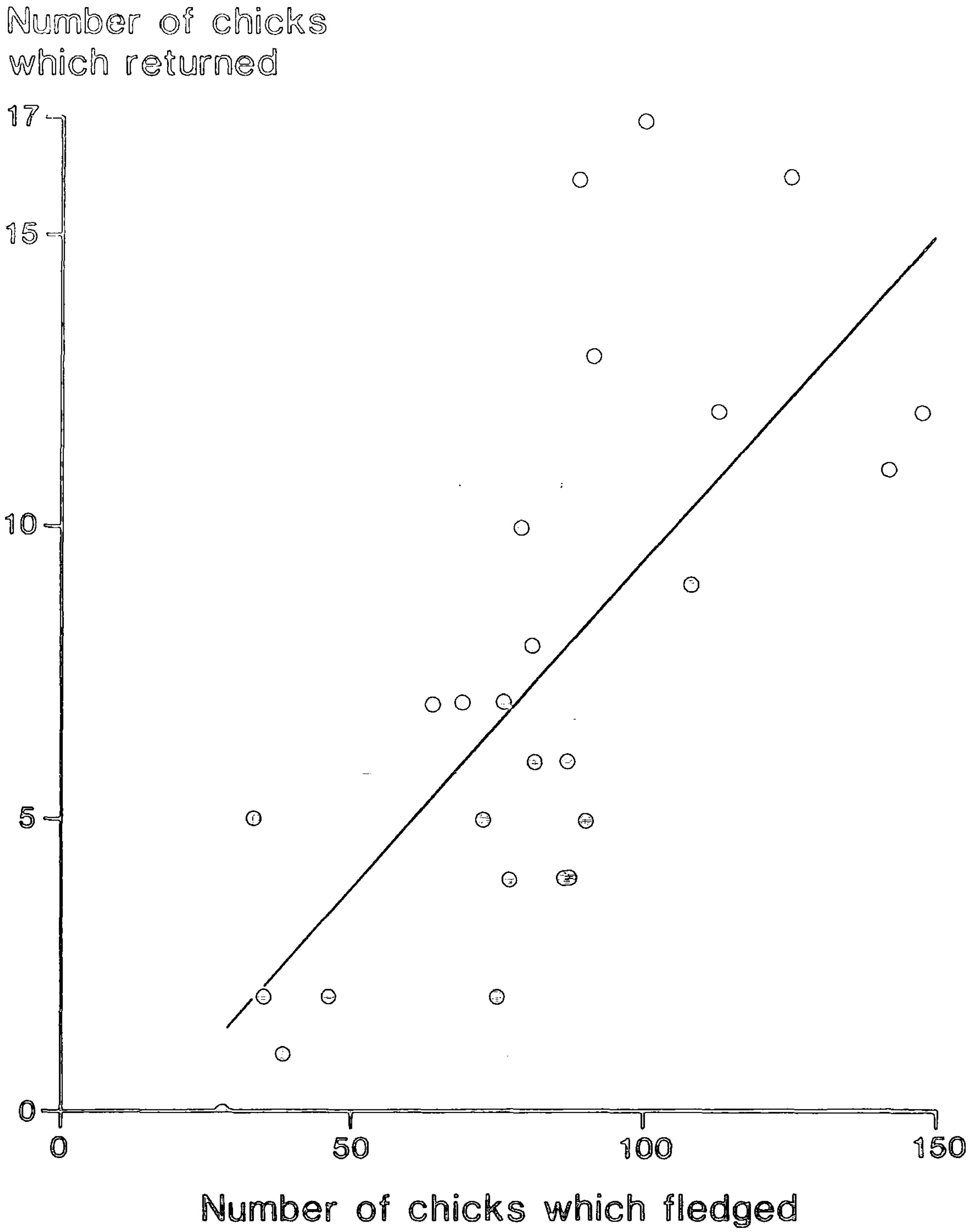

FIGURE 3.09: Relationship between the number of chicks which fledged from the North Shields colony in each year between 1954 and 1980 and the number which subsequently returned to North Shields to breed. The linear regression line is shown.

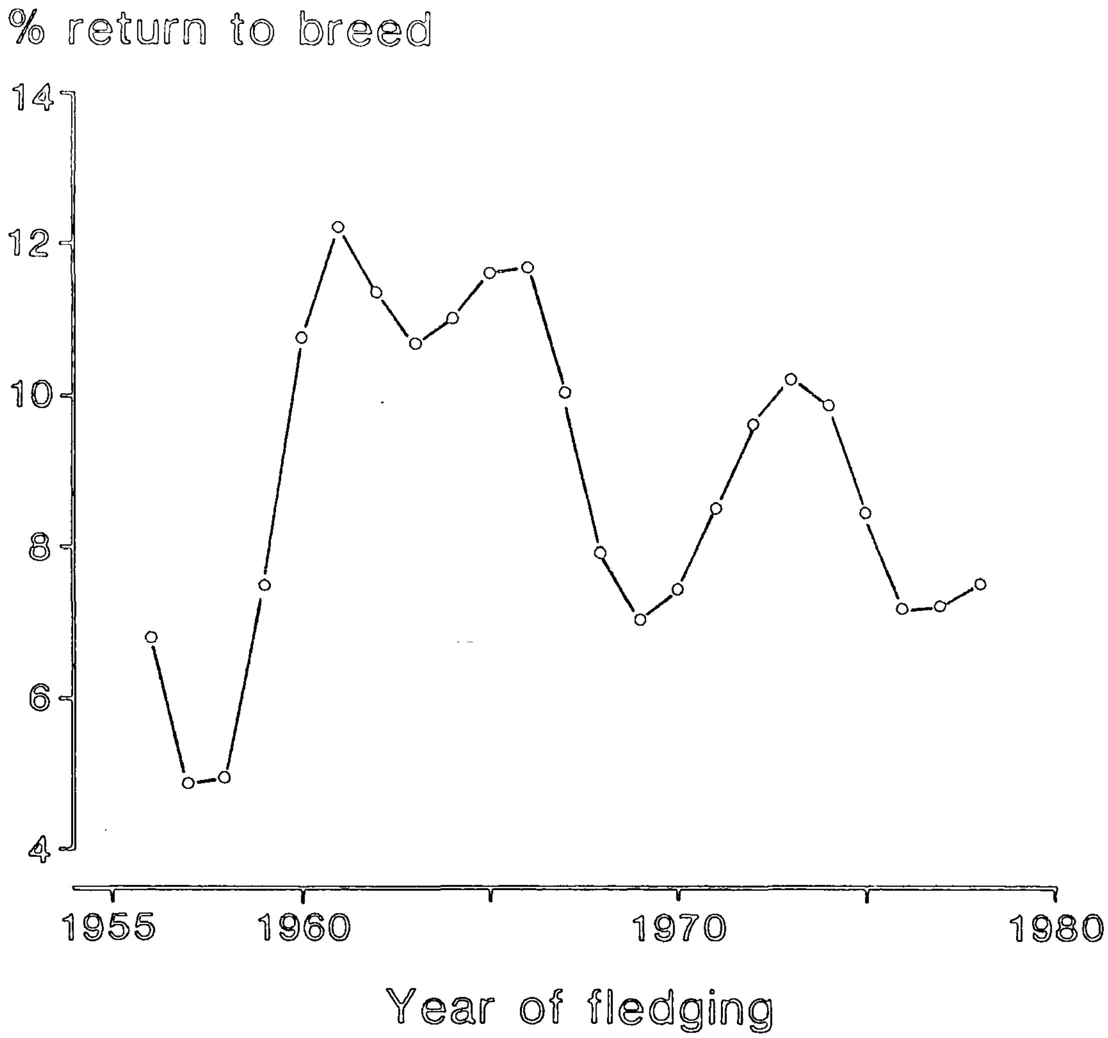

FIGURE 3.10: The five year running mean of the percentage of the chicks fledged from the North Shields colony in each year from 1954 to 1980 which subsequently returned to North Shields to breed.

Shields in a particular year) which returned is plotted against the year of fledging (five year running mean). Apart from the years of colony growth, the curve is similar to that of adult annual survival rates (Fig. 3.05), with a decline in the 1969 and 1970 cohorts. These cohorts would have recruited into the breeding group in 1973 and 1974, which were the years of lowest adult survival rates. If North Shields fledged Kittiwakes during their immature years suffered the same fluctuations in mortality as the adults did, there should be a correlation between the percent of each cohort which returned and the percent of that cohort which would have survived four years later with the known adult survival rates acting on them (tabulated in Appendix B). Fig. 3.11 shows that this was not the case. There was no significant linear correlation ($r_{25} = -0.04$). This supports the premise of Coulson & Thomas (1985) that mortality incurred by adults was prior to the breeding season when adults were associated with the colony and immatures were elsewhere (Coulson 1966a).

Although the proportion of birds which returned from each cohort can be explained by chick production, the balance of the recruits were made up from elsewhere. There seemed to be a constant input from North Shields (about 11% from each cohort), hence the remainder of recruits from outside the North Shields colony had to vary in order to make up the difference. The percent of the recruits which were immigrants is the compliment of the line in Fig. 3.08 and ranged from 42% to 100% (or nine to 31 recruits) for males. If this "quota" was completed from local colonies (e.g. Marsden, c. 4,000 pairs), that number of recruits would only be a very small proportion of their productivity.

3.4.2 Age at recruitment

Fig. 3.12 shows the five year running mean of the age of first breeding for males and females reared at North Shields which subsequently

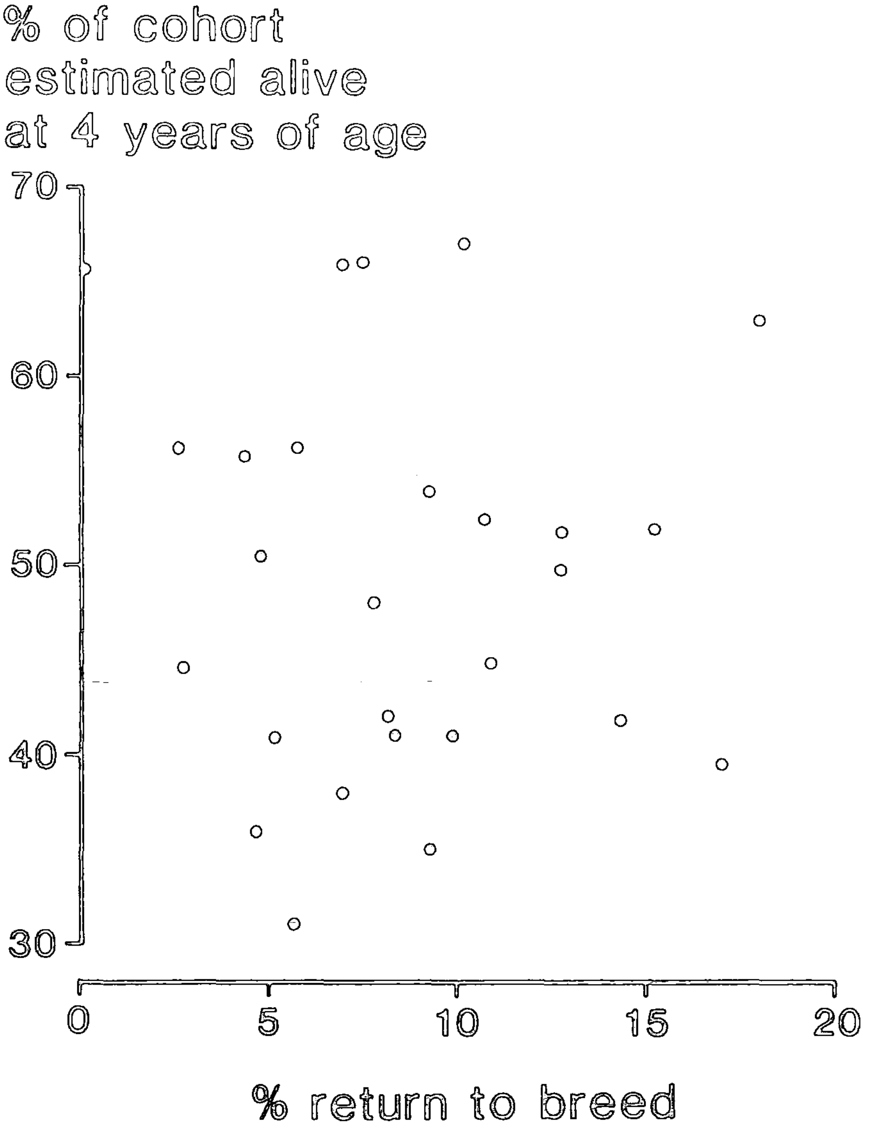

FIGURE 3.11: Relationship between the percentage of each cohort which returned to breed at the North Shields colony and the percentage of each of those cohorts estimated to be alive at four years of age with the known adult survival rates acting on them (see Appendix B), for each year between 1954 and 1980.

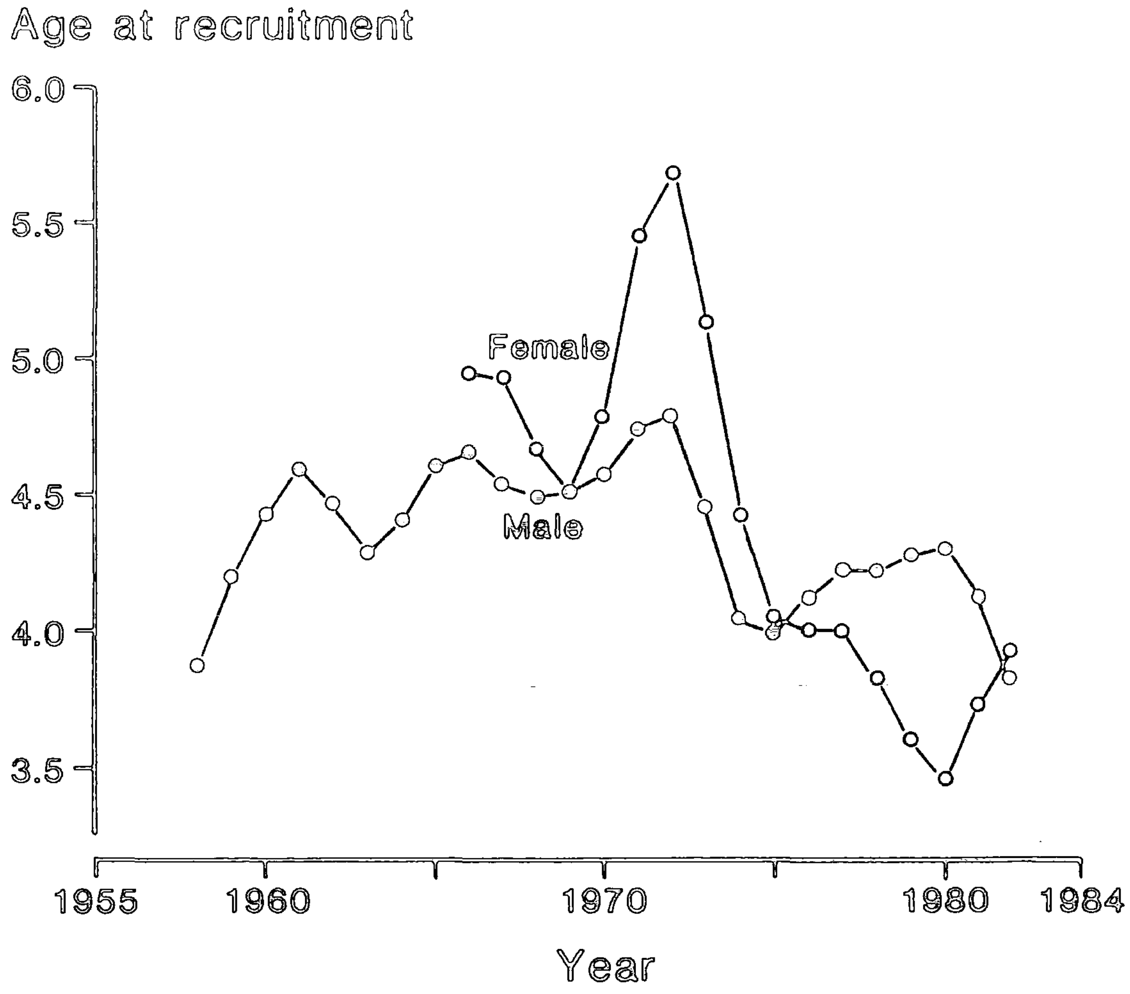

FIGURE 3.12: The five year running mean of the age at recruitment for natal male and female Kittiwakes at the North Shields colony over the period 1954 to 1984.

returned to breed. Females were represented by small samples, but they show a similar pattern to the males. The dramatic drop in age of first breeding in 1974 and 1975 was significantly different from the previous years and corresponds to the low adult survival rates following breeding in 1973 and 1974 (Fig. 3.05). Table 3.01 shows that the high mortality in the 1969 to 1974 period (column 3) differentially affected the breeding adults with one, two and three years of breeding experience, the most numerous breeders. Male age of recruitment recovered slightly, but not significantly and is presently declining again. This also corresponds to the current high mortality rates. Apparently, when annual survival rates dropped, the pool of potential recruits was drawn upon more heavily, and progressively younger Kittiwakes recruited into the breeding group.

3.4.3 Body size of recruits and prospectors

Fig. 3.07 demonstrated that the number of recruits increased to replace those breeders dying (see also Section 4.2), and Fig. 3.12 showed that the mean age of first breeding dropped by 18% by 1974/1975 to partially compensate for the loss of breeders. Concurrently, there was a drop in reproductive output (Fig. 3.03). Fig. 3.13 shows the five year running mean of body weights of male and female prospectors and recruits over time (from 1959 to 1984). Although males were heavier than females, breeders were significantly heavier than prospectors within a sex. The long-term trend of weights for male and female prospectors showed little fluctuation and no significant pattern. Indeed, there appeared to be a threshold weight for a healthy Kittiwake: males were about 375g and females 335g. On the other hand, there was a significant decline in both male and female recruits' mean body weights in 1972 and 1973. This may have corresponded to the low survival which followed years when recruits' body weights were low, and also to the subsequent decline in the age of first breeding.

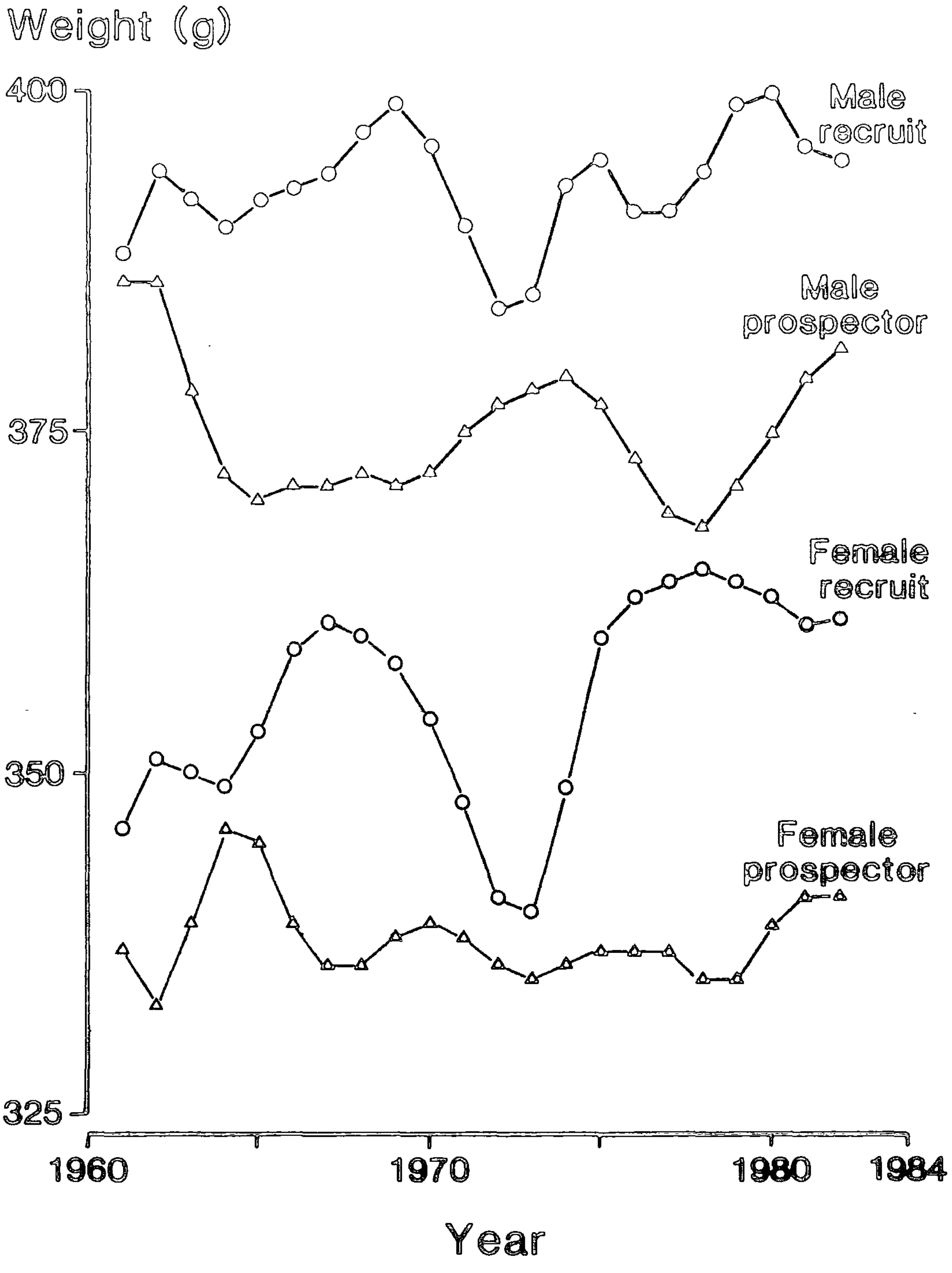

FIGURE 3.13: The five year running mean of body weights for male and female prospectors and recruits at the North Shields colony over the period 1959 to 1984.

Fig. 3.14 shows the five year running mean of the wing-length measurements of male and female recruits and prospectors from 1959 to 1984. Male prospectors and recruits did not differ significantly in their wing-lengths, while female recruits had significantly longer wings than female prospectors. In contrast to body weights, both recruit and prospector wing-lengths showed a significant decline (male and female, significant), although for prospectors it was in 1970-71, two years earlier than in recruits. If younger birds were drawn into the breeding colony during the decline in colony numbers and increased adult mortality rates, then younger (and possibly smaller) birds would move into the pool of prospectors. By 1970, this compensating mechanism must have depleted the pool and smaller birds were present at the colony as prospectors and recruits. The decline in wing-length of female prospectors started earlier (1967) and continued for longer (about 10 years) than that of recruits. For male prospectors, the decrease in wing-lengths appeared to recover before that of recruits, suggesting possibly that male prospectors opted out of breeding for a year. The decline in size of prospectors occurred about two years prior to that of the breeders. This implies that the larger, higher quality prospectors were extracted into the breeding group, following which there was a void, causing the mean size of recruits to decline. At the lowest point of the decline, recruits and prospectors had nearly the same body weight. In Sections 4.3.5 and 5.3.4. the implications of body size are considered in more detail.

