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Strowger, John

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ABSTRACT

Although much research has been undertaken into the status and biology of the Kittiwake *Rissa tridactyla* studies of a colony over an extended period are scarce with the notable exception of the North Shields colony for which 31 years of data were summarized by Coulson and Thomas (1985). The nearby colony at Marsden Bay, Tyne and Wear had however been the focus of study in the 1950s (Coulson and White 1956) and the 1970s (Dixon 1979). It was considered that a similar study in the early 1990s could be usefully combined with a review of data from these two previous periods.

Since the colony's formation in 1931 the nest count has increased from 308 in 1937 to 5768 in 1992. After rapid and steady growth through the 1940s and 1950s a period of relative stability occurred in the 1970s with about 4,600 nests present. In the last 15 years numbers have again risen substantially. Continuing changes in the cliff structure due to erosion are affecting the availability of nest sites and hence the number of nests.

Changes in the breeding biology have resulted in the Kittiwakes spending less time at the colony each year. Their later arrival in the spring has had little effect on the mean date of laying perhaps due to a more synchronised arrival of the colony. Evening departure by birds from the colony in the pre-breeding period was found to be related to the time the birds arrived in the colony in the spring and their subsequent attendance on the nest site.

Chick growth rates were slightly lower than in the 1950s and 1970s at North Shields, and chick neglect was frequent in 1992. However these factors did not appear to influence the fledging success.

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I would like to record my thanks and appreciation to Dr. J. C. Coulson for his advice and support which I have gratefully received.

Thanks also to members of the Durham Ringing Group for their assistance in the collection of adult and chick biometrics.

ASPECTS OF THE BREEDING BIOLOGY OF THE KITTIWAKE GULL *RISSA TRIDACTYLA* AT MARSDEN BAY, TYNE AND WEAR

JOHN STROWGER

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15 JUN 1994

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CHAPTER 1.

INTRODUCTION

The breeding biology of the Kittiwake gull *Rissa tridactyla* has been extensively studied and its status in the British Isles carefully documented since 1959 (Coulson 1963, 1974, 1983; Harris and Wanless 1990).

After a steady increase in numbers up to 1969 at the rate of 3-4% per annum, the next ten years showed a period of stabilization with the growth rate being reduced to 1% per annum, and only colonies bordering the North Sea showed consistent growth (Coulson 1983). However little information was available for these North Sea colonies except for a few notable exceptions e.g. Coulson and White (1956), Dixon (1979), Brown (1984), Coulson and Thomas (1985). A recent and comprehensive study of breeding success in colonies throughout the British Isles has provided data on a national scale but only for the period 1986-1988 (Harris and Wanless 1990). This demonstrated a negative relationship between breeding success and latitude in 1986 and 1987. In 1988, colonies further south in Britain were more successful than those further north although the more southerly colonies were also showing a reduction in breeding success following on from the Shetland experience of the mid and late 1980's.

The dramatic fluctuations in the breeding success of the Kittiwake in the Northern Isles in recent years has produced much speculation as to their cause. The exact nature and extent of these changes has not always been easy to assess due to the lack of reliable data from the past. Coulson and Thomas (1985) summarised 31 years of data for the North Shields, Tyne and Wear colony, 5 km north of Marsden, relating local changes to the national situation and demonstrated the value of such an approach.

At Marsden, no such continuous study has been performed, but detailed studies were carried out in the 1950's by Coulson and White (1956), who also summarized the early history of the colony, and in the 1970's by Dixon (1979). There is also some recently published information from 1988 (Harris and Wanless 1990). The current investigation coming 15 years after that of Dixon provided further data. This allows an analysis of the colony's development over a period in excess of 50 years and changes in the breeding biology as the colony has matured.

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Coulson and Thomas (1985) discussed various factors which may have been responsible for, or at least influenced, changes in the population dynamics and breeding behaviour of the Kittiwake colony at North Shields. Changes in the colony in its early formative years were considered to be associated with changing age structure. In later years, however, food availability, but not pesticides, was judged, on the basis of such evidence as existed on the feeding habits of Kittiwakes and fish stocks, to be responsible.

Much of the data available on fish stocks are linked with the requirements of commercial fisheries e.g. since 1946, Herring *Clupea harengus* has been monitored in the North Sea. Fisheries biologists have yet to make major contributions to the body of data required to aid the analysis of seabird population and breeding biology changes at specific colonies. Data collected in separate fields of study, have recently been collated by Aebischer, Coulson and Colebrook (1990). Long term trends were very similar in phytoplankton, zooplankton, Herring, Kittiwake breeding variables and westerly weather, during 1955-1987 in the northwestern quadrant of the North Sea. All were high in the late 1950s, declined, reaching a trough in the late 1970s, before showing a marked recovery during the 1980s. In addition, ornithologists must obtain.detailed information on the feeding areas and target food species of seabirds. In the Kittiwake this must include the pelagic "winter" season and the land-based phase of their life cycle at the breeding colony. The work of Pearson (1968) on the Farne Islands gives some valuable data for the seabirds off the Northumbrian coast, during the breeding season, which could form a basis for further studies.

As shown by Aebischer, Coulson and Colebrook (1990), certain Kittiwake breeding variables showed similar long term changes to three other sets of marine data and one set of climatic data. The breeding variables were mean laying date, clutch size and number of chicks reared per pair. These were some of the aspects of breeding biology investigated at Marsden Bay in my study. In addition, annual recolonisation, chick growth rates and adult attendance during chick rearing were also investigated as important aspects and possibly indicative of factors, including environmental conditions, influencing food supply, before breeding and during the chick rearing stage.

Much of my data collection depended on the use of selected areas within the colony which were photographed and the progress of individual nests followed. Colour-ringing of adults and chicks, in a small but accessible part of the colony was also undertaken. Some adults and chicks were ringed in 1990, then more intensive and systematic ringing took place during 1991 and 1992. This forms a solid base for the continuing study of a group of individually marked Kittiwakes at Marsden Bay. Previously, only individuals marked in other colonies and subsequently discovered at Marsden could be studied.

Data were also collected and analysed on colony size (1990-1992), annual nest site counts in areas of the colony , survival rates of adult Kittiwakes, evening departure and overnight occupation, hatching success, brood sizes, timing of chick mortality, adult body weights during chick rearing, and fledging success.

CHAPTER 2.

STUDY AREA AND METHODS

(i) Study Area

The Kittiwake colony at Marsden, Tyne and Wear (National Grid ref. NZ 403647), is on natural sea-cliffs composed of limestone. Kittiwakes were first observed at Marsden in 1930 when about 50 birds were seen on Marsden Rock (Temperley 1951). Breeding did not occur and assuming that this observation coincided with the first year of colonisation would be as expected. Colonisation depends upon an influx of young birds who prospect for a year or more before establishing a breeding colony. This behaviour is mirrored in the immigration of young non-breeding birds into an established colony. They are present as non-breeders in the colony at least one year before attempting to breed (Coulson and White 1960). Breeding first occurred in 1931 on the east face (original colony) of Marsden Rock. In 1933, Kittiwakes had colonised the south and north faces (areas A and B). It was not until 1940 that the mainland cliffs became colonised, non-breeding birds first being observed at the site in 1939. By 1953, four more colonies had developed with a total of 1923 nests (Coulson and White 1960).

In addition to Kittiwakes, other breeding seabirds include Fulmar *Fulmarus glacialis*, Cormorant *Phalacrocorax carbo*, and Herring Gull *Larus argentatus* with a few pairs each of Lesser Black-backed Gull *Larus fuscus* and Razorbill *Alca torda*. The Kittiwakes are by far the most numerous breeding species. During the period of this study the colony contained over 5,000 breeding pairs.

There is public access to the cliff-top above and to the sandy beach and rocky shore below the colony. From the Marsden Grotto north, the base of the cliffs is usually accessible even at high tide, whereas to the south access is limited to a period of about three hours either side of low water. The base of Marsden Rock, a large isolated stack opposite Marsden Grotto, is only accessible for a period of two hours either side of low water.

(ii) Methods

Coulson and White (1956) described 8 colonies in Marsden Bay (Figure 1a). I have followed their labelling of colonies for ease of comparison. Some modification has been necessary, mainly because the colonies have expanded and are much larger now than in the 1950s. As the previously individual colonies have in some cases merged and formed a continuum along the mainland cliffs, I have referred to "areas", rather than "colonies". Observations were made at various times both from the cliff top above and from the beach below the colony. The most detailed and comprehensive data were collected from areas F, G1 and G3 (Figure 1b). For area F, some observations were made from the cliff top just to the north but most were made from the beach below. Permission was obtained allowing access to the roof of the Marsden Grotto Public House which allowed direct access to some nests, in area F, and their eggs and chicks. Adults were also captured in this area. Adults were given a British Trust for Ornithology (BTO) monel ring and a unique colour combination composed of three colour rings. As far as I am aware there were no harmful effects to the birds or data biases caused as a result of my ringing activities. However, Calvo and Furness (1992) have drawn the attention of researchers using rings, and other marking devices, to be aware of potential problems, and take action to minimise the effect and where possible to attempt an assessment of their effect.

Observations were made using 10x40 binoculars and a 20-45x telescope. Monochrome photographs were taken of the main study areas, F, G1 and G3 using a 35mm SLR camera. The prints were enlarged to 25 x 15 cm and covered with a transparent sheet on which nest sites could be marked using waterproof ink. Each plot was identified by a combination of letters and/or numbers. The same photographs were used in 1990, 1991 and 1992 to allow direct comparison of the number of nests and their annual performance.

Colour transparencies were taken in 1992 of areas A, A1, B, D and F allowing numbers and density of nests to be calculated. Transparencies were projected onto a sheet of white paper, nest sites and prominent features marked, and nest diameters measured. As far as possible these maps of nest site distribution were checked in the field.

Colony Size

Colony size was measured as the number of apparently occupied nests (AON) during June of each year. Additional data were available for 1990. An AON was one considered to be capable of holding eggs with at least one adult present at the time of observation. This would give a slightly optimistic figure for the number of breeding pairs as not all nests identified as AONs would contain eggs. Non-attendance of adults at nests with chicks in June 1991 was not considered to be a significant cause of error in the final count of AONs. However in 1992 adult non attendance was significantly higher and could have lead to inaccuracies in AON counts. With care and experience, adults standing on nearby ledges could often be identified with nests, thus reducing the margin of error. Counts were made by dividing the colony into sections, delimited by obvious physical features, so that relatively small numbers of nests were counted at a time to increase the accuracy of the count . Coulson (1983) suggests that in small colonies the error in the count should be below 5%, only exceeding this in very large colonies or in those where there are difficulties with observation. Neither of these factors are relevant in this case.

Reoccupation of Colony

Observations in 1991 commenced on 20 February with no Kittiwakes observed. In the period 20 February 1991 to 2 May 1991, 47 visits were made to monitor reoccupation of the colony. Data were collected for eleven areas of the colony but none received the maximum 47 visits. Observations in 1992 commenced on 12 January although the first Kittiwakes were not seen on the cliffs until 7 February. Subsequently another 38 visits were made up to and including 7 May, specifically to monitor reoccupancy. The unit counted was an apparently occupied site (AOS), indicated by the presence of at least one adult. The number of pairs present on AOSs was also recorded. On count days in 1992, data were collected on wind direction and wind speed .

Annual nest site distribution

Information on colony size, as it was collected on a sectional basis, was used to investigate changes in the distribution and number of nests within the colony. Each section was the equivalent of a "small colony".

Survival rates of adult Kittiwakes

In 1990, 51 adult Kittiwakes were individually colour-ringed in early July in area F of the colony. In 1991, 42 of these were observed around area F. Due to the date of ringing in 1990, it is not known whether these were all breeding birds or included some non-breeding prospectors, visiting ledges in the colony. Any birds not returning in 1991 may not therefore have died. However in 1991, 33 adults were individually colour-ringed 28 of which were identified with nests. In addition 24 adults colour-ringed in1990 were also identified with nest sites in area F. In 1992, a further 35 adults were colour-ringed making a total of 119 during the period 1990-1992. The majority of adults captured were weighted and the head and bill length measured enabling many birds to be sexed (Coulson *et al.* 1983).

Once a Kittiwake has bred in a particular colony it is very rare for it to move to another colony (Coulson and Wooller 1976). Therefore, breeding birds which do not return the following year can be assumed to be dead. This enabled survival rates to be determined each year.

Evening departure and overnight occupation

Observations were largely restricted to area F of the colony in 1991, but in 1992 more widely spread areas were also examined. Individual nest sites were known and area F was compact enough to be covered easily from one position on the beach. These factors enabled accurate observations to be made in the poor light conditions of late evening. Observations in area F, enabled the reappearance of birds in February and March and their subsequent occupancy, on nest sites, to be recorded during regular visits. The number of times the nest site was observed as being occupied was expressed as a percentage of the maximum possible attendance (total number of my visits) since the date birds first reoccupied sites in this area. The mean evening departure time for adults at each nest site was calculated over the periods 28 April-16 May 1991, and 21 April-11 May 1992. For each nest site these figures were ranked and the resulting values used to calculate the Spearman Rank Correlation Coefficient. Elsewhere observations were restricted to counting or estimating the occupancy of a particular area. Few observations were made during the night or in the pre-dawn and immediate post-dawn period.

Date of laying and clutch size

Due to the inaccessibility of most nests and a wish not to unnecessarily disturb those accessible nests in area F, the laying date in 1991 was estimated from adult behaviour (sitting and incubating). In 1992, nests in area F were visited on ten occasions at seven day intervals, during 13 May to 15 July inclusive, nest contents being recorded. Using a ladder and pole-mounted mirror, data were collected on the clutch size of 35 nests in 1991 and 59 nests in 1992.

Hatching success

Observations were restricted to area F and the nests for which clutch size was known. Hatching success was defined as the proportion of eggs laid which successfully hatched.

Fledging success

Fledging success was calculated as the proportion of chicks which hatched that survived for over 35 days, the earliest at which fledging can occur (Coulson and Thomas 1985). If the date of hatching was not known an estimate of chick age was obtained using plumage features (Maunder and Threlfall 1972).

Chick growth rates

In area F, chicks were weighed to the nearest gram, using electronic scales between 18 June-2 July 1991 and 10 June-15 July 1992. The timing of visits, in an evening at seven day intervals, was arranged so as to minimize disturbance but at the same time to achieve regular and frequent weights on the chicks during the period between hatching and fledging. Care was taken not to cause undue disturbance to the study area. An area, F1, immediately adjacent to the study area was monitored to determine whether it was any more or less successful. On 10 July 1992, the mean brood size in area F1 was 1.58 chicks and 61% of nests held chicks. On the same day in area F, the mean brood size was 1.44 chicks and 58% of nests held chicks. From these data I suggest that research activities in area F had minimal impact on breeding activity.

In 1991 each chick was individually identified with an orange laminated Darvic ring on the left leg inscribed with a unique combination of white letter and number. A BTO ring was placed on the right leg. In 1992 chicks were identified with a blue laminated Darvic inscribed ring on the left leg and a BTO ring on the right. On 3 July 1990, 28 chicks had been individually marked with similarly inscribed green colour rings on the right leg, and a BTO ring on the left leg.

Brood size

Brood sizes were determined, within 7 days of hatching, for nests in area F by direct access to the nests. For nests in area G1 and G3 brood sizes were determined, as soon after hatching as chicks could be counted, by visual examination of the nests with a telescope from observation points on the cliff-top. All nests were numbered on photographs of the study plots and so nests were individually identifiable.

Additional observations were made elsewhere in the colony to obtain data for comparison.

Adult attendance and fledging success.

Observations were made on individually identified nests. In area F, observations were made during the period 11 June-7 August 1991, and 10 June-23 July 1992. In the other study areas observations were made between 17 June-5 August 1991 and 17 June-22 July 1992.

Brood sizes were recorded for each nest on the days of observation enabling data on chick mortality to be collected. Adult attendance was also recorded during these visits as was the progress of the chicks. These latter data enabled an estimate of fledging dates to be made. Broods left unattended occurred when both adults were absent, presumably feeding and not standing on a nearby ledge. Fledging success, defined as the percentage of chicks which hatched that eventually fledged. Chicks were judged to be fledged when over 35 days old, this being the earliest age at which chicks could fly.

FIGURE 1a

The position of Kittiwake colonies at Marsden Bay as described by Coulson and White (1956).

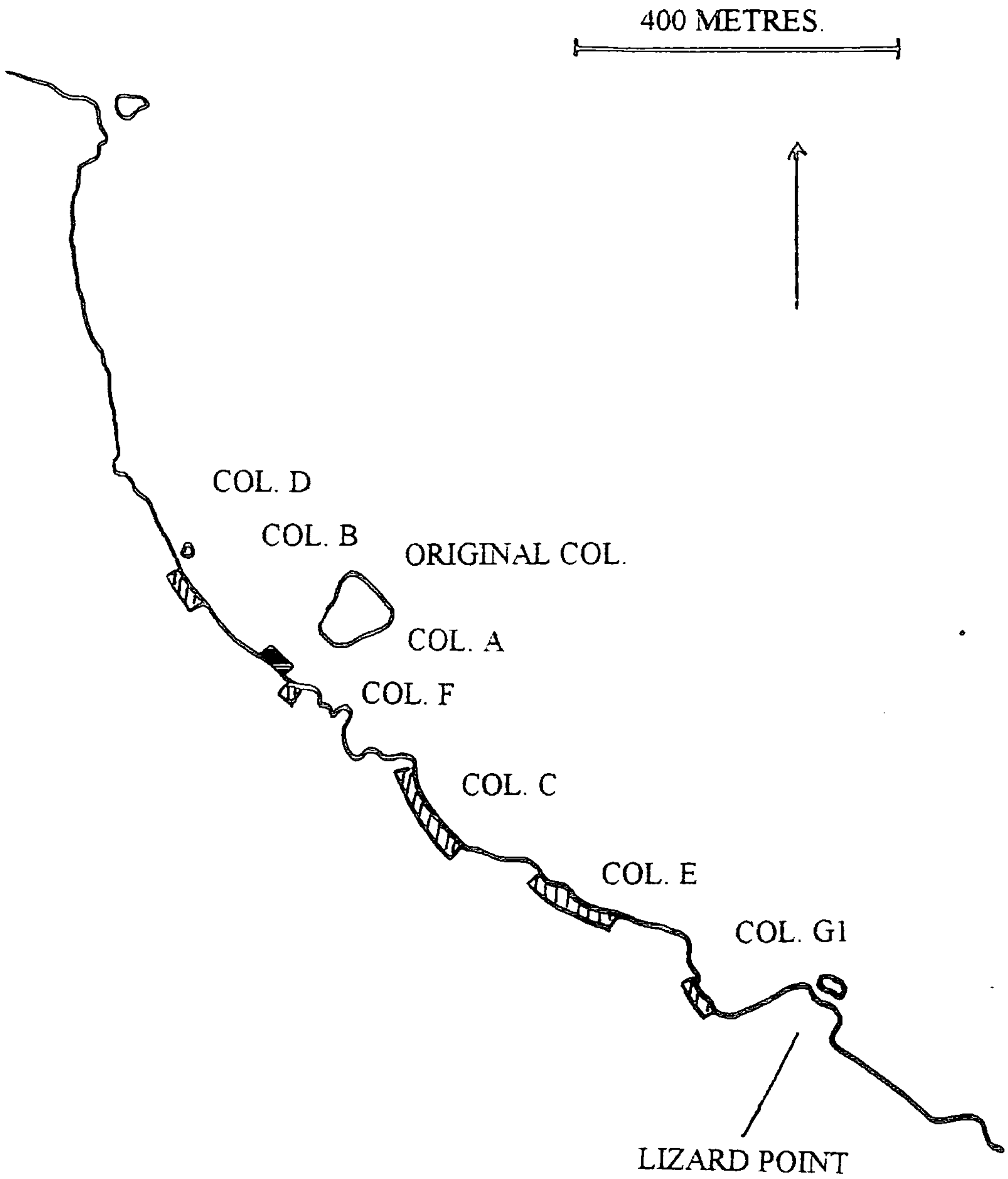
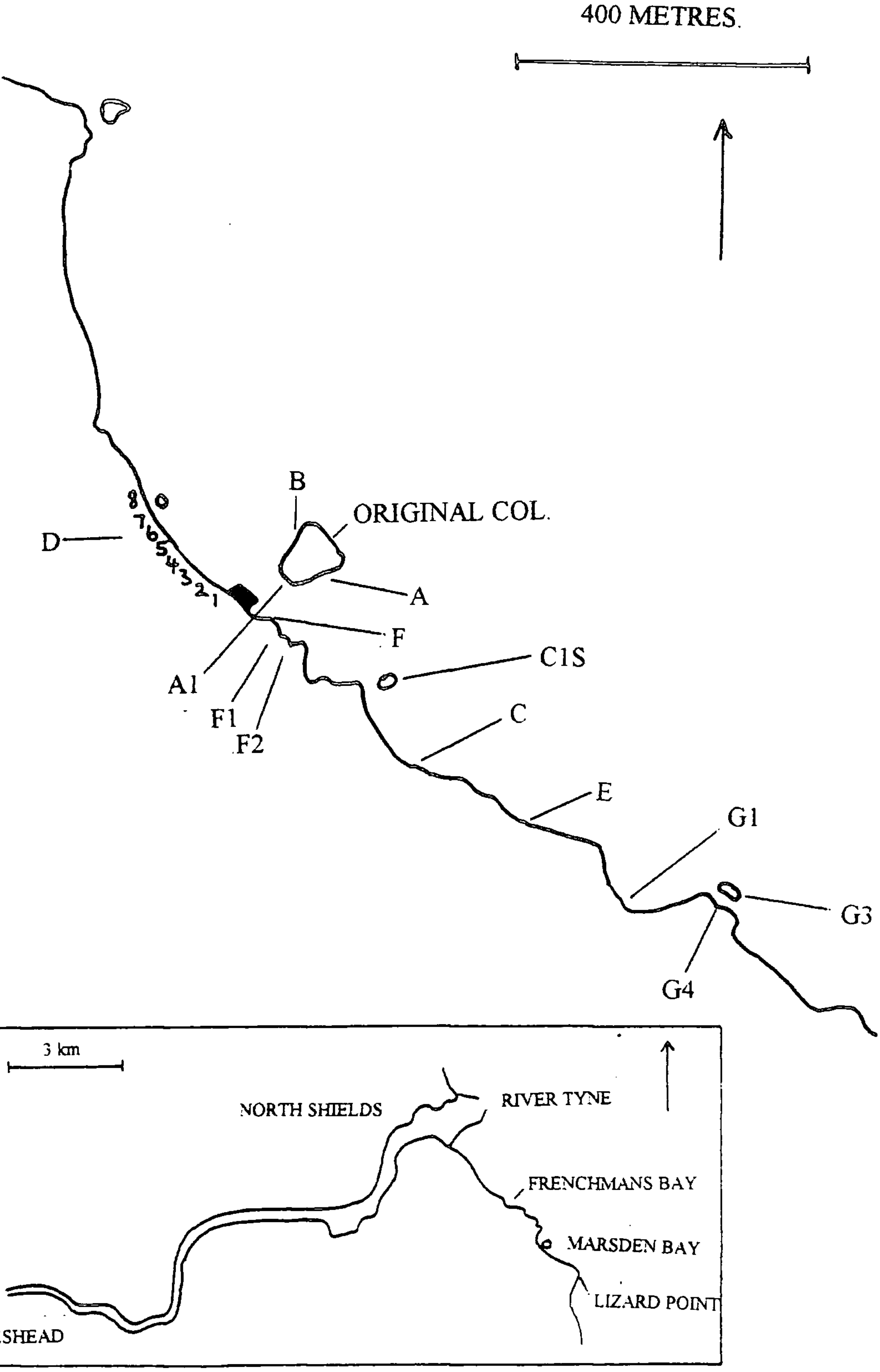


FIGURE 1b

The breeding distribution of Kittiwakes at Marsden Bay in 1991-1992. The discrete colonies described by Coulson and White no longer exist as such. Due to the increase in numbers of nesting Kittiwakes, greater areas of cliff are occupied and the original colonies are much larger and the distance separating each colony is much less.

Area D is subdivided into 8 sections.

Inset map shows the position of Kittiwake colonies in the North East of England referred to in the text.



CHAPTER 3.

COLONY SIZE AND NEST DENSITY.

Colony size

Results

In 1990 a count of apparently occupied nests (AON) produced a total of 5673. A similar count in 1992, using the same technique gave a figure of 5763 AON, an increase of 7%. The counts are shown in Table 2. The count in 1991 was incomplete, the original site of colonisation on the east face of Marsden Rock not being counted due difficulty of access. Excluding this area of the colony the number of AON was 4483. Using the comparable figures for 1990 and 1992 (5419 and 5613 respectively) gives a decrease of 17% between 1990 and 1991, and an increase of 25% between 1991 and 1992. The increase in AONs between 1990 and 1992 was 4%.

The lower total of AON in 1991 was due in large part to a decrease of 33% in area C, a decrease in areas A, A1 and B of 43% and a decrease of 32% in area D1. These areas account for 91% of the observed decrease between 1990 and 1991.

The fluctuations in AON in areas A, A1 and B were dramatic. Following the decrease, described above, between 1990 and 1991, there was an increase between 1991 and 1992 of 78%. Between 1990 and 1992 there was a 2% increase.

Although photographic records were not available for the whole colony in 1991, one was available for area A1 (J.C. Coulson). Counting AON from the photograph gave a figure of 158, confirming my own visual count and suggesting a consistent technique. A decrease of 17% occurred between 1990 and 1991, followed by an increase of 50% between 1991 and 1992. The fluctuations in area A1 were therefore real and suggest that the areas on Marsden Rock (A, A1 and B) behave differently and are subject to factors not experienced by those areas on the mainland.

The final count of AON in June 1991 agreed with the counts made during the reoccupation of the colony in March and April of that year, except on 2 May, when AOS (apparently occupied sites) were counted in area A as being 160% (n = 365) of the final total (n = 228). The reoccupation of areas A, A1 and B otherwise, followed a similar pattern to that of the rest of the colony.

Discussion

The origin of these birds, which initially colonised Marsden Bay, is open to much debate. However recent analysis of Kittiwake recovery data by Coulson and Neve de Mevergnies (1992) indicates that 43% of young Kittiwakes, mainly females, breed in another colony within 100 km of their natal colony. Few kittiwakes settle within 100-300 km of their natal colony, the next peak of colonisation occurring at 400-900 km. Coulson and Neve de Mevergnies also suggest that there is a link between colonies in Norway and Britain and that exchanges of birds have a tendency to be in a southerly direction.

Colonizing birds at Marsden in the 1930's may have originated from the few colonies on the Northumberland and Yorkshire coasts or from colonies on the east coast of Scotland. The presence of two adults, ringed as chicks in southern Norway, breeding at North Shields (Coulson and Neve de Mevergnies, 1992) suggests the possibility of some immigration more recently having taken place from that direction. However, in the 1930s colonies of Kittiwakes were not established so far south in Norway.

As the 19th century drew to a close there is evidence that the size of Kittiwake colonies had begun to increase but that there had been little or no increase in the number of colonies (Coulson 1963). From 1920 onwards however the number of breeding pairs and the number of colonies started to increase dramatically in a geometric manner, the increase being at an average rate of 3-4% per year. The colonisation of Marsden fits in well with this pattern as has the subsequent increase in the number of nesting pairs. The origin and development of the Marsden colony was therefore not an isolated event but part of a much wider change taking place throughout the British Isles.

One would assume that the increase in the size of colonies prompted a dispersal of young birds away from colonies in which density dependent factors were beginning to operate. Young birds returning to their natal colonies and finding conditions for recruitment into that colony unsuitable may have commenced a period of wandering which ultimately resulted in a new site being colonised. The initial location may have been close to an area previously used for roosting. The birds using the opportunity to assess the area as a future breeding site. However as initial colonisation requires the presence of a considerable number of birds, a collective dispersal and arrival at the new site was presumably necessary. The movements of Kittiwakes, of both adult breeding and non-breeding birds, is little understood outside of the breeding season, and is an area of research which could prove fruitful.

Coulson (1963) has also shown that since 1900 Kittiwakes began to occupy cliffs of a lower height. Before 1900, 45% of Kittiwake nests were on cliffs of 100-300 feet (30m-91m), but since 1900 over 60% were on cliffs of 50-100 feet (15m-30m). The cliffs at Marsden Bay fall into this category. Was this a change of behaviour in the Kittiwake or was it the result of birds emigrating to areas which were found to be otherwise suitable and the lower cliffs were not a critical factor any more? A similar trend was shown for the Fulmar (Fisher and Waterston 1941). A reduction in human persecution of seabirds in the early part of the twentieth century may have reduced the significance of high, relatively inaccessible, cliffs as an important factor in the selection of a suitable site for a colony. More recently, Coulson (1983), considered that the large increase in the number of nests in the Flamborough colony which had taken place over the previous 20 years was probably due to the cessation of egg collecting on the cliffs.

The Marsden colony, following initial colonisation, continued to grow at a rapid rate during the following 40 years (Figures 2 and 3). Coulson (1983) showed that small colonies grow at a much faster rate than larger ones; the relationship can be approximated to colony growth being proportional to the reciprocal of the square root of the colony size. During this period the number of potential nest sites would always be in excess of the number of breeding pairs and lack of nest sites would not be a limiting factor.

The 1970s were a period of change in the Kittiwake colonies of Britain (Coulson 1983). Many, particularly on the southern and western seaboards of the British Isles showed a decrease. On the east coast of Scotland and England increases of 37% and 42% respectively occurred (excluding the Flamborough colony which, if included, would give a figure of 81% for the English east coast) between 1969-1979. The rate of increase in the Marsden colony slowed during the 1970s, apparently in line with accepted population growth theory, that as limiting factors begin to operate, annual increases in population are reduced. The graph, of number of AON plotted against time, levelling off. However counts of AON in 1990-1992 indicate a further increase over the previous 15 years of 28%, an annual increase of 1.9%.

The annual adult survival rate at the North Shields colony, calculated as a 5 year running mean, showed a peak of 90% in 1963 decreasing to 80% during 1968-1975 (Coulson & Thomas 1985). After a slight recovery in 1977, it fell to 62% in 1986, before recovering to 85% in 1992. The removal of a limiting factor, reduced adult survival, since the mid 1980s, has allowed a further rise in the number of AON during the 1980s, to the present level. Although Harris (1990) showed that a decline had occurred in chick production in the North Sea in 1988, particularly in the northern sector, this has not, apparently, had a major impact on Kittiwake numbers at Marsden. Should this have happened at the Marsden colony, and there is no evidence to indicate that it did, it may simply have slowed the rate of increase in the early 1990s. The effect of a single years reduced chick production is in itself unlikely to produce a serious effect on future numbers of adult breeding birds, and as a result affect the size of colony. However, breeding success, defined as the mean number of young fledged per completed nest, appears to have remained relatively unchanged at least in areas A, A1 and B of the colony over the past five years. Harris (1990) gave a figure of 0.96 + 0.06 chicks per completed nest in 1988 for Marsden Rock (areas A, A1 and B). My own figures for 1992 were between 0.82 + 0.104 and 1.20 + 0.072 chicks per completed nest.

Changes in the density and the number of nests in the original eight colonies, 1930-1992.

Results

Coulson and White (1956) described 8 colonies in Marsden Bay. Using their map and colony designations, Tables 3a and b, and Figures 4a-c, show the changes which have taken place in the number of nests in each of these areas. Table 3c shows the current trend in the numbers of nests in these areas of the colony. The mean densities of nests and the percentage of nests with more than four nests in a 5' (1.52m) radius are shown, where available, for 1954, 1958, 1975 and 1992, in Table 4. The number and percentage of nests in each density range (number of nests within a 1.52m radius) are shown in Tables 5a and b. Up to the late 1950s the Kittiwakes formed a number of discrete colonies in Marsden Bay. Since then these colonies have merged in many instances and so direct comparisons are difficult. The absence of counts in all years between 1952 and 1992 invariably reduces the degree of certainty which can be attached to any conclusions.

Discussion

The first three colonies formed (Original, A and B) are all now showing signs of decline, in terms of the number of nests present. The Original area, colonised in the early 1930s, increased slowly up to 1956, when it contained 366 nests. There then followed a slow decline to 255 nests in 1990. A rapid decrease occurred over the next 2 years resulting in the 1992 total being only 47% of that in 1952. Continuous monitoring of the rock structure on this cliff face has not occurred. However observations in 1992 indicate that this area is probably not now capable of supporting over 300 Kittiwake nests. The exposed nature of this cliff to the wind and waves has resulted in erosion which has changed its topography and consequently the number of available nest sites.

Areas A and B together, held on average 1340 nests in 1974-1977. In 1990 and 1992 the mean number of nests was 1011. In both cases the trend is one of declining numbers. Falls of rock and extensive erosion of the top of the stack have been noted, changing the pattern of occupancy by Kittiwakes and Herring Gulls. The latter are encroaching further down the cliff on a newly extended slope caused by erosion. The large number of Kittiwake nests towards the top of the cliff occupied in area A in the 1950s, can be seen in an illustration from Coulson and White (1959) and repeated here as Figure 5. The number of nests then exceeded 700, as it did in the 1970s (Dixon 1979). In 1990 and 1992 the mean number of nests was 446. A large decrease but one confirmed by duplicate counts from photographs for 1992.

The number of nests in area C has continued to increase over the period of its existence as Kittiwakes have exploited more of the cliff face. Although the cliff in this area is subject to erosion, the effect appears to have been beneficial to the Kittiwakes allowing expansion of this area of the colony.

The number of nests in area D peaked in 1975 and has remained relatively unchanged since. Although in recent years the number of nests have levelled out, slight changes in the nature of the cliff continue, but are insufficient to affect numbers of nests.

The three remaining areas from the original eight, E, F and G1,are all continuing to increase, with 1992 being the year of the highest known count. The Kittiwakes in these areas are continuing to exploit the available cliff face with area F showing the most dramatic rise between 1958 and 1974. Ample space was available and ready to be exploited by new recruits. Areas E and G1 are both on sites where erosion is frequently changing the nature of the cliff face and hence the number of potential nest sites. In area E, the erosion has largely been favourable, increasing the number of nest sites. Area G1 of the colony is in comparison on a site where erosion frequently replaces suitable cliff structure with one totally devoid of nest sites, the cliff face becoming smooth with no ledges. The cause of the erosion is due to both wind and wave action and to the seepage of ground water through the porous limestone.

Recruitment into the areas, E, F and G1, after initial colonisation, required birds to settle onto peripheral sites, on the edge of the area already occupied by breeding birds. This would result in expansion, as ther is a limit on the extent to which the density of nests in the initial area of colonisation can increase. This limit is influenced by cliff structure and the behavioural responses of nesting Kittiwakes to their neighbours. Birds which are responsible for this expansion are late arrivers in the spring, which take up nest sites immediately and in relatively poor locations (Porter 1990). These birds, at least in their first year of breeding, may perform less well in terms of chicks fledged per pair. This is in part due to them pairing with another recruit. Porter (1990), demonstrated that 60% of these "late-immediate" recruits did so. Although these birds may be "less fit" to breed, they are nevertheless an essential component of the expanding colony. Porters "late- delayed" birds, increase the nest density in the centre of the colony, if sites are available. These birds will play an important role in contributing initially a greater number of fledged chicks than the "late-immediate" recruits. But in subsequent years, as peripheral areas themselves are absorbed and become more central, breeding performance will improve. New peripheral areas will then develop as the colony continues to expand.

Coulson and White (1956) also describe a colony about 1 km north of Marsden Bay. This colony,which they designated G2, has since become extinct, due largely to the changes which have occurred in the nature of the cliff face as a result of erosion.

By 1958, area A was well established containing 770 nests. The figures for mean density and percentage of nests with more than four nests in a 1.52 m radius were similar in both 1958 and 1992, as were the nest counts of 770 and 711 respectively (area A, the south face, in 1958 was considered to extend slightly onto the west face, A1, of Marsden Rock, whereas the 1992 nest count is restricted to the south face only). This area probably peaked in the mid 1970s, when its mean nest density was 16.4, and is now showing a trend of decreasing nest numbers.

Area D, one of the first on the mainland cliffs, has shown an increase of mean nest density from 3.8 to 5.2 /1.52 m (5 ft) radius between 1952 and 1992. The nest count has increased over the same period, from 271 to 355. This denser nest distribution is further illustrated by the percentage of nests with more than four nests in a 1.52 m radius, 17% in 1958 increasing to 47% in 1992.

Areas F and G1, low density areas in 1958, are now among the densest areas. Area F has a mean nest density of 7.6 nests / 1.52 m radius, and area G1 a density of

5.8 nests / 1.52 m radius. These represent increases of 3.2 and 1.7 times. In area F, no nests in 1958 had more than four nests in a 5 ft radius, 86% did in 1992. Dixon (1979) reported a nest density of 4.3 nests / 1.52 m radius and a substantial increase in the number of nests since 1958. The nest numbers then almost doubled up to 1992.

Area A, having peaked and now apparently showing a decline, has density values similar to those reported by Coulson and White (1959) when it was still increasing in size.

Area D has probably stabilized after showing an increase in nest density from 1958 to 1975.

Areas F and G1 were low density and relatively new colonies in 1958 being only eight years and five years old respectively. They have continued to grow over the past 32 years passing through, during this time, a period of rapid growth, expected of healthy young developing colonies. Increased nest density has accounted in part for the increased number of nests but in addition a greater area of cliff has also been used.

When viewing the colony as a whole, a pattern of increasing numbers is seen. Since its inception in the 1930s, the numbers of nest has increased steadily with only a slight slowing in the rate in the 1970s. However examination of specific areas within the colony show a different pattern with some now decreasing, others static and others increasing. While it is important to observe what is happening to the whole colony, sight should not be lost of the small scale changes within the colony which may account for those observed on the larger scale.

Table 1

Number of apparently occupied nests (AON) in the Marsden Bay colony during 1937-1992.

Year	AON	log no. of nests
1937	308	2.49
1945	750	2.87
1952	1344	3.13
1953	1661	3.22
1954	1905	3.27
1955	2196	3.34
1956	2424	3.38
1957	2448	3.39
1958	2665	3.43
1974	4293	3.63
1975	4534	3.66
1976	4561	3.66
1977	4465	3.65
1990	5673	3.75
1991	4700	3.67
1992	5768	3.76

Source of figures

1937.	Grey (1937).
1945.	Temperley (1951).
1952-1958.	Coulson and White (1960)
1974-1977.	Dixon (1979).
1990-1992.	this study.

Table 2

Numbers of apparently occupied nests in the Marsden Bay colony, by area, for 1990-1992.

Area	1990	1991	1992
A,A1,B,Orig.	1258	728-828	1169
C	770	519	726
C1	278	277	386
C1S	130	131	170
D	1632	1540	1529
E	344	240	356
F		65	66
F1	485	32	41
F2		359	423
G1	269	228	302
G3	238	259	313
G4	269	260	286
TOTAL	**5673**	**4638-4738**	**5768**

Numbers of apparently occupied nests during 1990-1992 on the four faces of Marsden Rock and the extensive mainland section, area D, subdivided for ease of counting.

Marsden Rock

	1990	**1991**	**1992**
ORIG.	255		150
A	458	228	474
A1	190	158	237
B	355	187	308
Mainland			
D1	520	353	386
D2	300	264	254
D3,4	345	368	357
D5	230	270	246
D6,7	187	240	224
D8	50	45	62

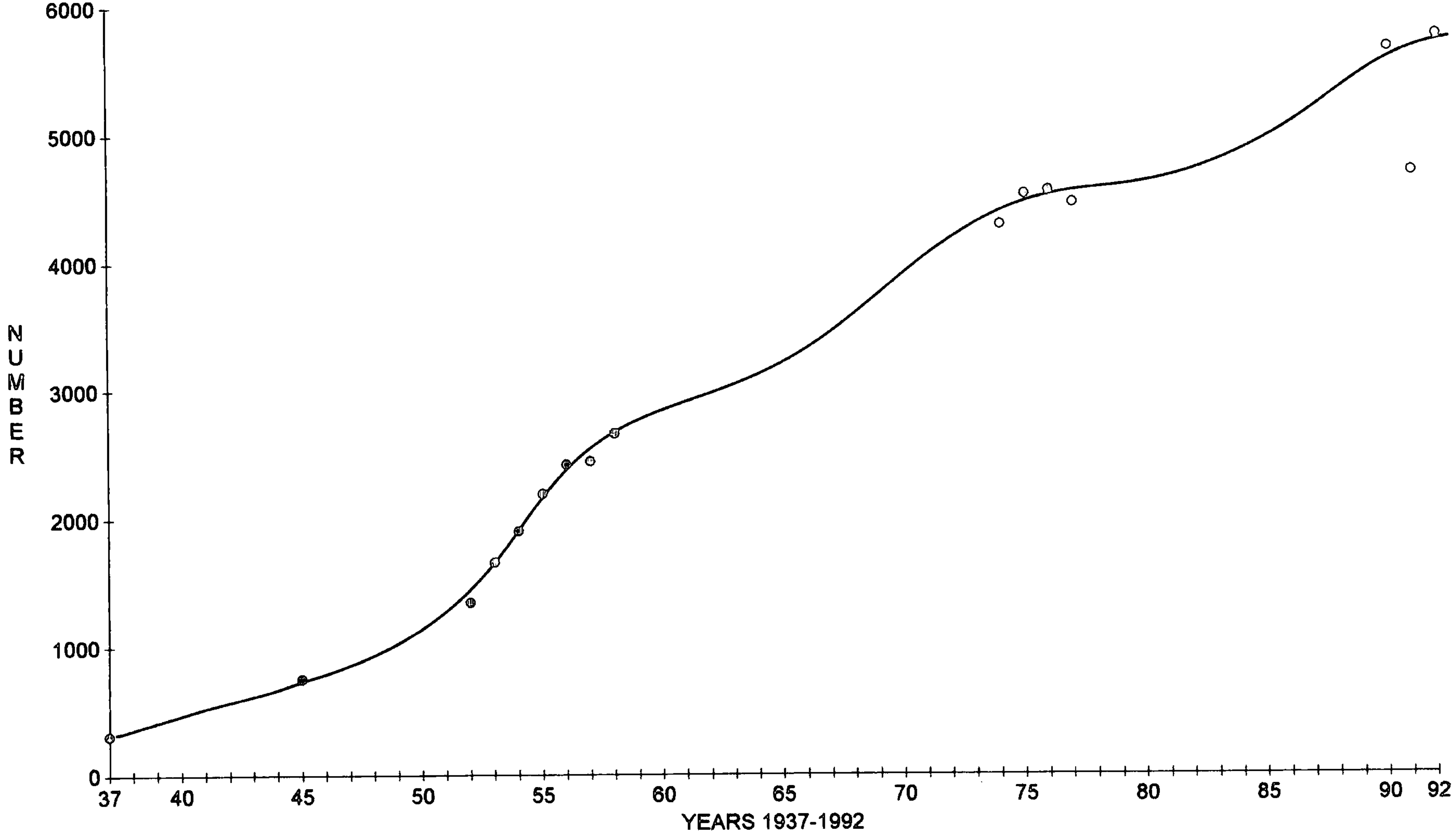
FIGURE 2

The growth of the Kittiwake colony in Marsden Bay between 1937 and 1992. The data and its sources are shown in Table 1. The portion of the graph between 1937 and 1957 shows a steady rate of increase in the number of nests. By the mid 1970s the rate of increase had slowed, but subsequently quickened again to give the population of the early 1990s.