3.5 Colony growth

3.5.1 Model of unrestricted colony growth

Coulson (1983) described the relationship between the size of 47 Kittiwake colonies in Britain in 1959, and their percentage increase between 1959 and 1969 by the equation: $Z = -0.44W + 3.09$, where $Z = \log_{10}$ percent

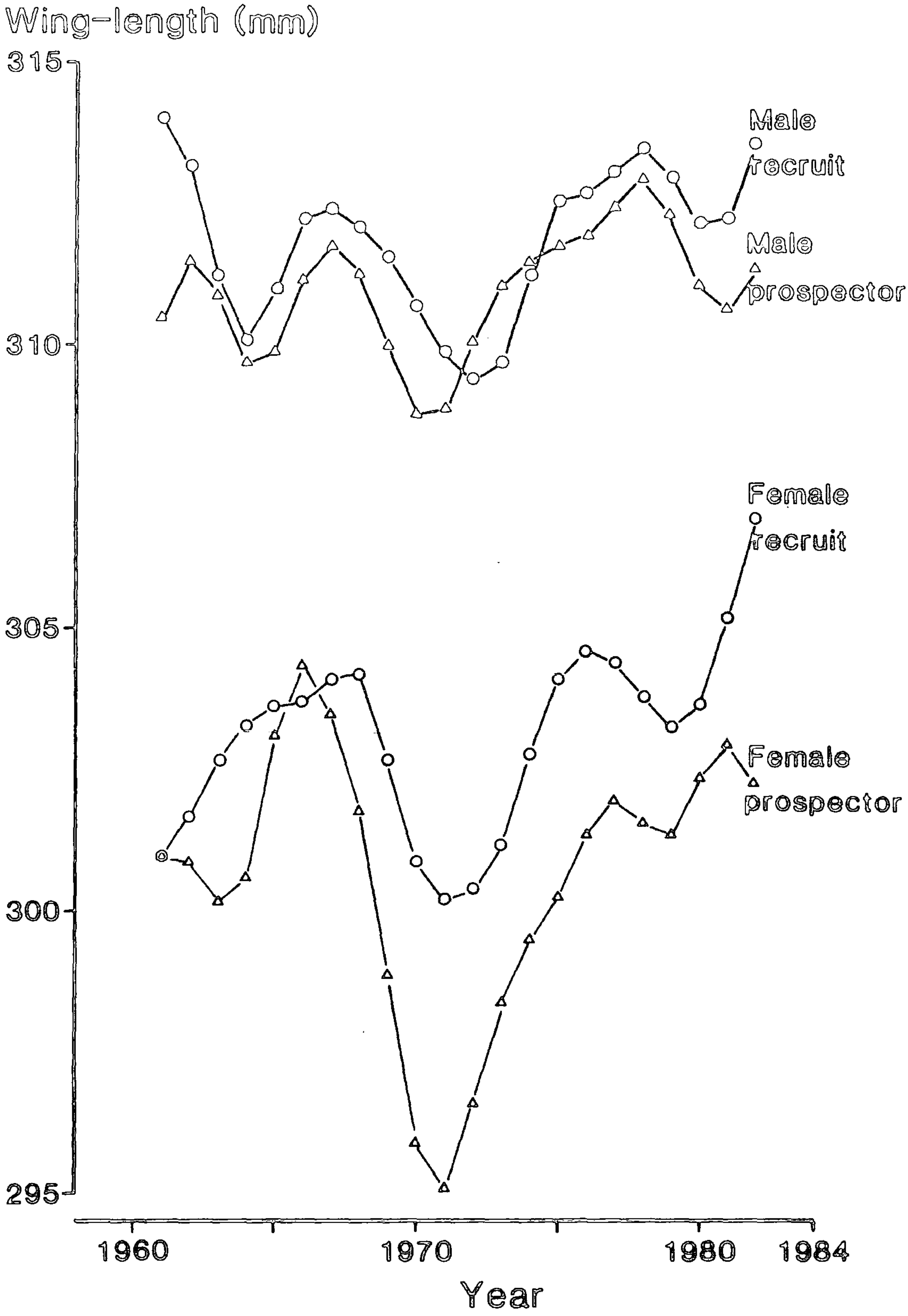

FIGURE 3.14: The five year running mean of wing-lengths for male and female prospectors and recruits at the North Shields colony over the period 1959 to 1984.

increase over 10 years and $W = \log_{10}$ colony size (see Appendix C). Although the general situation in Britain for the Kittiwake at that time was a four percent per annum increase, Coulson demonstrated that small colonies grew at a much faster rate than large colonies. He used this relationship to explain, at least in part, why colonies in the same region often grew at different rates and why the rate of growth could be higher in regions with a higher proportion of small colonies. He suggested that, in proportional terms, small colonies are more attractive to recruits to the breeding population.

While the relationship in Coulson's (1983) investigation described the size and percent increase for 47 colonies at a particular point in time, that same relationship can be used to describe the way a single colony grows and matures over time. Coulson's equation has been used to model the expected pattern of growth of a single Kittiwake colony. Appendix C describes the calculations involved in this model.

Fig. 3.15(a) shows the expected pattern of growth of a Kittiwake colony over a 200 year period. The model assumes that growth of the colony is not restricted (e.g. by food or space). Fig. 3.15(b) shows the rate of growth by plotting colony size on a logarithmic scale. In fact, colony growth is not exponential; it does not increase by a constant factor. Although absolute numbers increase each year, the small colony grows at a faster rate than does the large colony. This point is further illustrated in Fig. 3.16(a) which shows that the percent increase in numbers per year declines progressively with time. In order for the colony to grow at the calculated rate, more and more recruits are required in each year (see Appendix C for values), but the proportion of breeders in the colony which are recruits declines each year as colony size increases (Fig. 3.16(b)). Hence, in the small, young colony the rate of increase and the recruitment

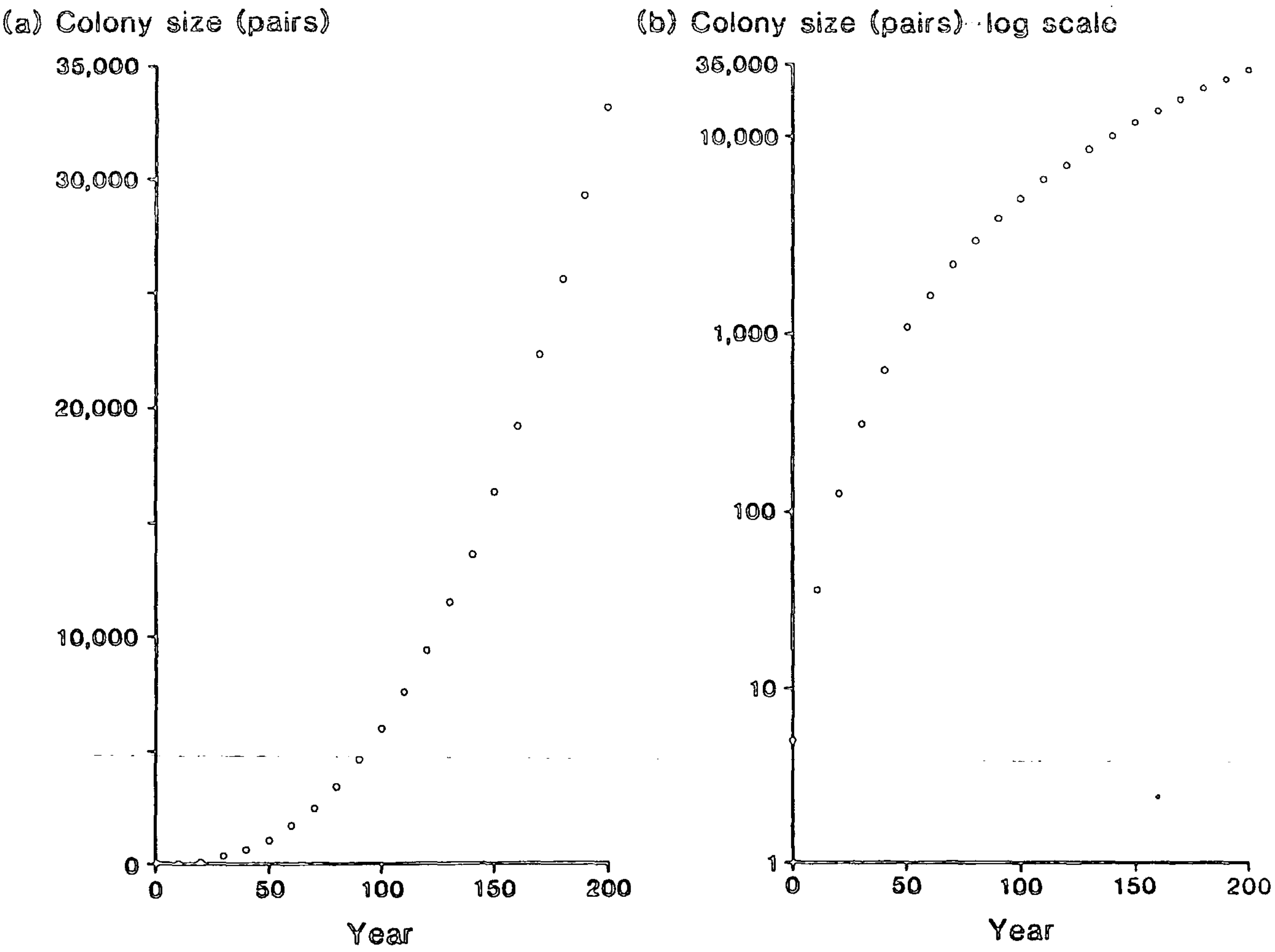

FIGURE 3.15: Pattern of growth of a single Kittiwake colony over a 200 year period on (a) linear and (b) logarithmic scales. See Appendix C for calculations.

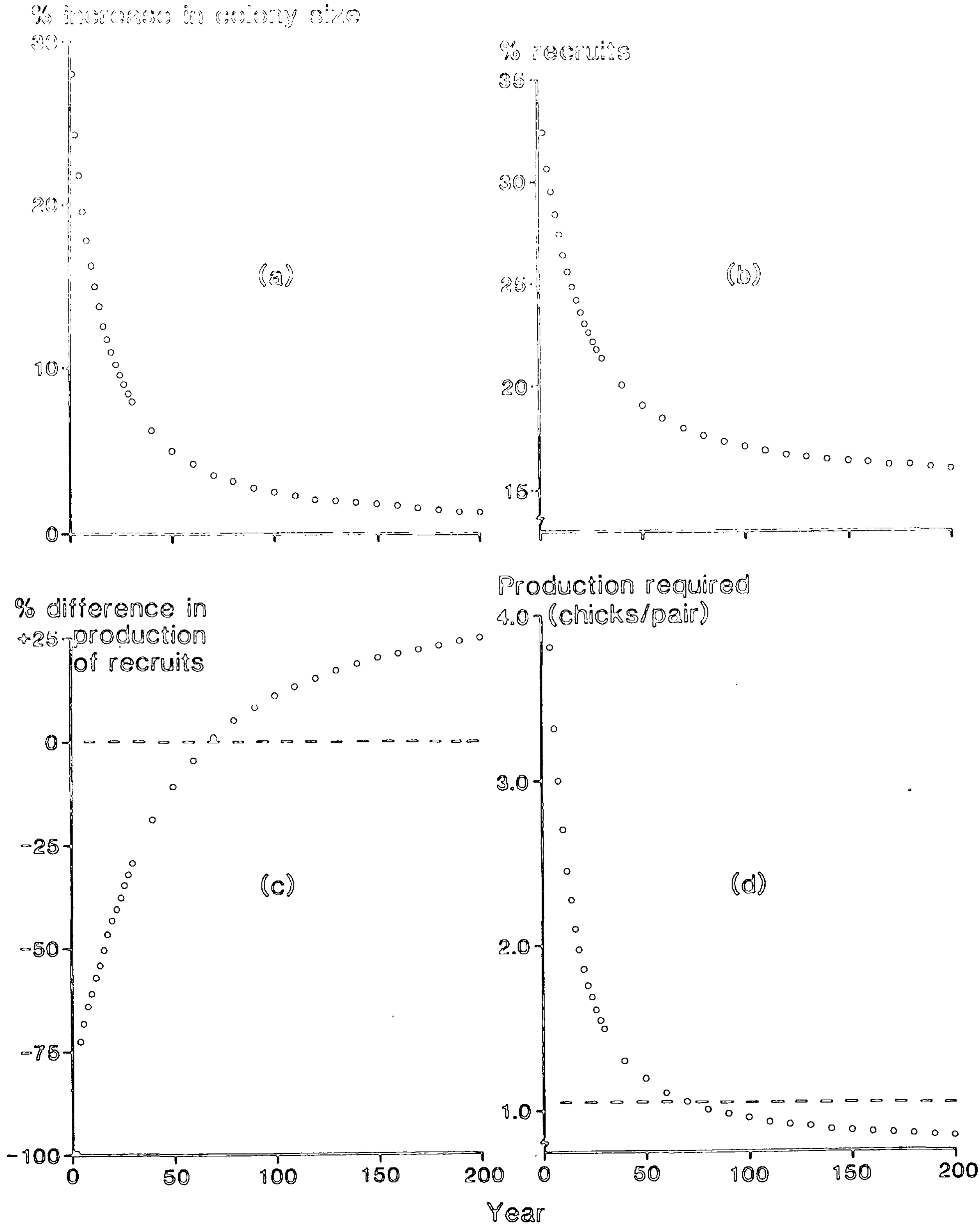

FIGURE 3.16: Pattern of (a) percentage per annum increase in colony size; (b) annual recruitment rates; (c) percentage difference in the number of recruits a colony of a particular size is capable of producing, and the actual number required to maintain the pattern of growth in Fig. 3.15; and (d) the production (number of chicks fledged per pair) required to supply enough recruits four years later to maintain the pattern of growth in Fig. 3.15. See Appendix C for calculations.

rate are much higher than in the large, old colony. That is, small colonies are proportionately more attractive than large ones.

If chick production is the same in all colonies, a large colony needs proportionately fewer recruits due to its slower rate of growth, and would appear to produce a surplus of recruits, while small colonies can only be sustained by immigration. On the other hand, if colonies are discrete units, chick production needs to be much greater in young colonies than in old ones.

Fig. 3.16(c) shows the percent difference in the number of recruits a colony of a given size is capable of producing (assuming chick production of 1.05 per pair per year, Section 3.2.2; age of first breeding of four, Section 3.4.2; and the survival rate from fledging to breeding of 0.40, Appendix C) and the actual number required to maintain the pattern of growth as modelled. For the first four years no recruits are supplied by the colony, as it takes four years for Kittiwakes to attain sexual maturity. Initially, the percentage difference between the number of chicks produced and the number required is -100%. Not until the colony is nearly 70 years old, does the chick production of the colony meet the recruitment needs. Another way to illustrate this point, is to calculate the chick production required to supply enough recruits four years later to maintain the pattern of growth. This is shown in Fig. 3.16(d). The point where the production required reaches 1.05 chicks per pair is nearly 70 years as in Fig. 3.16(c). Even if other, but reasonable values of chick production are used, similar conclusions are reached. In the natural situation, either old colonies are less productive, or they supply young colonies with recruits, or both. Certainly young colonies have to be supported by immigration. On the other hand, Furness & Birkhead (1984) have suggested that large colonies have a lower reproductive output per pair than do small colonies.

3.5.2 Limits of colony growth at North Shields

Fig. 3.17 shows the growth of the North Shields colony compared with the pattern of growth predicted by the model. North Shields growth was similar to the model until about 1965 when numbers at North Shields began to decline and stabilized at about 90 pairs. What limited the maximum colony size at North Shields to just over 100 pairs? Fig. 3.18 shows the relationship between colony size and the percentage of attractive sites which were available for all years at North Shields. Attractive sites are defined here as those sites in the "centre" of the colony (Coulson 1968). Coulson (1968) showed a higher reproductive success for Kittiwakes nesting in the centre of the North Shields colony. He defined the centre as those ledges occupied when the colony was one half its maximum size. Fig. 3.18 reveals that the percent of attractive sites available at North Shields declined with colony size. This significant relationship from 1954 to 1967 is described by the equation: $y = -0.603x + 68.0$ (where y is the percent of attractive sites available and x is colony size; $r_{12} = -0.97$). Extrapolating this line to the x-axis gives a maximum colony size of 113 pairs, which is very close to the actual maximum of 104 pairs. Fig. 3.18 also shows a similar pattern during the decrease in colony size ($y = 1.084x + 112.7$; $r_{13} = -0.85$). This figure suggests that numbers at North Shields were limited by the availability of attractive sites. On the other hand, there were apparently suitable ledges, which were never used by breeders in any year, and ledges occupied in some years but not in others. In other words, there was not a <u>physical</u> shortage of nest sites at North Shields in any year.

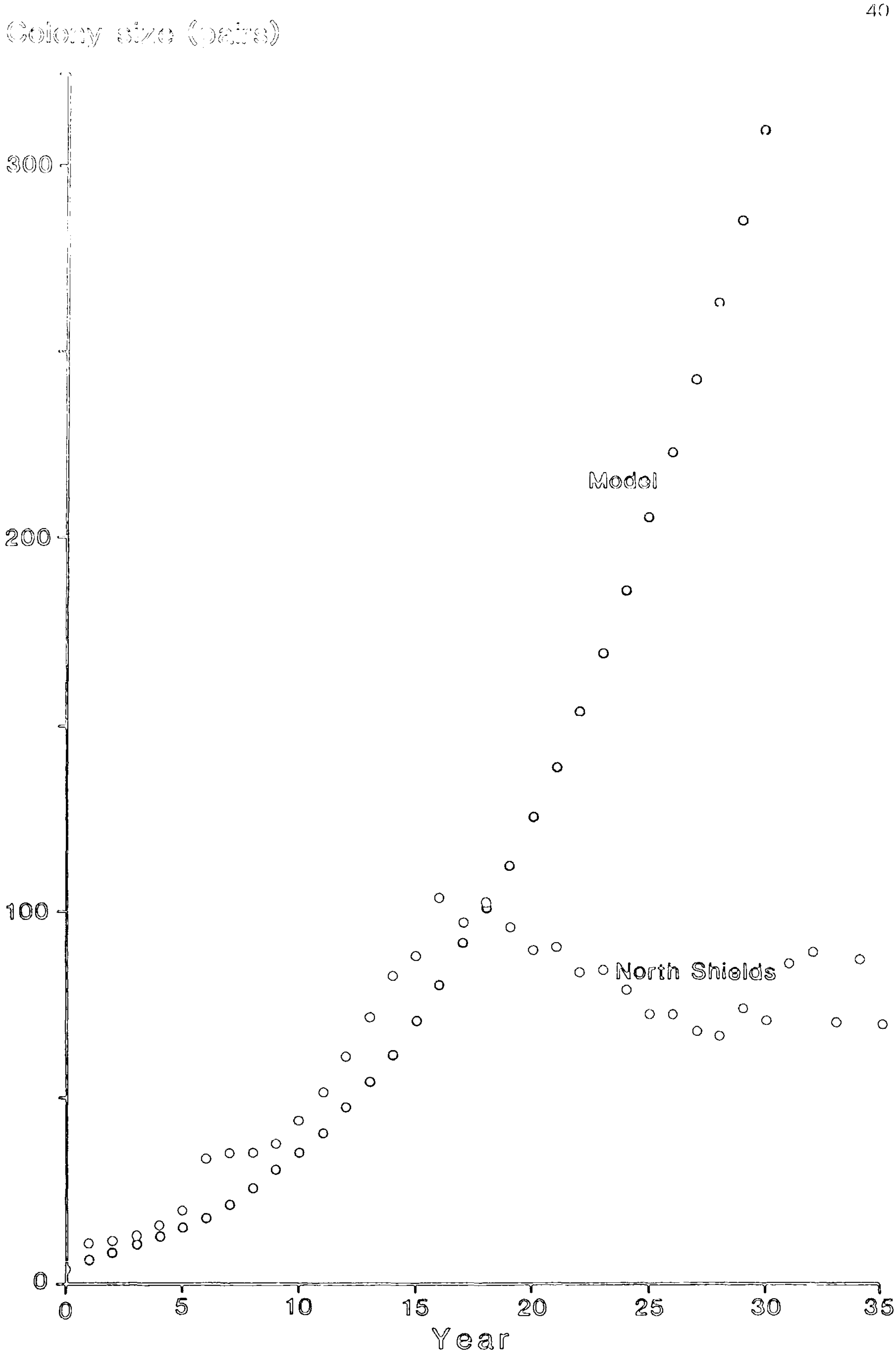

FIGURE 3.17: Relationship between the colony size at North Shields between 1949 and 1984, and the expected colony size based on the model in Appendix C.

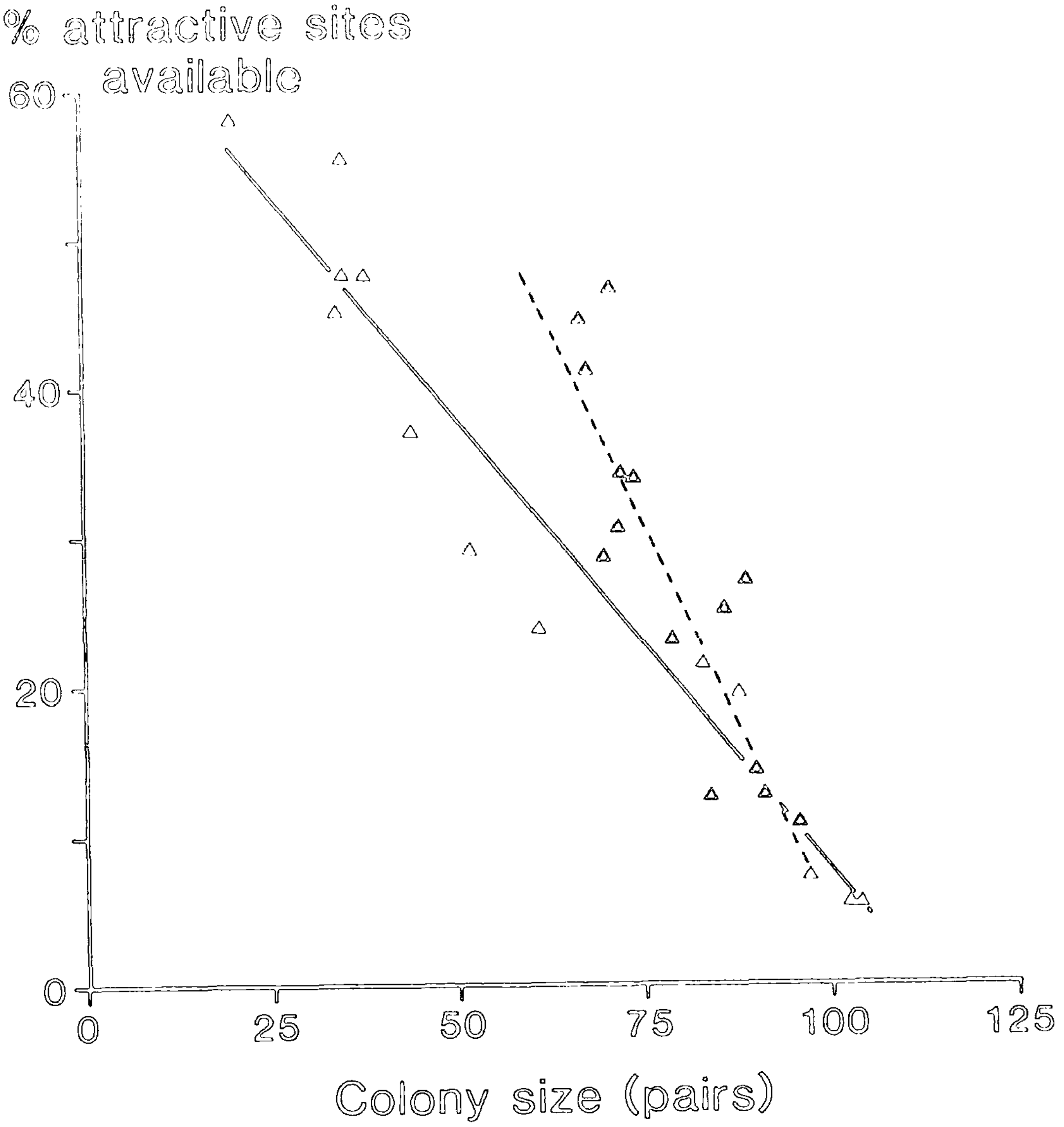

FIGURE 3.18: Relationship between the colony size and the percentage of attractive sites available (number of sites in the centre not occupied/total sites in the centre) at the North Shields colony in each year between 1954 and 1982. Solid triangles are 1954 to 1967 (solid linear regression line), open triangles are 1968 to 1982 (broken linear regression line).

CHAPTER 4. BEHAVIOUR AND ATTENDANCE OF RECRUITS AND PROSPECTORS

4.1 Introduction

Section 3.5.2 showed that there was not a physical shortage of nest sites at North Shields, and that the colony size after 1965 was 10 to 20 pairs below the maximum size. As the availability of attractive sites declined, presumably competition for these sites increased and may have restricted some birds from breeding. On the basis of this, I propose that nest sites are socially limited. That is, the social structure of colonies actually inhibit some birds from breeding. That being the case, there must be a pool of potential breeders associated with the colony which are restricted from breeding.

This chapter describes two forms of indirect evidence which suggest there is an excess of potential breeders associated with the colony. Then there is a description of this pool based on direct observations in 1982 to 1984.

4.2 Indirect evidence for a pool of potential recruits

Fig. 3.07 showed the positive relationship between the number of deaths from one breeding season to the next and the subsequent number of recruits, which demonstrated that there is a compensatory effect for deaths. This mechanism whereby recruits replaced mortality (at least partially), could only operate if there was a pool of birds waiting to breed.