FIGURE 3

The growth of the Kittiwake colony in Marsden Bay between 1937 and 1992. The annual nest counts are plotted as their logarithms (base 10). The portion of the graph between 1937 and 1957 has a linear form and indicates that the population was increasing at a constant rate. Since the late 1950s the rate of increase in the number of nests in the colony has slowed, although their was a further smaller surge in numbers between 1977 and the early 1990s.

Figure 2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5000
4000
3000
2000
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37
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65
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75
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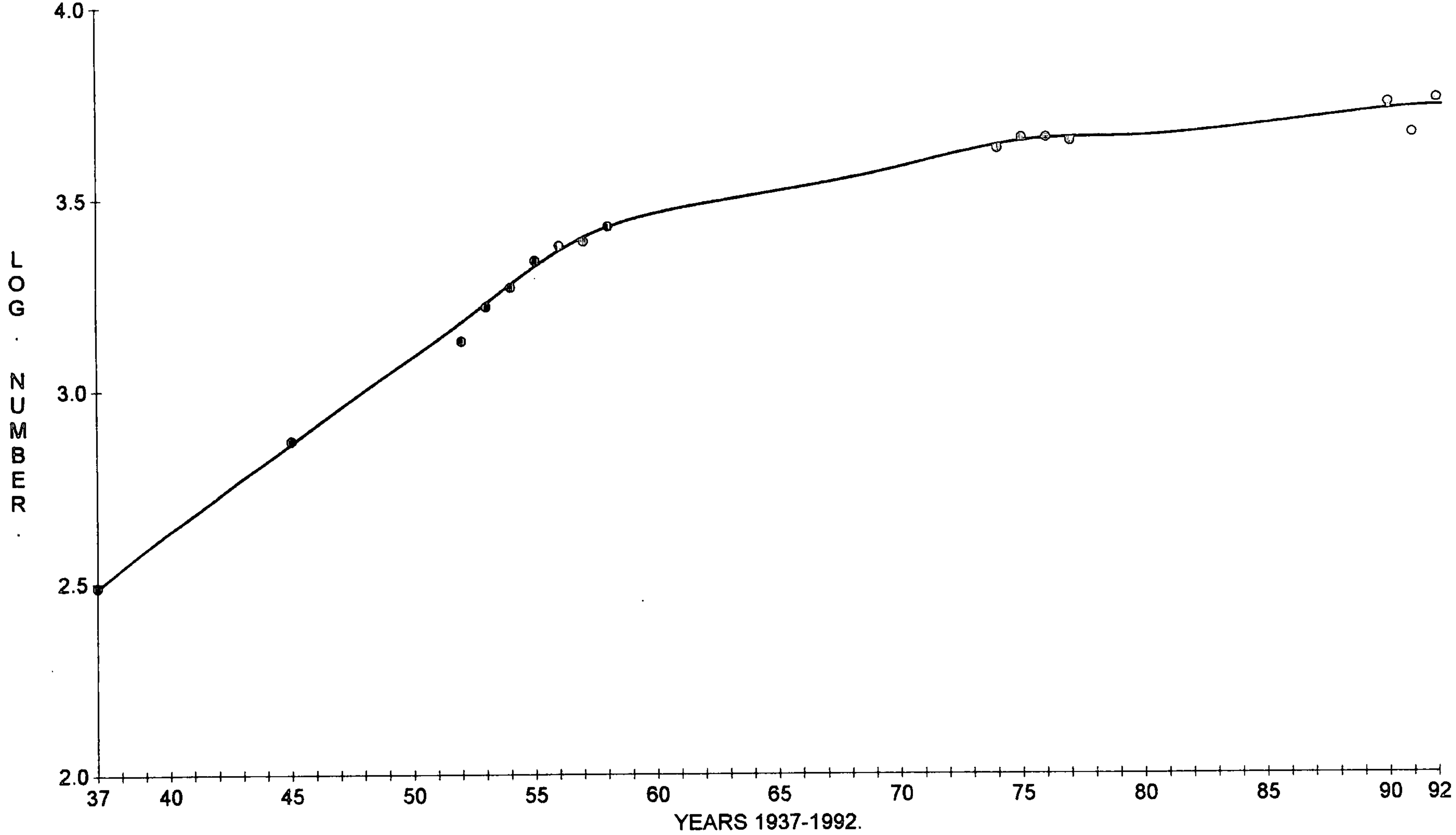
85
90
92
YEARS 1937-1992

Figure 3


4.0
3.5
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LOG . NUMBER .
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40
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85
90
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YEARS 1937-1992.

Table 3.

a) Number of nests in the colonies described by Coulson and White (1956) at the Marsden Bay colony during 1952-1992

							Years							
Colony	1952	1953	1954	1955	1956	1957	1958	1974	1975	1976	1977	1990	1991	1992
Original	318	316	337	359	366	363	355	276	301	300	300	255		150
A	429	591	648	705	733	744	770	1003	991	946	885	648	386	711
B	299	359	422	457	493	474	533	436	324	394	383	355	187	308
C	130	172	197	254	299	293	332	371	449	466	486	770	519	726
D	70	85	111	155	189	218	271	389	396	376	345	345	368	355
E	99	120	157	198	230	226	246	165	317	327	314	344	240	356
F	5	8	13	17	24	40	44	290	310	319	274	485	456	530
G1	0	10	20	51	90	90	114	128	159	154	172	269	228	302
ALL	1344	1661	1905	2196	2424	2448	2665	3058	3247	3286	3159	3471	2384*	3438

b) Number of nests, expressed as a percentage of the 1952 count, (1953 for G1) in the colonies described by Coulson and White (1956), during 1952-1992.

							Years							
Colony	1952	1953	1954	1955	1956	1957	1958	1974	1975	1976	1977	1990	1991	1992
Original	100	99	106	113	115	114	112	87	95	95	95	80		47
A	100	140	153	167	173	176	182	237	234	224	209	161	88	168
B	100	120	141	153	165	158	178	146	108	132	128	119	62	103
C	100	132	151	195	230	225	255	285	345	358	374	592	399	558
D	100	121	159	221	270	311	387	556	566	537	493	493	526	507
E	100	121	159	200	232	228	248	167	320	330	317	347	242	360
F	100	160	260	340	480	800	880	5800	6200	6380	5480	9700	9120	10600
G1		100	200	510	900	900	1140	1280	1590	1540	1720	2690	2280	3020
ALL	100	124	142	163	180	182	198	227	242	242	235	258	177*	256

*** excludes a count for the original colony site.**

c)

Colony	**First year of beeding**	**Year of maximum known nest count**	**Current trend in numbers of nests**
Original	1931-1933*	1956*	decreasing
A	1933-1937*	1974#	decreasing
B	1933-1937*	1958*	decreasing
C	1940*	1990	increasing
D	1941-1945*	1975#	static
E	1947*	1992	increasing
F	1950*	1992	increasing
G1	1953*	1992	increasing

* Coulson and White (1956)
# Dixon (1979)

FIGURES 4a, b, c

The percentage changes, since 1952, in the number of nests in areas of the colony designated by Coulson and White (1956). The number of nests counted in 1952 was taken as the base and given the value of 100. Changes between 1952 and 1992 are expressed as a percentage of the 1952 count.

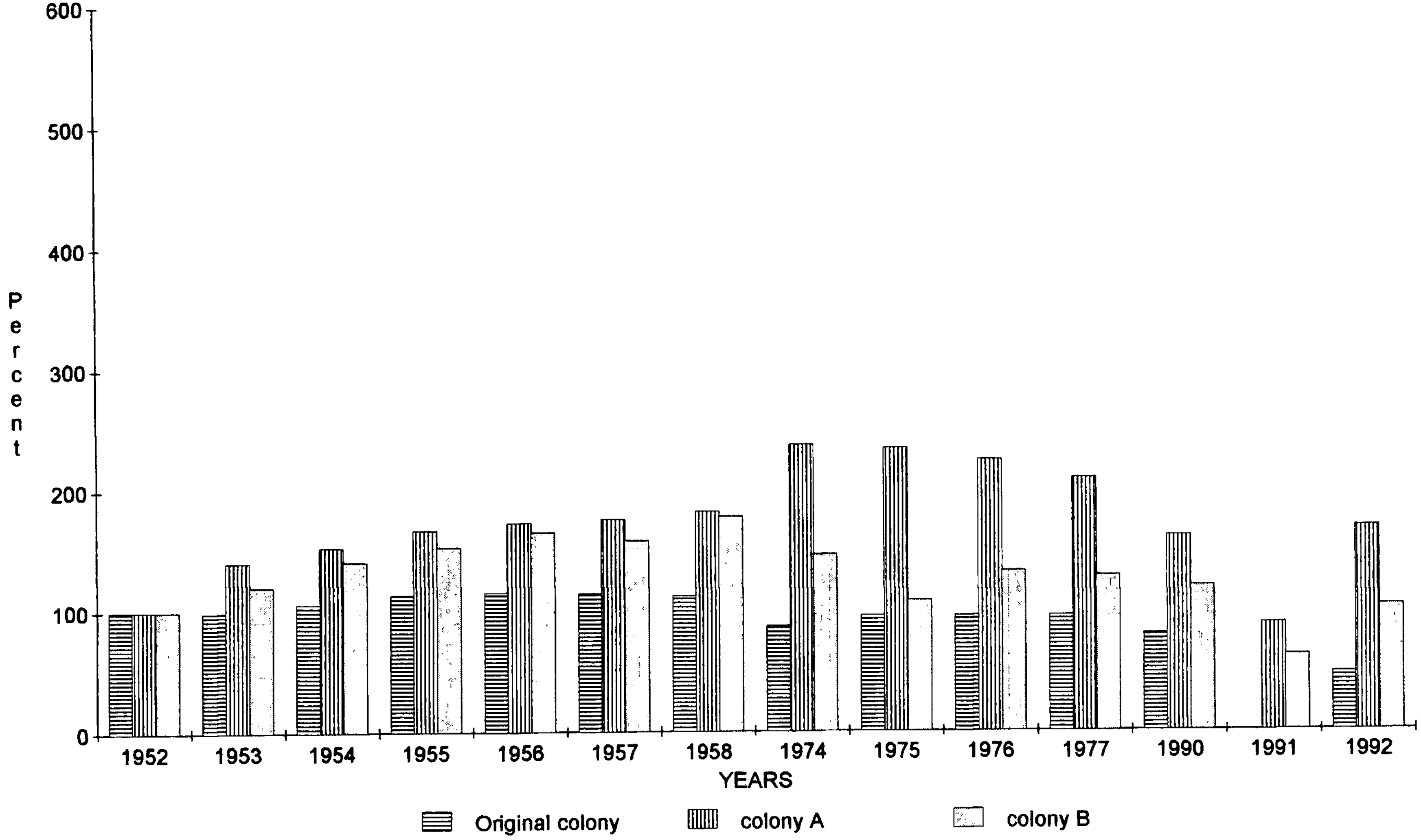
Caution is necessary in interpreting the graphs because 1952 was taken as the base year for all areas of the colony. The original colonisation of these areas did not occur simultaneously. Each area had therefore been developing for a different length of time by 1952. Table 3c gives the dates for the first year of breeding in each area. The Original area and area B both reached their peak in the late 1950s, whereas areas E, F and G1, which started in 1947, 1950 and 1953 respectively, had maximum counts in 1992. Future counts may be higher.

Figure 4a Original, A and B areas

Figure 4b C, D and E areas

Figure 4c F and G1 areas

Figure 4a


600
500
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200
100
0
Percent
1952
1953
1954
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1956
1957
1958
1974
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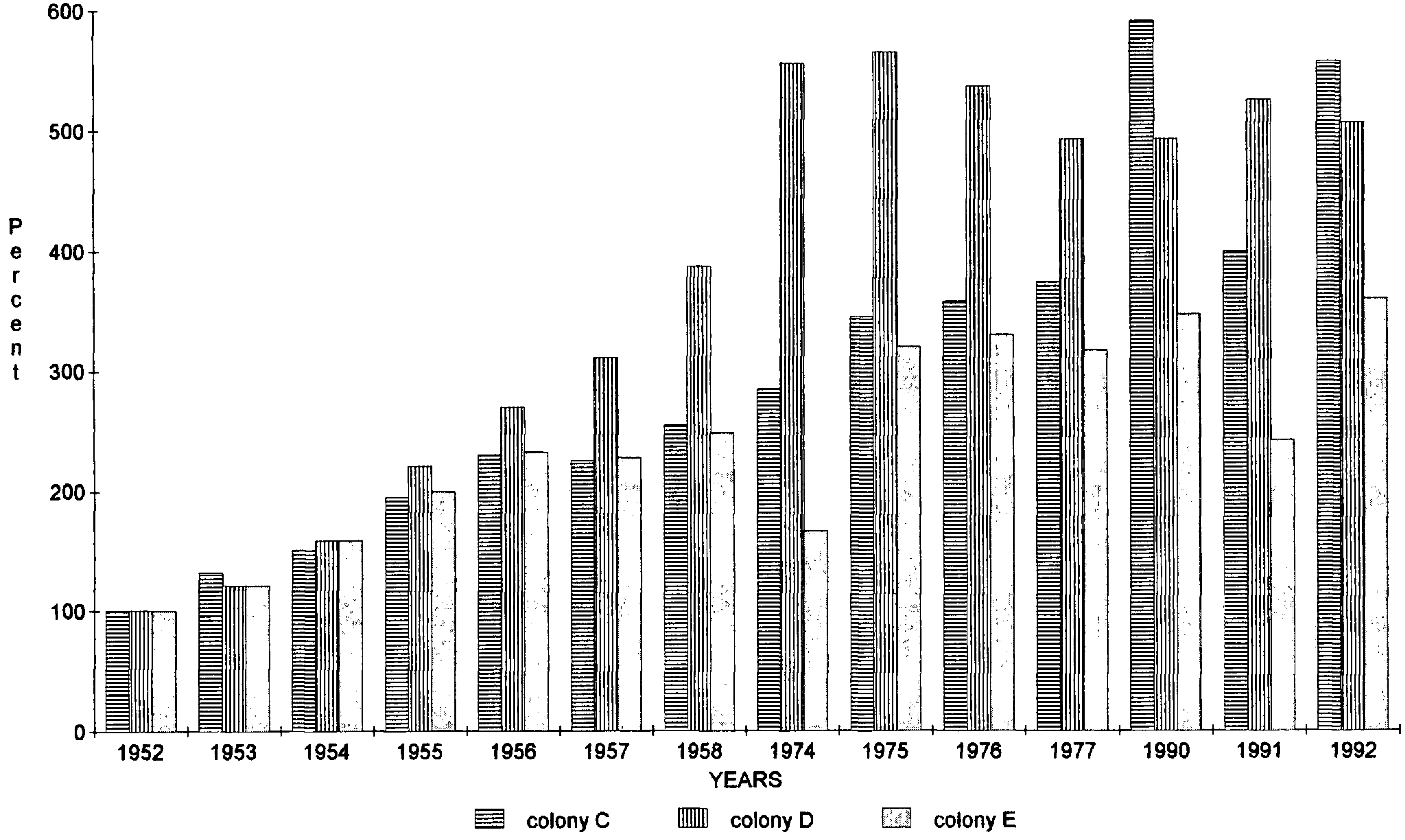
1976
1977
1990
1991
1992
YEARS
Original colony
colony A
colony B

Figure 4b


Percent
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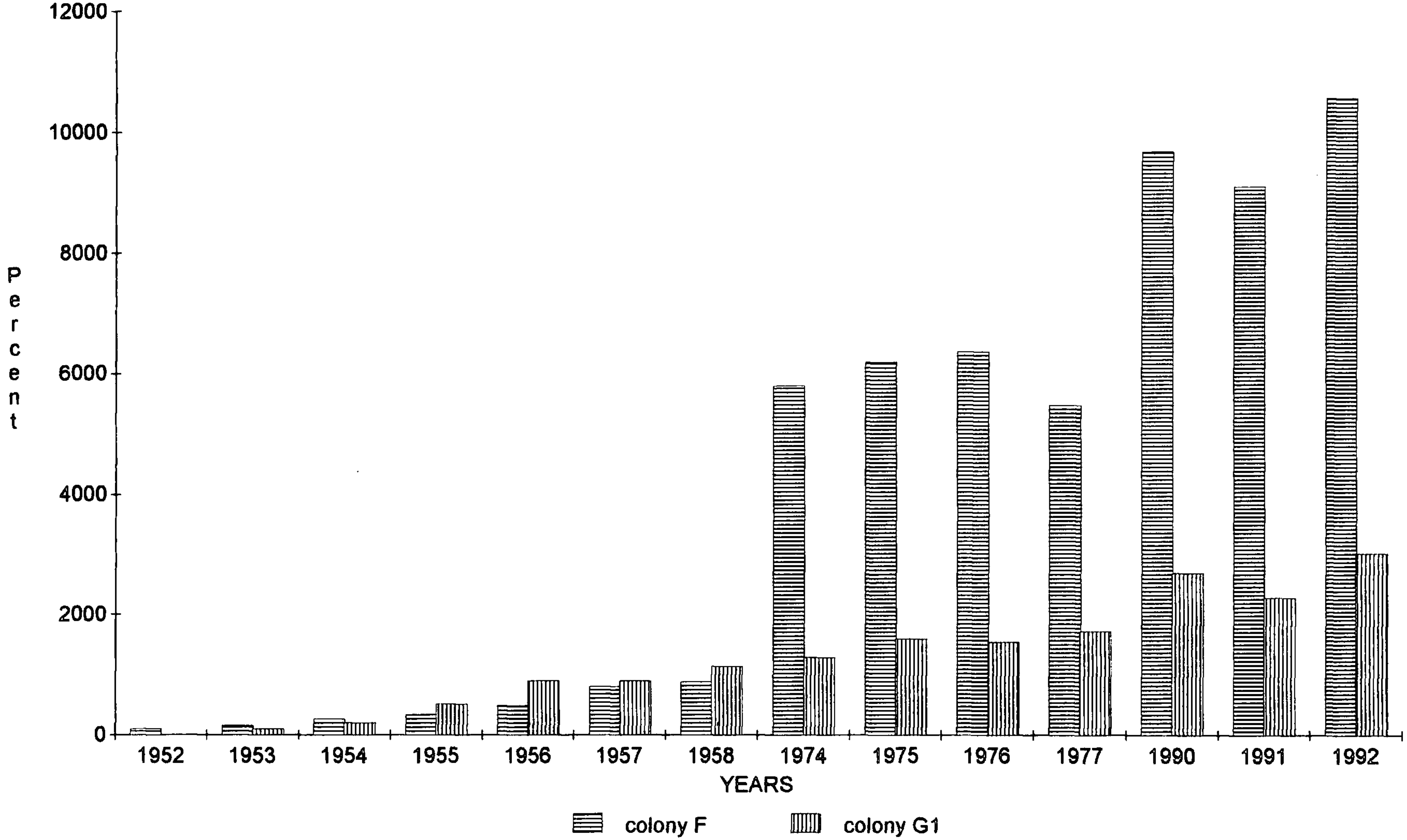
YEARS
▤ colony C
▥ colony D
▨ colony E

Figure 4c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Percent
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1975
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1977
1990
1991
1992
YEARS
▤ colony F
▥ colony G1

Table 4

a) Mean number of other nests in a circle of radius 1.52 m of each nes in selected areas of the Marsden Bay colony in 1958, 1975 and 1992.

Area	1958	1975	1992
A	8.0	16.4	7.4
B			6.9
C			
D1	3.8	9.3	5.2
E		3.1	
F	2.4	4.3	7.6
G1	3.3	3.4	5.8

Sample sizes for 1992 are shown in Table 5a

b) Percentage of nests with more than 4 nests within a 1.52 m radius in selected areas of the Marsden Bay colony in 1958, 1975 and 1992.

Area	1954	1975	1992
A	68	99	77
B	34		73
C	15	60	
D	17	94	47
E	6		
F	0		86
G1	16		80

1954,1958 data from Coulson and White (1959)
1975 data from Dixon (1979)

Table 5a

The number of other nests within a 1.52 m radius for selected areas of the Marsden Bay colony in 1992.

	Areas												
Density group	A	A1	B	D1	D2	D3	D4	D5	D6	D7	D8	F	G1
0	2	3	4	0	0	2	2	3	2	0	1	1	1
1	5	4	12	4	3	3	5	7	3	4	4	2	0
2	18	4	22	11	5	10	4	20	6	8	11	1	1
3	15	9	22	25	12	9	6	16	11	11	3	1	9
4	16	9	24	25	8	16	5	18	17	11	6	1	10
5	20	9	35	33	25	19	2	13	5	8	5	2	27
6	22	16	31	31	21	17	6	19	2	4	1	4	19
7	14	9	35	22	14	20	6	10	1	2		3	18
8	30	10	25	15	19	21	2	9		4		8	10
9	28	15	24	16	13	9	3	3		6		7	8
10	26	4	18	3	3	4	2	2		2		9	1
11	13	6	16	3	3	2	4			1		1	
12	8	1	15	4	1					3		2	
13	6	1	9	1						1			
14	9	2	10							1			
15	1		3										
16	0		1										
17	2		1										
18			0										
19			1										
20													
All	235	102	308	193	127	132	47	120	47	66	31	42	104

Density group - the number of other nests within a 1.52 m radius.

Table 5b

The percentage of nests in areas of the Marsden Bay colony in 1992, in each density range ie. the number of other nests within a 1.52 m radius.

Number of nests within 1.52m radius	Areas of colony												
	A	A1	B	D1	D2	D3	D4	D5	D6	D7	D8	F	G1
0	1.0	3.0	1.5	0.0	0.0	1.5	4.3	2.5	4.3	0.0	3.2	2.4	0.9
1	2.0	4.0	4.0	2.0	2.4	2.3	10.7	5.8	6.4	6.0	12.9	4.8	0.0
2	7.5	4.0	7.0	5.5	3.9	7.6	8.5	16.6	12.8	12.0	35.5	2.4	0.9
3	6.5	9.0	7.0	13.0	9.4	6.8	12.8	13.3	23.4	16.0	9.7	2.4	8.6
4	6.5	9.0	7.5	13.0	6.3	12.1	10.7	14.9	36.2	16.0	19.3	2.4	9.6
5	8.5	9.0	11.0	17.1	19.7	14.4	4.3	10.8	10.6	12.0	16.1	4.8	26.0
6	9.0	15.5	10.0	16.1	16.5	12.9	12.8	15.8	4.3	6.0	3.2	9.5	18.3
7	6.0	9.0	11.0	11.5	11.0	15.1	12.8	8.3	2.1	3.0		7.1	17.3
8	12.5	10.0	8.0	7.8	14.9	15.9	4.3	7.5		6.0		19.0	9.6
9	12.0	14.0	9.0	8.3	10.2	6.8	6.4	2.5		9.0		16.7	7.7
10	11.0	4.0	6.0	1.6	2.4	3.0	4.3	1.7		3.0		21.4	0.9
11	5.5	6.0	5.0	1.6	1.4	1.5	8.5			1.5		2.4	
12	3.5	1.0	5.0	2.0	0.8					4.5		4.8	
13	2.5	1.0	3.0	0.5						1.5			
14	4.0	2.0	3.0							1.5			
15	0.5		1.0										
16	0.0		0.5										
17	1.0		0.5										
18			0.0										
19			0.5										
20													

Table 5c

Mean date of hatching, related to the mean density of nests in areas of the Marsden Bay colony in 1992 (density is expressed as the mean number of nests in a circle of radius 1.52 m.)

Area	Number of nests	Mean density	Mean date of hatching
A	235	8.4	11/06
A1	102	7.6	11/06
Afa	96	8.0	11/06
B	308	7.9	11/06
D1	193	6.7	12/06
D2	127	7.3	11/06
D3	264	6.8	11/06
D4	93	6.2	13/06
D5	120	5.5	13/06
D6	93	4.4	13/06
D7	131	6.4	15/06
D8	62	3.9	16/06
F	42	8.6	11/06
G3			12/06
G1	104	6.8	12/06

(Afa - a small section of area A, described and studied by Dixon 1979)

FIGURE 5

The distribution of Kittiwake nests on the south face (area A) of Marsden Rock.

Figure 5a (taken from Coulson and White 1959) shows the distribution of nests in the mid 1950s.

Figure 5b shows the distribution of nests in 1992. The figure was produced from colour transparencies taken in 1992 to determine the number and density of nests in this area of the colony.

Figure 5a

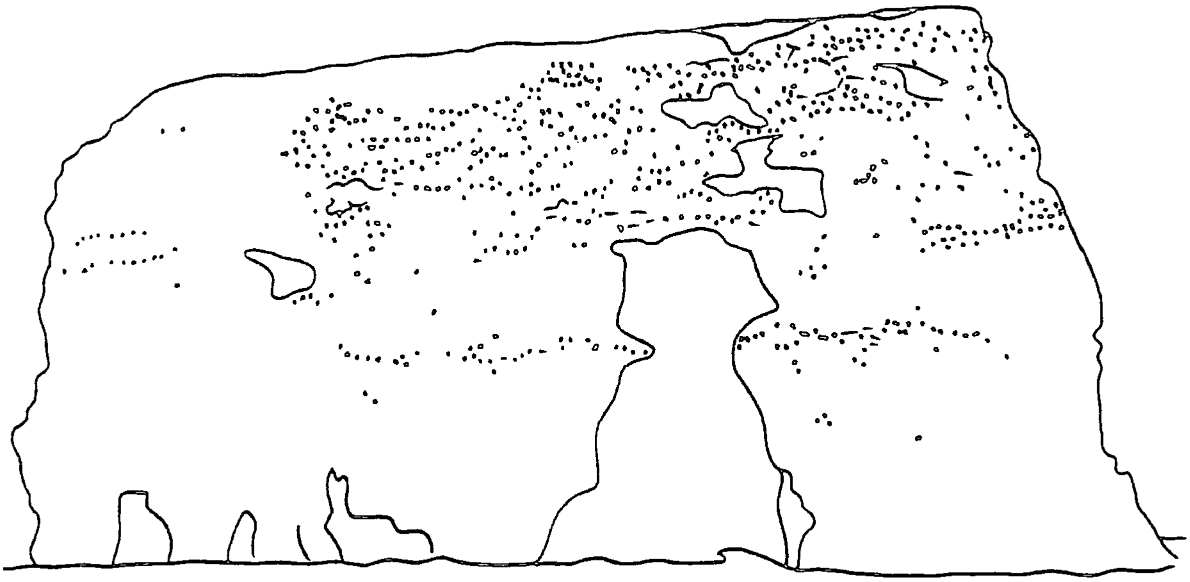


Figure 5b

CHAPTER 4.

DATE OF RETURN TO THE COLONY, ANNUAL REOCCUPATION OF THE COLONY, ADULT SURVIVAL RATES AND EVENING VACATION OF NEST SITES

Date of return and annual reoccupation of the colony

Results

Reoccupation commenced on 21 February 1991, with 31 Kittiwakes present on ledges. Observations continued until 2 May (Table 6a, Figure 6a).

Throughout March the number of occupied ledges increased steadily. As a percentage of the total number of nests subsequently built, 50% occupancy was achieved by 17 March. After achieving 90% occupancy on 23 March, on 1 April occupancy was only 15% in the colony as a whole, and in some sections fell below 5%. The cliffs were almost silent, the colony had been virtually deserted. The subsequent return to the colony was spread over the following fourteen days with 95% occupancy achieved by 16 April. In mid April, numbers fell below 40%, before recovering in the last week of April to produce occupancy very similar to that of the eventual nest count. Area G1 experienced a similar pattern of recolonisation, but with more extreme fluctuations. It had 1% occupancy on 1 April, and was deserted on 7 April, 9 April and 23 April.

Areas A and B, which had fewer AON in 1991 than in 1990, appeared to resist these fluctuations. Fluctuations did occur and followed a similar pattern, but were less dramatic, numbers of AOS remaining higher than elsewhere in the colony (Table 6b).

In 1992 reoccupation commenced on 7 February and data collection continued until 7 May (Table 7b). Numbers of AOS increased slowly during February and by 3 March 50% occupancy was achieved. However on 9 March numbers were down with 17% occupancy of sites. Throughout the rest of March and April although numbers of AOS fluctuated, the overall pattern was one of increasing occupancy (Figure 7a). The dramatic fall in numbers at the end of March 1991 did not occur.

Reoccupation of sites by pairs followed a very similar pattern although the number of sites occupied by pairs was, on any one day, much less than the number occupied by single birds (Figures 6b and 7b).

This general pattern of reoccupation occurred throughout the colony although there were minor differences between areas (Table 7b). Although birds were seen first in areas A and D on 7 February, no further sightings occurred at the latter site until 17 February. However at the former site there was 0.2- 4% occupancy between 8-17 February. Meanwhile birds had started reoccupying area B from 12 February. Areas C, F and G1 were reoccupied from 19 February and area E from 23 February. Within area D, nest sites at the extreme northern end, in D8, were not reoccupied until 27 February, ten days after the main reoccupation commenced, although twenty days after the first birds were seen in this area (Table 7b).

At Marsden, annual survival was 82% (SE 5.4) between 1990-1991 and 92% (SE 3.2) between 1991-1992. These are high survival rates. At North Shields, on only three occasions since 1955, has the adult annual survival rate exceeded 90% (Coulson and Fairweather, unpublished). At Marsden Bay they have occurred in years when the date of return to the colony in spring was much later than that observed in the 1950s and 1970s. Figures for annual adult survival are not available for these earlier periods at Marsden. Annual survival figures are available, for the period 1955-1992, for the North Shields colony (Coulson and Fairweather, unpublished) and as adult survival is influenced by factors exerting their effect on the birds when away from the colony, these figures should also reflect the situation at Marsden Bay.

Accuracy of counts

Spot counts of birds on nest sites produce an underestimate of the true level of occupancy. Between 19-30 March 1992, twelve counts were made in area F, where nests were individually identified. A spot count of birds on nest sites was made initially and over the following 30 minutes the total number of nest sites which were visited was then recorded. The "period" counts were on average 18% higher for single bird occupancy of AOS and 51% higher for pairs on AOS than those recorded in the initial spot count. However assuming that all spot counts are made using the same technique, errors should be constant and comparisons are still valid when discussing variations in reoccupation.

Because individual nests were known in this area and could be separately monitored, a measure of occupancy based on serial observations was obtained. Reoccupation commenced on 19 February 1992 at this site. By 6 March, 75% of sites had been occupied and by 19 March, 85% of sites had been occupied. Seventy five percent occupancy was not recorded in a spot count until 19 March 1992 and 85% occupancy not until 31 March. By the latter date, 76% of sites had been occupied at least once by pairs, whereas the highest spot count of sites with pairs by that date was 57%. The situation is however clouded by the likelihood of some birds landing on more than one nest site when they visit the cliff. Unless all birds were individually identifiable it is not feasible to elliminate this factor.

Discussion

Date of return and adult survival rates.

Temperley (1951), Coulson and White (1959) and Dixon (1979) give data regarding date of return and annual reoccupation of colonies for 1946, 1954-1955 and 1975 respectively. In 1946, the first birds were seen on 14 February. In 1954-1955 and 1975 Kittiwakes were present by the middle of January, at least three or four weeks before those in 1991 and 1992. Considerable variation in the date of return to the North Shields colony was noted by Coulson and Thomas (1985) in their summary of data covering 31 years. During 1955-1960, the mean date of return, by birds with previous breeding experience, to the colony was comparitively late. It became progressively earlier from 1960 to 1978. The advance in the mean date of return was approximately 50 days. In the early 1970s, the first birds were seen in the second half of December. In the 1960s, and since 1978, the first birds were seen in early January and more recently, not until early February.

As Kittiwakes spend the winter away from the breeding colony, conditions in the wintering area may influence their time of return. It would seem likely that the physical condition of the adults dependent on the availability of adequate food supplies may be a controlling element. Changes in the availability of food may influence their return. Scarce food supplies and their resultant poor condition may force the birds to remain at sea for a longer period in the late winter. The converse is that birds finding good feeding may remain away from the breeding colony for longer, reaching a higher level of physical fitness, to take them through the rigours of breeding, but forcing a later return to the colony. A late return also reduces the time that the adults spend at the breeding colony. Reducing time spent at the colony may mean that the pressures on breeding birds are reduced, increasing their chance of survival the following winter.

In the North Shields colony annual adult survival was highest in the late 1950s and early 1960s. From the late 1960s to the late 1970s it stabilized at a lower level. Over the next 10 years it fell to an all-time low of 63% (based on a 5 year running mean) (Coulson and Fairweather, unpublished). Subsequently it has returned to its mid-1960s level.

The adult annual survival rate, at North Shields, decreased as the return of birds to the colony became progressively later. In recent years, since the mid-1980s, the adult annual survival rate has been increasing but the date of return has remained unchanged, the birds returning to the colony in early to mid-February. A high adult survival rate would increase the number of birds with previous experience of breeding. This should lead to an earlier return, by birds with previous breeding experience, but this has not happened. The pattern of later return appears to have remained. At Marsden, the high annual adult survival rates during 1990-1992, are accompanied by a relatively late return to the colony. These survival rates are similar to those at North Shields in the 1960s when return to that colony was in early January.

Effect of wind speed on annual reoccupation

After a steady build up in numbers of AOS during late February and March in 1991, the fall in numbers at the end of March was dramatic. Wind speed and direction data were not recorded but data collected at Durham University Observatory and supplied to Newcastle Weather Centre were obtained. Advice was sought from the Weather Centre regarding the compatibility of data from Durham with conditions on the coast. Conditions should be similar when winds are from a generally westerly direction, but when the wind is in the east, measurements of wind speed at Durham may slightly underestimate wind strength. The overall pattern of wind direction and wind speed should however be similar. Winds were light, force 1-2 (1-6 knots), in late March when the decline in AOS commenced. During the first week of April the wind was W or SW, force 4 (11-16 knots). Birds may have left anticipating these conditions. However during this period birds started returning again to the colony. Although through the rest of April wind speed was generally force 1-2, occasionally force 3, another dip in occupancy occurred in the second half of the month and did not appear to be linked with wind speed and direction.

After a steady build up in numbers in 1992, a pronounced fall in numbers of AOS occurred on 9 March, although not as dramatic as at the end of March and early April in 1991. Early March,1992, was generally a windy period with winds from a westerly direction, only changing to easterly in the last three days. Mean wind speeds peaked during 10-13 March, with 18.7 knots being recorded on 12 March (Durham University data). My own estimate of wind speed on the coast was 22-27 knots. These stronger winds coincided with an increasing number of AOS after the dip on 9 March. Wind speed on 8 March was 2.8 knots (Durham University data, my estimate was 4-6 knots on the coast), a surprisingly low figure to cause a drop in numbers of AOS.

In both 1991 and 1992, after a pronounced fall in numbers, the subsequent recolonisation, shown by increasing numbers of AOS occurred during periods of strong winds, in excess of 10 knots. The relationship between wind speed and occupancy appears to be variable.

Daily reoccupation of the colony

During late February 1992 daily reoccupation commenced shortly after sunrise reaching its daily peak by mid-morning. Numbers remained high throughout the early afternoon before declining sharply from about 1500 h. Observations on the behaviour of birds in areas A, A1, B and D strongly suggested that birds at the first three of these arrive earlier and leave later each day. Rafting and panic flighting are not essential before birds settle on the cliffs on any day after initial colonisation as some birds, particularly in areas A, A1 and B, arrived straight off the sea.

General observations, on a number of dates, relating to the behaviour of birds in relation to weather conditions were made and are described below.

During the morning of 27 February 1992 the wind was SSW and estimated at 11-16 knots. Despite this moderate wind, Kittiwakes were in areas A, A1, B and D in numbers normal for this stage of colonisation and consistent with previous counts. However during the late morning, numbers, particularly in areas A, A1 and D, decreased markedly. Numbers in area B, which is north facing, were reduced only slightly. By midday area D was virtually deserted (from 281 AOS at 0915 h) and only 5 AOS (from 36 AOS at 0910 h) were noted in area A1. Numbers in area A fell to 18 AOSs (from 85 AOS at 0910 h). During the afternoon the wind moderated to an estimated 4-6 knots and became NW behind a cold front which had moved south across NE England during the day. The change in wind direction resulted in the now more sheltered areas, A and A1, showing a marked increase in AOS, from 3% to 19% and from 8% to 27% respectively. The now more exposed face on the north side, area B, showed a continuing decrease in AOS from 29% at noon to 14% by 1650 h. Areas A and A1 had virtually recovered to their 0900 h levels by this time. Despite being the most exposed, area A showed the most resilience in resisting the effect of the wind. Area D did not recover that day, although over 150 birds were on the sea off this area at 1630 h. Raft formation was also noted throughout the morning despite the strong wind e.g. off area D, 140 at 0850 h and 190 at 1030 h. Dixon (1979) found winds in excess of 11 knots drastically reduced the number of birds and prevented the formation of rafts. Rafts off area D were still present at 1630 h with groups of 103, 11 and 25 being observed. Dixon (1979) indicates that from her observations in the 1970s, rafts dispersed after midday, the birds flying out to sea. Dixon (1979) concluded that wind speed was the sole environmental factor having a marked effect on the numbers of birds present. While wind speed is certainly important, a wind speed of 11-16 knots on 27 February did not prevent substantial initial colonisation, although during the morning its effect was considerable. Wind direction also appeared to play a part as illustrated by the changing numbers of AOS in areas A, A1 and B. Other factors may play a part. On 23 February 1992 the daily reoccupation of areas A, A1 and B proceeded normally with a wind of 1-3 knots. Area D remained virtually deserted throughout the morning despite a raft of up to 380 birds being present. Even at 0800 h, 78 birds were off the beach, but only for a short time in mid-morning were 3 sites occupied. However by mid-afternoon, 1515 h there were 221 AOS with 197 still occupied at 1640 h. A similar pattern of occupancy was shown by area F birds. Kestrels *Falco tinnunculus* can cause a similar effect and they are frequently present, however none were observed on this occasion. The possibility remains, however, that a Kestrel was responsible.

A cold day with an estimated 11-16 knot wind occurred on 10 March 1992 with a very heavy sleet shower in mid-afternoon. Despite the unpromising nature of the day, counts of between 42-68% occupancy were obtained. The previous day, although conditions were calm, counts were well down showing only 15-17% occupancy.

Evening vacation of nest sites and overnight occupation in area F and the colony as a whole.

Results

On twelve evenings between 28 April and 16 May 1991, and on six evenings between 21 April and 11 May 1992, observations were made in area F on nest site occupancy. Times were recorded when nests were deserted each evening and the mean time of departure calculated (Table 8). On occasions, particularly during May, birds were still occupying nest sites when observations ceased due to failing light.

These birds were allocated the time when observations ceased, purely for the purpose of ranking departure times.

Up until 3 May 1991 all sites in area F were vacated by 21.07 h . After 3 May, and up to 9 May, birds remained later, and some were still present when failing light prevented further observation. In these cases birds were standing on nest sites and not incubating. On 14 May 1991, sitting, and apparently incubating, birds were still present at 22.35 h , occupying 26% of nest sites. On 16 May 1991, 54% of nest sites were occupied by sitting birds at 22.00 h .

In 1992, all nest sites in area F up to 1 May were vacated by 21.05 h . Subsequently, birds remained later in the evening. By 11 May, 10% of nest sites were occupied by sitting birds at 22.40 h . Behaviour suggesting incubation (birds sitting into darkness), was first observed in areas A1, D, G1 and G3 on 7 May 1992. By 22 May all the original colonies (areas A, A1, B, C, D, E, F, G1) had at least 58% of AOS occupied by sitting birds. In area D, Kittiwakes sitting late into the evening were first observed in areas of highest nest density on 7 May. By 22 May, areas D1-3 had 95% of AOS occupied by sitting birds but area D8 had only 52% of sites similarly involved. Of the mainland sites, area D was more advanced than areas F, G1 and G3. By 22 May 1992, the mainland areas, D, F and G1, appeared to be ahead, in terms of percentage occupancy of nests by sitting birds, of areas A, A1 and B on Marsden Rock..