In 1962 and 1983 new ledges were added to the warehouse, increasing the density of possible nest sites in the apparently favoured centre of the colony (Coulson 1968; Section 2.1). This experiment can be likened to a breeder removal experiment (e.g. Manuwal 1974) as each results in an increased number of available sites. Both 1962 and 1983 showed very high recruitment rates of about 35% (Table 4.01), compared to an overall mean

TABLE 4.01: Results of the experiments where new ledges were added to the North Shields warehouse before the 1962 and 1983 breeding seasons.

	Year new ledges were added	
	1962	1983
% recruitment in that year (colony size)	35.4 (72)	34.5 (87)
% new ledges occupied in that year (n)	81.8 (11)	84.2 (19)
% nests on new ledges occupied by recruits in that year	100.0	100.0

recruitment rate of 27%. Table 4.01 shows that in both years, over 80% of the new ledges were occupied, all by pairs with at least one recruit. Established breeding birds did not move from existing sites onto the new ones. Thus sites were made available in the attractive centre of the colony and were occupied by recruits. In Section 5.3.1, evidence is presented to show that the overall use of sites at the colony was approximately 65% of those available. The fact that 80% of the new ledges were used indicates a strong attraction to the new sites. There were still unoccupied ledges at the periphery of the colony which were not used.

Hence, when sites were made available either through death or the addition of new ledges, recruitment rates increased. In order for this effect to occur, there had to be a pool of potential recruits (Kittiwakes of breeding age which had not bred previously) ready and waiting to breed.

4.3 Direct observations of the pool of prospectors associated with the North Shields colony

4.3.1 Size of the pool

In 1982 and 1983, direct observations were made of the non-breeders associated with the North Shields colony. Prospectors (Kittiwakes which had not bred previously) were seen loafing on the roof of the warehouse and on ledges unoccupied by breeders. Based on the relative frequency of sighting of ringed and unringed potential recruits at the colony during spot observations from April to August, the size of the pool of potential recruits was estimated (Lincoln Index; Table 4.02). Table 4.03 shows that there were over 100 potential recruits associated with the colony in each year and about 40% actually recruited. This left the remaining Kittiwakes of breeding age, which did not breed, associated with the North Shields colony.

TABLE 4.02: Estimation of the size of the pool of potential recruits[1] at the North Shields colony in 1982 and 1983 using the Lincoln Index.

	1982	1983
Number of marked animals in sample (M_S)	2095	802
Total number of animals in sample (T_S)	4460	3063
Number of marked individuals in total pool of potential recruits (M_P)	31	21
Total size of pool of potential recruits[1] ($T_P = T_S \cdot M_P/M_S$)	66.0	80.2

Notes: [1] Potential recruits which did not breed in those years.

TABLE 4.03: Size and composition of the pool of potential recruits at the North Shields colony in 1982 and 1983. The number of individuals fledged from North Shields are in parentheses.

	Year	
	1982	1983
Total number of potential recruits	104 (24)	139 (23)
Number of recruits	38 (7)	59 (8)
Remaining potential recruits which did not breed[1]	66 (17)	80 (15)
Number of breeding birds	140 (19)	174 (31)

Notes: [1] Calculated in Table 4.02.

4.3.2 Proportion of natal prospectors

About 20% of the birds in the pool were hatched at North Shields; the others originated from elsewhere. This proportion of natal to immigrant Kittiwakes was not significantly different from that which actually recruited into the colony (Table 4.03; $\chi^2_1 = 1.54$, n.s.), suggesting that natal Kittiwakes were not favoured.

4.3.3 Age structure

Table 4.04 shows the number of natal Kittiwakes seen in the three years of study according to their status and age. There were only four one year olds seen at the colony, only 3% of those estimated alive. These young Kittiwakes spent very little time on land. About 50% of two and three year olds estimated to be alive were seen at the colony, although some of the latter were breeding. There were only about 30% of four and five year olds and 10% of six year olds seen. This was due to the decline in the number of prospectors aged four and over. Fifty percent of the prospectors seen were two years old, while only 11% were four or over.

4.3.4 Sex of prospectors

Many of the prospectors seen in 1982 to 1984 could not be sexed, hence it is not possible to detect sex-related differences in behaviour or attendance of prospectors. Since 1954, 614 Kittiwakes marked on the North Shields warehouse were caught as prospectors. Of those, 51% returned to breed and all of those were sexed. The ratio of males to females (1.44:1) among those Kittiwakes was significantly higher than expected based on the ratio of 1.07 males : 1.0 female among recruits ($\chi^2_1 = 6.56$).

All of the natal Kittiwakes of both sexes which recruited in 1983 and 1984 were seen in the previous year (10 males and two females). Hence, the higher than expected ratio of males to females caught as prospectors

TABLE 4.04: Observations in 1982 to 1984 of North Shields fledged Kittiwakes at North Shields according to their age and status.

Age	Number seen at North Shields		Number estimated alive[1]	% alive which were seen
	Prospectors	Breeders		
1	4	0	134	3.0
2	56	0	114	49.1
3	39	10	93	52.7
4	10	13	80	28.8
5	2	15	59	28.8
6	0	6	48	12.5

Notes: [1] Estimated from 60% survival from fledging to age one, and 82% thereafter.

which subsequently returned to breed, possibly reflects a behavioural difference in catchability between males and females; males may be on ledges more often as prospectors, although there is no evidence to support this.

For 296 of the 312 known-sex Kittiwakes which prospected in one year and bred the next year, data are available for the site each individual was caught on and the site where it subsequently recruited. For males and females, 35% and 18%, respectively, bred on the same site where they prospected. This significant difference between males and females (χ_1^2 = 10.12) reflects the stronger site tenacity of males. There was no significant difference for males or females in body weights or adult survival rates, according to whether or not they recruited onto the same site they were caught on as prospectors.

Hence, although many prospectors could not be sexed, evidence presented suggests that males spent more time on ledges than did females and showed a stronger site tenacity.

4.3.5 Body size

In Section 3.4.3 the long-term changes in the body weights and wing-lengths of male and female breeders and prospectors were discussed. Fig. 3.13 showed that body weights of prospectors were relatively constant, implying that there is a threshold weight for a healthy Kittiwake. In fact, the mean weights of male and female recruits were significantly heavier than those of prospectors (Table 4.05). The wing-lengths of males were not significantly different, although those of females were. Thus if body weight within a sex is taken as a measure of condition, then only the Kittiwakes in the best condition recruit into the breeding population.

TABLE 4.05: Mean body weights and wing-lengths (± s.e.) of male and female prospectors and recruits between 1959 and 1984.

	Male		Female	
	Prospectors	Recruits	Prospectors	Recruits
Weight (g)	375.0 ± 1.92	391.6 ± 1.72	335.6 ± 1.54	354.2 ± 1.74
Wing-length (mm)	311.0 ± 0.41	311.2 ± 0.37	299.8 ± 0.55	303.1 ± 0.42
n	175	258	146	264

4.3.6 Intercolony movements

A portion of this pool of prospectors was also associated with neighbouring colonies (e.g. Marsden, Gateshead, Tynemouth). Coulson & Wooller (1976) reported that no birds which had bred at North Shields were seen at neighbouring colonies. In contrast, of those which were caught as prospectors at North Shields which did not breed at North Shields, 23% were seen at another colony. In the sample of 614 Kittiwakes caught as prospectors between 1954 and 1983 (including the sample from Coulson & Wooller 1976), 299 did not breed at North Shields. Of those, 26% were seen at another colony.

Table 4.06 shows that only two and three year old prospectors were seen at more than one colony in the same season. Older prospectors and all breeders were seen only at one colony.

4.4 Attendance at the colony

The observations in this section were made in 1983, unless otherwise stated. Table 4.07 summarizes the chronology of reproductive events at the North Shields colony in 1983. When detailed observations began on 14 April, 25% of the ringed recruits and all of the established breeders had arrived.

4.4.1 Seasonal attendance

The presence of Kittiwakes at the colony which were not on nests or nest sites was recorded and expressed as the mean number seen at any one time (on the roof and vacant sites). Table 4.08 and Fig. 4.01 show the seasonal pattern of attendance for these Kittiwakes. The mean number of off-duty breeders (breeding birds not on their nest site) increased significantly from 0.79 in 7-20 April to 2.18 in 21 April-4 May, and remained relatively constant until late June (about 1.7 Kittiwakes at any

TABLE 4.06: Observations in 1982 to 1984 of North Shields fledged Kittiwakes at North Shields, Marsden, Tynemouth and Gateshead colonies according to their age and status.

Status Where seen	Age 1	 2	 3	 4	 5	 6
Prospectors						
North Shields only	4	56	39	10	2	0
Other colony only[1]	0	5	12	13	0	0
North Shields + other colony	0	4	2	0	0	0
Breeders						
North Shields only	-	-	10	13	10	3
Other colony only	-	-	2	2	2	1
North Shields + other colony	-	-	0	0	0	0

Notes: [1] Other colonies = Marsden, Tynemouth, Gateshead.

TABLE 4.07: Chronology of events in the reproductive cycle during detailed observation periods at the North Shields colony in 1983.

Weekly periods beginning	Event
14 April	All established breeders on sites; 80% of recruits arrived.
21 April	95% of recruits arrived.
28 April	All recruits arrived.
5 May	First clutch laid (7 May).
12 May	50% of clutches laid (by 17 May)
19 May	All recruits paired on sites.
26 May	75% of clutches laid (by 28 May).
2 June	First chick hatched (5 June)
9 June	Last clutch laid (11 June).

TABLE 4.08: Seasonal pattern of attendance of off-duty breeders and prospectors at the North Shields colony in 1983. The mean number (± s.e.) of individuals seen at one time is shown.

Two week period beginning	Number of spot observations	Number of individuals/scan		
		Off-duty breeders	Marked 2 year olds	Other prospectors
7 April	45	0.79 ± 0.14	0	0.29 ± 0.09
21 April	145	2.18 ± 0.16	0.01 ± 0.01	3.15 ± 0.29
5 May	95	1.64 ± 0.17	0.05 ± 0.02	5.77 ± 0.38
19 May	122	1.96 ± 0.19	0.26 ± 0.05	6.73 ± 0.34
2 June	74	1.68 ± 0.17	0.08 ± 0.04	6.74 ± 0.36
16 June	45	1.21 ± 0.18	0.44 ± 0.10	4.84 ± 0.36
30 June	34	2.44 ± 0.25	0.62 ± 0.11	8.38 ± 0.56
14 July	28	3.46 ± 0.37	0.29 ± 0.09	10.70 ± 0.62
28 July	23	1.29 ± 0.27	0.04 ± 0.04	3.07 ± 0.38

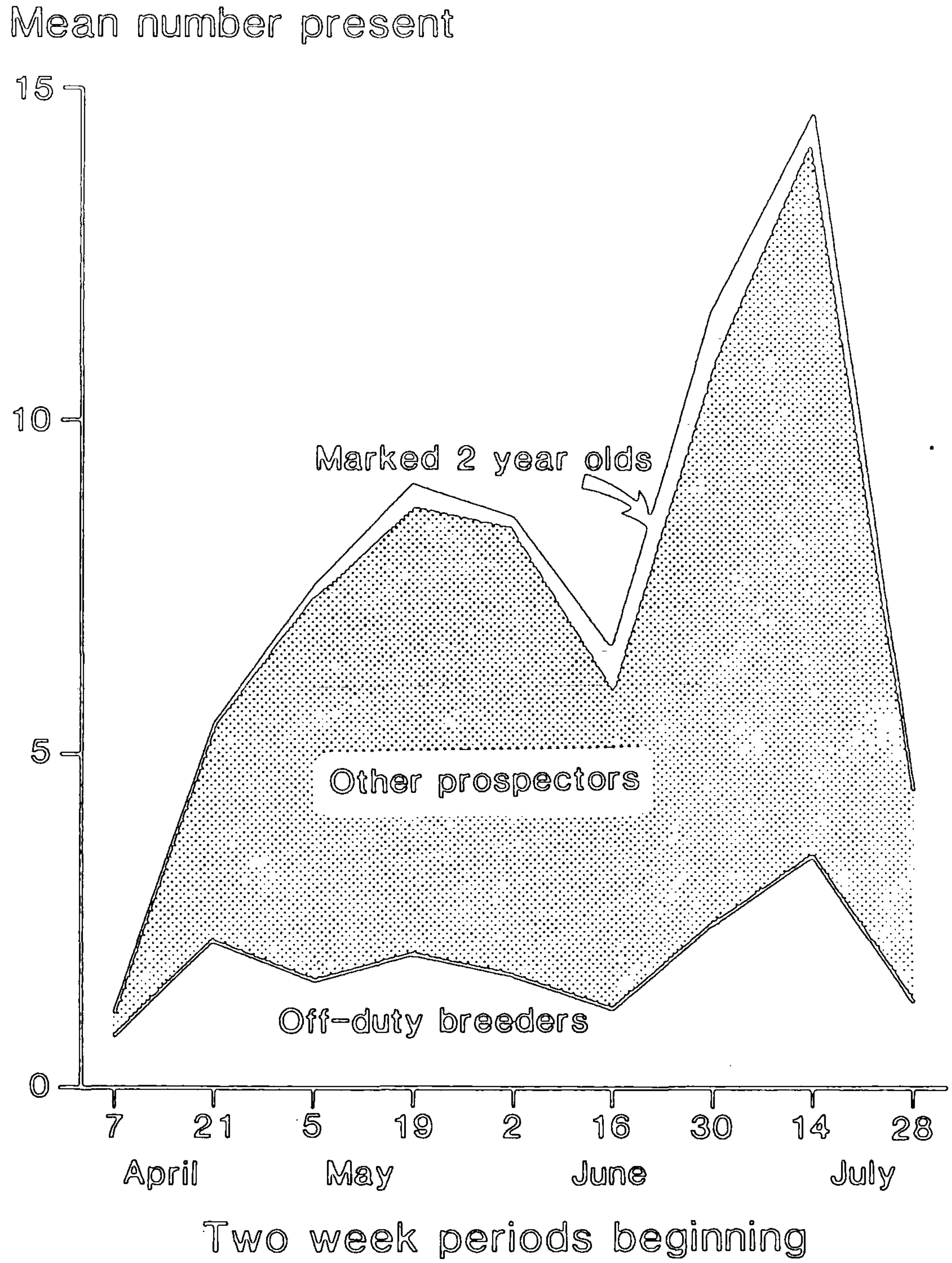

FIGURE 4.01: Seasonal pattern of attendance of off-duty breeders and prospectors (marked two year olds and others) at the North Shields colony in 1983. The cumulative mean number of Kittiwakes seen at one time is shown.

time). There was a significant increase in July corresponding to the time when parents were feeding chicks and a further increase after chicks fledged. Numbers declined in August as breeders deserted the colony.

Prospectors are divided into those which were ringed two year olds (all ringed as nestlings at North Shields), and the remaining ringed birds plus unringed birds. Ringed two year olds were not present in the 7 - 20 April period. They were first seen in the 21 April-4 May period; their numbers peaked in late June and early July (0.62) and dropped off following 13 July. Other prospectors increased in numbers to a mean of about six (at a time) at the beginning of the incubation stage. There was a significant decline in late June followed by a peak of 10.7 Kittiwakes in the 14-27 July period. The decline in late June coincided with the relative inactivity at the colony at the end of incubation when very few birds were paired on nests (pers. observ., Hodges 1974). The subsequent peak was a result of an influx of non-breeding birds at the time chicks fledged. It is important to note that the number of prospectors per scan initially peaked in late May; a date which was too late for breeding in 1983 (Section 4.4.2).

Fig. 4.02 illustrates the percent of each two week observation period each ringed prospector and recruit was seen. This was calculated for 1983 recruits until 18 May when most had established their sites, and over the entire season for ringed two year olds and ringed prospectors at least three years old. Individually marked recruits were seen, on average, 50 to 60% of the time prior to their site occupation. They were present a mean of 17.8 ± 0.56 of the 19 observation days in May. In contrast, prospectors at least three years old were seen less than 5% of the time from 7 April - 4 May, and only 20% of the time until early June. In fact they were present only on a mean of 3.1 ± 1.36 of the 19 observation days in May.

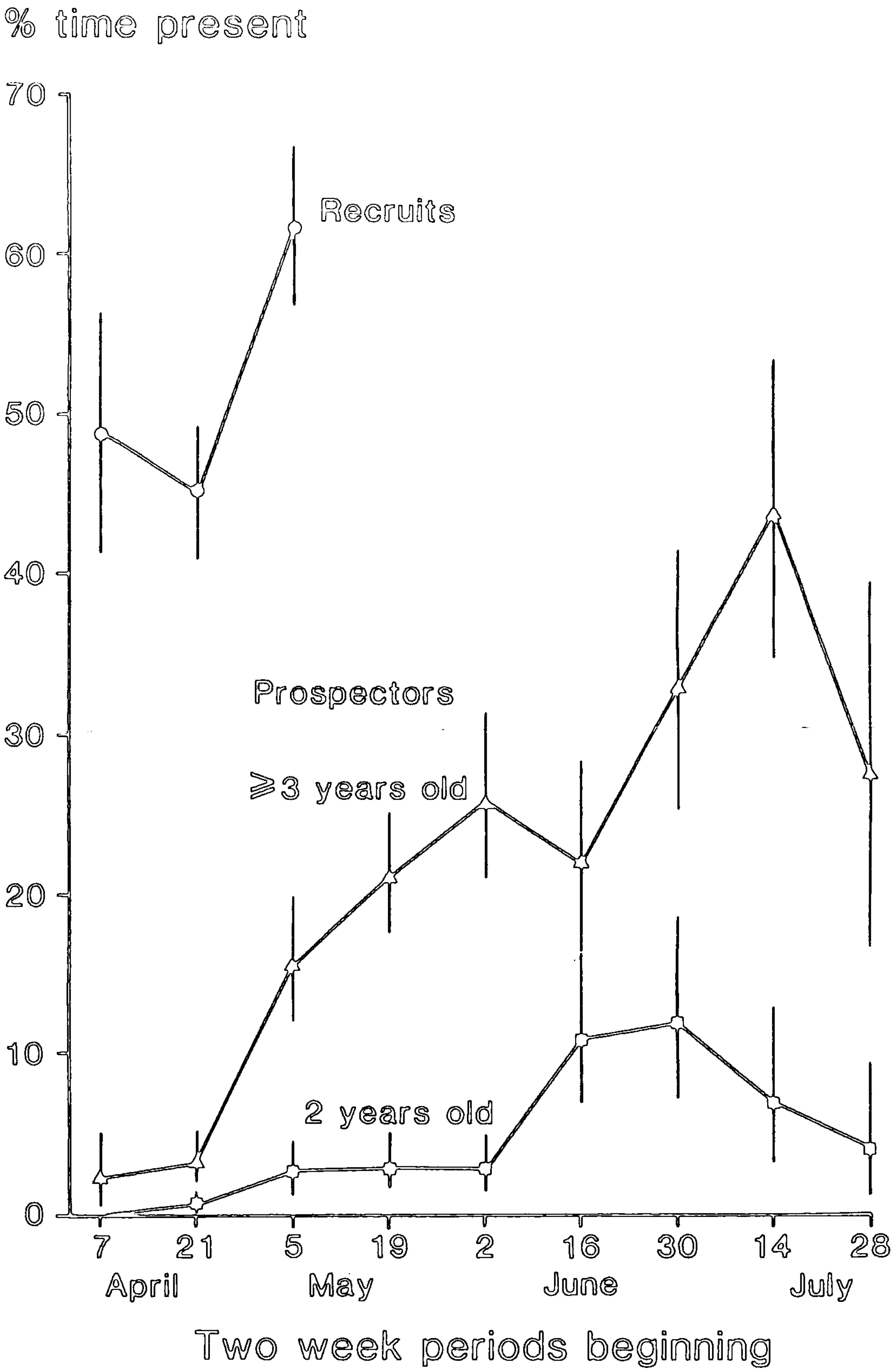

FIGURE 4.02: Mean percentage (± s.e.) of the time during each two week observation period which ringed prospectors (two years old and at least three years old) and recruits were seen at the North Shields colony in 1983.

These prospectors were seen progressively more of the time until late July, following which their attendance dropped off. Two year olds showed a similar seasonal pattern to the older prospectors, their presence did not exceed 12% of the time during observations.

The pattern of an increased number of prospectors seen at any one time in July in Fig. 4.01, can be partly accounted for by the increased attendance of individuals at the colony in Fig. 4.02. On the other hand, the number of marked Kittiwakes at the colony increased from April to May and declined in August (Table 4.09). Although the number of marked individuals present in a month was constant from May to July, Table 4.09 shows considerable turnover. Marked prospectors at least three years old seen in April were more likely to be seen in another month suggesting a stronger attachment to the colony for early arriving Kittiwakes.

4.4.2 Arrival dates, departure dates and duration of stay

Arrival dates, departure dates and duration of stay of prospectors were considered in relation to age. Kittiwakes ringed as chicks at North Shields were used in calculations, as their age, arrival and departure dates were known. Data from all three years of study were combined. Kittiwakes which were seen only on one occasion were used in mean arrival dates and duration of stay calculations. They were omitted from mean departure date calculations. Duration of stay was the number of days between the earliest (arrival) and latest (departure) sightings of individuals in a season.

Fig. 4.03 shows the arrival and departure dates of prospectors and breeders according to age. There are several points to note: (1) Older birds arrived earlier than younger birds. For individuals seen in consecutive years, only one of 37 examples arrived later than in the previous year. Table 4.10 shows that the greatest change in arrival dates between consecutive years occurred in the youngest birds. (2) For birds of a

TABLE 4.09: Number of individually marked prospectors seen in each month and in subsequent months at the North Shields colony in 1983; (a) prospectors at least three years old, (b) two year old prospectors.

(a)

Month	No. seen	No. not seen in another month	No. seen subsequently in each month				% seen in another month
			May	June	July	August	
April	7	2	5	3	3	1	71
May	11	4	-	5	5	1	64
June	11	4	-	-	7	3	64
July	11	4	-	-	-	3	64
August	3	0	-	-	-	-	100

(b)

Month	No. seen	No. not seen in another month	No. seen subsequently in each month		% seen in another month
			June	July	
May	7	4	3	1	43
June	6	1	-	3	83
July	7	4	-	-	43

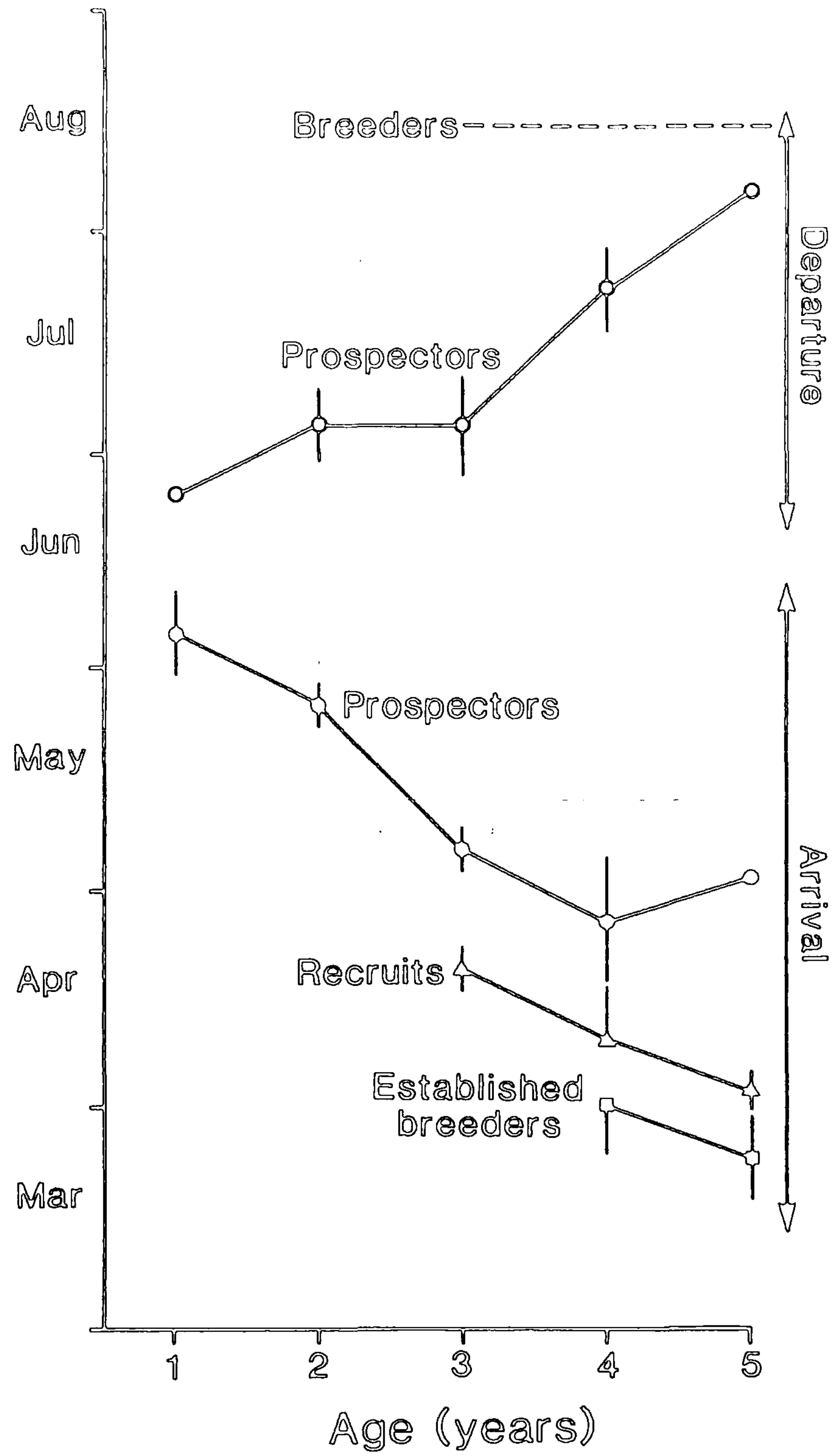

FIGURE 4.03: Mean arrival and departure dates (± s.e.) of prospectors, recruits and established breeders according to age at the North Shields colony between 1982 and 1984.