In area F on 14 May at 04.00 h , only 13 nests had sitting birds, although it was known for certain that 20 nests contained eggs on 13 May. Nine of these nests contained full clutches and all except two of these had sitting birds. Of the other nests occupied by sitting adults, three would have completed clutches within 24 hours.

For each nest site in area F, the mean time of evening departure (y) and the number of observed attendances (x), maximum of 37 attendances, since the area was first reoccupied that year, were ranked. The resulting values were used to calculate the Spearman Rank Coefficient. The results of these calculations give a highly significant correlation for individual nest sites, between the time of evening departure and the occupancy of that site ($r = 0.67$, df 30, $P<0.01$,for 1991; $r = 0.43$, df 31, $P<0.01$, for 1992). The earlier the site is occupied and the more frequently it is occupied, the later will be the time of evening departure from the site in the pre-egg laying period. The data are displayed graphically in Figure 8, for 1991 and 1992. Regression analysis describes the relationship by the equation, $y = 61.2 + 1.66\ x$, for 1991, and $y = 40.22 + 1.09\ x$, for 1992, where x represents occupancy and y the time of evening departure. For every attendance recorded at a nest site (in excess of 14 in 1991, and 13 in 1992) after the first nest site was occupied, the nest site was vacated on average 1.7 minutes later each evening in 1991 and 1.1 minutes later in 1992.

Observations in 1992 indicated a clear variation in the order of departure times between 31 March and 11 May for different areas in Marsden Bay (Table 9). The general tendency was for areas F and D4-D8 to vacate first, followed by D1-D3, G1 and G3. Areas A, A1 and B were always partly occupied when observations ceased between 21.00-22.00 h. In area D the sequence of vacation was from the peripheral area D8, to the more central and densely populated areas, D1-3.

On two occasions when direct comparisons were made, area D vacated earlier than area G1. On the first occasion area D vacated at 20.08 h and area G1 at 20.35 h . On the second, area D vacated at 20.40 h and area G1 at 20.45 h . Birds in area G3, on an isolated stack, vacated later than those in G1. But from 21 April, G3 did not vacate completely, the birds behaving in a similar way to those in areas A, A1 and B, also on an isolated stack. However earlier in the season, area G3 was vacated while areas A, A1 and B held at least a few birds until late into the hours of darkness even in very bad weather conditions, e.g. 26 March at 20.00 h some Kittiwakes, estimated at about 50 in darkness, were still present despite a gale force easterly wind with rain.

Discussion

Wooller (1973) states that overnight occupation of the nest site, at the North Shields colony, starts when the pair first comes together each season. In seven out of twelve pairs considered, the first overnight of the year took place on the same day that the pair were re-united. Dixon (1979) observed that by the time 50% of nest sites were regularly occupied, Kittiwakes were remaining at the colony until several hours after sunset, although the colonies were eventually vacated each night until about two weeks before egg laying. Experienced birds returning in February and early March were paired soon after arrival and yet widespread overnight occupancy at Marsden was not indicated until early May. These early returning birds, which are more likely to be experienced breeders (Coulson 1972), establish nest sites earlier, are in attendance for a greater proportion of the time and stay on the nest site longest before evening departure. This behaviour makes them less likely to lose what they consider to be better quality nest sites.

The order of evening departure from different areas of the Marsden colony is not related to the order of annual return to the colony or nest density. The areas, which are the last to be vacated each evening, are located on two stacks and isolated from the mainland cliffs. As a result, they are surrounded by the sea for a proportion of each day and the extra security which this offers, may be a contributory factor in delaying the departure of the birds.

From my observations it appears that adult Kittiwakes were not occupying their nest sites overnight until late in the pre-laying period. At Marsden, areas in late April and even early May were being deserted and not apparently occupied overnight. These nest sites had, in many cases, been occupied since mid-February. By early May, birds were staying later and some were still present when observations ceased. These birds may have stayed overnight. As the period of egg-laying approached in mid-May, late evening occupancy was noted (Table 9). The slightly higher count for sitting birds on 12 May, involving 18% of AOS, suggests that some, but not all Kittiwakes, cover clutches before incubation proper commences, although this may not be continuous.

Table 6a
The reoccupation of the Marsden Bay colony in 1991, by nest sites (AOS) and pairs between 21 February 1991 and 2 May 1991. Figures are expressed as a percentage of the final nest count in June 1991 (Table 2, page 21). Data from nest counts in the study areas were used to give a mean value from which the percentage was calculated to reflect changes in the whole colony.

Date	AOS	Pairs
21/02	3	0
22/02	<1	0
23/02	<1	0
24/02	<1	0
25/02	2	0
26/02	5	0
28/02	7	0
01/03	11	<1
06/03	17	2
08/03	30	3
12/03	27	3
13/03	32	6
14/03	29	5
15/03	40	4
17/03	56	15
18/03	57	15
19/03	54	15
20/03	65	22
21/03	76	27
23/03	84	26
24/03	68	23
29/03	86	25
30/03	50	5
31/03	35	3
01/04	10	<1
02/04	18	3
03/04	43	5
07/04	35	7
08/04	73	17
09/04	62	13
10/04	64	10
11/04	70	9
12/04	59	11
16/04	90	42
17/04	36	7
18/04	40	10
19/04	30	5
20/04	41	4
21/04	44	5
22/04	58	7
23/04	28	3
24/04	50	6
25/04	40	3
26/04	75	24
30/04	95	50
01/05	95	38
02/05	107	57

Table 6b

Annual reoccupation of nest sites during 1991 expressed as a percentage of the final nest count in June 1991 (Table 2, page 21) for the colonies described by Coulson and White (1956) in Marsden Bay

Areas

Date	A		B		C		D		E		F		G1	
	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs
21/02	3		6				<1				0		0	
22/02	1		0				0				2			
23/02	1		1				0				0		0	
24/02	1												0	
25/02	6		5				<1				0		<1	
26/02	1		6				1				19		1	
28/02	9		13				3				9		1	
01/03	27	2					7	<1						
06/03			34	5			14	2			14	4	16	1
07/03			59	6										
08/03											17	4		
10/03														
12/03	35	5			4	1	36		3	<1			0	
13/03	64	20	58	15	12	2	36	6	17	2	29	10	12	2
14/02					25	5							33	6
17/03	114	37			58	16	47		74	23	50	12	50	
18/03													50	13
20/03	118	48					60	19			61	27	58	20
21/03													64	27
23/03	117	37	128	29	88	36	79	24			66	38		
24/03									62	23			70	29
29/03			116										63	
30/03	75	4	80	7	57	8	42	5					56	12
31/03	55	3	43	4			28	2			36	2	30	5
01/04	40	4	21	1	4	<1	6	0			6	0	1	0
02/04	59	11	67	10			8	1			15	0	6	0
03/04	70	7	70	6			40	4			41	21		
07/04	77	15											0	0
08/04													58	20
09/04	99	31									71	19	0	0
10/04	96	13	102	16			57	7			59	27	48	15
11/04	90	11			70	10			54	4	70	33		
12/04							57	9					60	20
16/04											83	54		
17/04	70	4	48	7			19						50	7
18/04			68	24									13	2
19/04	59	15	45	5			19						25	5
20/04	75	7	69	8			34	3			31	15		
21/04	88	14	64	8	43	5	90	4	50	10			14	2
22/04	66	9	43	5										
23/04	57	4									31	14	0	0
24/04			80	12			42	4						
25/04	46													
26/04											66	27	77	35
30/04													85	54
01/05							93						96	41
02/05	160	79			98	59			133	67			81	59

FIGURES 6a and 6b

The reoccupation of the Marsden Bay colony in 1991. The number of sites occupied on each date, by single birds or pairs, is expressed as a percentage of the final nest count in June 1991. Counts of nests at sites described by Coulson and White (1956) were used to produce a figure reflecting the reoccupation of the colony as a whole.

Figure 6a the reoccupation of nest sites by either single birds or pairs.

Figure 6b the reoccupation of nest sites by pairs.

Figure 6a

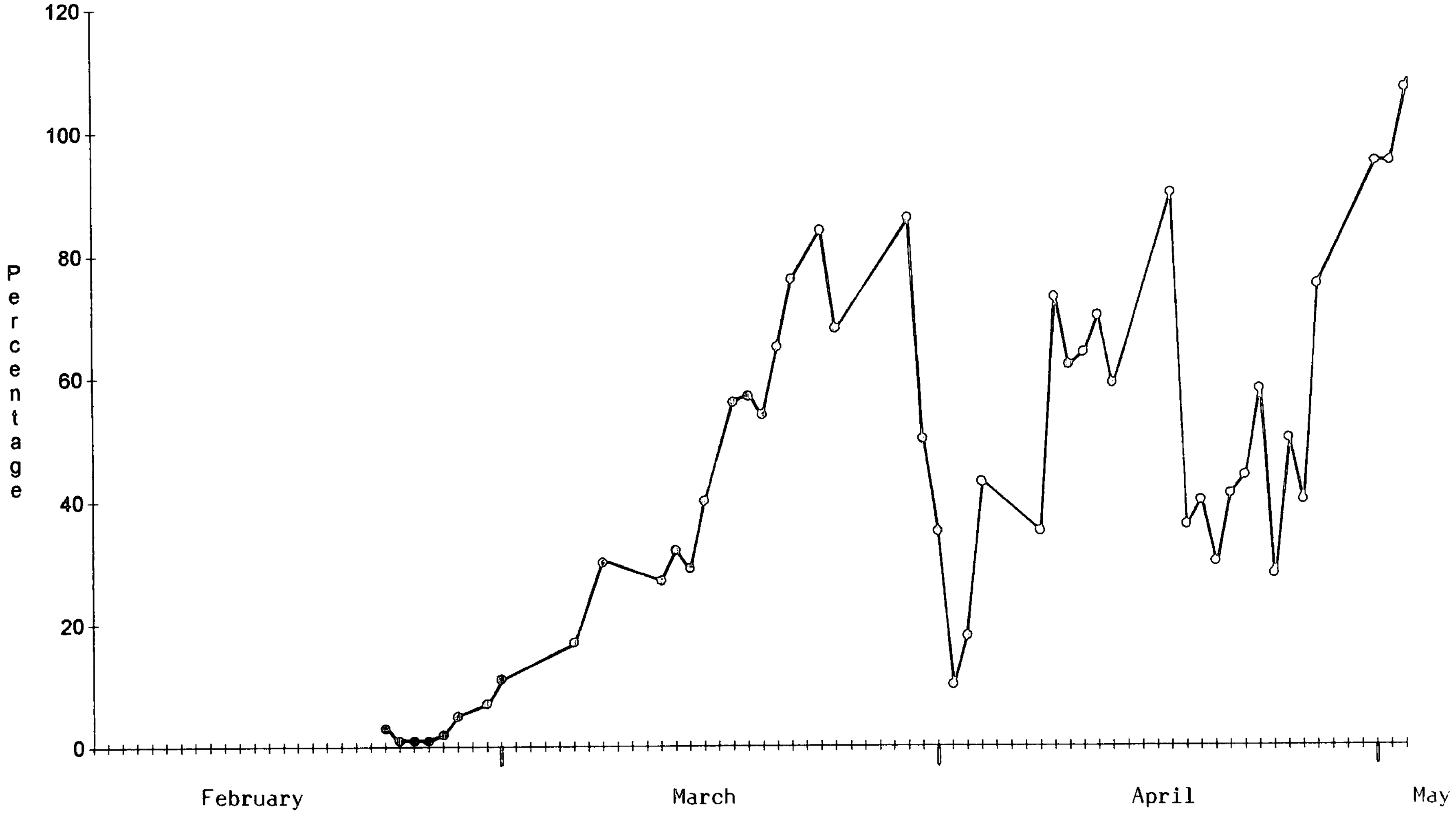


Figure 6b

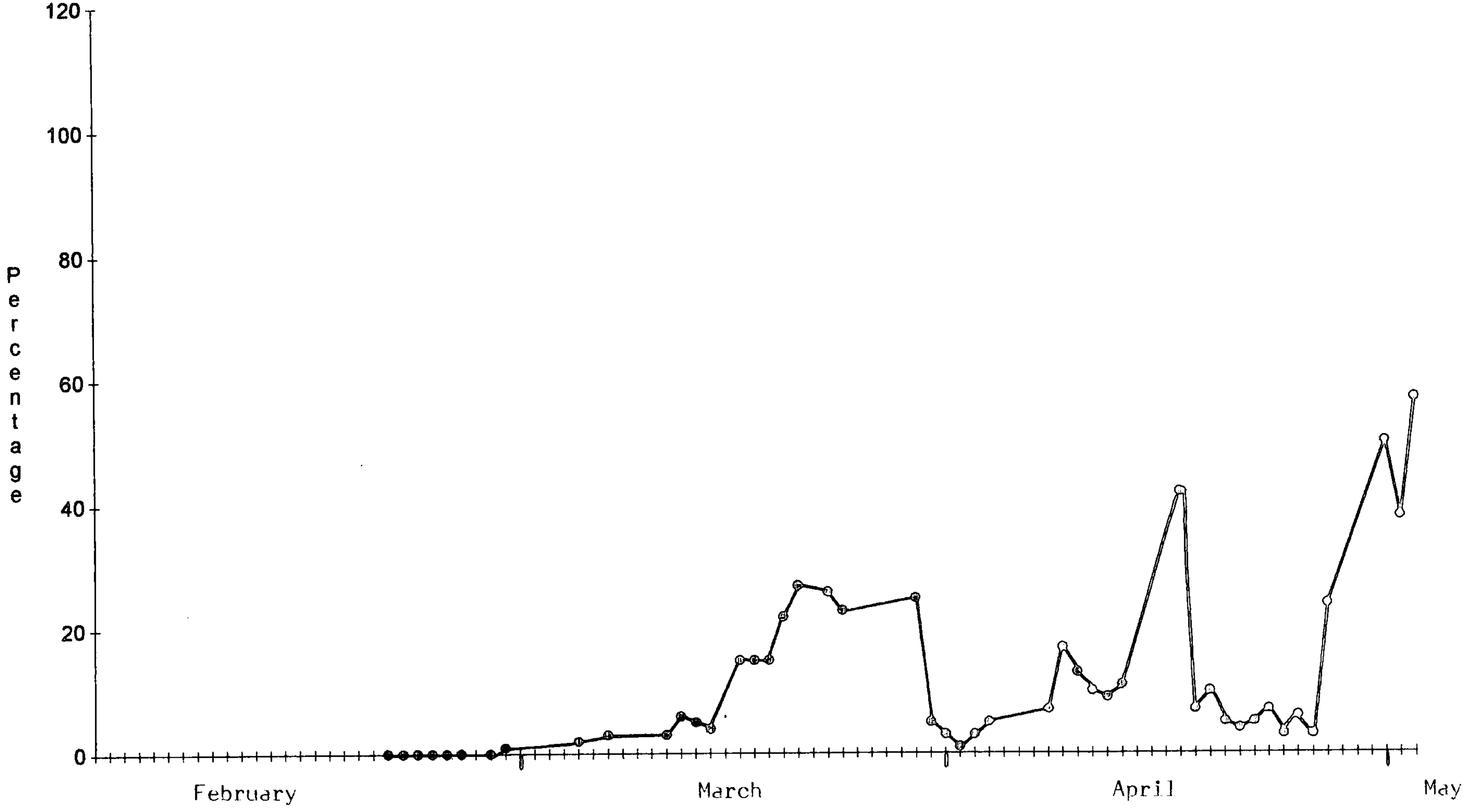


Table 7a
The reoccupation of the Marsden Bay colony in 1992 by nest sites (AOS) and pairs between 7 February-7 May. Figures are expressed as a percentage of the final nest counts in June 1992 (Table 2, page 21). Data from nest counts in the study areas were used to give a mean value from which the percentage was calculated to reflect changes in the whole colony.

DATE	AOS	PAIRS
07/02	<1	0
08/02	<1	0
09/02	0	0
10/02	0	0
11/02	1	0
12/02	<1	0
17/02	4	<1
19/02	5	<1
20/02	9	<1
21/02	6	<1
23/02	12	1
26/02	21	2
27/02	13	1
28/02	33	5
04/03	51	11
05/03	51	14
06/03	50	15
09/03	17	3
10/03	49	16
11/03	51	14
12/03	43	9
13/03	41	8
14/03	45	8
15/03	56	13
17/03	45	9
18/03	47	8
19/03	67	17
23/03	50	8
25/03	57	10
26/03	50	9
27/03	62	12
31/03	84	24
02/04	66	17
04/04	71	22
09/04	87	43
14/04	81	32
22/04	90	33
07/05	83	21

Table 7b

Annual reoccupation of nest sites during 1992 expressed as a percentage of the final nest count in June 1992 (Table 2, page 21) for the original colonies described by Coulson and White (1956) in Marsden Bay.

	Areas													
Date	A		B		C		D		E		F		G1	
	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs
07/02	1	0	0	0	0	0	0.1	0	0	0	0	0	0	0
08/02	<1	0	0	0	0	0	0	0	0	0	0	0		
09/02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10/02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12/02	<1	0	3	0			0	0			0	0		
13/02	2	0	1	0	0	0	0	0	0	0	0	0	0	0
17/02	4	0	9	<1			6	<1			0	0	0	0
19/02	7	1	11	<1	2	<1	6	<1			2	0	1	<1
20/02	9	<1	14	<1	5	<1	13	1			2	0	0	0
21/02	9	1	11	<1	4	<1	7	<1	0	0	2	0		
23/02	22	3	20	3	7	<1	15	1	3	0	8	2	0.5	0
26/02	19	3	30	3			25	1			21	3	10	2
27/02	18	1	28	2	12	1	18	1			6	2	1	0
28/02			34	5			45	5			27	6	36	4
04/03	39	9	57	9			59	13			60	20	47	10
05/03	39	13	47	11	43	10	55	16	51	13	56	20	60	14
06/03	37	11	52	17			57	12			62	26	29	4
09/03	15	1	16	1			15	1			17	3	17	2
10/03	42	13	49	17			62	15			68	23	53	17
11/03	46	13	62	18	49	12	64	16	56	14	45	12	60	17
12/03	31	5	46	10	20	5	60	10			55	12	51	10
13/03	35	6	52	12	14	1	44	10			48	12	63	8
14/03	31	5	43	8			50	6			57	15		
15/03	45	6	57	9							53	14	62	15
17/03	38	7	49	8	41	6					50	18		
18/03	33	5	46	5	45	6	55	7	49	7	64	23		
19/03	54	13	57	16	55	15	75	20	67	17	79	18	77	23
23/03	36	5	36	6			57	10			47	9		
25/03	41	5	52	8			71	12			45	9	74	15
26/03	41	10	49	7			63	8			50	14	50	7
27/03	46	6	52	10			72	13			61	11	75	17
30/03	58	15	72	20			98	34			71	41	77	22
31/03	63	22	75	24			69	26			88	52	90	30
02/04	48	13	67	11			72	16			56	15	64	18
03/04													68	15
04/04	62	17	65	20			81	20			73	23	73	26
09/04	73	33	76	33	100	49	107	49	87	37	83	58	87	48
14/04	65	27	67	28							88	52	82	28
17/04													79	32
21/04													80	27
22/04	80	27	69	19			113	58			88	55		
07/05	72												91	33

Table 7c
Number of apparently occupied sites (AOS) in area D of Marsden Bay during the reoccupation phase of 1992, between 7 February-22 April.
During 7-28 February (inclusive) areas combined due to small numbers of AOS.