TABLE 4.10: Difference in mean arrival dates (± s.e.) of North Shields fledged prospectors in consecutive years (data from 1982 to 1984).

Consecutive ages (years)	Advancement of arrival dates (days)	(n)
One -- two	69.0 ± 19.0	(3)
Two -- three	33.3 ± 5.4	(22)
Three -- four	22.4 ± 4.1	(12)
Four -- five	17.4 ± 4.2	(9)

similar age, established breeders arrived earlier than recruits (Kittiwakes breeding for the first time), and recruits arrived earlier than prospectors. (3) No birds arriving after 4 May bred. These later arrivals rarely obtained mates and never built nests. (4) Older prospectors left the colony later than younger prospectors. (5) Breeders' departure dates did not vary with age or their breeding status. The mean date of departure for breeders (16 August ± 3.1) was later than that of prospectors, regardless of age.

Fig. 4.04 shows that the duration of stay varied with age, older birds were seen over a longer period than younger birds, even though about half of two and three year old prospectors were seen only on one occasion. No Kittiwake which bred in the next year was seen on only one occasion at the North Shields colony in the year prior to breeding; 31% of Kittiwakes which prospected in the next year and 56% of Kittiwakes which were not seen again at the colony were seen only once.

Mean arrival dates of prospectors were significantly earlier for all age groups if the individuals were present in the previous year (Table 4.11(a)). Departure dates did not vary with experience at the colony. In addition, two year olds which bred the next year, regardless of whether they were present at the colony last year (i.e. two years prior to breeding) arrived significantly earlier (about 11 days) than two year olds which did not breed the next year, and they stayed three times as long, on average (mean of 75.5 ± 14.7 days, Table 4.11(b)).

All marked recruits prospected at least one year prior to breeding; there was no age-related difference in arrival or departure dates or duration of stay among prospectors which bred the next year (Table 4.11(b)). All birds which bred in the next year arrived by 11 June (mean of 10 May) and stayed on average 74.5 days. Thus the evidence implies that early arrival and high attendance in one year reflects the Kittiwakes' tenacity

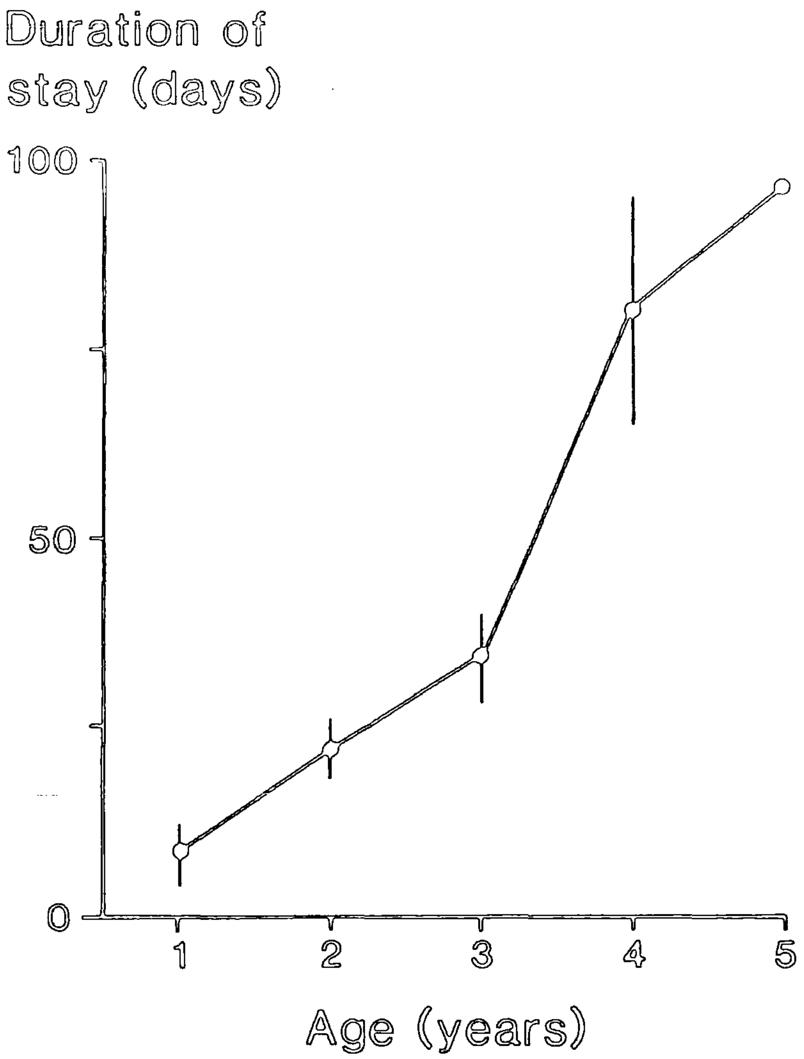

FIGURE 4.04: Mean duration of stay (± s.e.) of prospectors according to age at the North Shields colony between 1982 and 1984.

TABLE 4.11: Mean arrival dates, departure dates and duration of stay (± s.e.) of prospectors (a) according to age and whether they had had experience at the colony in the previous year (data for prospectors seen in 1983 and 1984), and (b) in the year prior to breeding for the first time and according to age (data for prospectors seen in 1982 and 1983).

(a)

Age	Status	(n)	Arrival date	Departure date	Duration of stay (days)
2	inexperienced	(28)	1 Jun ± 4.5	24 Jun ± 7.1	16.1 ± 4.0
	experienced	(4)	17 May ± 6.1	27 Jun ± 16.1	43.8 ± 11.3
3	inexperienced	(11)	24 May ± 7.1	12 Jul ± 15.1	21.5 ± 10.7
	experienced	(14)	30 Apr ± 4.4	29 Jun ± 8.0	38.4 ± 10.7
4	inexperienced	(1)	15 Jul –	22 Jul –	7.0
	experienced	(5)	27 Apr ± 9.2	13 Jul ± 3.8	61.0 ± 19.0

(b)

Age of prospectors which bred next year	(n)	Arrival date	Departure date	Duration of stay (days)
2	(6)	16 May ± 3.1	31 Jul ± 14.1	75.5 ± 14.7
3	(5)	5 May ± 12.1	14 Jul ± 22.5	69.4 ± 18.6
4	(2)	4 May ± 26.5	28 Jul ± 4.5	84.0 ± 22.0

to the colony in subsequent years and is important to the recruiting process. Although the mechanism to return to the colony as prospectors is age related, there is individual variation such that the process is earlier in some individuals of similar ages.

4.4.3 Diurnal patterns of attendance

Fig. 4.05 shows the diurnal attendance patterns for the period 5 May to 15 June during which time the numbers (Fig. 4.01) and attendance (Fig. 4.02) of prospectors were relatively constant. The mean number of Kittiwakes over the day was considered in relation to their location on the colony (ledges or roof) and breeding status (prospectors or off-duty breeders not on nests). For prospectors both on the roof and on the ledges, numbers were still increasing at the beginning of observations (0530 GMT) and had a morning peak at 0630-0700. The attendance of prospectors on the ledges declined progressively over the day; this was due to the "regular" site holders leaving over the course of the day. In contrast, the number of prospectors on the roof fluctuated over the day, with two peaks (0630-0700 and 1630-1700). There was considerable turnover of individuals on the roof. Marked individuals on the roof were only seen one to three times per day, while marked birds on ledges were there for a large part of the day.

Off-duty breeders fluctuated around two at any time over the course of the day. The main feature common to off-duty breeders and to prospectors on the roof and ledges was the decline in numbers after 1800 until nightfall. No prospectors or off-duty breeders spent the night at the colony.

Fig. 4.06 gives data on diurnal attendance for the 51 breeding pairs on the west side of the colony which can be compared with Fig. 4.05. The percent of sites with pairs present on the warehouse over the day is shown, and this was split into three, two week periods. Time spent paired was

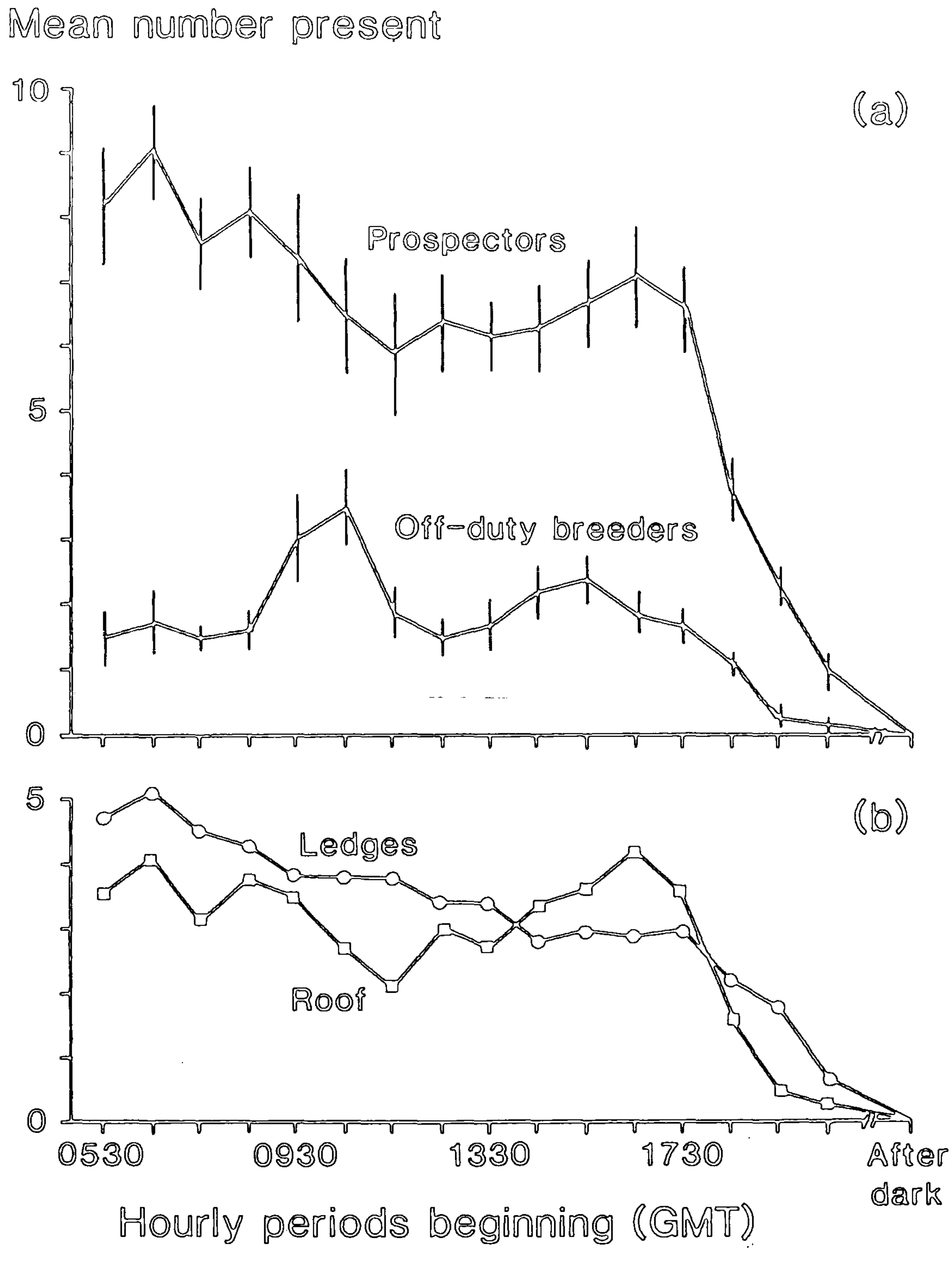

FIGURE 4.05: Mean number (± s.e.) of prospectors and off-duty breeders seen at one time, over the day, at the North Shields colony from 5 May to 15 June, 1983 (a). The diurnal pattern of attendance of prospectors on the roof and the ledges of the warehouse is also shown (b).

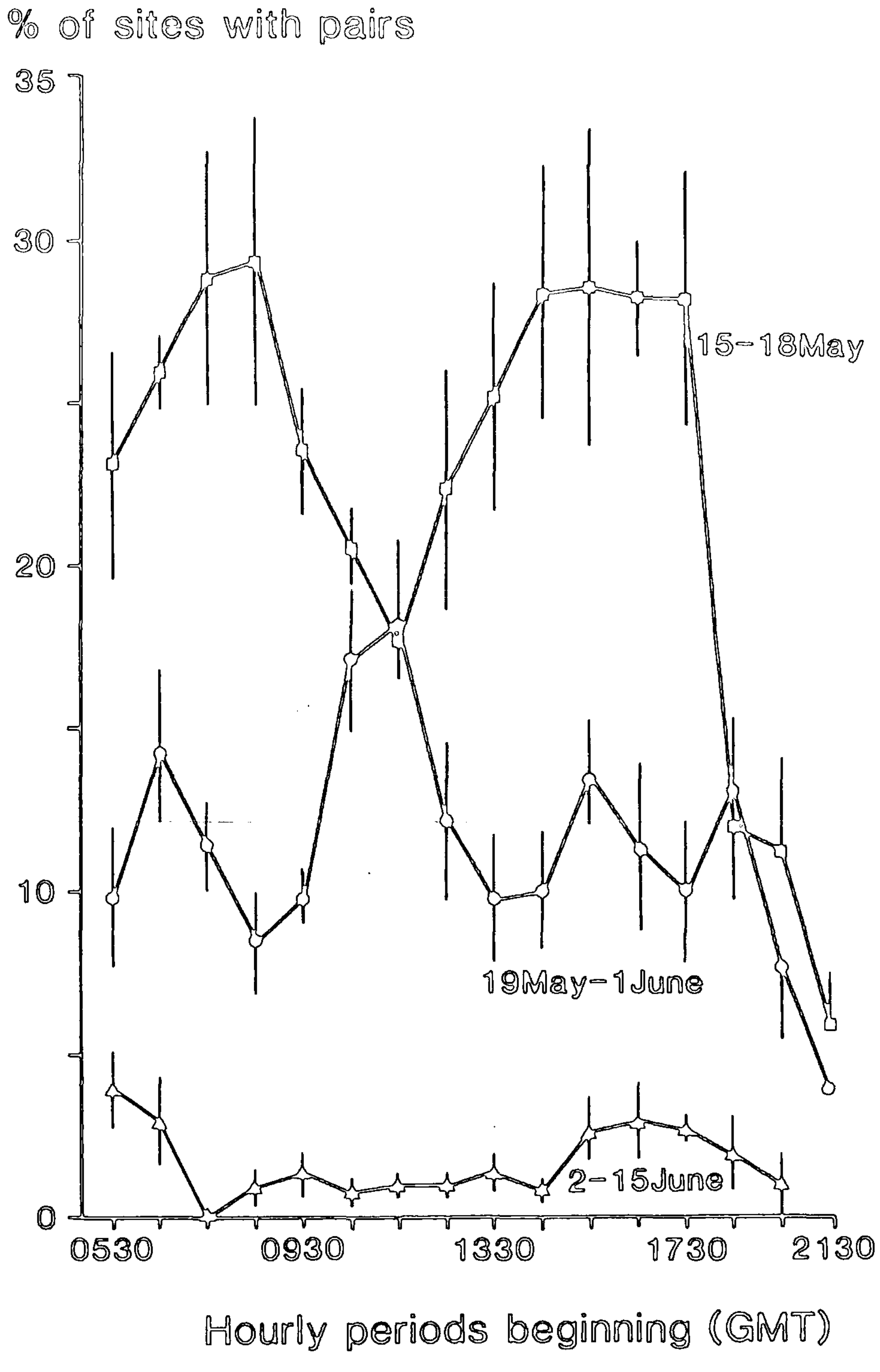

FIGURE 4.06: Mean percentage (± s.e.) of sites occupied by breeders which contained pairs, over the day at the North Shields colony for three, two week periods in 1983.

highest in the 5-18 May period (about 25%) and lowest from 2-15 June. This seasonal pattern in time spent paired was noted by Hodges (1974). During the day, the number of pairs of breeding birds decreased after about 1800. Hence all Kittiwakes not involved with incubation began to leave the colony after 1800 in order to go to their night roost.

4.4.4 Effects of weather on attendance

Coulson & White (1956) noted a weather-related difference in attendance at the Marsden colonies prior to laying. Fig. 4.07 shows a comparison of attendance of prospectors at the North Shields colony in relation to wind conditions (when the wind was above Force 3, or Force 3 or less). There was no difference between windy and not windy conditions before 4 May, but after this date a consistent difference existed throughout the season.

To show this effect more dramatically, Table 4.12 compares attendance of prospectors at the colony during extremes of weather for the period from 5 May to 15 June when numbers were relatively constant. On sunny, calm days (wind ⩽ Force 2) numbers were significantly higher on both the roof and ledges, than they were on days with a strong wind (⩾ Force 7). On the sunny, calm days, there were significantly more prospectors on the roof than on ledges; in contrast, on very windy days there were more prospectors on ledges than on the roof. This reflects the greater tenacity of birds which were on ledges than those on the roof. No two year old prospectors were seen on days which were very windy. The largest number of ringed two year olds (four) seen on one day was seen on a sunny, calm day.

4.4.5 Anti-predator responses

On 5 April 1982, 78 nest sites were occupied by Kittiwakes; on 8 April a Kestrel was sitting on a site on the south side of the warehouse and only one Kittiwake was present (on the north side of the warehouse). When the

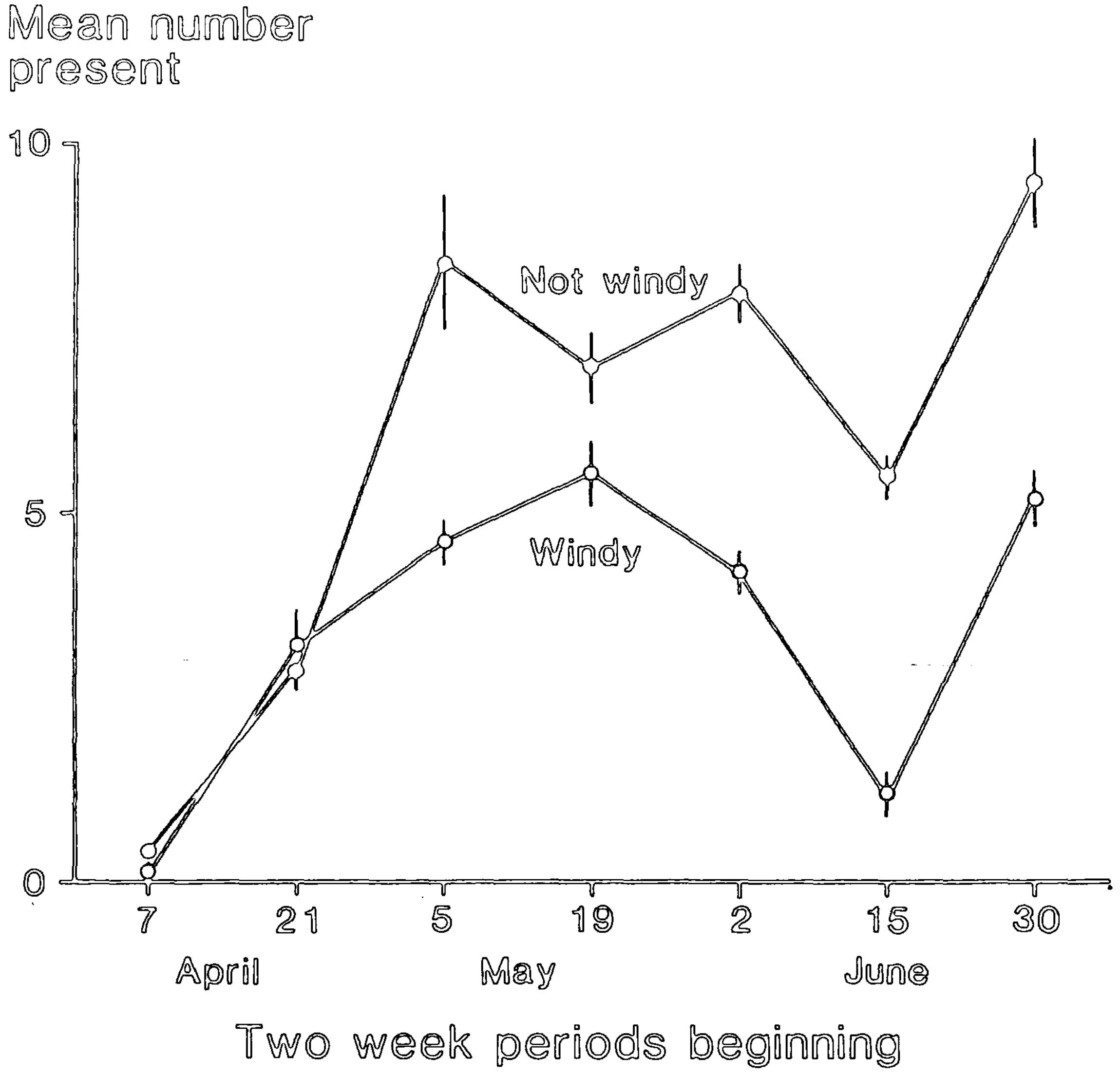

FIGURE 4.07: Mean number (± s.e.) of prospectors present at one time according to wind conditions over the season at the North Shields colony in 1983. Windy refers to ⩾ Force 4 and Not windy to ⩽ Force 3.

TABLE 4.12: Mean number (± s.e.) of prospectors seen at one time at the North Shields colony from 5 May to 15 June 1983 according to extremes in weather.

Weather conditions[1]	Number of prospectors seen at one time		
	Roof	Ledges	(n)
Sunny, calm	6.57 ± 0.51	4.67 ± 0.22	(27)
Very windy	1.00 ± 0.17	2.71 ± 0.19	(38)

Notes: [1] See text for further explanation.

Kestrel departed, the first Kittiwakes to return were old birds (which had arrived earliest at the colony).

On other occasions, a hunting Kestrel or a Carrion Crow caused panic flights. Only prospectors, recruits prior to site establishment, and off-duty breeders on the roof left the warehouse; the remaining birds on sites were very quiet until the danger passed.

4.4.6 Seasonal attendance at the North Shields Fish Quay

The North Shields Fish Quay is the loafing area closest to the North Shields colony. It is regularly used by North Shields breeders and prospectors, as well as those from Tynemouth and Marsden colonies. On several occasions each month, the numbers of Kittiwakes at the Fish Quay were counted and ringed individuals noted.

Fig. 4.08 shows the mean number of Kittiwakes per visit per month from January to September 1983. Numbers increased to about 70 per visit in February and dropped dramatically in March to less than 10. In January and February, all 17 ringed birds were North Shields or Marsden breeders. The decline in March corresponded to the reoccupation of the breeding colonies. Although numbers increased from April to July, the number of ringed birds per visit did not increase. In fact 25% of the ringed birds were prospectors, and this suggests that there was an influx of non-breeders (most of which would be unringed). In August, there were nearly 100 Kittiwakes per visit at the Fish Quay and all of the ringed birds were breeders from North Shields and Marsden. Hence, this peak corresponded to post-breeding movements of adults; the non-breeding birds had apparently departed. No Kittiwakes were seen on two visits in September although in other years there have been some Kittiwakes seen at the Fish Quay from September to December.

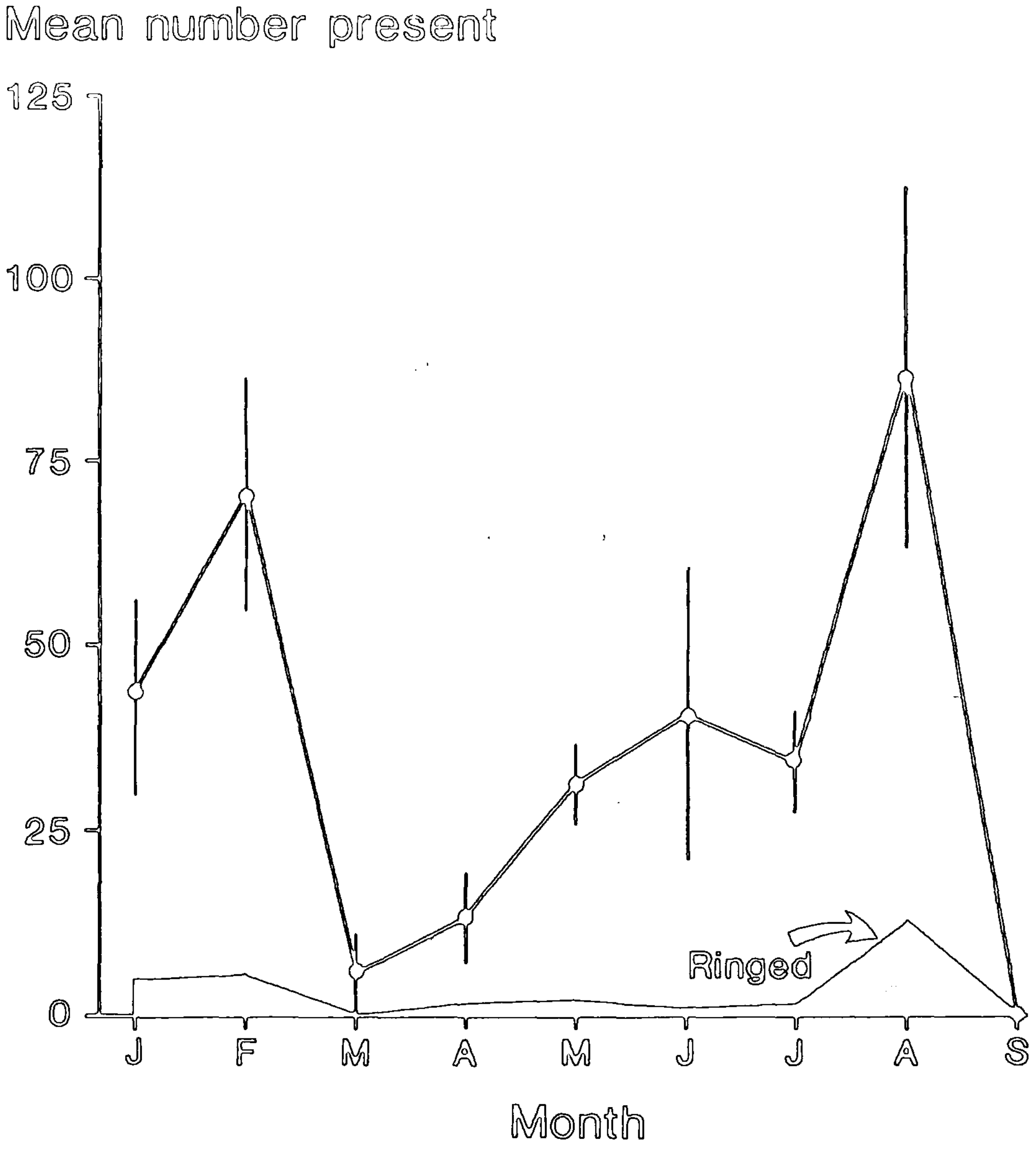

FIGURE 4.08: Mean number (± s.e.) of Kittiwakes present per visit per month at the North Shields Fish Quay in 1983. The shaded area represents the mean number of ringed Kittiwakes seen.

CHAPTER 5. MECHANISM OF RECRUITMENT AT THE NORTH SHIELDS COLONY

5.1 Introduction

The previous chapter showed several characteristics which distinguished recruits and prospectors. Recruits arrived at the colony earlier (Section 4.4.2), spent more time at the colony (Section 4.4.1), and were heavier (Section 4.3.5). This chapter describes the process of pair formation and the way recruits established sites following their arrival at the colony in 1983. The positive effects of density on reproductive output (Section 3.2.2) are illustrated by the recruits' nest site selection and reflect the quality of the individual. Once all of the evidence of this investigation is presented, the control of recruitment at North Shields is summarized.

5.2 Pair formation

5.2.1 Recruiting strategies

In 1980, the mean number of days from pair formation to laying for 12 pairs of recruits was 26.3 ± 5.34 (Chardine pers. comm.). The same measure in 1983 for 19 pairs was 23.1 ± 1.89 days. These two means do not differ significantly. In 1983, observations showed that there were two patterns of recruitment: recruits which took up sites immediately upon their arrival at the colony, and those which arrived at the colony but delayed taking up a site for two to three weeks. In 1983, the mean number of days from site occupation to laying for the 19 pairs of recruits was 29.4 ± 1.86 (10 nests) and 16.0 ± 0.90 (9 nests) for the immediate and delayed occupiers, respectively.

Table 5.01 summarizes the timing of events in the reproductive cycle of recruits in relation to their type of site occupation. All of the 19 pairs where both members were recruits were considered. In addition, six

TABLE 5.01: Timing of events in the reproductive cycle and breeding characteristics of recruits in relation to the type of site occupation at North Shields in 1983. Mean ± s.e. is shown.

	Type of site occupation (n)[1]	
	Immediate (15)	Delayed (10)
Arrival date of male	14.7 Apr ± 4.40	22.3 Apr ± 3.68[2]
Date of site occupation by pair	19.1 Apr ± 3.51	16.9 May ± 1.79
Laying date	22.5 May ± 2.00	2.0 Jun ± 1.84
Clutch size	1.80 ± 0.13	1.44 ± 0.18
No. days from arrival of pair at the colony to laying	33.4 ± 2.76	35.0 ± 2.28
No. days from male arrival to site occupation	0 ± 0	18.9 ± 2.07
No. days from site occupation to laying	33.4 ± 2.76	16.1 ± 0.81
% time paired (site occupation to laying)	36.9 ± 5.50 (9)	40.9 ± 4.77 (7)
No. days from site occupation by male to laying at nearest nest	32.0 ± 4.86	-3.6 ± 1.07
Laying date of nearest nest	16.7 May ± 1.77	13.3 May ± 1.32

Notes: [1] All pairs where male was a recruit (unless the female held the site from previous year and mate was a recruit - two cases).

[2] Only arrival dates of the 4 marked males used.

other pairs were used where only the male was a recruit and where that male established the site. This excluded two instances where the female retained her site from the previous year and mated with a recruiting male. In other words, pairs where the recruiting male had to establish the site, in order to attract a mate are shown in Table 5.01.

There was no significant difference in the arrival dates of males according to their recruiting strategy (although some recruits were unmarked making arrival dates difficult to determine). The mean date of site occupation differed by 28 days. The laying date was significantly later in the delayed site occupiers and the mean clutch size was consequently lower (but not significantly). Although the mean number of days from the arrival of the pair at the colony until they laid eggs did not differ for the two strategies, both the number of days from the arrival of the male to site occupation, and the mean number of days from site occupation to laying did differ significantly. The delayed site occupiers had a mean of 16.1 ± 0.81 days from site occupation to laying; the minimum was 13 days.

Fig. 5.01 illustrates the timing of events in the reproductive cycle of recruits and compares them to that of established breeders. Established breeders and immediate site occupiers among recruits had usually paired on sites within a week of the arrival of the male. The delayed site occupiers took about three weeks to occupy sites. Chardine (1983, pers. comm.) showed that once pairs were formed, recruits spent about 39% of the time paired, which was twice the percentage of time spent paired by established breeders for the last two weeks before laying. There was no significant difference in the percentage of time spent paired for the delayed and immediate site occupiers in 1983; they spent 39% of the time paired, as in 1980.

5.2.2 Behaviour of delayed site occupiers

Table 5.01 shows that delayed site occupiers were present at the colony

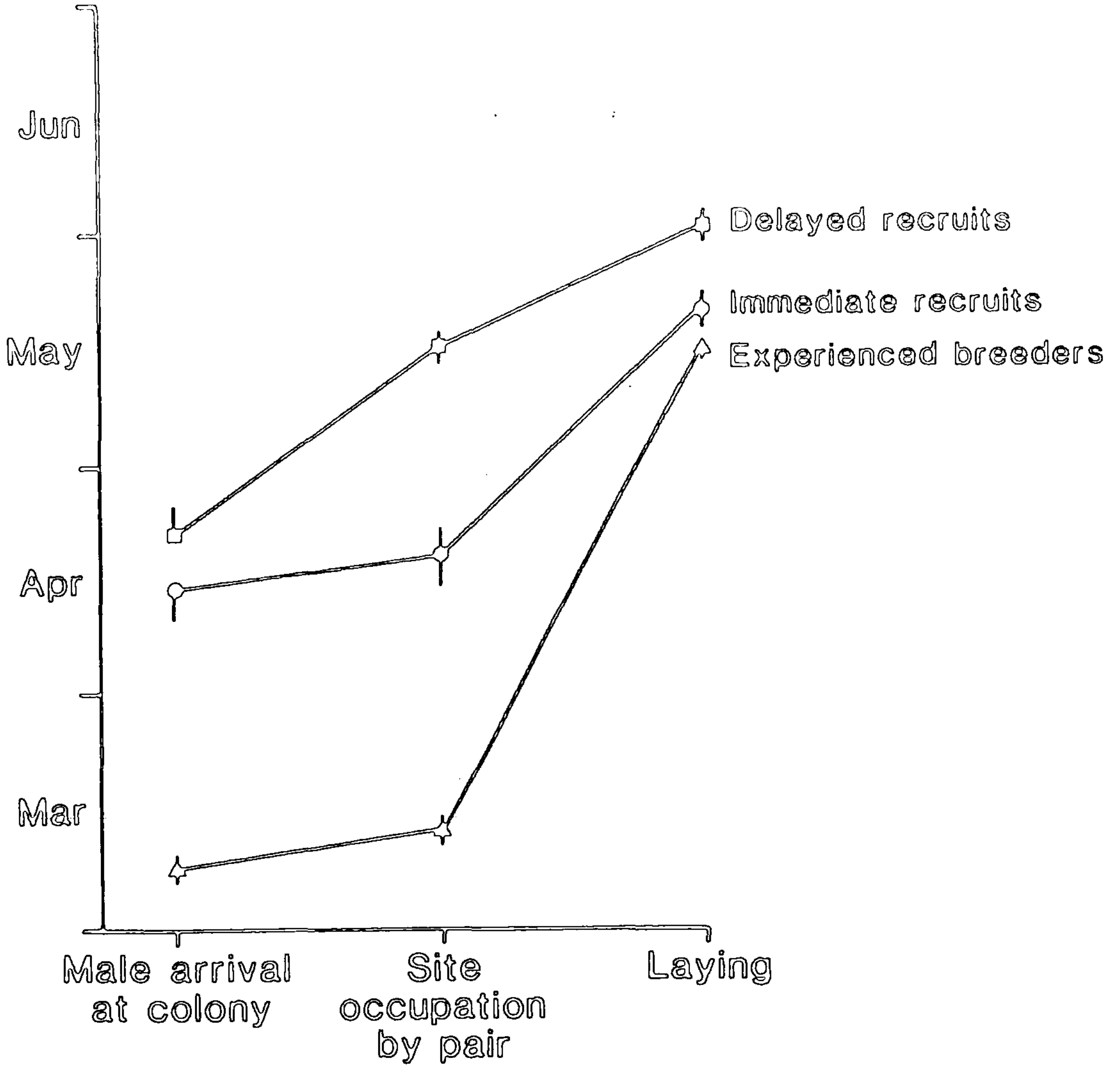

FIGURE 5.01: Timing of events (mean ± s.e.) in the reproductive cycle of delayed and immediate recruits, and established breeders at the North Shields colony in 1983.

for about 19 days prior to site occupation. This section describes their activities during the time prior to establishment. Observations showed that in order to attract a mate, males had to establish and defend a site (see also Coulson & Thomas 1983). To be successful in obtaining a site, they had to be at the colony regularly. Section 4.4.1 showed that recruits were at the colony on about 90% of the observation days in May and 50 to 60% of the time during observation periods.

Of the nine west side pairs which had delayed site occupation, four were unmarked and were not consistently identifiable. Their approximate time of arrival at the colony was known, but no detailed observations were made until they took up sites.

Of the remaining west side pairs, all five females arrived before the male. All of the females and three of the males were ringed. One male was not ringed but was identifiable by plumage. He was a bigamist. The females of these five pairs were seen with, on average, 4.6 ± 0.67 males (range 3-7) on 12.2 ± 1.24 sites (range 9-17). One female copulated with four males, another with two males. All of the "pre-marital" matings were with males which had bred before and had changed mates from the previous year, and had formed pairs in April. Females only copulated with males on sites, which emphasized the importance of site establishment for the male. The promiscuous behaviour of females may stem from the apparent shortage of males in the breeding population. In 1983, there were four bigamist pairs, one female-female pair and one trio, giving a ratio of 1.09 females to one male. Obviously, competition for males was very high.

The recruiting males, on the other hand, were seen with 2.5 ± 0.86 females, but they only copulated with their mates and only when they had established their site. These males concentrated their efforts on a small number of sites (mean 4.5 ± 1.9), as it was the male which established the site. Over two thirds of these sites were on the same window as an established pair. Although there were vacant sites alone on a window (usually at the periphery of the colony), these males attempted to establish sites close to other breeding Kittiwakes.

5.3 Nest site selection

The two strategies for recruits are distinct which provokes the questions, Why should there be two strategies? and What determines when the delayed occupiers take up sites? Nest sites at North Shields are all physically the same and differ only in their location on the warehouse and in their proximity to neighbours. The sites taken up by recruits have been classified according to the proximity of the nearest occupied nest at the time of recruitment. These are as follows: 0.3m to the nearest nest (two pairs nesting on the same ledge, within pecking distance), 0.7m (nearest pair nesting on the same window, but not on the same ledge), 1.5m (nearest pair nesting on the adjacent window) and $\geqslant$ 2.5m (nearest pair nesting beyond the next window). Although distances between nests at North Shields are discrete, the above categories correspond to the situation at cliff colonies (e.g. variable distances to the nearest nest).

5.3.1 Use of sites

The sites taken up by recruits in each year (from 1954 to 1984) were classified according to the proximity of the nearest occupied nest at the time of recruitment. In addition, unoccupied sites used in the previous year were classified in a similar way. Thus two values were calculated: (1) those sites <u>used</u> and (2) those sites <u>available</u> (the sum of those used in one year and those used in the previous year but not in the present year). This excluded all empty sites which remained so in successive years.

If site choice was random, it would be expected that the use of sites in a particular distance category would be proportional to the availability of sites in that category. Table 5.02 reveals that this was not the case. There was a significantly greater proportional use of nests in the 0.7m category than any other. At North Shields, this is the closest a pair can establish to another nest without being within pecking distance. The use of sites in the 0.3 and 1.5m distant categories was the same, and beyond 1.5m distant, very few sites were used.

Table 5.03 shows the proximity of the nearest nest for the delayed and immediate site occupiers in 1983. None of the immediate site occupiers took up sites on the same ledge (0.3m distant) as another pair. Eight took up sites on the same window, but alone on a ledge (0.7m distant) and seven were alone on a window ($\geqslant$ 1.5m distant). On the other hand, over half of the delayed site occupiers nested on the same ledge as another pair. On closer inspection, it was found that all sites which delayed breeders eventually occupied were defended by another pair. In the case of the recruit alone on a window, the site had been occupied by a pair which moved onto a site next to another pair.

5.3.2 Ease of entry onto sites

This use of sites prompts the questions, Why is there differential use of sites in the various distance categories? and Is there a difference in the ease of entry onto sites according to the distance to the nearest occupied nest?

Table 5.01 also shows the mean number of days from site occupation by the male to the date of laying of the nearest nest. The mean for pairs taking up sites immediately was 32 days whereas delayed site occupiers took up their sites 3.6 days after the first egg of their nearest neighbour's clutch had been laid (which corresponds to when these neighbours began incubating).

TABLE 5.02: Use of sites and ease of entry onto sites at the North Shields colony by recruits according to the distance to the nearest nest. Use was calculated from data for 1954 to 1984; ease of entry was calculated from observations in 1983. See text for further details.

Distance to nearest nest (m)	Use ± s.e.[1] (n)	Ease of entry ± s.e.[2] (n)
0.3	65.6 ± 2.52% (355)	17.9 ± 1.9% (406)
0.7	77.8 ± 4.29% (94)	32.4 ± 1.7% (730)
1.5	66.0 ± 2.72% (303)	57.6 ± 2.0% (613)
2.5	33.3 ± 19.2% (6)	100 ± 0% (3)
3.0	0 (0)	100% ? (0)

Notes: [1] (a) ANOVA, all categories, $F_{3,754} = 2.85$, $P < 0.05$: the distance to the nearest nest has a significant effect on the use of sites; (b) 0.3m vs 0.7m, $t_{447} = 2.45$, $P < 0.02$; (c) 0.7m vs 1.5m, $t_{395} = 2.32$, $P < 0.05$: the use of sites is highest in the 0.7m category.

[2] ANOVA, all categories, $F_{3,1748} = 69.50$, $P < 0.001$: the distance to the nearest nest has a significant effect on the ease of entry onto sites.

TABLE 5.03: Distance to the nearest nest for immediate and delayed site occupiers at the North Shields colony in 1983.[1]

Distance to nearest nest (m)	Type of site occupation (n)	
	Immediate (15)	Delayed (10)
0.3	0	6
0.7	8	3
1.5	7	1

Notes: [1] *G*-test of independence (a) All categories, $G_2 = 39.96$, $P < 0.001$: the frequency of the type of site occupation is dependent on distance to the nearest nest; (b) 0.3m vs $\geqslant$ 0.7m, $G_1 = 14.09$, $P < 0.001$: there were significantly fewer immediate site occupiers on nests 0.3m distant than on more distant nests.

Kittiwake laying dates are usually highly synchronous (Coulson & White 1958). Table 5.04 shows that in 1983 the mean number of days between laying of two established pairs nesting 0.3m distant was only 4.6 days, compared to 21.3 days for one recruiting pair and one established pair nesting together on a ledge. Section 3.2.1 demonstrated that during the years the colony was growing, the number of ledges with two pairs nesting together (density) also increased. Table 5.04 shows the mean number of days between laying of established pairs and recruits for a sample of these ledges which had previously only been occupied by a single pair. A similar sample from each year of two established pairs on a ledge was taken for comparison. As in 1983 (differences were not significant), two established pairs were highly synchronous in their laying dates, while the laying dates of a recruiting and an established pair differed by about three weeks.

In 1983 levels of aggression were examined according to the proximity of the nearest occupied nest to the site used. Each arrival onto a site of a prospector or potential recruit was recorded, and the subsequent fate of that bird. An arrival was scored '0' if no aggression was shown to the arriving bird, '1' if another bird flew by or showed a threat posture, but had no contact with the arriving bird, and '2' if there was contact aggression shown towards the arriving bird (which always resulted in displacement of the arriving bird).

Fig. 5.02 shows the mean attack score over the season for all arrivals on sites 0.3, 0.7 and 1.5m distant from the nearest nest. There were only three arrivals seen beyond 1.5m distant and none involved an attack. Aggression decreased with increasing distance to the nearest nest; hence closest sites were the most difficult to land on and stay. For the week beginning 14 April, both the 0.5 and 1.5m distant categories had a mean attack score of under 1.0. This allowed immediate site occupiers arriving at that time to take up sites which were alone on a ledge. Beginning 21

TABLE 5.04: Mean number of days (± s.e.) between laying of two pairs nesting 0.3m distant according to their breeding status for 1983 and for 1954 to 1967.

	Number of days between laying date of neighbours 0.3m distant (n)	
	1983	1954-1967
Two established pairs	4.6 ± 1.10 (10)	4.2 ± 0.63 (30)
One recruit, one established pair	21.3 ± 1.41 (6)	21.5 ± 1.46 (30)

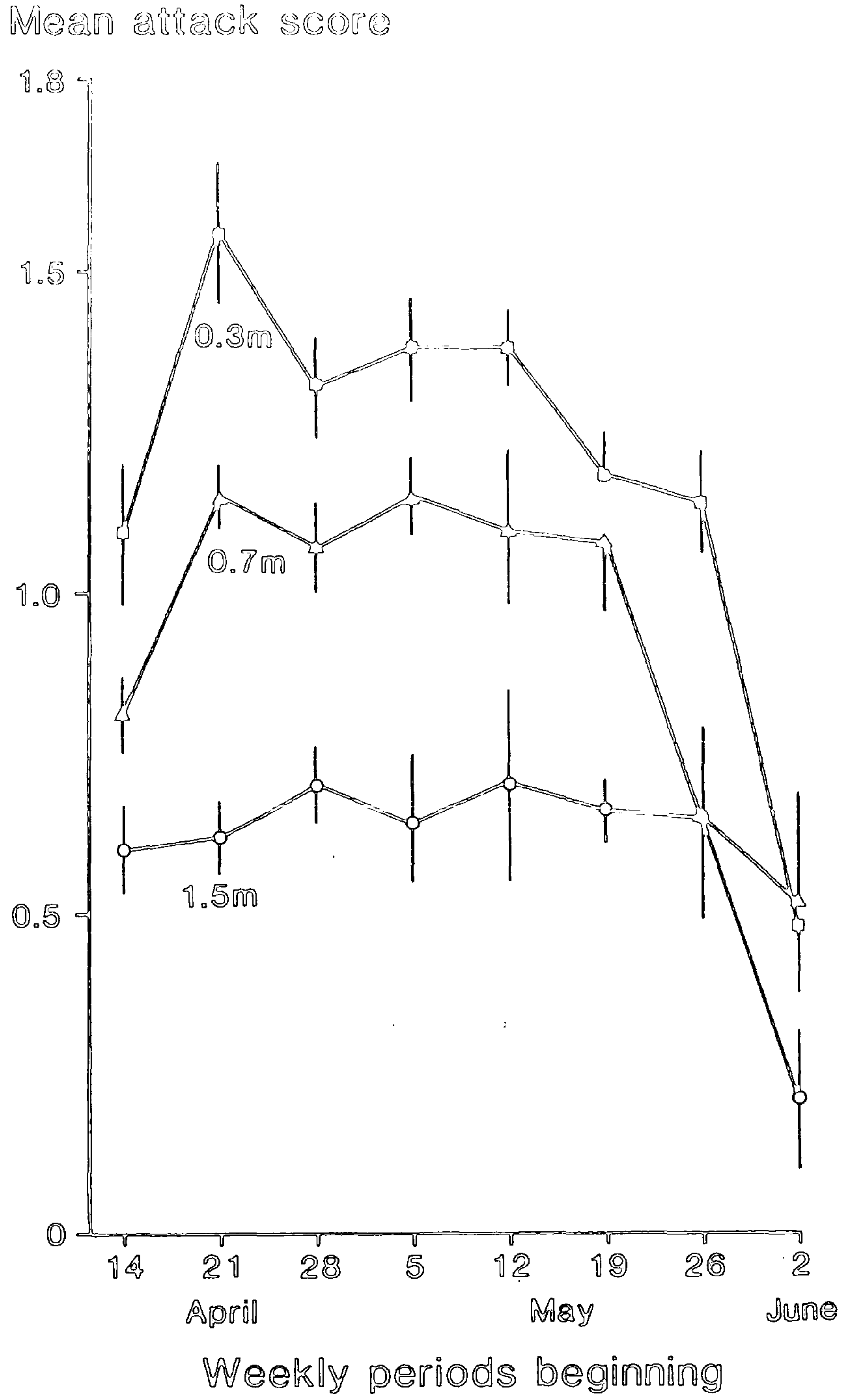

FIGURE 5.02: Mean attack score (± s.e.) for all arrivals of prospectors and recruits on sites according to the distance to the nearest nest at the North Shields colony over the season in 1983.