Date	D1/D2		D3/D4		D5/6/7a,b		D8	
	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs
07/02	1	0	1	0	0	0	0	0
09/02	0	0	0	0	0	0	0	0
10/02	0	0	0	0	0	0	0	0
11/02	0	0	0	0	0	0	0	0
12/02	0	0	0	0	0	0	0	0
13/02	0	0	0	0	0	0	0	0
17/02	45	1	25	0	28	1	0	0
19/02	34	1	34	2	20	1	0	0
20/02	98	4	47	3	50	2	0	0
21/02	27	2	40	3	35	0	0	0
23/02	97	5	76	3	48	4	0	0
26/02	176	8	96	5	109	8	0	0
27/02	135	6	80	9	95	5	5	1
28/02	300	26	140	13	175	20	9	2

Table 7c (continued)

Date	D1		D2		D3		D4		D5		D6		D7a		D7b		D8	
	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs	AOS	Pairs
02/03	103	6	50	4	38	3	4	0	27	5	11	2	8	0	4	1	4	1
04/03	250	80	170	45	130	16	45	6	180	31	46	5	42	4	22	5	19	3
05/03	238	80	146	42	146	31	49	11	138	38	43	14	37	8	21	8	20	6
06/03	221	61	132	30	140	25	45	15	121	30	35	7	41	8	17	4	21	4
09/03	62	5	60	6	42	2	8	1	20	2	5	1	15	2	2	1	10	1
10/03	280	77	180	36	187	40	42	13	138	32	40	13	36	5	27	7	21	4
11/03	259	73	192	48	190	39	44	10	156	39	46	8	40	8	26	9	23	9
12/03	260	34	180	28	165	22	43	8	149	24	34	13	32	9	21	4	24	6
13/03	230	45	153	30	140	18	35	8	104	20	32	5	36	6	25	8	22	6
14/03	220	35	180	20	151	15	32	4	99	10	19	2	22	4	22	3	19	3
15/03	54	3	43	6	56	3	16	0	47	3	15	1	16	2	8	0	8	2
17/03	180	10	120	8	99	7	30	4	104	8	23	6	23	4	19	2	12	1
18/03	254	20	159	20	143	18	37	7	130	14	34	4	32	7	27	4	14	3
19/03	327	119	217	64	248	68	58	6	143	23	53	9	45	9	28	5	24	6
23/03	280	55	180	33	143	23	30	4	110	18	49	4	32	6	19	4	26	4
25/03	308	71	238	36	207	27	36	4	168	25	50	7	38	5	17	2	19	2
26/03	260	30	202	20	180	24	46	6	163	25	50	7	38	5	17	2	19	2
27/03	326	55	236	36	160	30	53	14	142	26	60	10	54	12	35	8	38	7
30/03	446	190	278	96	246	90	53	16	260	80	95	18	46	12	27	9	37	11
31/03	399	108	275	86	250	70	60	15	262	68	90	15	56	14	28	8	42	15
02/04	314	64	188	40	208	48	52	12	66	42	54	10	55	12	20	4	35	8
04/04	344	89	240	44	258	48	47	16	190	46	54	14	59	17	25	10	32	8
09/04	431	190	310	140	300	150	59	30	261	120	100	40	76	34	36	19	60	26
22/04	425	220	290	140	330	170	76	42	300	140	107	58	82	47	39	25	70	40
01/06	386		254		357*				246		224^						62	

* includes areas D3 and D4

^ includes areas D6, 7a and b

FIGURE 7a and b

The reoccupation of the Marsden Bay colony in 1992. The number of sites occupied is expressed as a percentage of the final nest count in June. Counts in the areas described by Coulson and White (1956) were used to produce a figure reflecting the reoccupation of the colony as a whole.

Figure 7a the reoccupation of nest sites

7b the reoccupation of nest sites by pairs

Figure 7a

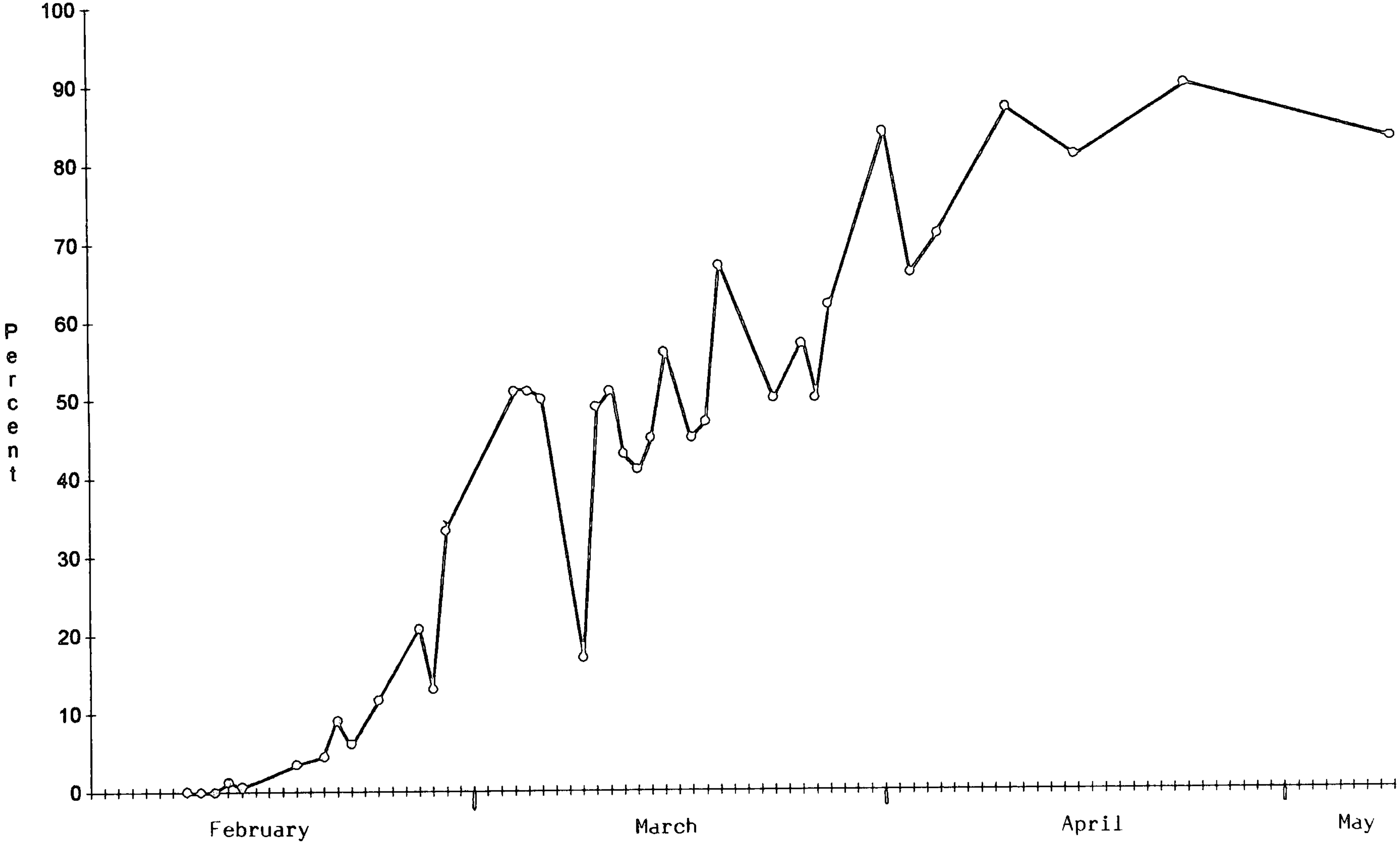

100
90
80
70
60
50
40
30
20
10
0
Percent
February
March
April
May

Figure 7b

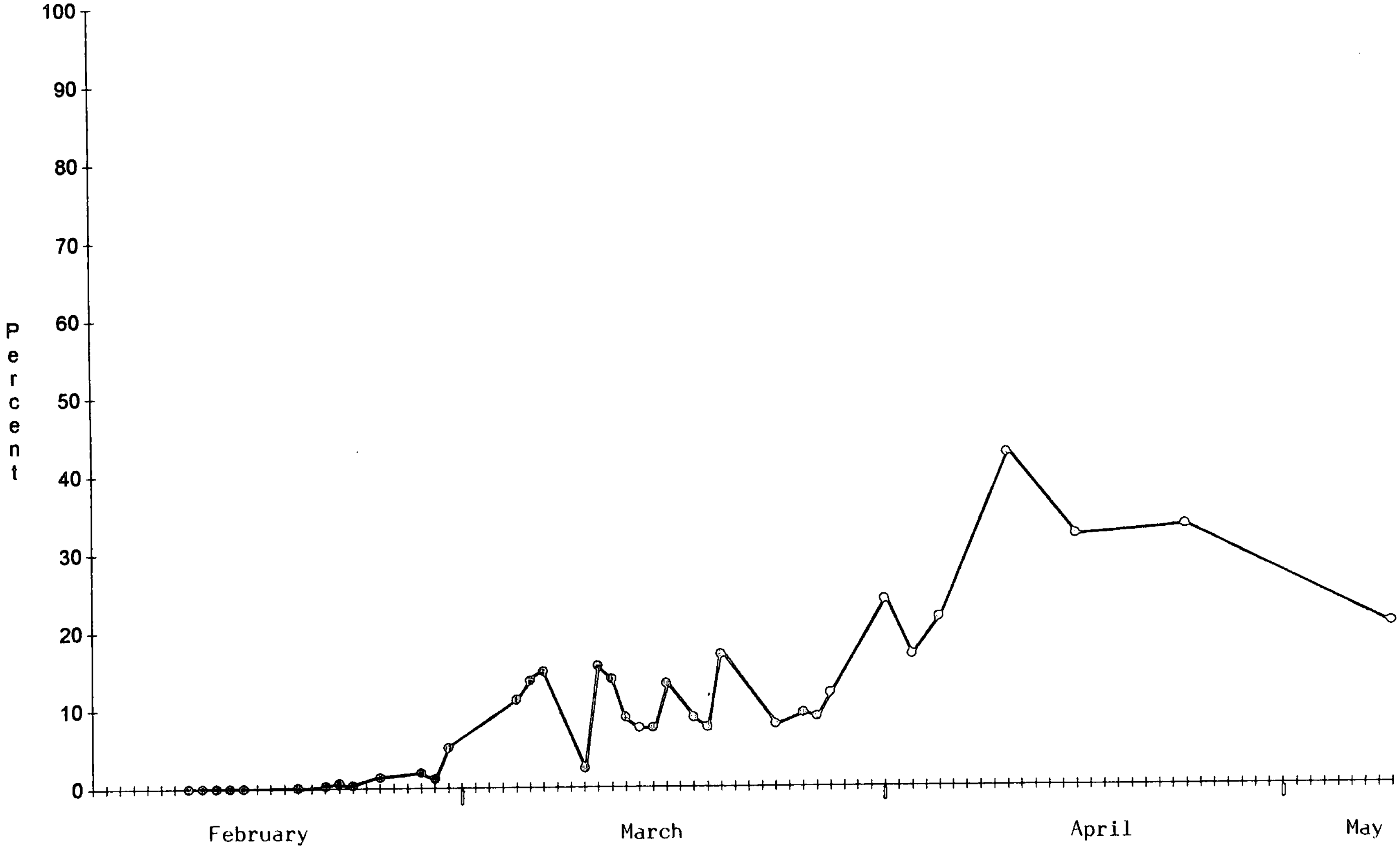

Percent
100
90
80
70
60
50
40
30
20
10
0
February
March
April
May

Table 8

The mean evening departure times (BST) in 1991 and 1992 for adults leaving specific nests in area F of the Marsden Bay colony. The number of observed attendances at the nest site since area F was first occupied in 1991 and 1992 is also shown.The maximum possible number of observed attendances was 37 in both 1991 and 1992.

Nest no.	Mean departure time,1991 28 April-16 May	Mean departure time,1992 21 April-11 May	No. of attendances 1991	No. of attendances 1992
1a	21:41	20:59	18	19
1b	21:13	20:42	8	13
2	21:40	21:24	30	29
3	21:56	21:20	31	32
4	21:36	21:18	21	27
5	21:39	21:22	27	14
6a	21:29	21:20	23	17
6b	21:19	20:29	14	20
7	21:36	20:25	19	16
8	21:46	21:17	27	31
9	21:35	21:16	24	30
10	21:38	20:48	29	34
11	21:42	21:10	27	28
12	22:02	21:08	28	31
13	21:55	21:22	26	31
15	22:02	20:57	30	34
16	21:57	21:16	28	34
17	21:52	21:07	25	20
18	21:48	21:25	20	27
20	21:34	21:16	24	28
21	21:48	21:21	28	27
22	21:33	21:17	25	27
23	21:40	21:22	22	22
24	21:39	21:24	28	30
25	21:50	21:07	31	30
26	21:47	20:57	27	21
27	21:43	20:53	27	27
28	21:37	20:56	24	17
29	21:53	21:26	30	28
30a	21:33	20:56	23	17
30b	21:56	20:52	29	15

FIGURE 8

The number of observed attendances by adult birds at the nest site, between 28 April-16 May 1991 (filled circles) and 21 April-11 May 1992 (filled squares), since area F was first occupied in that year, plotted against mean evening departure time, also for that year. The maximum number of observed attendances possible in each year was 37, ie. the number of visits made for recording purposes

Figure 8

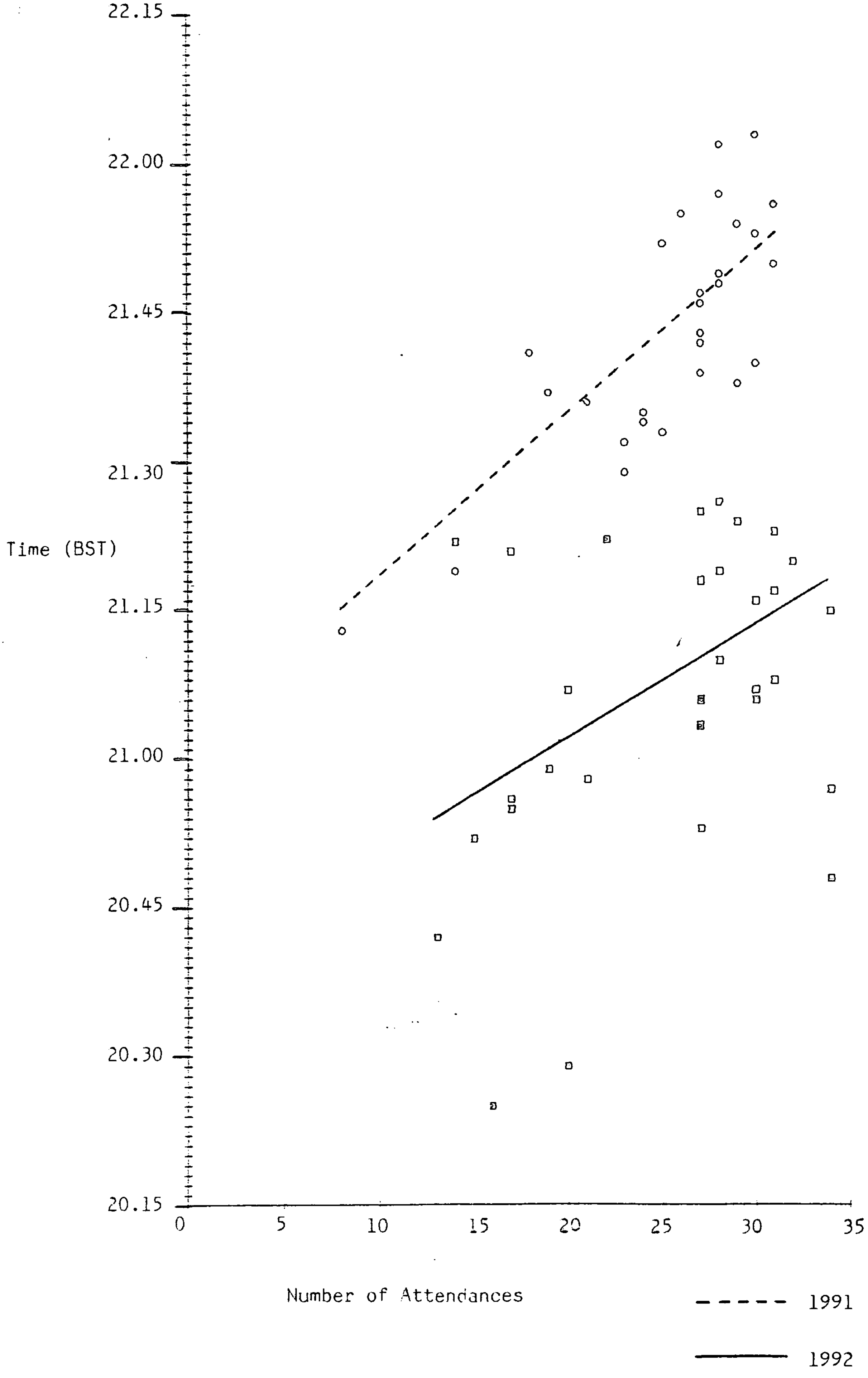

22.15
22.00
21.45
21.30
21.15
21.00
20.45
20.30
20.15
Time (BST)
0
5
10
15
20
25
30
35
Number of Attendances
1991
1992

Table 9
Evening departure times in areas of Marsden Bay colony
during 31 March-11 May 1992.

	Areas													
Date	A	A1	B	D1	D2	D3	D4	D5	D6	D7	D8	F	G1	G3
31.3				20:15	20:20	20:15	20:08	20:15	20:05	20:05	20:05	20:00		
3.4	23:00*													
4.4	20:45*	20:45*		20:10	20:10	20:10	20:05	20:05	20:05	20:05	20:05	19:55		
9.4	20:15*	20:15*	20:15*	20:15	20:15*	20:15*	20:10	20:13	20:10	20:10	20:10	20:07	20:30	20:38
17.4	20:40*	20:40*	20:40*	20:08	20:08	20:00	19:50	19:50	19:50	19:50	19:50	19:50	20:35	20:36
21.4	20:40*	20:40*	20:40*	20:36	20:40	20:40	20:30	20:34	20:22	20:22	20:22	20:24	20:45	21:00*
26.4	21:20*	21:20*	21:20*	21:20*	21:20*	21:20*	21:10	21:20	21:05	21:00	21:00	21:05	21:43	21:40*
1.5	21:20*	21:20*	21:20*	21:20*	21:20*	21:20*	21:20	21:25	21:15	20:55	20:50	21:15	21:40	21:50*
6.5	21:35*	21:35*	21:35*	21:35*	21:35*	21:35*	21:35	21:35*	21:10	20:50	20:20	21:35*		
7.5	22:00*	22:00*	22:00*							21:25	21:25	21:55*	21:50*	21:50*
11.5	21:40*	21:40*	21:40*	21:40*	21:40*	21:40*	21:30	21:40*	21:40*	21:30	21:30	22:40*		

* area still occupied when observations ceased.

Number of nests occupied, as a percentage of the final nest count ,by sitting birds during 7-22 May 1992.
in areas of the Marsden Bay colony.

	Areas						
Date	A	A1	B	D	F	G1	G3
7.5		6		9		10	18
11.5		25			8	33	49
12.5	26	23		16	24	31	42
13.5					17		
14.5				24	20		
15.5	35	40	35	44	38	46	60
18.5	54	60	46		54	66	62
19.5				62	62		
22.5	66	68	58	83	71	72	70

	Areas							
Date	D1	D2	D3	D4	D5	D6	D7	D8
7.5		2	1	0	0	0	0	0
11.5				0	4	7	1	0
12.5	23	18	11	15	13	18	6	7
14.5	28	29	26	15	28	14	10	0
15.5	65	59	45	28	28	21	18	20
19.5	78	79	59	36	47	59	49	38
22.5		95		53	71	72	67	52

CHAPTER 5

CLUTCH SIZE, HATCHING SUCCESS AND FLEDGING SUCCESS

Clutch size

Results

The mean clutch size in area F in 1991 was 1.87 (n=8) and in 1992 was 1.95 (n=59) (Table 10). The majority of nests, 82% in 1991 and 86% in 1992, in area F contained two eggs as reflected in the mean clutch sizes. Clutch completion dates were not available for 1991, but closer monitoring of egg laying was undertaken in 1992. The majority of clutches in 1992 (52%, n=27) were completed in the period 13-20 May, and 92% of these (n=24), were clutches of two eggs. Three clutches of 3 eggs were laid, all in this most prolific spell. Clutches containing a single egg were laid early and late. One, completed before 13 May, and 4 completed between 3-17 June.

Discussion

Cullen (1957) recorded a mean clutch size on the Farne Islands of 1.94 and Coulson and White (1958a) quote a figure of 2.01 for the North Shields colony between 1952 and 1957. Between 1960 and 1981 the mean clutch size at North Shields fell erratically from 2.18 to 1.89, but in 1982 it rose sharply to 2.07 (Coulson and Thomas 1985). During the period 1952-1957 at North Shields the percentage of clutches with one, two and three eggs was 10%, 77% and 13% respectively (n=149) (Coulson and White 1958a). In area F in 1991 the corresponding figures were 8%, 87%, and 5% (n=38) and in 1992 the were 8%, 86% and 6% (n=59). Few clutches of 3 eggs were laid. Coulson and Porter (1985) propose that 3 egg clutches are laid by higher quality individuals and Coulson and White (1961) demonstrate the relationship between clutch size and previous breeding experience of the female. In addition, they show that clutches, on average, are smaller in females breeding for the first time, relative to those clutches of more experienced breeders laying at the same time. However few clutches of either 1 or 3 eggs were laid

(13% of all clutches in 1991 and 14% of all clutches in 1992). This would lead one to suggest that few inexperienced birds were nesting in area F in 1992. The annual adult mortality rate in area F, 18% in 1990-1991 and 8% in 1991-1992, would have required only 9 new recruits in 1991 and 6 in 1992 to maintain the breeding population. In any one year their would be few new breeders present.

Mean clutch size laid decreased from 14-20 May to 11-17 June 1992 (Table 10 and Figure 9). This pattern is almost identical to that shown by Coulson and White (1961) in their comparison of clutch size and time of laying in five widespread east coast colonies At North Shields, during 1952-1959, the mean clutch size was 2.07 eggs per nest. In 1958, by 13 May, 10% of nests at North Shields had eggs (Coulson and White 1961). In 1992, in area F at Marsden, 15% of nests had full clutches by 13 May, the final mean clutch size being 1.95.