April, the mean attack score on sites 0.7m distant was over 1.1. On the other hand, the mean attack score for those arriving on the 0.3m distant sites was already 1.26 ± 0.16 in the first week of observations and remained above 1.3 until mid-May. The mean attack score on ledges 1.5m from the nearest nest was never more than 0.7. Fig. 5.03 shows the proportion of all arrivals which were on sites 0.3m from the nearest nest over the season; this proportion increased steadily from the week beginning 21 April, which was when the mean attack score began to decline (Fig. 5.02). In other words, as aggression to birds arriving on sites beside an occupied nest declined, proportionately more of the arrivals were on those sites. The mean date of site occupation by delayed site occupiers was 17 May which was when aggression levels began to drop considerably. Although there was little aggression to birds landing on sites alone on a window, the delayed site occupiers attempted to obtain sites 0.3m from the closest occupied nest. The aggression by established breeders resulted in these recruiting birds taking up sites very late in the season. The data on aggression levels would suggest that vacant ledges alone on windows were available to recruiting birds throughout the season.

In Table 5.02, a simplified value for ease of entry is shown according to the proximity of the nearest nest. This value is the number of arrivals on a distance category followed by no attack as a percent of the total arrivals, during the five week period from 14 April to 18 May. The ease of entry increased with increasing distance to the nearest occupied nest.

Given that sites 0.3m distant from the nearest nest are the most difficult to land on and stay, do recruits nest on them as often as established breeders? Fig. 5.04 shows the five year running mean of the percentage of nests which were 0.3m from the nearest pair, comparing pairs where the male was a recruit with established pairs. On average in each

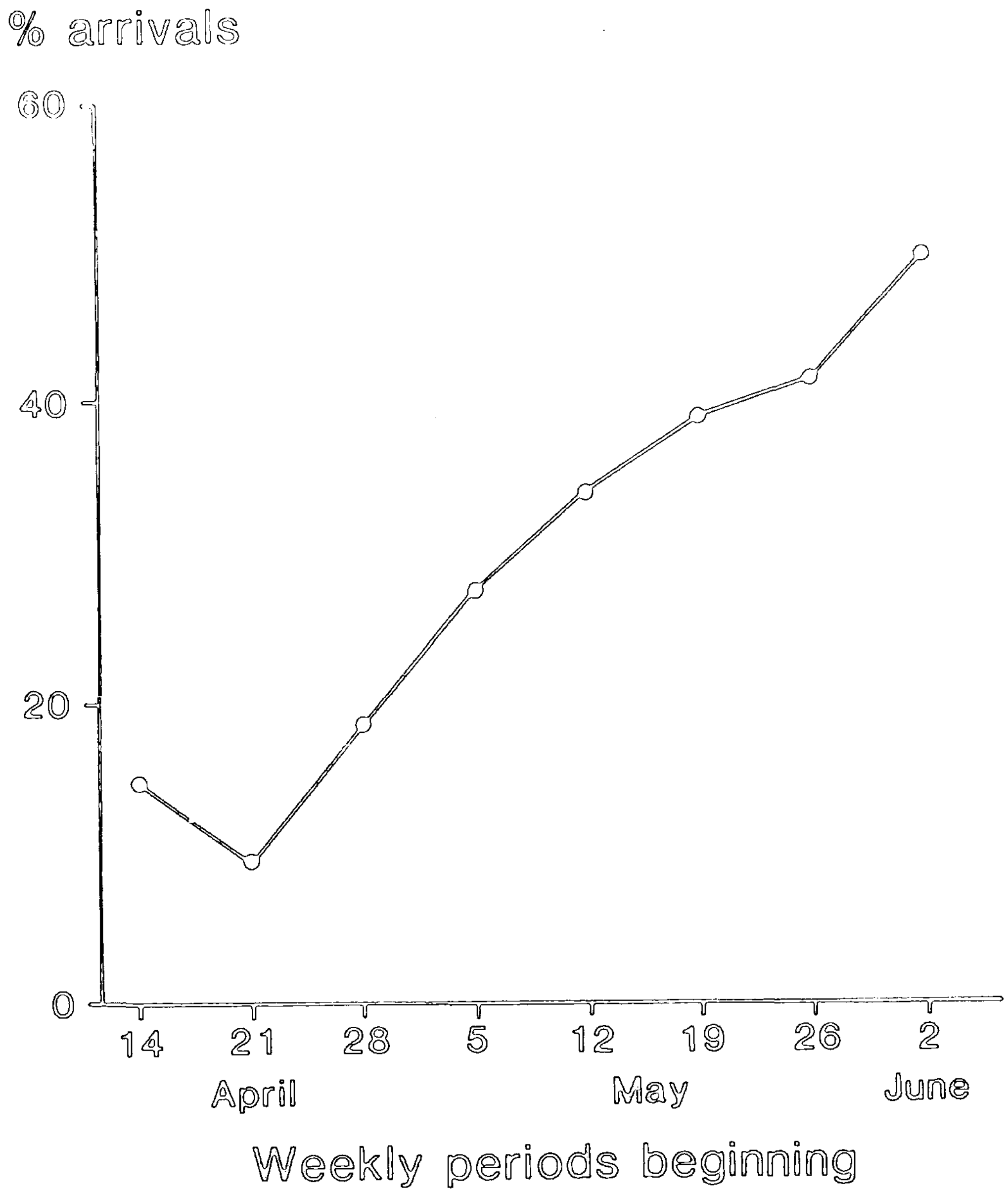

FIGURE 5.03: Percentage of all arrivals of prospectors and recruits which were on sites 0.3m from the nearest nest at the North Shields colony over the season in 1983.

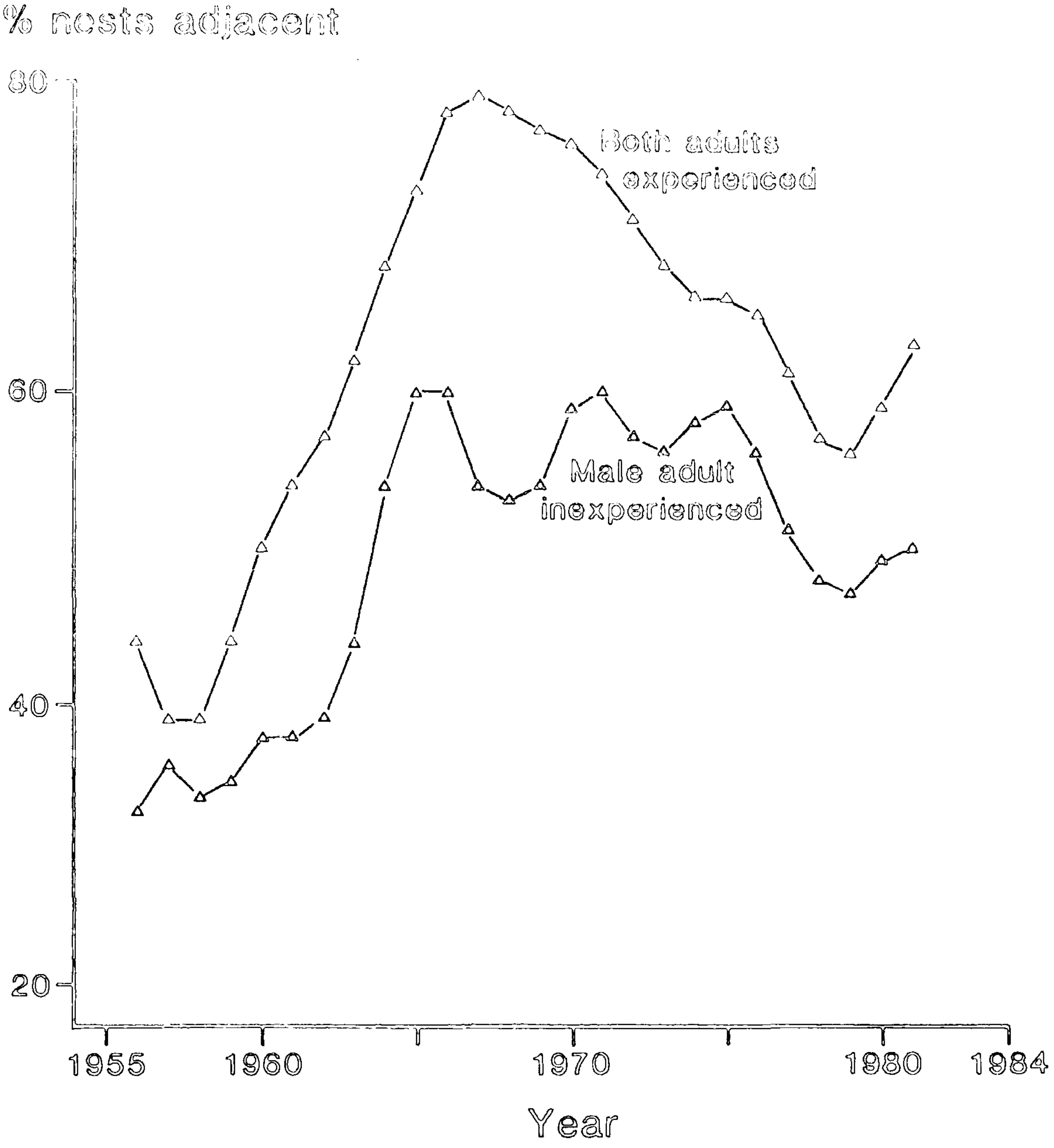

FIGURE 5.04: The five year running mean of the percentage of nests which were 0.3m from the nearest nest according to breeding experience at the North Shields colony over the period 1954 to 1984.

year, the difference between recruits and established breeders was 13.9 ± 2.2% (significant). Recruits were less likely to nest on these sites with a low ease of entry value. Their late arrival ensures that only a few can occupy sites close to other pairs, and then only late in the season when aggression levels are lower.

5.3.3 Preference of sites

In Fig. 5.05 the use of sites and their ease of entry value for all distance categories are plotted (from Table 5.02). The use of sites is the product of the ease of entry and the preference. Hence the preference has been determined for each distance category. Fig. 5.05 shows that Kittiwakes prefer sites as close as possible to others, but aggression forces a compromise. Therefore the most used sites were just out of pecking distance. The strong tendency to nest close still remained.

Table 5.05 examines the tendency of male Kittiwakes, which had bred at North Shields at least twice, to change sites within the colony according to the distance to the nearest nest in the year prior to their move. Birds nesting at least 1.5m from their nearest neighbour were twice as likely to move (63%) than those nesting 0.3 or 0.7m from the nearest nest (35% move, χ^2_1 = 12.63, significant). Of those 37% of Kittiwakes nesting 0.3m from the nearest nest, which moved, 68% moved to a site also 0.3m from the nearest nest; only 5% of Kittiwakes which nested at this distance moved to windows where no other Kittiwakes were nesting. On the other hand, of those experienced male Kittiwakes which nested alone on a window and moved sites, 73% moved to a site 0.3 or 0.7m distant from the nearest nest (Table 5.05). These experienced birds preferred to nest close to other birds; they were less likely to move if they nested on the same window as another pair and very few birds actually moved to a site farther away from the nearest nest than they were before.

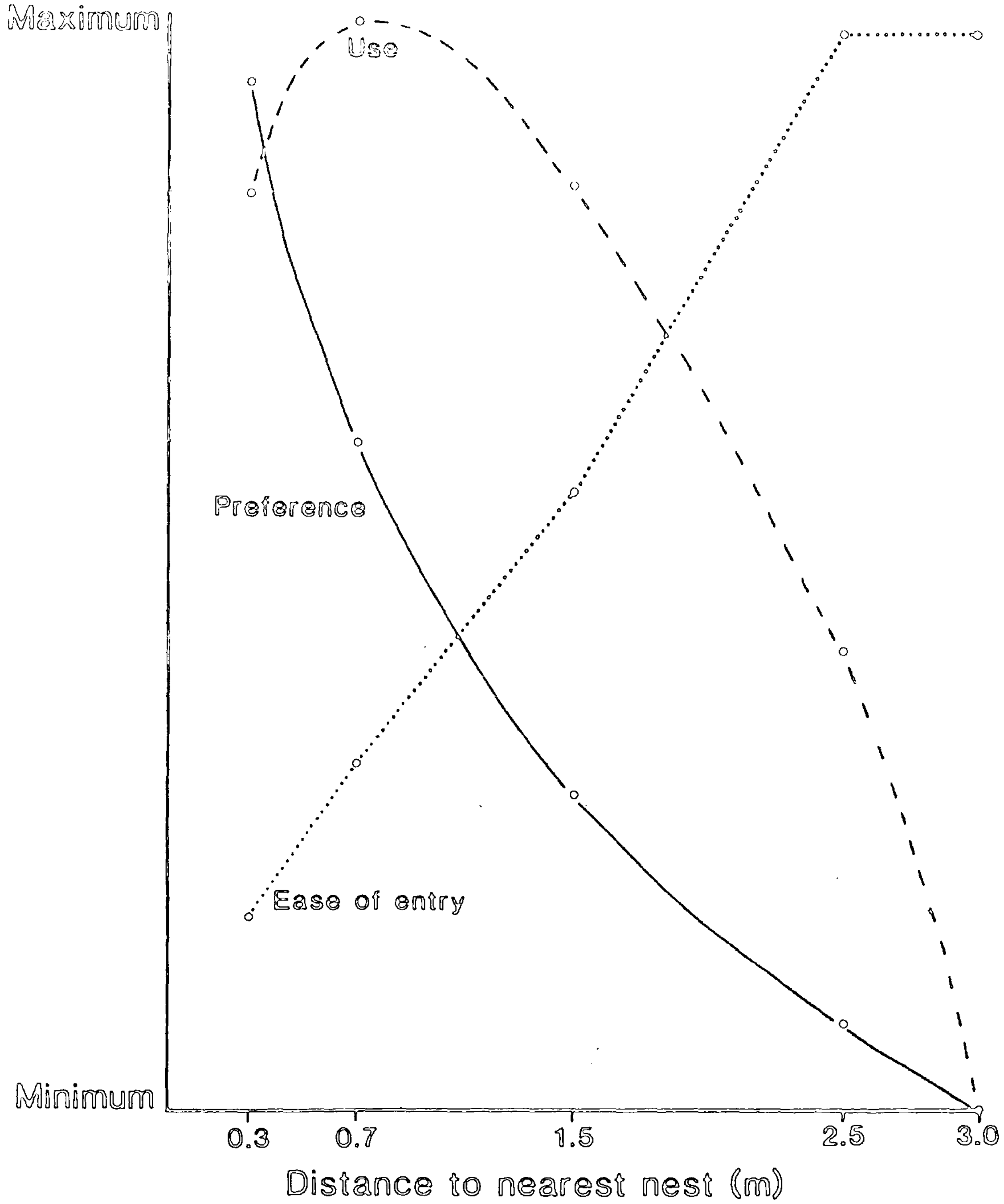

FIGURE 5.05: Model showing the use of sites, ease of entry onto sites and preference for sites according to the distance to the nearest nest. See text for explanation.

TABLE 5.05: Tendency of male Kittiwakes which have bred at least twice to change sites within the North Shields colony according to the distance to the nearest nest in the year prior to the move (1954 to 1984).

	Distance to nearest nest		
	0.3m	0.7m	⩾ 1.5m
% move (n)	36.7 (120)	29.4 (17)	62.5 (64)
Of those which move,			
% with same distance to nearest nest	68.2	60.0	27.5
% which reduced distance to nearest nest	-	40.0	72.5
% which increased distance to nearest nest	31.8	0	-
n	44	15	40

5.3.4 Advantages of nest site types

What is the biological significance of Kittiwakes' preference for sites close to other birds? Table 5.06 shows the number of chicks fledged per pair for two time periods and for three age categories, according to the distance to the nearest occupied nest. There was no significant difference in the number of chicks fledged per pair on sites 0.3 and 0.7m from the nearest nest and they are combined. For all age groups and year groups, the number of chicks fledged per pair was higher for nests which were on the same window as the nearest nest (0.3 and 0.7m distant) than for nests alone on a window (⩾ 1.5m distant), although this difference was only significant for the Kittiwakes aged 2-10. Thus reproductive success as measured by the number of chicks fledged per pair, was higher in the close categories.

In Section 4.3.5, body weight was demonstrated to be a factor which determined whether or not the potential recruits actually bred. Table 5.07 shows the body weight and wing-length measurements for male and female recruits according to the distance to the nearest occupied nest. There were no significant differences between measurements of recruits nesting 0.3 and 0.7m distant from the nearest neighbour and they are combined in Table 5.07. The mean body weights of both males and females were significantly higher for birds which nested on the same window as their nearest neighbour (0.3 and 0.7m distant categories) than for those nesting alone on a window (⩾ 1.5m distant). Male wing-lengths did not differ between the two, while females which nested in the 0.3 or 0.7m categories had significantly longer wings than those in ⩾ 1.5m categories.

Although birds may have had to compromise and take a nest site 0.7m away from the nearest nest, they did not compromise on reproductive output. These birds in the two close categories were also the heaviest birds. Less

TABLE 5.06: Mean number of chicks fledged per pair (± s.e.) according to breeding experience of the pair and distance to the nearest nest in two time periods. Sample sizes are in parentheses.

Breeding experience[1]	Number of chicks/pair			
	1954 - 1967		1968 - 1982	
	0.3-0.7m	≥ 1.5m	0.3-0.7m	≥ 1.5m
1	1.18 ± 0.06 (138)	1.12 ± 0.07 (131)	0.97 ± 0.05 (294)	0.82 ± 0.07 (151)
2-10	1.58 ± 0.05 (204)	1.41 ± 0.07 (128)	1.27 ± 0.03 (524)	1.15 ± 0.05 (132)
≥ 11	-	-	1.25 ± 0.08 (107)	1.18 ± 0.16 (33)

Notes: [1] Breeding experience is '1' if the male or female was breeding for the first time; breeding experience is '2-10' if the male and female had bred at least twice and the female had bred for less than 11 years; breeding experience is '≥ 11' if the female had bred ≥ 11 years.

TABLE 5.07: Mean body weights and wing-lengths (± s.e.) of male and female recruits nesting 0.3-0.7m or ≥ 1.5m from the nearest nest (1959-1984).

	Male		Female	
	0.3-0.7m	≥ 1.5m	0.3-0.7m	≥ 1.5m
Weight (g)	394.0 ± 2.09	386.8 ± 2.97	358.3 ± 1.95	344.5 ± 3.38
Wing-length (mm)	311.4 ± 0.48	310.8 ± 0.58	303.7 ± 0.53	301.7 ± 0.65
n	171	87	185	79

fit birds were forced to take up the more distant sites and appeared to be unable to compete successfully for these preferred sites and were less productive.

5.4 Control of recruitment

As a result of this investigation, it has been shown that there is an excess of potential recruits at North Shields, that there are physically available sites, and Coulson & Porter (1985) have shown that there was no regular or long term shortage of food for chicks. The evidence suggests that the restriction on colony growth, that is on recruitment, is a social one.

The previous sections have revealed certain prerequisites for Kittiwakes in order to recruit into the breeding colony at North Shields. These are summarized as follows:

(1) Age -- Recruits must be at least three years old (Section 3.4.2).

(2) Experience -- Recruits must have been present at the colony in the previous year. As prospectors in the year prior to breeding, they must arrive by early June and stay about two months, on average (Sections 4.4.1, 4.4.2).

(3) Arrival date -- Recruits must arrive by early May (Section 4.4.2).

(4) Attendance -- Recruits must be present at the colony in May for over 90% of the days and about 50% of the daylight hours (Section 4.4.1). In order to be at the colony this often, they must have good body condition as measured by their body weight (Sections 3.4.3, 4.3.5).

Fig. 5.06 is a flow diagram summarizing how recruitment is controlled. In any breeding season, there exists a pool of potential recruits, as well as a group of one and two year olds incapable of breeding. Some of these birds may be shared with neighbouring colonies. Considering only the pool of potential breeders, the first selection is made when birds

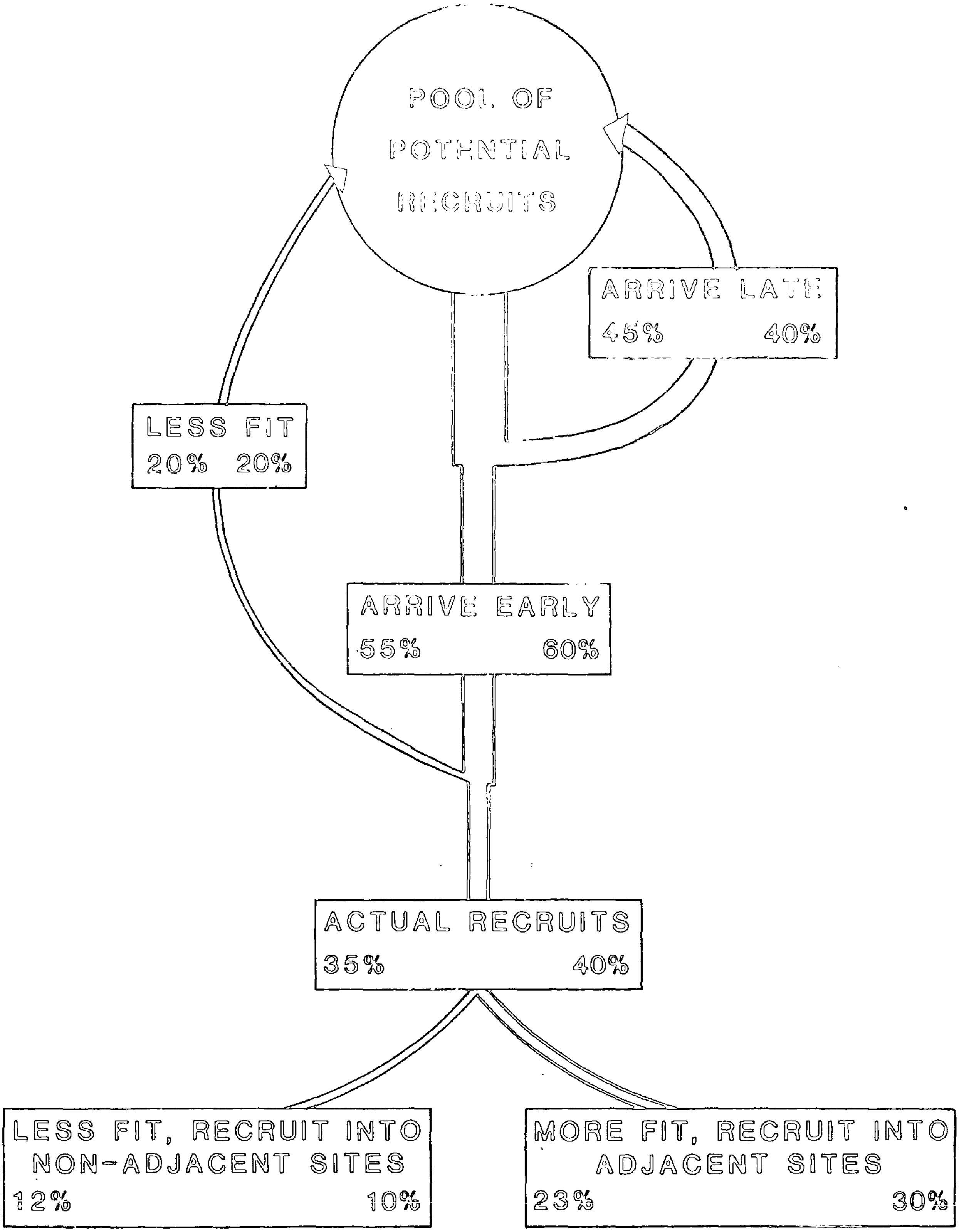

FIGURE 5.06: Flow diagram summarizing how recruitment is controlled at the North Shields colony. The percentage of potential recruits at each stage are shown for 1982 (left corner) and 1983 (right corner). See text for explanation.

arrive too late or do not have the required experience. In 1982 and 1983 this was about 45% and 40%, respectively, of the original pool. None of these birds held sites or built nests. Of those Kittiwakes arriving early enough, the less fit ones (those with the lower body weights which could not put in the required attendance) also remain in the pool. This represented about 20% of the pool in each year. Some of these birds temporarily held a site or mate. About 35% and 40% of the pool in 1982 and 1983, respectively, actually recruited into the breeding group. There is further selection at the time of recruitment; high quality birds choose sites close to other birds and do better reproductively.

CHAPTER 6. DISCUSSION

Three important concepts regarding Kittiwake colony growth and recruitment to the breeding group are revealed in this thesis. Firstly, the model of colony growth showed that small colonies are proportionately more attractive to recruits in that they grow at a faster rate and have a higher recruitment rate. Because of this high recruitment rate, these small colonies do not contribute as many young to the pool of future breeders as they extract. Secondly, the process of recruitment is difficult; there is a pool of potential recruits at the colony which are restricted from breeding by the social structure of the colony. Thirdly, there is considerable selection at the time of recruitment based on the quality of the individual. This results in two strategies where the high quality recruits compete for sites in the denser areas of the colony, and subsequently do better reproductively.

The model of colony growth, based on the growth rates of British Kittiwake colonies (Coulson 1983), shows that recruitment rate is inversely related to colony size, implying that small colonies are proportionately more attractive to recruits. Virtually nothing is known about the Kittiwakes which form new colonies. Since competition for sites is low in a new colony, they may be similar to the less competitive birds which cannot obtain sites in the dense central areas of existing colonies. This study has shown that these less competitive birds have a lower reproductive rate, hence this could account for (at least in part) the lower reproductive output per pair in the early years of young colonies (Coulson & White 1956, Coulson & Thomas 1985). The model illustrates that small and young colonies do not have high enough young production to balance their recruitment needs for about 70 years and therefore draw heavily on the pool of potential breeders. Thereafter, chick production is in excess of the needs of the colony. Gaston et al. (1983) claim that Brunnich's Guillemot chick fledging weights were negatively correlated with colony size, and Birkhead & Furness (1985) have shown an inverse relationship between Kittiwake colony size and various breeding parameters (although their results must be treated with caution as their regression is based on data from a very wide range of latitudes and longitudes). If reproductive output does decline with colony size, it is more difficult to explain why birds choose to nest in these large aggregations since, presumably, any advantageous effects of reduced predation are taken into account in the lower reproductive output.

The pattern of growth in the North Shields colony followed that predicted by the model for about 17 years, after which numbers stopped increasing. Colony size at North Shields was limited by the availability of attractive sites, although since 1967 there were available sites which were not used. Several forms of evidence have been presented which indicate that there is a pool of potential recruits which are temporarilty restricted or prevented from breeding. When sites were made available by death or by adding new sites, these were occupied by recruits, even though apparently suitable sites at the periphery of the colony were still not used. Manuwal (1974) used removal experiments to demonstrate this effect with Cassin's Auklets. He believed that colony size was regulated by territorial behaviour, and this appeared to be the case. When adult mortality at North Shields was particularly high in the early 1970's, age of first breeding for males and females declined in order to replace the shortage of breeders. Studies of Herring Gull on the Isle of May (Chabrzyk & Coulson 1976, Duncan 1978, Coulson et al. 1982) show the effects of a dramatic removal experiment through extensive culling. Prior to the cull, Chabrzyk & Coulson (1976) showed that the gulls preferred to nest at the higher densities but could not immediately obtain a site, and therefore recruited to the medium density areas. They did not recruit extensively to low density areas. The result of the cull was that the age of recruitment decreased, overall recruitment rates in previously dense areas increased, emigration decreased and the density of nests was reduced (Coulson et al. 1982).

Direct observations of this pool of potential breeders at the Kittiwake colony in North Shields demonstrated that they preferred to nest as close as possible to others but were restricted by aggression from established breeders. The most fit Kittiwakes (those with heavier body weights) recruited onto sites close to other birds and they subsequently bred more successfully. Birkhead (1977) and Harris (1980) have shown that alcids nesting at higher densities have higher breeding success; they attributed this to the greater degree of protection in dense groups from predators. The higher breeding success in dense areas at North Shields was not caused by reduced predation; there has been no predation at the colony in 33 years of study. Kittiwakes appear to be segregated by quality at the time of recruitment. The heavy birds are apparently able to withstand the intense competition for sites located close to other birds, and less fit birds recruit to sites which are alone on a window ledge. In fact, the evidence suggests that potential recruits which fail to obtain a breeding site are individuals of even poorer quality than those which succeed in aquiring a site in less dense areas (see also Ainley 1978).

The findings of the present study relate closely to the investigation at North Shields by Coulson (1968) where he examined the difference in the quality of Kittiwakes breeding in the centre and on the edges of the colony. Male Kittiwakes which recruited into the centre were, on average, heavier and had a higher reproductive output. Coulson showed that the weight of Kittiwakes at recruitment was also related to their subsequent survival; the birds nesting in the centre also lived longer, thus their lifetime reproductive output was higher than that of birds on the edges. Coulson's central sites are also the more dense areas of the North Shields warehouse colony. In fact, in 1982 and 1983, 99% of the nests in the centre were on the same window as another nest. On the other hand, 40% of the nests on the edge were alone on a window. Therefore Coulson's divisions described the density of the nests and the classifications in the present study merely provide a more functional division in order to study behaviour of recruits. The fact remains that Kittiwakes compete for sites close to other birds and are thus segregated by quality on the basis of their ability to obtain sites in dense areas. Sites alone on a window are usually on the periphery of the colony and easily accessed by recruits during the season but are less attractive.

There is no obvious reason why sites in dense areas should attract the high quality recruits. In the North Shields situation, predation is unimportant, although these Kittiwakes do respond to the presence of a potential predator (e.g. Kestrel). In other situations, close nests may have less predation or a more effective defense against predators. Alternatively the advantage may be a social one (Darling 1938, Coulson & Dixon 1979; see also Nelson 1978 for Gannets) which results in earlier, more synchronous breeding and higher annual production of young. However there is a danger of producing a circular argument since young production is the criterion used to identify high quality individuals.

In this study, the first time breeders arrived much later in the season than established breeders and therefore had much less time to go through courtship in order to establish and maintain a pair bond (Coulson 1966b, Coulson & Thomas 1983). This appears to be counteracted by the intensity of their courtship once at the colony. Chardine (1983, pers. comm.) showed higher rates of greeting for first breeders and this study showed that they spent twice as much time paired than did established breeders (Chardine

1983). Similar observations of higher levels of greeting in newly formed pairs have been reported in several species (Adelie Penguins, Le Resche & Sladen 1970; Ring Dove, Erickson & Morris 1972; Stilt Sandpiper, Jehl 1973; Greenshank, Nethersole-Thompson 1951 in Jehl 1973; Gannets, Nelson 1978). Rather than spreading courtship over a long period, Kittiwake recruits have a short burst of intense courtship. This may be assisted by the social stimulation at the colony (Nelson 1978, Coulson & Dixon 1979). The combination of the intense competition for dense sites and the need for high attendance at the colony during pair formation indicates the need for individuals to be fit in order to recruit, and this explains the differences in mean body weights between recruits and prospectors, and recruits in dense and less dense areas.

Two strategies were demonstrated for recruits; some took up sites immediately on their arrival at the colony, others delayed their site occupation for several weeks. It might be expected that birds which moved directly onto sites would do better reproductively, but the converse was true. Although delayed site occupiers had a slightly lower mean clutch size, they produced, on average, more chicks per pair and this was more pronounced in subsequent breeding seasons. It is an ultimate advantage to delay site occupation until aggression by established breeders wanes when they start incubation. The strategy of delayed site occupiers appears to be a deliberate attempt to nest on sites close to other birds - otherwise they would take up sites which are available on the periphery (which are more easily established). Such a behaviour pattern is necessary to retain the structure of the colony. These delayed site occupiers do not initially establish on a peripheral site and then move to a preferred site. Rather, they wait until the sites in the dense areas are available and then form the pair. The trade-off in the reproductive benefits must outweigh the extra effort in establishing on such a site. On the other hand, the costs of competing for sites in the dense areas to the less fit birds (those with the lower body weights) may be prohibitive in the long-term and they take up sites where aggression is low.

The scope of this thesis has been restricted to the regulation of numbers in a colony. Although there appears to be a social restriction on recruits at the colony level, this does not necessarily regulate Kittiwake numbers over a greater geographical area. Birds prevented from entering one colony may move to form new colonies (see Coulson 1983). The factors which limit seabird numbers on a larger scale are more likely to be a shortage of food, colony sites or nest sites (see review by Birkhead & Furness 1985). Thus while a behavioural mechanism may operate to limit numbers in a colony, this is unlikely to be responsible for the regulation of seabird numbers as a whole (cf. Wynne-Edwards 1962).

This investigation has demonstrated that the pool of potential recruits is associated with more than one colony. This group of birds provides a reservoir of potential breeders. The 20% of the pool in Fig. 5.06 which arrived early enough to breed but did not, act as a buffer. They could be drawn into the breeding group when mortality was high (as shown by the long-term trends in Chapter 3). In the early 1970's, the data on recruitment and survival rates, and body weights of recruits suggest that the pool was reduced, which meant the buffering effect of the pool could not operate effectively and, in fact, there was a shortage of males. Hence, the number of nests declined and bigamy and female-female pairing was observed (Coulson & Thomas 1985).

Figure 6.01 illustrates these processes with a simple model. In a healthy colony there is a large non-breeding pool which supplies the breeding group. At the onset of stress (e.g. reduction in food supply, pesticides

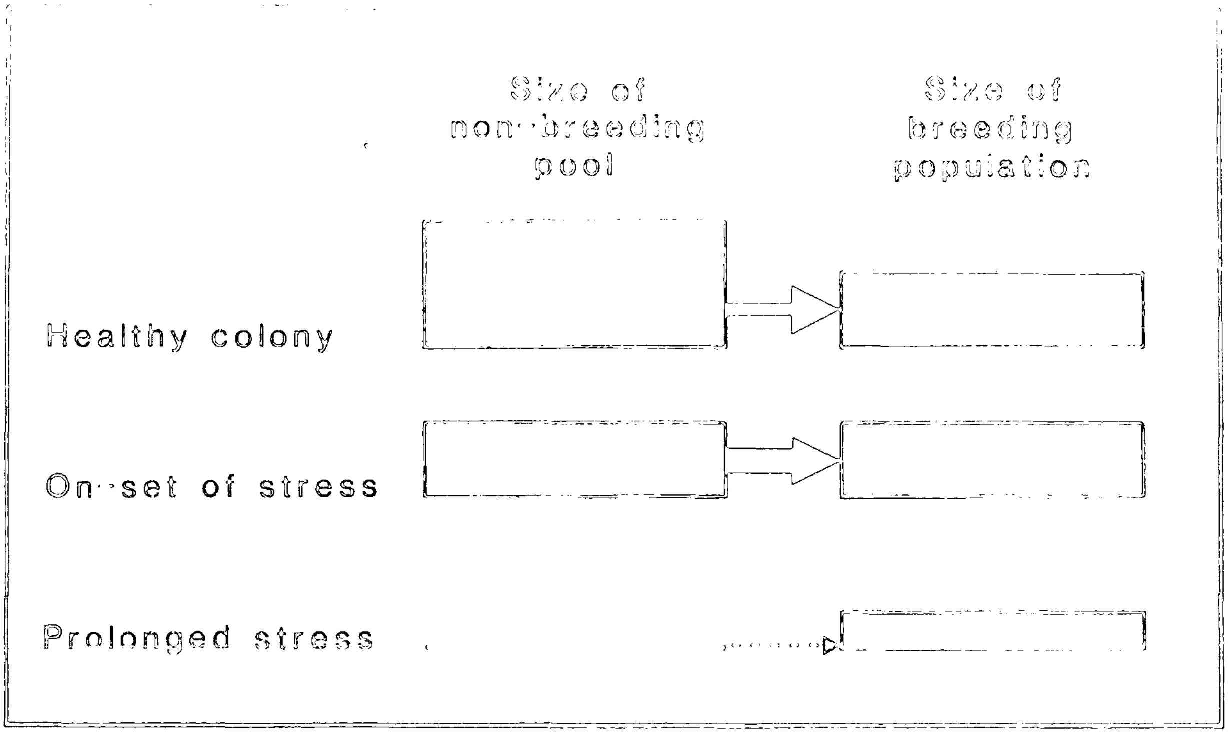

FIGURE 6.01: Schematic representation of the effect of stress on the size of the pool of non-breeders and the breeding population of a colony. See text for explanation.

causing high mortality) more birds are able to enter the breeding population, thus the size of the pool is radically reduced. After prolonged stress the pool is deplcated and there are not enough recruits to sustain the number of breeders, and there is a decline.

Thus information about this non-breeding pool can act as an earlier and more sensitive measure of both the condition of the population and of the environment: that is, the health of the population. By the time a change is detected in the number of breeders, the adverse effects could have been operating for several years and it may be too late to apply conservation measures; the damage to the total population has occurred.

The presence of a non-breeding surplus of reproductively able individuals has been documented in many groups of animals (e.g. mammals, birds: Silver-backed Jackal, Moehlman 1979; Florida Scrub Jay, Woolfender 1981). Emlen (1978, 1984) has shown in his reviews that ecological constraints (such as a shortage of sites or mates, or high costs of breeding independently) prevent some animals from breeding and this has lead to the evolution of cooperative breeding. Helping others is thought to be a strategy which increases the helpers' breeding prospects for the future. Studies have shown that when the death of a breeder causes a vacancy, non-breeding auxillaries from nearby territories attempt to take over the site very quickly (reviewed by Emlen 1984).

However, this situation where there is a surplus of potential recruits can occur without cooperative breeding but is usually thought to be imposed by a shortage of suitable sites (e.g. Rufous-collared Sparrow, Smith 1978; Great Tit, Krebs 1971; Blue Tit, Dhondt & Eyckerman 1980; White-throated Sparrow, Rappole et al. 1970; White-crowned Sparrow, Petrinovich & Patterson 1982; Blue Grouse, Jamieson & Zwickel 1983). On the other hand, several workers have shown that area-specific experience prior to breeding may be important in subsequent breeding attempts (Smith 1978, Yasukawa 1979, Jamieson & Zwickel 1983, Patterson & Grace 1984). Ainley (1978) in his study of Adelie Penguins showed that non-breeders (which were physiologically capable of breeding) were less active socially and made poorer nests. Carrick & Ingham (1967 in Carrick & Ingham 1970) showed that the weight of female Adelie and Royal penguins determined whether or not they bred. They suggested that after the first year or two of life, age, as such, is less important than experience and social status, which were expressed in the arrival date and weight, and in breeding status and performance. They felt this separation was primarily determined by the capacity to obtain food. The social limitation on nest sites at North Shields serves to temporarily exclude less fit individuals from breeding, but may benefit these unsuccessful recruits in terms of their life-time reproductive output (through improvement with experience).

A polygamous mating system also leads to an excess of potential breeders. In birds and mammals polygamy occurs when some males defend good resources (e.g. Long-billed Marsh Wren, Verner 1964; Yellow-bellied Marmot, Downhower & Armitage 1971) or groups of females (e.g. Northern Elephant Seals, Le Boeuf 1972, 1974); other males with poor resources may never mate. Lewis & Zwickel (1981) found that adult male Blue Grouse which are polygamous preferred certain territorial sites over others. Sites were either occupied each year (persistent) or used intermittently (transient). There were more transient sites but only half were ever used in a year. Males on persistent sites survived longer and had more females in their territories during the breeding period. Further, both adult and yearling males preferred persistent sites when both were made available in a removal experiment (Lewis & Zwickel 1980). Thus these birds were able to assess territorial quality and were "willing" to delay breeding for a year in order to take up high quality sites.

As with Kittiwakes, the benefits of the high quality sites may be outweighed by the costs of competition for these sites. Thus Kittiwakes with lower weights should take up the sites in less dense areas as the costs of competition for dense sites may be high, or they should not breed at all in that year. Emlen (1984) suggested that helpers may exist in some instances because the costs of breeding may be too high; it is more advantagous for them to gain experience before attempting to breed themselves (carnivores reviewed by Macdonald & Moehlman 1982, also Lawton & Guindon 1981). The segregation of recruits on the basis of their quality may act as a mechanism for mate choice (see Parker 1983). High quality females may be attracted to high quality males and can identify them or their ability to compete for sites, but at this stage of knowledge this is only speculation.

SUMMARY

1. This study was initiated to examine the methods and biology of recruitment to the breeding group in the Kittiwake. The study colony is at North Shields where all of the breeders are individually marked. These Kittiwakes nest on the window ledges of a warehouse. The colony has been studied intensively since 1952 and much is known about Kittiwake breeding biology, although little is known about the Kittiwake prior to breeding for the first time.

2. The North Shields Kittiwake colony began in 1949 and reached a peak of 104 pairs in 1965; thereafter there have been 70 to 90 pairs. Density (measured as the proportion of window ledges with two pairs) was positively correlated with colony size. Reproductive output (the number of chicks fledged per pair) increased with density, although the values of chick production were lower after 1967.

3. Adult females had a higher survival rate than adult males which resulted in higher recruitment rates for males. There is a positive correlation between the number of deaths and the number of recruits in each year implying a compensatory mechanism.

4. About 11% of the chicks fledged in each year returned subsequently to breed at North Shields which did not account for more than 40% of the recruits in any year (usually less). A large proportion of recruits at North Shields originated from other colonies. The number of recruits supplied by the North Shields colony did not balance its loss of breeders through mortality. Immature Kittiwakes did not suffer the same fluctuations in mortality that adults did, as they winter in different areas.

5. The mean age of first breeding dropped from 4.5 years of age to less than 4.0 in response to the high mortality in the early 1970's. At the same time,

male and female recruits' (Kittiwakes breeding for the first time) body weights and wing-lengths declined. There was little fluctuation in male and female prospectors' (Kittiwakes which had not bred before) body weights, implying a threshold weight for a healthy Kittiwake.

6. The model of colony growth based on the rate of increase of British colonies between 1959 and 1969 demonstrated that small colonies grow at a faster rate than large ones and have higher recruitment rates. Small colonies are proportionately more attractive to recruits. Small colonies do not supply enough chicks to the pool of potential breeders to support their losses through mortality and needs through growth. After about 70 years, production is in excess of the colony's needs. Colony size at North Shields was limited by the number of attractive sites; there were physically available sites which were not used.

7. Evidence is presented to show that there is a pool of potential recruits (prospectors at least three years old) which are temporarily restricted from breeding. When sites were made available either through death or the addition of new ledges, recruitment rates increased. Direct observations in 1982 and 1983 showed that there were over 100 potential recruits associated with the colony, only about 40% of which actually recruited.

8. About 20% of the pool of potential recruits had fledged from North Shields which did not differ from the proportion which recruited into the colony. Fifty percent of the prospectors were two years old, while only 11% were four years or older. As many prospectors were unmarked, their sex ratio could not be determined. However, evidence suggests that males spent more time on ledges and showed a stronger site tenacity than did females. The mean weights of male and female recruits were heavier than those of prospectors. The wing-lengths of males were not significantly different, although those of females were. No birds which bred at North Shields were seen at other

colonies. In contrast, North Shields prospectors were also seen at other colonies in the same or subsequent years.

9. The mean number of prospectors seen at one time increased from early April to mid-May while breeders were incubating eggs. There was a further increase in numbers in July corresponding to an influx of non breeding birds. Two year olds were not seen until late April and their numbers declined in mid to late July. Individual recruits were seen about 60% of the time in April and May, while prospectors were seen less than 20% of the time. The peak number of marked individual prospectors was seen in May to July although there was a considerable turnover of individuals.

10. Older prospectors arrived at the colony earlier in the season than younger prospectors. For birds of the same age, recruits arrived earlier than prospectors, and established breeders earlier than recruits. Older prospectors departed the colony later than younger prospectors, and breeders departed later than prospectors; thus duration of stay at the colony was age-related. Arrival dates were advanced if the prospector was present in the previous year or if the prospector bred in the next year. All recruits prospected at least one year prior to breeding.

11. All Kittiwakes not involved with incubation (off-duty breeders and prospectors on the roof and ledges) began to leave the colony after 1800 GMT. More prospectors were seen on days which were not windy. In the presence of a potential predator, prospectors and off-duty breeders left the colony, while breeders stayed on their nests. The seasonal pattern of attendance at the North Shields Fish Quay (the nearest loafing area to the North Shields colony) reflected the activities at the colony.

12. Male Kittiwakes establish the site and attract a female to form the pair. There were two patterns of recruitment: recruits which took up sites immediately on their arrival at the colony, and those which arrived at the

colony but delayed taking up sites for two to three weeks. Arrival dates of the males did not differ between the two strategies. Because the delayed site occupiers took up their sites later, they only had a mean of 16.1 days from site occupation to laying (minimum 13 days). There was no difference between the percentage of time spent paired for the two strategies (39%), but it was twice that of the established pairs.

13. Delayed site occupiers attempted to establish on sites close to other birds. Females only copulated with males which defended sites, and females showed promiscuous behaviour prior to pair formation. Males only copulated with their future mate, and then only when the site was established.

14. Sites were classified according to the proximity of the nearest neighbour. Over the history of the colony, those sites 0.7m distant from the nearest nest (as close as possible to another nest without being in pecking distance) were used proportionately more than others. Beyond 1.5m distant, very few sites were used. In 1983, all of the delayed site occupiers took up sites which had been defended by another pair; over half were on the same ledge as another pair. No immediate site occupiers took up sites on the same ledge as another pair.

15. Delayed site occupiers did not take up sites until incubation began at the nearest nest of established breeders. Two established pairs on a ledge were highly synchronous in laying dates, while laying dates of one established pair and one recruiting pair nesting together on a ledge differed by three weeks. Aggression from established breeders increased with decreasing distance to the nearest nest, and the closest sites were most difficult to land on and stay. The proportion of all arrivals by potential recruits which were on sites 0.3m to the nearest nest increased steadily from the week beginning 21 April, which was when the mean attack score began to decline. Recruits were less likely to nest on sites 0.3m distant from the

nearest nest than were established breeders.

16. The use of sites is the product of the ease of entry onto sites and the preference for those sites. Kittiwakes prefer to nest as close as possible to other birds, but aggression forces a compromise. The strategy of delayed site occupiers was a deliberate attempt to nest on the preferred sites. Experienced birds were less likely to change sites between years if they nested on the same window as another pair and very few established breeders actually moved to a site farther away from the nearest nest than they were before.

17. Reproductive success, as measured by the number of chicks fledged per pair, was highest in the close categories (two pairs nesting on the same window). Male and female recruits in the two close categories were significantly heavier than those nesting ⩾ 1.5m from the nearest nest.

18. The control of recruitment at North Shields is summarized. The pre-requisites for recruits are as follows: their age must be at least three years; they must have experience at the colony in the previous year; recruits must arrive by early May; and they must have high attendance in May which requires high body weights. There is further selection at the time of recruitment; high quality birds choose sites close to other birds and do better reproductively.

19. The results are discussed in terms of the importance of individual quality which segregates birds on the basis of their ability to obtain sites in dense areas. This competition for sites serves to limit the numbers in the colony, although it does not necessarily limit Kittiwake numbers on a broader scale. The pool of potential recruits which are temporarily restricted from breeding are important as a buffer to fluctuations in colony numbers, as demonstrated by the long-term population biology at North Shields.

Information about this non-breeding pool can act as an earlier and more sensitive measure of the health of the population. Competition for resources has lead to a pool of reproductively able non-breeders in other animals, as seen in cooperative breeding and polygamous mating systems. Higher quality animals gain the best resources, although lower quality individuals prevented from breeding may increase their fitness by gaining experience before they are able to enter the breeding group.

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APPENDICES

APPENDIX A: Common and scientific names of species mentioned in the text.

Adelie Penguin *Pygocelis adeliae* (Hombron & Jacquinot)
Blue Grouse *Dendragapus obscurus* (Say)
Blue Tit *Parus caeruleus* L.
Brünnich's Guillemot *Uria lomvia* (L.)
Carrion Crow *Corvus corone* L.
Cassin's Auklet *Ptychoramphus aleuticus* (Pallas)
Common Guillemot *Uria aalge* (Pontoppidan)
Florida Scrub Jay *Aphelocoma coerulescens* (Bosc)
Fulmar *Fulmarus glacialis* (L.)
Gannet *Sula bassana* (L.)
Great Tit *Parus major* L.
Greenshank *Tringa nebularia* (Gunnerus)
Herring Gull *Larus argentatus* Pontoppidan
Kestrel *Falco tinnuculus* L.
Kittiwake *Rissa tridactyla* (L.)
Lesser Sheathbill *Chionis minor* Hartlaub
Long-billed Marsh Wren *Cistothorus palustris* (Wilson)
Manx Shearwater *Puffinus puffinus* (Brünnich)
McCormick's Skua *Catharacta maccormicki* (Saunders)
Northern Elephant Seal *Mirounga angustirostris* Gill
Puffin *Fratercula arctica* (L.)
Ring Dove *Streptopelia risoria* L.
Royal Penguin *Eudyptes schlegeli* Finsch
Rufous-collared Sparrow *Zonotrichia capensis* (Müller)
Shag *Phalacrocorax aristotelis* (L.)
Silver-backed Jackal *Canis mesomelas* Schreber
Stilt Sandpiper *Calidris himantopus* (Bonaparte)
Wandering Albatross *Diomedea exulans* L.
White-crowned Sparrow *Zonotrichia leucophrys* (Forster)
White-throated Sparrow *Zonotrichia albicollis* (Gmelin)
Yellow-bellied Marmot *Marmota flaviventris* (Audubon & Bachman)

APPENDIX B: Data for annual values presented as five year running means in the text and annual values for North Shields fledged Kittiwakes which returned to North Shields.