Hatching success

Results

In area F in 1991, hatching success was 62% (SE 5.7) and in 1992 it was 78% (SE 3.8) (Table 11). Percentage hatching success based on clutch size was obtained for area F in 1991 and 1992 (Table 11). Clutches of one (n=11), two (n=82) and three eggs (n=4) had 27% (SE 14.0), 73% (SE 3.4) and 92% (SE 8.2) hatching success in 1991 and 1992 combined. Clutches of one and three eggs were few in number and so small changes in the number of chicks hatching can produce large percentage fluctuations in the figure for hatching success. Hatching success for all eggs (n=187) over the period 1991-1992 was 72% (SE 3.3). The mean number of chicks hatched per clutch was 1.38.

[Standard errors of percentages, such as hatching and fledging succes were calculated from the usual binomial relationship ($\sqrt{p.q/N}$) where $p+q = 100$. Since no high and low percentages were involved, no arcsine transformations were considered necessary]

Discussion

Hatching success in area F, was higher in 1991-1992 than that at North Shields, during 1952-1957, which Coulson and White (1958a) give as 69%. That level of hatching success at North Shields continued until the 1970s when it decreased to a little over 60%, before showing a slight upturn in the late 1970s and early 1980s.

My figures for hatching success compare with 42%, 69% and 79% for clutches of one, two and three eggs at North Shields during 1952-1957 (Coulson and White 1958a). Clutches containing only one egg were most likely to have been laid by birds breeding for the first time (Coulson and White 1959b) and lack of breeding experience may have been responsible for the poor hatching success of 27%. However the figures for hatching success in clutches of one are based on a total of only 11 clutches.

Fledging success

Results

Fledging success in 1991 and 1992 was 47% (SE 5.9) and 54% (SE 5.2) respectively for area F (Table 12). Coulson and White (1958a) rightly consider breeding success in relation to brood size to be essential in a consideration of the importance of food supply. Fledging success, in 1991-1992 combined, for broods of one, two and three chicks was 55% (SE 11.4), 51% (SE 4.7) and 44% (SE 19.0) respectively (Table 12). The mean number of chicks fledged per brood in 1991-1992 was 0.92 in area F, 1.30 in area G1 and 1.39 in G3.

The observed difference in fledging success in broods of one between 1991 and 1992 was statistically significant (χ^2= 5.57, $P<0.05$, Yates correction applied). There was no statistically significant difference for fledging success in broods of one and broods of two between 1991 and 1992. Percentage fledging success, based on brood size, also showed variation between the study areas. Fledging success in areas G1 and G3 combined in 1991-1992 were 82% (SE 2.9), 86% (SE 1.7) and 90% (SE 6.7) (Table 13).

In area F, 1992 was a more successful year for the number of nests built and number of chicks fledged. The breeding success of group Fa nests was only slightly less than that in areas G1 and G3, which in 1991 had been much more successful. Group Fb nests were also more successful in 1992. Nest occupancy of ringed birds in 1990 is lacking. Hence the presence of birds on nests in 1991 no indication of either a first or subsequent breeding attempt. However in 18 group Fb nests in 1992, at least 12 of the adults were known to have nested in the same section of the colony in 1991. Although not breeding for the first time, they may still have been inexperienced breeders.

In area F in 1992, there were six new nests. Six eggs were laid, but only one chick hatched. It did not fledge. The adults involved may well have been inexperienced and breeding for the first time.

Discussion

In Harris and Wanless (1990), figures for breeding success at North Shields for 1986, 1987 and 1988 are given as 1.40, 1.34 and 1.16 respectively (J.C. Coulson). For area A1 in 1988, a figure of 0.96 ± 0.6 is given (D. Turner).

Coulson and White (1958a) combined their data from North Shields with data from Cullen (1957). This produced a figure of 1.84 chicks per brood and 1.59 chicks fledged per brood (n=214) (my calculation). The discrepancy between brood size and number of chicks fledged, in area F at Marsden, suggests problems in the chick-rearing stage.

In looking for reasons for the poor breeding success in area F, judged on the number of chicks fledged per completed nest, the position of the nest appears to be important (Table 14). In 1991 a number of nests, group Fa, (n=34) on the open area of cliff face had a breeding success of 0.94 ± 0.15 chicks fledged per completed nest. Another group, Fb, (n=16), consisting of nests low down on the cliff and others close to and behind a lift shaft, produced 0.11 ± 0.08 chicks per completed nest. The group Fb nests were subject to more daily disturbance by workmen than group Fa nests and the lift shaft on occasions produced severe wind turbulence, largely affecting group Fb nests. Both factors which may have affected the behaviour of the nesting Kittiwakes. These figures above for 1991 compare with 1.0 ± 0.13 chick fledged per completed nest in group Fa (n=40), and 0.45 ± 0.14 chicks fledged per completed nest in group Fb (n=20) in 1992. The lower success of group Fb nests therefore exerts a considerable influence on the figures for overall breeding success in area F.

Harris and Wanless (1990), without explanation, considered a figure of less than 0.7 young fledged per completed nest as being important and listed colonies where this had occurred in 1988. Area F, although only a section of the Marsden Colony, fell into this category in 1991. The main reason for the low figure being the poorer performance of group Fb nests.

Chick deaths between hatching and fledging

Data were collected for colonies G3, G1 and F. In 1991, no chick deaths were recorded between 16 July and the time chicks fledged. In 1992, 5% of observed mortality occurred after this date. Between the years there was a noticeable difference in the timing of chick mortality. In 1991, 24% occurred between 22- 25 June and 51% took place between 29 June-7 July. In 1992, 51% took place between 4-11 July and 23% between 12-16 July. A movement of about a week in the main periods of mortality. Adult non-attendance was significantly higher in 1992. This may have been a contributory factor, although overall breeding success between the years remained unchanged. The number of chick deaths observed may be normal, a natural process, which occurs in most years unless conditions are exceptionally good.

Table 10

Clutch completion dates and size of clutches between 13 May-17 June in area F of the Marsden Bay colony.

Clutch completed	No. of eggs	No. of nests	Mean clutch size
by 13/05	17	9	1.88
14-20/05	57	27	2.11
21-27/05	20	10	2.00
28/05-3/06	12	5(6)	2.00
4-10/06	11	7	1.57
11-17/06	1	1	1.00
Total	117	59(60)	1.95

Clutch completed	No. of clutches containing		
	1 egg	2 eggs	3 eggs
by 13/05	1	8	0
14-20/05	0	24	3
21-27/05	0	10	0
28/05-3/06	0	6*	0
4-10/06	3	4	0
11-17/06	1	0	0
Total	5	52	3

( ) includes a replacement clutch of 2 eggs
* includes a replacement clutch of 2 eggs.

FIGURE 9

The mean clutch size of the Kittiwake at Marsden in 1992 in relation to the date of laying

Figure 9

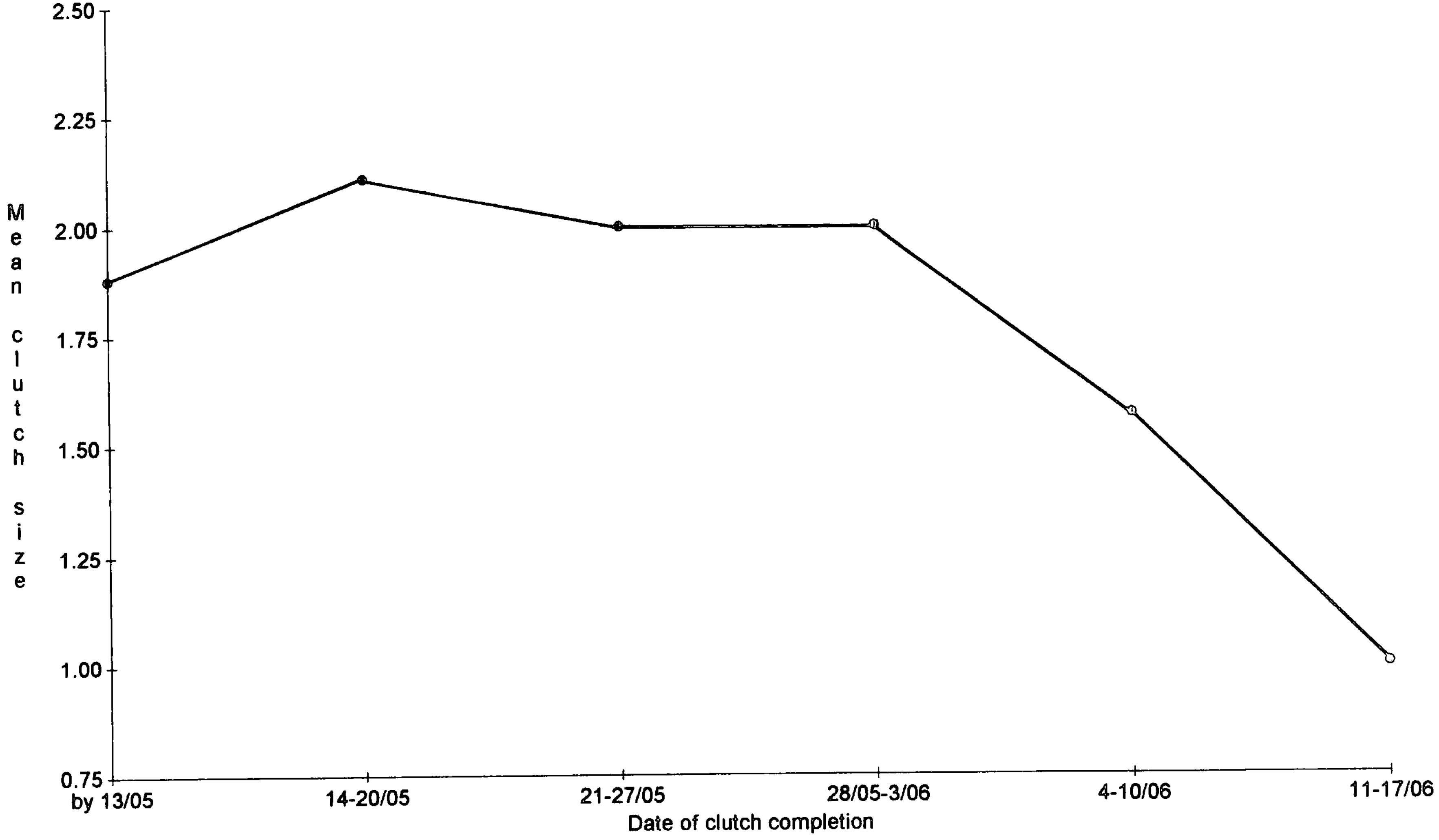

Mean clutch size
2.50
2.25
2.00
1.75
1.50
1.25
1.00
0.75
by 13/05
14-20/05
21-27/05
28/05-3/06
4-10/06
11-17/06
Date of clutch completion

Table 11

Hatching success in area F in 1991 and 1992.
(data only used from nests in which the clutch size was accurately known)

1991

Clutch size	No. of clutches	No. of eggs	No. hatched	Hatching success,%	SE
1	6	6	2	33	21
2	31	62	39	63	5.8
3	1	3	3	100	
All	**38**	**71**	**44**	**62**	**5.7**

1992

Clutch size	No. of clutches	No. of eggs	No. hatched	Hatching success,%	SE
1	5	5	1	20	17.9
2	51	102	81	79	4.0
3	3	9	8	89	10.4
All	**59**	**116**	**90**	**78**	**3.8**

Table 12

Fledging success in area F in 1991 and 1992.
(data only used from nests in which the brood size was accurately known)

1991

Brood size	No. of broods	No. of chicks	No. fledged	Fledging success,%	SE
1	8	8	2	25	16.4
2	30	60	29	48	6.5
3	1	3	2	67	33.2
All	**39**	**71**	**33**	**47**	**5.9**

1992

Brood size	No. of broods	No. of chicks	No. fledged	Fledging success,%	SE
1	12	12	9	75	13.1
2	36	72	38	53	5.9
3	2	6	2	33	21.0
All	**50**	**90**	**49**	**54**	**5.2**

Table 13

Number of chicks fledged according to brood size in areas F, G1 and G3 of the Marsden Bay colony in 1991 and 1992

Site	Brood size	Number of broods		No. of chicks		No. fledged		Fledging success, %			
		91	92	91	92	91	92	91	SE	92	SE
Fa	1	6	6	6	6	2	5	33	20.9	83	16.7
	2	21	26	42	52	27	33	64	7.5	64	6.7
	3	1	2	3	6	2	2	67	33.2	33	20.9
	All	28	34	51	64	31	40	61	6.9	63	6.1
Fb	1	2	6	2	6	0	4	0		67	7.5
	2	9	10	18	20	2	5	11	7.7	25	9.9
	3	0	0	0	0	0	0	0		0	
	All	11	16	20	26	2	9	10	6.7	35	9.5
G1	1	58	36	58	36	43	33	74	5.8	92	4.5
	2	50	53	100	106	90	90	90	3.0	85	3.5
	3	0	1	0	3	0	2	0		66	33.5
	All	108	90	158	145	133	126	84	2.9	87	2.8
G3	1	30	49	30	49	26	46	87	6.2	94	3.4
	2	46	49	92	96	82	79	89	3.3	83	3.8
	3	3	3	9	9	9	8	100		89	11.1
	All	79	101	131	154	117	133	89	2.9	86	2.9
G1 G3	1	88	85	88	85	69	73	81	4.0	93	2.80
	2	96	102	192	202	172	169	88	2.2	83	6.50
	3	3	4	9	12	9	10	100		83	33.20

Table14

Breeding data for areas G1, G3 and F in the Marsden Bay colony in 1991 and 1992

1991	G1	G3	F	Fa	Fb
Total no. of nests	128	94	52	34	18
No. of chicks hatched	158	131	71	51	20
No. hatched per nest	1.28 + 0.061	1.39 + 0.082	1.36 + 0.124	1.50 + 0.146	1.11 + 0.226
No. of successful nests	107	79	39	28	11
No. of chicks fledged	133	117	33	31	2
No. fledged per successful nest	1.24 + 0.067	1.48 + 0.073	0.85 + 0.135	1.11 + 0.157	0.18 + 0.122
Chicks fledged per nest (all)	1.10 + 0.067	1.25 + 0.084	0.64 + 0.113	0.94 + 0.148	0.11 + 0.076
1992					
Total no. of nests	105	116	60	40	20
No. of chicks hatched	145	154	90	64	26
No. hatched per nest	1.38 + 0.072	1.33 + 0.068	1.50 + 0.104	1.60 + 0.128	1.30 + 0.179
No. of successful nests	90	101	50	34	16
No. of chicks fledged	126	133	49	40	9
No. fledged per successful nest	1.40 + 0.063	1.33 + 0.055	0.98 + 0.112	1.18 + 0.136	0.56 + 0.157
Chicks fledged per nest (all)	1.20 + 0.072	1.15 + 0.068	0.82 + 0.104	1.00 + 0.134	0.45 + 0.135

CHAPTER 6

GROWTH RATES OF CHICKS

Results

In 1991, weights of chicks were recorded in area F between 18 June-2 July (Table 15a). In 1992, weights were recorded between 11 June-15 July (Table 15b).

Coulson and White (1958a) in estimating the linear growth rate per day of individual chicks used weights between 100 g and 300 g as it is within these limits that growth rate is constant. Later, Coulson and Porter (1985) extended the lower end of the range to 60 g . In my sample of chicks in 1991, 27 paired weights were within the former range and in 1992 there were 38. Calculating a mean daily growth rate for these chicks gives a figure of 13.5 g per day (SD 4.5) in 1991 and 12.05 g per day (SD 3.9) in 1992. Within the revised range, in 1991 there were 30 paired weights to give a mean daily growth rate of 13.4 g. (SD 4.6) and in 1992, 56 paired weights gave a growth rate of 12.2 g. (SD 4.6). There is therefore little difference in the figures for either year irrespective of the method used.

Chick growth rates in area F, during 18 June-2 July 1991, are shown in Table 15a. Chick weights and growth rates are shown in Table 16a, in which the data are related to date of weighing. Chicks were weighed when of a suitable size to ring and therefore the designation A1 and B1 broadly reflect chick age in 1991; A1 chicks were those which hatched approximately a week before B1 chicks.

The data from 1992 for chick daily growth rates and chick weights are more comprehensive and they can be linked with three periods of clutch completion (Table 16b, Figure 10a and b). Chicks indicated as belonging to groups A2, B2 and C2 are from clutches completed 13 May, 20 May and 27 May respectively. Growth rates of chicks at Marsden, North Shields and Gateshead in 1992 are shown in Table 17. These figures include all chicks weighed on a particular date. The figures are for comparative purposes only and so chick weights in the 60-300 g. range have not been specifically selected. The data for North Shields and Gateshead are unpublished (J.C. Coulson). Figure 1b shows the location of these colonies.

Published data for mean daily weight increase over the period of most rapid growth include 15.5 g (Farne Islands, Pearson 1968), 15.64 g (North Shields; Coulson and White 1958), and 16.1 g (North Shields, Coulson and Porter 1985). The mean growth rates per day, during 1991 and 1992 in colony F at Marsden, when chicks were in the 60-300 g range, were 13.6 g (SD 4.6, SE 0.8, n=29) and 12.7 g (SD 4.6, SE 0.6, n=34).

Tables 15b,15c, 16a and b, and Figure 12 show data on chick weights and growth rates for 1992, comparing those for chicks of similar age (from clutches completed by 13 May, group A2 ; during 13-20 May, group B2 : during 20-27 May, group C2). To compare the progress of these groups over a period of time, all chicks, irrespective of weight, have been included in the calculation of means. Comparing groups at a similar age, group A2 experienced a higher initial growth rate, than group B2 and C2. The difference between group A2 and group B2 growth rates was significant ($t = 2.6$, df 27, $P < 0.02$), but there was no significant difference between those of group B2 and group C2 ($t = 1.3$, df 27, n.s.).

Discussion

During their period of most rapid growth groups A1 and B1 had daily growth rates of 16.2 g and 13.3 g respectively. At the same stage of growth, groups A2, B2 and C2 had daily growth rates of 17.2 g, 13.5 g and 11.4 g respectively. The good start achieved by groups A1 and A2 may well be a major factor in their 78% and 89% fledging success. However, Coulson and Porter (1985) could not identify any significant relationship between fledging success and mean growth rate in any year. The fledging successes of 57% for group B1, and 46% and 44% for groups B2 and C2 respectively, with their lower maximum growth rates, do suggest the possibility, although the sample size was much less than that available to Coulson and Porter. Other factors undoubtedly play a part in fledging success and may have been influential in producing this relationship between the sets of data. Parental experience probably played a part. Five nests were involved, three of which produced the first chicks in 1991. At least four out of the six adults involved in these three nests occupied the same site in both years. In the other two nests the pairs were the same in each year.

The most successful broods in 1991 and 1992 in area F were those from clutches laid early, probably by older and more experienced females, able to protect and feed the chicks and withstand the physical stress involved.

The comparative data in Table 17 show changes in growth rate in three colonies over the chick rearing period. In all cases, chicks weighed in the early part of this period showed greater daily growth rates. This is in part due to the faster growth experienced by chicks initially during their development. As they approach a weight of 300 g the daily increase in weight becomes less. In addition, as shown above, chicks which hatch later have a smaller daily growth rate and it tends to vary more between chicks, and this further contributes to the effect. The standard deviation figures tend to increase with time showing a greater variation in chick growth rates in the chicks measured later in the chick rearing period. Growth rates for the Gateshead colony, which is about 15 km from the sea, are comparable with those from Marsden, a coastal colony. Adults are therefore having to make much longer foraging trips, which increases the physical demands on themselves, if they are to maintain a degree of fitness sufficient to obtain an adequate supply of food to meet the energy requirements of the chicks. Further investigation of the Gateshead colony in terms of adult behaviour and biometrics and how they cope with the extra demands imposed by the location of the colony would be of interest.

Table 15

15a Daily growth rates of chicks in area F of the Marsden Bay colony in 1991 (growth rates are in grams per day and are shown for two periods, 18-25 June and 25 June -2 July.)

Outcome is expressed as

the number of chicks fledged . the number of chicks in the brood

eg. 0.2 means that no chicks fledged from a brood of two.

15b Growth rates of chicks in area F of the Marsden Bay colony in 1992. (growth rates are expressed in grams per day and are shown for five periods, 10-17 June, 17-24 June, 24 June-1 July, 1-8 July and 8-15 July).