TABLE B.1: Colony size, density of nests (% ledges with two pairs), and number of chicks fledged per pair in each year from 1949 to 1984.

Year	Colony size (pairs)	% ledges with two pairs (n)	Mean number of chicks fledged/pair
1949	4	0	-
1950	11	0	-
1951	12	0	-
1952	13	0	-
1953	16	0	-
1954	20	7.1 (14)	1.05
1955	34	14.8 (27)	1.03
1956	35	17.2 (29)	1.06
1957	35	22.2 (27)	1.09
1958	38	16.1 (31)	1.29
1959	44	20.0 (35)	1.61
1960	52	28.9 (38)	1.40
1961	61	28.9 (45)	1.34
1962	72	28.8 (52)	1.28
1963	83	38.6 (57)	1.40
1964	88	44.1 (59)	1.49
1965	104	53.0 (66)	1.49
1966	97	56.7 (60)	1.09
1967	103	56.3 (64)	1.42
1968	96	50.0 (62)	1.14
1969	90	45.0 (60)	1.08
1970	91	48.3 (60)	1.25
1971	84	44.6 (56)	1.15
1972	84	49.1 (55)	1.14
1973	79	42.6 (54)	1.09
1974	72	45.8 (48)	1.07
1975	72	43.8 (48)	1.05
1976	68	48.9 (45)	1.08
1977	67	30.6 (49)	0.99
1978	74	36.5 (52)	1.07
1979	71	36.5 (52)	1.03
1980	86	35.5 (62)	1.06
1981	89	40.3 (62)	1.00
1982	70	44.7 (47)	1.12
1983	87	(29.7)(64)	0.94
1984	69	(7.9)(63)	1.24

TABLE B.2: Annual survival rates of male and female breeding Kittiwakes at North Shields between 1954 and 1984. Numbers at risk are in parentheses. Data from 1954 to 1974 are from Coulson & Wooller (1976).

At risk between	Male survival rate	Female survival rate
1954-5	1.00 (15)	1.00 (14)
1955-6	0.70 (30)	0.97 (34)
1956-7	0.93 (29)	0.84 (38)
1957-8	0.86 (29)	0.89 (37)
1958-9	0.75 (32)	0.83 (36)
1959-60	0.86 (44)	0.85 (47)
1960-1	0.92 (51)	0.95 (54)
1961-2	0.82 (60)	0.92 (64)
1962-3	0.92 (72)	0.95 (72)
1963-4	0.82 (77)	0.92 (85)
1964-5	0.88 (85)	0.89 (92)
1965-6	0.89 (102)	0.91 (106)
1966-7	0.75 (102)	0.75 (104)
1967-8	0.86 (102)	0.85 (112)
1968-9	0.69 (98)	0.76 (105)
1969-70	0.83 (81)	0.84 (92)
1970-1	0.88 (74)	0.92 (87)
1971-2	0.72 (87)	0.77 (106)
1972-3	0.82 (82)	0.95 (95)
1973-4	0.62 (86)	0.74 (95)
1974-5	0.77 (75)	0.80 (75)
1975-6	0.85 (71)	0.88 (75)
1976-7	0.78 (72)	0.83 (82)
1977-8	0.92 (66)	0.86 (80)
1978-9	0.83 (75)	0.88 (78)
1979-80	0.69 (78)	0.74 (87)
1980-1	0.84 (83)	0.80 (92)
1981-2	0.80 (90)	0.82 (88)
1982-3	0.72 (82)	0.73 (89)
1983-4	0.66 (93)	0.61 (96)
All years	0.80 (2123)	0.84 (2317)

TABLE B.3: Recruitment rates (proportion of Kittiwakes breeding for the first time), and the percent and age of recruits which had fledged from North Shields for males and females at North Shields for each year from 1954 to 1984.

Year	Male			Female		
	Recruitment rates (number of recruits)	% natal recruits (n)	Age of recruitment	Recruitment rates (number of recruits)	% natal recruits (n)	Age of recruitment
1954	75.0 (15)	0 (0)	-	50.0 (10)	0 (0)	-
1955	58.8 (20)	0 (0)	-	58.8 (20)	0 (0)	-
1956	40.0 (14)	7.1 (1)	3.0	25.7 (9)	0 (0)	-
1957	28.6 (10)	0 (0)	-	25.7 (9)	0 (0)	-
1958	39.5 (15)	0 (0)	-	39.5 (15)	0 (0)	-
1959	54.5 (24)	12.5 (3)	4.0	40.9 (18)	0 (0)	-
1960	32.7 (17)	17.6 (3)	4.3	32.7 (17)	0 (0)	-
1961	31.1 (19)	10.5 (2)	5.0	23.0 (14)	0 (0)	-
1962	37.5 (27)	0 (0)	-	33.3 (24)	0 (0)	-
1963	26.5 (22)	13.6 (3)	4.0	30.1 (25)	0 (0)	-
1964	29.5 (26)	15.4 (4)	4.5	23.9 (21)	9.5 (2)	3.5
1965	30.8 (32)	31.3 (10)	4.5	25.0 (26)	11.5 (3)	4.7
1966	24.7 (24)	20.8 (5)	5.2	27.8 (27)	7.4 (2)	5.5
1967	31.1 (32)	28.1 (9)	4.0	30.1 (31)	16.1 (5)	4.8
1968	15.6 (15)	46.7 (7)	4.7	19.8 (19)	21.1 (4)	4.8
1969	34.4 (31)	38.7 (12)	4.5	33.3 (30)	10.1 (3)	4.3
1970	34.1 (31)	22.6 (7)	4.4	27.5 (25)	4.0 (1)	4.0
1971	28.6 (24)	45.8 (11)	4.7	31.0 (26)	7.7 (2)	6.0
1972	22.6 (19)	57.9 (11)	5.3	22.6 (19)	10.5 (2)	6.5
1973	24.1 (19)	57.9 (11)	4.5	17.7 (14)	14.3 (2)	5.0
1974	36.1 (26)	30.8 (8)	3.7	27.8 (20)	5.0 (1)	4.0
1975	19.4 (14)	35.7 (5)	3.8	16.7 (12)	8.3 (1)	4.0
1976	25.0 (17)	23.5 (4)	4.3	23.5 (16)	12.5 (2)	4.0
1977	26.9 (18)	44.4 (8)	4.4	23.9 (16)	6.3 (1)	4.0
1978	25.7 (19)	57.9 (11)	4.0	23.0 (17)	5.9 (1)	^{a}
1979	33.8 (24)	20.8 (5)	4.2	25.4 (18)	0 (0)	-
1980	39.5 (34)	12.5 (3)	4.7	38.4 (33)	3.0 (1)	3.0
1981	31.5 (28)	14.3 (4)	4.0	31.5 (28)	7.1 (2)	4.0
1982	24.3 (17)	35.3 (6)	3.8	30.0 (21)	4.8 (1)	4.0
1983	33.3 (28)	21.4 (6)	3.5	35.6 (31)	6.5 (2)	4.0
1984	29.9 (20)	20.0 (4)	3.8	34.8 (24)	0 (0)	-

Notes: ^{a}no data.

TABLE B.4: Percentage of each cohort (chicks fledged from North Shields in a particular year) which subsequently returned to North Shields to breed, and the percentage of that cohort which would be expected to be alive four years later after year-specific annual survival rates (Table B.2) had acted on them.

Year fledged	Number fledged	Number return		% return (male + female)	% alive four years later[1]
		Male	Female		
1954	28	0	0	0	65.7
1955	33	5	0	15.2	52.0
1956	35	2	0	5.7	56.2
1957	38	1	0	2.6	56.2
1958	46	2	0	4.3	55.6
1959	72	5	0	6.9	66.1
1960	69	3	4	10.1	66.9
1961	89	12	4	18.0	63.3
1962	81	3	3	7.4	65.5
1963	113	9	3	10.6	52.3
1964	125	12	4	12.8	51.7
1965	148	9	3	8.1	42.4
1966	100	14	3	17.0	39.6
1967	142	11	0	7.7	47.5
1968	108	6	3	8.3	41.4
1969	86	4	0	4.7	50.5
1970	81	7	1	9.9	40.9
1971	87	3	1	4.6	35.9
1972	91	11	2	14.3	41.6
1973	87	5	1	6.9	37.9
1974	79	10	0	12.7	49.5
1975	76	7	0	9.2	53.9
1976	75	2	0	2.7	44.6
1977	64	5	2	10.9	45.2
1978	77	3	1	5.1	41.1
1979	76	5	2	9.2	34.9
1980	90	5	0	5.6	31.0

Notes: [1] Calculated from the product of the number of young fledged per year and adult annual survival rates for the following four years (from Table B.2).

TABLE B.5: Annual mean male and female body weights according to their status (recruits or prospectors) at the time of capture from 1959 to 1984. Sample sizes are in parentheses.

Year	Male weights (g)		Female weights (g)	
	Recruits	Prospectors	Recruits	Prospectors
1959	365 (11)	360 (3)	336 (4)	321 (5)
1960	365 (5)	357 (8)	325 (4)	348 (4)
1961	400 (4)	419 (1)	359 (4)	346 (1)
1962	398 (7)	370 (5)	347 (10)	315 (1)
1963	388 (9)	389 (4)	357 (17)	337 (4)
1964	389 (17)	361 (2)	339 (10)	361 (2)
1965	388 (23)	371 (4)	349 (17)	340 (1)
1966	399 (7)	373 (4)	370 (2)	- (0)
1967	394 (15)	368 (11)	358 (27)	334 (5)
1968	386 (5)	373 (3)	358 (7)	337 (1)
1969	417 (6)	372 (5)	367 (8)	335 (3)
1970	385 (5)	366 (9)	345 (4)	346 (7)
1971	397 (18)	380 (10)	354 (16)	337 (9)
1972	385 (10)	375 (10)	342 (9)	333 (9)
1973	366 (9)	378 (6)	321 (7)	335 (7)
1974	402 (17)	382 (28)	355 (11)	338 (14)
1975	414 (4)	379 (15)	366 (6)	333 (14)
1976	361 (2)	369 (4)	366 (4)	338 (10)
1977	412 (1)	371 (2)	355 (4)	342 (3)
1978	377 (1)	364 (2)	379 (2)	330 (5)
1979	407 (9)	369 (8)	352 (12)	332 (7)
1980	410 (20)	379 (4)	370 (21)	343 (4)
1981	385 (13)	- (0)	361 (6)	- (0)
1982	392 (11)	379 (9)	350 (16)	341 (13)
1983	403 (16)	383 (6)	377 (19)	341 (3)
1984	404 (12)	394 (6)	363 (19)	343 (9)
$\bar{X}$ ± S.D.	391.6 ± 25.4	375.0 ± 25.4	354.2 ± 28.3	335.6 ± 18.6

TABLE B.6: Annual mean male and female wing-lengths according to their status (recruits or prospectors) at the time of capturing from 1959 to 1984. Sample sizes are in parentheses.

Year	Male wing-lengths (mm)		Female wing-lengths (mm)	
	Recruits	Prospectors	Recruits	Prospectors
1959	312 (11)	307 (3)	308 (4)	301 (5)
1960	313 (5)	310 (8)	299 (4)	303 (4)
1961	315 (4)	- (0)	300 (4)	298 (1)
1962	315 (7)	311 (5)	302 (10)	303 (1)
1963	310 (9)	314 (4)	303 (17)	302 (4)
1964	308 (17)	306 (2)	303 (10)	293 (2)
1965	311 (23)	310 (4)	304 (17)	309 (1)
1966	314 (7)	312 (4)	304 (2)	- (0)
1967	312 (15)	312 (11)	302 (27)	302 (5)
1968	311 (5)	312 (3)	308 (7)	305 (2)
1969	314 (6)	310 (5)	302 (8)	298 (3)
1970	309 (5)	308 (9)	299 (4)	295 (7)
1971	310 (18)	307 (10)	301 (16)	293 (9)
1972	310 (10)	312 (10)	300 (9)	297 (9)
1973	307 (9)	310 (6)	299 (7)	299 (7)
1974	312 (17)	313 (28)	305 (11)	300 (14)
1975	315 (4)	310 (15)	303 (6)	299 (14)
1976	311 (1)	314 (4)	306 (4)	302 (10)
1977	- (0)	310 (2)	304 (4)	303 (3)
1978	315 (1)	315 (2)	304 (2)	302 (5)
1979	312 (9)	314 (8)	303 (12)	299 (7)
1980	313 (20)	308 (4)	302 (21)	304 (4)
1981	310 (13)	312 (2)	306 (6)	303 (1)
1982	314 (11)	310 (9)	306 (16)	304 (13)
1983	316 (16)	313 (6)	311 (19)	299 (3)
1984	316 (12)	315 (6)	307 (19)	301 (9)
$\bar{X}$ ± S.D.	311.2 ± 5.9	311.0 ± 5.4	303.1 ± 8.0	299.8 ± 6.6

APPENDIX C: Calculations for a model of unrestricted growth of a Kittiwake colony as discussed in Section 3.5.1.

Coulson's (1983) equation, describing the relationship between colony size in 1959 and the percent increase between 1959 and 1969 for 47 Kittiwake colonies in England, was used to calculate the pattern of growth for a single hypothetical colony. The equation was used to calculate the colony size and from that the number of recruits required to sustain the expected pattern of growth was determined, as well as the chick production of the colony. The following shows how calculations were made. Values for each of the first 30 years are shown in Table C.1 and values for 200 years at 10 year intervals are shown in Table C.2.

Calculations of expected pattern of growth of a Kittiwake colony

Where: I = survival of immatures from fledging to breeding at four years (= 0.40)[1]

P = chick production/pair/year (= 1.05)

R = number of recruits required

S = annual adult survival rate (= 0.85)

W = $\log_{10}$ (colony size)

X = year

Y = colony size in pairs

Z = $\log_{10}$ (% increase/10 years)

Colony size:

Given $Y_0 = 5$, using Coulson's equation $Z = -0.44W + 3.09$

$$Z = -0.44 (\log_{10} 5) + 3.09 = 2.782$$

% increase/10 years = 606%

$$\therefore Y_{10} = (5 \cdot 6.06) + 5 = 35.3$$

Notes: [1] Based on adult annual survival rates of 0.80 and chick production of 1.05/pair; immature survival rate from fledging to breeding required is 0.40.

TABLE C.1: Pattern of growth of a single colony for the first 30 years showing colony size, percent increase per annum, recruitment requirements and production requirements.

Year	Colony size (pairs)	% increase per annum	% recruits required	No. recruits required	No. recruits produced	Production required (chicks/pr)
0	5.0	27.9	100.0	10.0	0	-
1	6.4	25.8	33.6	4.3	0	-
2	8.0	24.2	32.4	5.2	0	-
3	10.0	22.9	31.6	6.3	0	-
4	12.3	21.7	30.8	7.6	2.1	3.80
5	14.9	20.6	30.1	9.0	2.7	3.52
6	18.0	19.6	29.5	10.6	3.4	3.31
7	21.6	18.7	28.9	12.5	4.2	3.13
8	25.6	17.8	28.4	14.5	5.2	2.95
9	30.1	17.1	27.9	16.8	6.3	2.82
10	35.3	16.2	27.4	19.3	7.6	2.69
11	41.0	15.6	26.9	22.0	9.1	2.55
12	47.4	14.9	26.4	25.1	10.8	2.45
13	54.5	14.3	26.0	28.4	12.6	2.36
14	62.3	13.7	25.6	32.0	14.8	2.27
15	70.8	13.2	25.2	35.7	17.2	2.18
16	80.1	12.6	24.9	39.8	19.9	2.10
17	90.2	12.2	24.5	44.2	22.9	2.03
18	101.2	11.7	24.2	49.1	26.2	1.97
19	113.1	11.3	23.9	54.2	29.7	1.91
20	125.8	10.9	23.6	59.3	33.6	1.85
21	139.5	10.5	23.3	65.1	37.9	1.80
22	154.2	10.2	23.1	71.3	42.5	1.76
23	169.9	9.8	22.9	77.7	47.5	1.72
24	186.6	9.5	22.6	84.4	52.8	1.68
25	204.4	9.2	22.4	91.6	58.6	1.64
26	223.3	9.0	22.2	99.1	64.8	1.61
27	243.3	8.7	22.0	107.0	71.4	1.57
28	264.4	8.4	21.8	115.2	78.4	1.54
29	286.7	8.2	21.6	123.9	85.8	1.52
30	310.2	8.0	21.4	133.0	93.8	1.49

TABLE C.2: Pattern of growth of a single colony for 200 years showing colony size, percent increase per annum, recruitment requirements and production requirements.

Year	Colony size (pairs)	% increase per annum	% recruits required	No. recruits required	No. recruits produced	Production required (chicks/pr)
0	5	27.9	100.0	10	0	--
10	35	16.1	27.4	19	8	2.69
20	125	10.9	23.6	59	34	1.85
30	310	8.0	21.4	133	94	1.49
40	616	6.2	20.1	247	201	1.29
50	1065	5.0	19.1	408	364	1.18
60	1675	4.2	18.5	620	592	1.10
70	2460	3.6	18.0	886	892	1.04
80	3436	3.2	17.6	1211	1269	1.00
90	4611	2.8	17.3	1599	1729	0.97
100	5997	2.5	17.1	2051	2275	0.95
110	7602	2.3	16.9	2571	2912	0.93
120	9436	2.1	16.7	3161	3644	0.91
130	11506	1.9	16.6	3822	4473	0.90
140	13819	1.8	16.5	4558	5403	0.89
150	16381	1.7	16.4	5369	6437	0.88
160	19200	1.6	16.3	6259	7577	0.87
170	22280	1.5	16.2	7228	8827	0.86
180	25629	1.4	16.2	8279	10188	0.85
190	29250	1.3	16.1	9412	11663	0.85
200	33150	1.2	16.0	10630	13254	0.84

In the same way, the colony size was determined at 10 year intervals for 200 years. A polynomial equation was then fitted to these 21 values, using the "least squares" criterion. The equation of best fit was:

$$Y = A_0 + A_1X + A_2X^2 + A_3X^3 + A_4X^4 + A_5X^5 + A_6X^6 + A_7X^7 + A_8X^8$$

where: $A_0 = 4.99$
$A_1 = 1.39$
$A_2 = 8.80 \times 10^{-2}$
$A_3 = 8.11 \times 10^{-3}$
$A_4 = -4.97 \times 10^{-5}$
$A_5 = 2.57 \times 10^{-7}$
$A_6 = -8.97 \times 10^{-10}$
$A_7 = 1.83 \times 10^{-12}$
$A_8 = 1.64 \times 10^{-15}$

The sum of (Y-Y calculated)^2 was 1.40×10^{-2} for the 21 points. An eighth order polynomial equation was used to obtain a close fit to the colony size in the first forty years; a lower order was a close fit to the upper points, but not the early years when numbers were small. Solving for this polynomial equation, the colony size in any year could be calculated.

The following calculations were made:

% increase/annum:

% increase/annum in Year X = $\left(\frac{Y_X - Y_{X+1}}{Y_X}\right) \times 100\%$

Recruits required:

recruits required in Year X = $\frac{R_X}{Y_X}$

Recruits produced:

recruits produced for Year X = $(Y_{X-4})\cdot(P)\cdot(I)$

Production required

production required in Year X

to supply recruits in Year X + 4 = $\frac{R_{X+4}}{Y_X \cdot I}$

% difference in production of recruits:

% difference between the number of recruits produced by the colony and those required (for Year X) $= \frac{(\text{recruits produced for Year } X) - R_X}{R_X} \cdot 100\%$

APPENDIX D: Details of statistical tests used in the text.

Page	Line	Statistic	d.f.	Significance level (P)
13	24	$r = +0.97$	12	< 0.001
15	20	$r = +0.66$	10	< 0.02
15	20	$r = +0.70$	13	< 0.01
15	25 (slope)	$t = 0.46$	23	ns
15	25 (intercept)	$t = 2.09$	23	< 0.05
21	22	$r = +0.49$	27	< 0.01
24	17	$r = +0.72$	25	< 0.001
28	12	$r = -0.04$	25	ns
31	3 (male)	$t = 2.42$	109	< 0.02
31	3 (female)	$t = 4.51$	25	< 0.001
31	9	$t = 1.30$	38	ns
31	21 (male)	$t = 6.44$	431	< 0.001
31	21 (female)	$t = 8.00$	408	< 0.001
31	25 (male)	$t = 3.25$	189	< 0.01
31	25 (female)	$t = 3.59$	196	< 0.001
33	3	$t = 0.36$	431	ns
33	4	$t = 4.77$	408	< 0.001
33	6 (m. recruit)	$t = 2.14$	189	< 0.05
33	6 (m. prosp.)	$t = 2.21$	130	< 0.05
33	6 (f. recruit)	$t = 2.69$	196	< 0.01
33	6 (f. prosp.)	$t = 2.81$	107	< 0.01
39	16	$r = -0.97$	12	< 0.001
39	20	$r = -0.85$	13	< 0.001
47	5	$\chi^2 = 1.54$	1	ns
47	24	$\chi^2 = 6.56$	1	< 0.05
49	9	$\chi^2 = 10.12$	1	< 0.01
49	11 (male)	$t = 0.58$	149	ns
49	11 (female)	$t = 0.37$	104	ns
49	12 (male)	$t = 0.69$	149	ns
49	12 (female)	$t = 0.29$	104	ns
49	23 (male)	$t = 6.44$	431	< 0.001
49	23 (female)	$t = 8.00$	408	< 0.001
49	24 (male)	$t = 0.36$	431	ns
49	24 (female)	$t = 4.77$	408	< 0.001
51	26	$t = 6.54$	188	< 0.001
56	1	$t = 3.99$	77	< 0.001
56	11	$t = 3.73$	177	< 0.001
62	17 (2)	$t = 2.05$	30	< 0.05
62	17 (3)	$t = 2.87$	23	< 0.01
62	17 (4)	$t = 8.59$	3	< 0.01
62	18 (2)	$t = 0.17$	30	ns
62	18 (3)	$t = 0.76$	23	ns
62	18 (4)	$t = 2.37$	3	ns
62	21	$t = 2.37$	21	< 0.05
62	22	$t = 3.02$	21	< 0.01
68	16	$t = 10.36$	63	< 0.001
68	17	$t = 6.74$	63	< 0.001
68	18	$t = 3.42$	52	< 0.01
68	20	$t = 6.70$	74	< 0.001
73	17	$t = 0.56$	29	ns
75	7	$t = 1.32$	17	ns
75	9	$t = 7.06$	23	< 0.001
75	10	$t = 3.86$	23	< 0.001
75	11	$t = 1.62$	23	ns
75	12	$t = 0.45$	23	ns
75	13	$t = 9.13$	23	< 0.001
75	14	$t = 6.01$	23	< 0.001
75	26	$t = 0.55$	14	ns
79	27	$t = 7.15$	23	< 0.001
82	5	$t = 9.34$	14	< 0.001
82	11 (estab.)	$t = 0.32$	38	ns
82	11 (1 recr.)	$t = 0.10$	34	ns
82	13	$t = 10.88$	58	< 0.001
88	2	$t = 6.30$	29	< 0.001
88	19	$\chi^2 = 12.63$	1	< 0.001
91	11 (1, early)	$t = 0.65$	267	ns
91	11 (1, late)	$t = 1.74$	443	ns
91	11 (2-10, early)	$t = 1.98$	330	< 0.05
91	11 (2-10, late)	$t = 2.06$	654	< 0.05
91	11 (≥ 11, late)	$t = 0.39$	138	ns
91	20 (males)	$t = 1.98$	256	< 0.05
91	20 (females)	$t = 3.54$	262	< 0.001
91	23	$t = 0.80$	256	ns
91	24	$t = 2.38$	262	< 0.02