Table 15a

Ring no.	Growth rate	Growth rate	Outcome
	18-25.6.91	25.6-2.7.91	
A1			0.2
K7	5.7	11.1	
A6	12.9	15.1	2.2
A2	7.9	14.0	
A7	23.0	4.9	2.2
A3	22.7	6.3	
A8	22.1	10.0	2.2
A5	17.0	13.1	
A9	18.1	12.6	1.2
J6		12.6	
J7		9.1	2.3
J8			
K1		15.1	2.2
J9		15.2	
C7		3.3	2.2
C5		16.3	
K0		19.4	1.1
K2		15.9	1.2
K3		12.4	
K4		20.1	2.2
K5		7.9	
K6		20.0	1.2
L2		11.7	0.2
L3			
P3			0.1
K8		16.0	1.2
K9		6.6	
L0		14.0	1.2
L1		13.7	
J4		14.3	2.2
J5		15.1	
C9		18.8	0.2
C6		5.7	
L4		13.4	0.2
L5		10.3	0.2
L7		9.7	0.2
L6		16.8	
L8		16.0	1.2
L9			
C0		13.4	1.2
C3		7.7	
C1		18.8	0.1

Table 15b

Ring no.	Growth rates					No. fledged from brood
	10-17.6	17-24.6	24.6-1.7	1-8.7	8-15.7	
AL	16.3	17.1				2.2
AK	17.6	13.7				
AX	19.4	4.6				1.2
AT	14.3	8.6	7.7			
AB	15.7	12.9				2.2
AC	17.1	8.3				
AS	20.8	15.4				1.1
AU	15.7	20.0				2.2
AW	18.0	14.3				
AF						1.1
AM		16.3				0.2
AD						
AP		12.0	10.6			2.2
AZ		4.6	10.3			
AN		16.3	15.7			1.3
AG						
AA		18.3	6.6	6.0		2.2
AY		15.4	7.1	1.2		
48		8.8	14.6	-8.8		1.2
42		15.1	12.8	4.8	-9.8	
46		6.0	9.4			2.3
47		15.1	12.3			
43		12.3	23.1			2.2
41		17.7	7.1			
44						
45						
49		13.4				0.2
96						
91		15.1				0.3
93		13.4	8.6			
99		7.4	16.3			
BA		14.7				0.2
DZ		14.0				
BB		16.6	8.0	8.6		1.2
BC		16.0	10.0	2.0		2.2
BD		18.3	10.6	5.4		
AE		15.1				2.3
AH		6.6	17.7	0.0	15.7	
AR		9.1	15.7	-1.0	8.6	
CS			8.0			1.2
BH			17.1	10.0		
BG			9.9	15.4		1.2
BE			11.7			
BF			17.4	11.1	6.9	1.1
DT			11.7			0.2
DN			8.6			
DV			22.0	5.4		1.2
BY			10.3			
BW						0.2
BN						
CX						
CG						
CR				14.3		1.2
CA						
CF			13.4	-5.4		1.2

Table 16a

Mean growth rates, in grams per day, of chicks in area F of the Marsden Bay colony, related to date of weighing, in 1991.

Group A1

	Date	
	18-25.6	25.6-2.7
mean growth rate	16.2	10.9
n	8.0	8.0
SD	6.7	3.7
SE	2.4	1.3

Group B1

	Date
	25.6-2.7
mean growth rate	13.4
n	29.0
SD	4.4
SE	0.8

Mean weights, in grams, of chicks in area F of the Marsden Bay colony, related to day of weighing, in 1991.

Group A1

		Date	
	18.6	25.6	2.7
mean wt	165.3	278.2	354.5
n	9.0	8.0	8.0
SD	31.6	43.1	43.5
SE	10.5	15.2	15.4

Group B1

		25.6	2.7
mean wt		151.0	249.6
n		32.0	29.0
SD		54.8	71.6
SE		9.8	13.2

Table 16b

Mean growth rates, in grams per day, of chicks in area F of the Marsden Bay colony, related to clutch completion dates in 1992

Clutch completion date Group A2	13 May	Date	
		10-17.6	17-24.6
	mean growth rate	17.2	12.8
	n	9	9
	SD	2.0	4.8
	SE	0.7	1.6

Clutch completion date Group B2	20 May	Date		
		17-24.6	24.6-1.7	1-8.7
	mean growth rate	13.5	11.7	4.7
	n	20	15	6
	SD	3.9	4.4	2.7
	SE	0.9	1.1	1.1

Clutch completion date Group C2	27 May	Date	
		24.6-1.7	1-8.7
	mean growth rate	11.4	11.3
	n	9	4
	SD	3.6	2.9
	SE	1.2	1.5

Table 16b (continued)
Mean weights, in grams, of chicks in area F of Marsden Bay colony related to clutch completion dates in 1992

Clutch completion date 13 May
Group A2

	Date 10.6	17.6	24.6
mean wt	70.8	189.6	280.7
n	9	11	9
SD	18.8	23.8	39.8
SE	6.3	7.2	13.3

Clutch completion date 20 May
Group B2

	Date 17.6	24.6	1.7	8.7
mean wt	88.5	186.0	275.0	282.3
n	24	22	15	6.0
SD	31.2	40.4	49.1	56.4
SE	6.4	8.6	12.6	22.6

Clutch completion date 27 May
Group C2

	Date 24.6	1.7	8.7
mean wt	120.3	197.0	296.0
n	9	9	4
SD	49.4	49.0	40.3
SE	16.5	16.3	10.0

Table 17

Growth rates, in grams per day, of chicks at Marsden Bay in 1991 and 1992, and at North Shields and Gateshead in 1992.

	Date				
Marsden 1991		18-25 June	25 June-2 July		
n		9	40		
growth rate		16.2	12.8		
SE		2.2	0.7		
SD		6.7	4.2		
Marsden 1992	11-17 June	17-24 June	24 June-1 July	1-8 July	
n	9	34	28	10	
growth rate	17.2	13.0	12.1	7.4	
SE	0.7	0.7	0.8	2.5	
SD	2.0	4.1	5.0	7.9	
North Shields 1992		15-24 June	24-30 June	30 June-7 July	7-14 July
n		12	22	18	11
growth rate		15.1	12.6	11.5	12.9
SE		0.1	1.1	1.2	2.0
SD		1.7	5.0	5.1	6.7
Gateshead 1992	9-14 June	14-21 June	21-28 June	28June- 5July	5-10 July
n	7	19	34	32	10
growth rate	16.0	12.9	12.0	11.9	8.4
SE	3.1	1.0	0.7	1.0	3.3
SD	8.1	4.5	4.1	5.6	10.3

FIGURES 10a and b

10a Mean daily growth rate of chicks hatched at Marsden from clutches completed during 6-13 May 1992, 14-20 May 1992 and 21-27 May 1992, plotted against time (10 June-8 July 1992)

10b Mean weight, in grams, of chicks hatched at Marsden from clutches completed during 6-13 May 1992, 14-20 May 1992 and 21-27 May 1992, plotted against time (10 June-8 July 1992).

Figure 10a

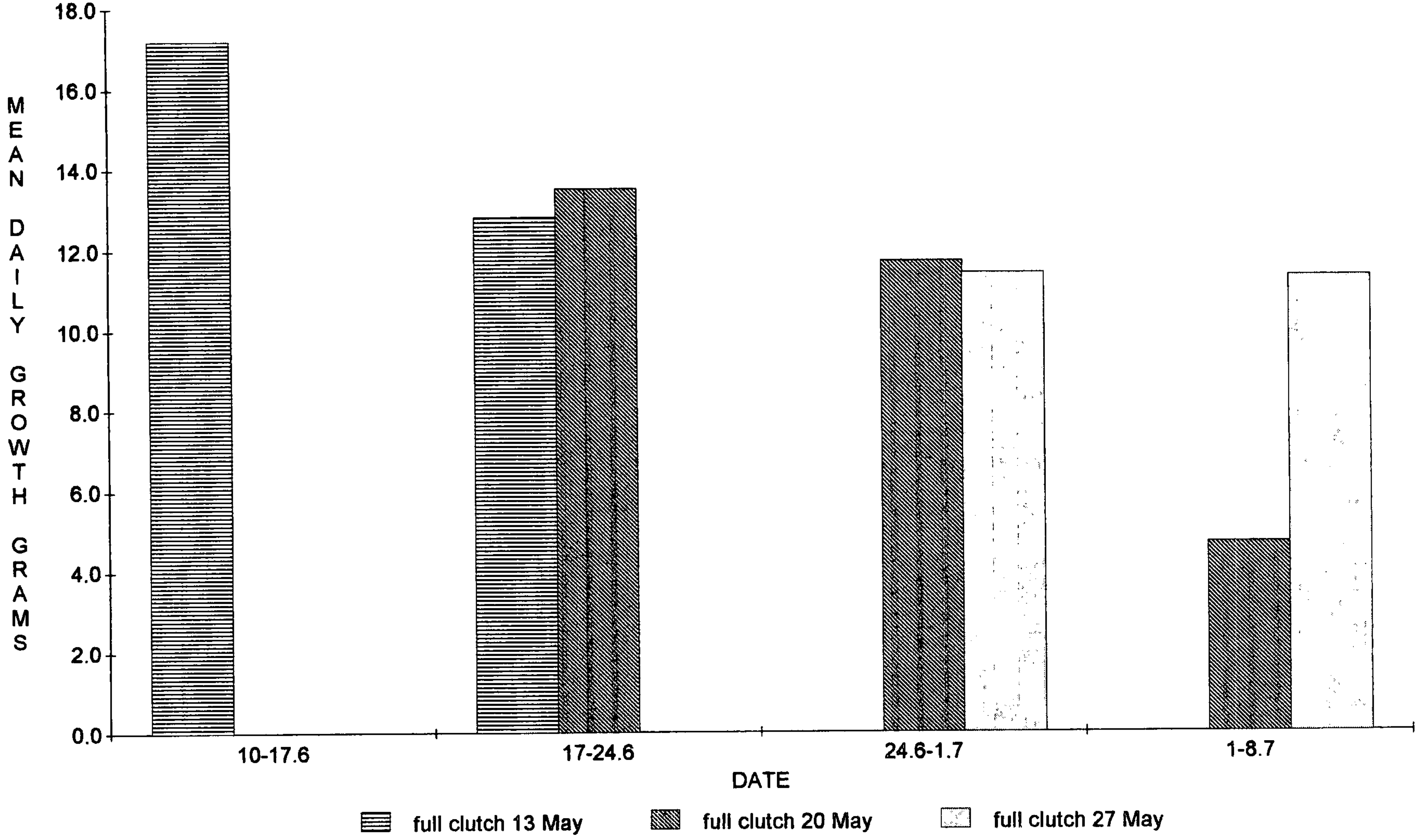
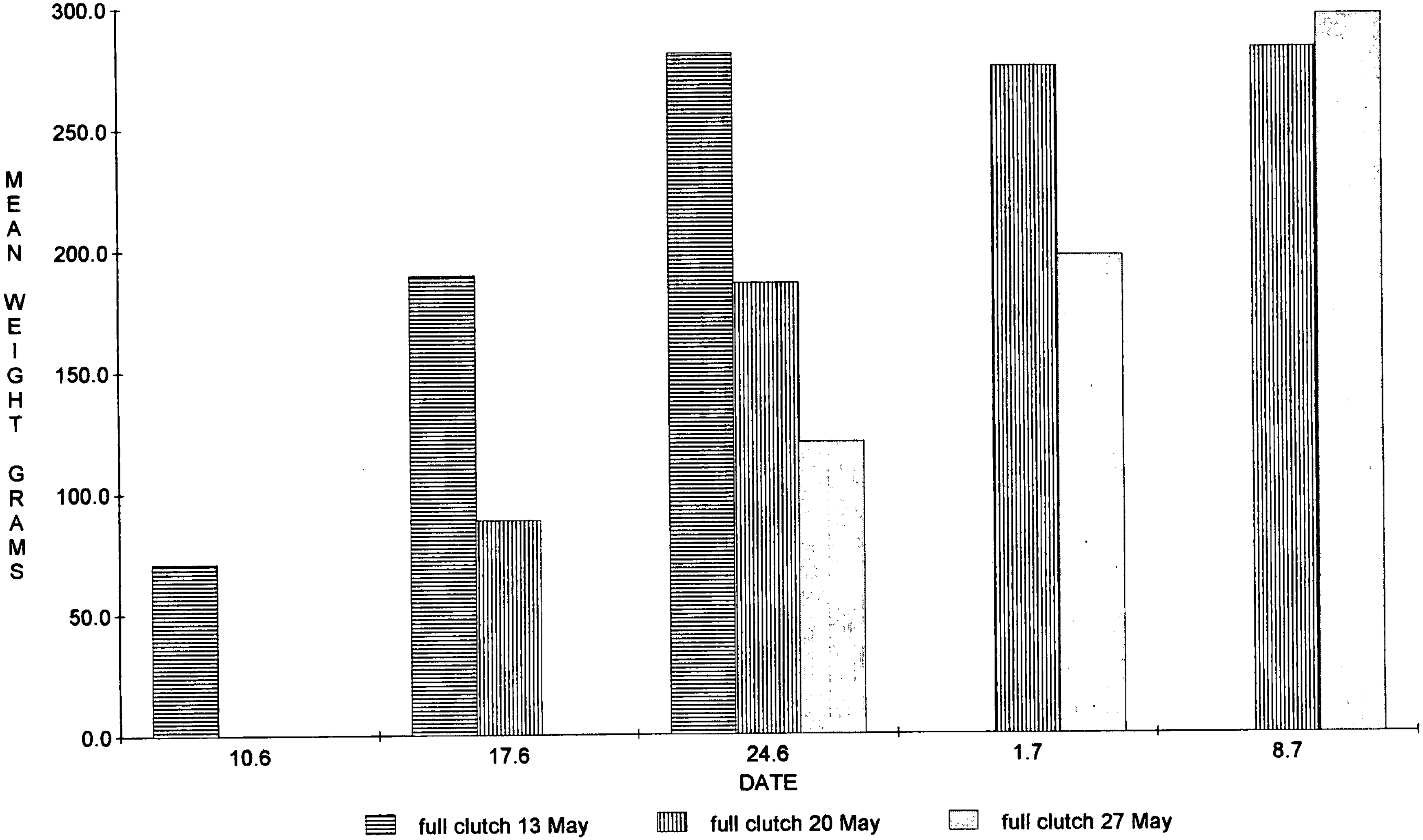

MEAN DAILY GROWTH GRAMS
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
10-17.6
17-24.6
24.6-1.7
1-8.7
DATE
▤ full clutch 13 May
▨ full clutch 20 May
☐ full clutch 27 May

Figure 10b


300.0
250.0
200.0
150.0
100.0
50.0
0.0
MEAN WEIGHT GRAMS
10.6
17.6
24.6
1.7
8.7
DATE
full clutch 13 May
full clutch 20 May
full clutch 27 May

CHAPTER 7

ADULT BIOMETRICS

Results

Weights and head and bill measurements were recorded for the majority of adults caught in area F for ringing during 1990, 1991 and 1992 (Table 18). Mean weights for all adults and males and females separately are shown in Table19. Data for head and bill measurement (arbitrarily designated x) was plotted against weight (arbitrarily designated y), (Figure 11a), for all birds weighed in May, June and July 1990-1992, to investigate the relationship between these biometrics. A regression analysis, using the least squares method was performed, for each month separately and all months combined, followed by a calculation to measure the significance of the regression lines. This showed a positive relationship between head and bill measurement and weight, for all months combined. This relationship was also statistically significant ($t = 11.1$, d.f. 104, $P<0.01$) and is described by the regression equation, $y = -438.8 + 8.79x$. Similar positive relationships existed for the data from May, June and July separately, although the relationship for May was not statistically significant. The regression equations and levels of significance are as follows :-

May $y = -536.29 + 9.91x$

$t = 1.23$, $n = 6$, d.f. 4, not significant

June $y = -399.4 + 8.47x$

$t = 5.69$, $n = 35$, d.f. 33, $P<0.01$. significant.

July $y = -322.7 + 7.52x$

$t = 8.52$, $n = 65$, d.f. 63, $P<0.01$. significant.

Figure 11b shows regression lines for males and females separately in June and July 1990-1992.

The regression equations and levels of significance for males and females separately, in 1990-1992, are as follows:-

June males $y = -747.0 + 12.2\,x$

$t = 3.5$, $n = 22$, d.f. 20, $P<0.01$. significant.

females $y = -1604.1 + 22.4\,x$

$t = 6.1$, $n = 8$, d.f. 6, $P<0.01$. significant.

July males $y = -578.2 + 10.1\,x$

$t = 3.3$, $n = 16$, d.f. 14, $P<0.01$. significant.

females $y = -223.3 + 6.28\,x$

$t = 2.35$, $n = 32$, d.f. 30. significant

Considering the data for all adults, Figure 11a, demonstrates that for any given head and bill measurement, the weight of that bird would be expected to decrease from May to June to July. May and June weights are heavier, and July weights lower than the mean for all months.

The data plotted separately for males and females, Figure 11b, similarly shows that, except at the lower end of the female head and bill range, June weights exceed July weights for a given head and bill measurement.

Adult re-weights were obtained for 4 birds in 1992. On head and bill measurements, 3 were males, the other was probably male. In all 4 birds, the initial weight recorded was the heaviest. The weights subsequently obtained all showed that a weight loss had occurred, over periods ranging from one to five weeks.

Data on adult weights from other colonies and geographical areas are shown in Table 21. This table includes data on birds from Norway, Russia and Newfoundland. These birds from northern latitudes are larger than our own birds which is to be expected and the figures are consistent with Bergmann's Rule.

Discussion

Although birds were generally caught on nests it was not known whether all the birds were breeders. Some may have been prospectors, visiting the cliff and nests in area F. Birds which had not experienced the rigours of chick rearing may as a result be heavier than breeding birds. This would produce a distortion in the mean weights, which if we assumed we were dealing only with breeders, would suggest a mean weight greater than was the case in reality.

The data and the regression analysis shows that the greater the head and bill measurement the heavier the body weight of the adult Kittiwake. It has already been demonstrated by Coulson *et al.* (1983) that adult gulls, Laridae, can be sexed on head and bill measurements. On the basis that adult male Kittiwakes generally have head and bill measurements greater than those of females, it can be seen from the data above that adult males have a tendancy to be heavier.

In addition, both males and females show a tendancy to lose body weight during May-July. Small birds of both sexes are affected less than larger birds, Small females however are noticably less affected than small males. The stress of breeding, incubating and feeding themselves and their chicks being a possible reason for the weight loss. Coulson and Wooller (1984) demonstrated that overall females performed 54% of incubation in their study at North Shields. The males did on occasion show less consistent attendance patterns and this was compensated for by the females. However the resulting variations in attendance give no indication as to the cause of the differences in amount of weight loss in males and females during incubation.

This loss of weight over the breeding season may be normal and not, for example, indicative of food shortage. Alternatively it could suggest limited food availability in 1990-1992. Shortage of food may manifest itself initially through adult weight loss before it affects the chicks directly. The adults acting as a buffer between shortage of food and the well-being of the chick.

Table 18

Biometrics of adult Kittiwakes in area F of the Marsden Bay colony during 1990-1992

H & B - Head and bill measurement in millimetres

Weight - weight in grams

Males (M)- head and bill measurement 92mm or greater

Females (F)-head and bill measurement 89mm or less.

1990

	H & B	Weight	Sex		H & B	Weight	Sex
03/07	85	310	F	**12/07**	86	288	F
	91	340			88	338	F
	92	360	M		89	324	F
	94	310	M		90	344	
	92	360	M		89	320	F
	89	340	F		88	286	F
	89	360	F		86	316	F
	87	330	F		90	368	
	92	330	M		92	360	M
					89	328	F
					89	306	F
					93	358	M
					90	346	
					86	342	F
					94	374	M
					88	324	F
					94	384	M
					86	304	F
					89	294	F
					88	330	F
					93	372	M
					88	314	F
					88	306	F
					94	394	M
					86	296	F
					88	360	F
					89	326	F

1991

	H & B	Weight	Sex		H & B	Weight	Sex		H & B	Weight	Sex
18/06	86	322	F	**25/06**	92	384	M	**02/07**	92	348	M
	90	320			90	335			89	358	F
	92	385	M		90	334			92	348	M
	95	398	M		88	330	F		91	358	
	89	362	F		94	354	M		96	404	M
	94	420	M		95	410	M				
	92	384	M		92	366	M				
	96	420	M		95	450	M				
	94	398	M								
	87	340	F								

1992

	H & B	Weight	Sex		H & B	Weight	Sex		H & B	Weight	Sex
13/05	89	304	F	**20/05**	94	385	M	**10/06**	90	400	
	94	384	M		94	381	M		91	346	
	92	396	M		91	420			92	360	M
									95	384	M
									88	394	F
									88	368	F
									88	382	F
									88	354	F
									95	460	M

Table 18 (continued)

	H & B	Weight	Sex		H & B	Weight	Sex		H & B	Weight	Sex
17/06	93	394	M	01/07	92	372	M	08/07	91	384	
	96	430	M		91	350			94	386	M
	94	404	M		93	352	M		96	384	M
	94	370	M		88	348	F				
	93	414	M		85	298	F	15/07	94	382	M
	93	384	M		96	378	M		91	346	
	95	394	M		91	338					
	92	372	M		91	316					
					95	386	M				
					92	322	M				

FIGURE 11a

Head and bill measurements plotted against weight for adult Kittiwakes captured for ringing in area F of the Marsden Bay colony during May, June and July 1990, 1991 and 1992.

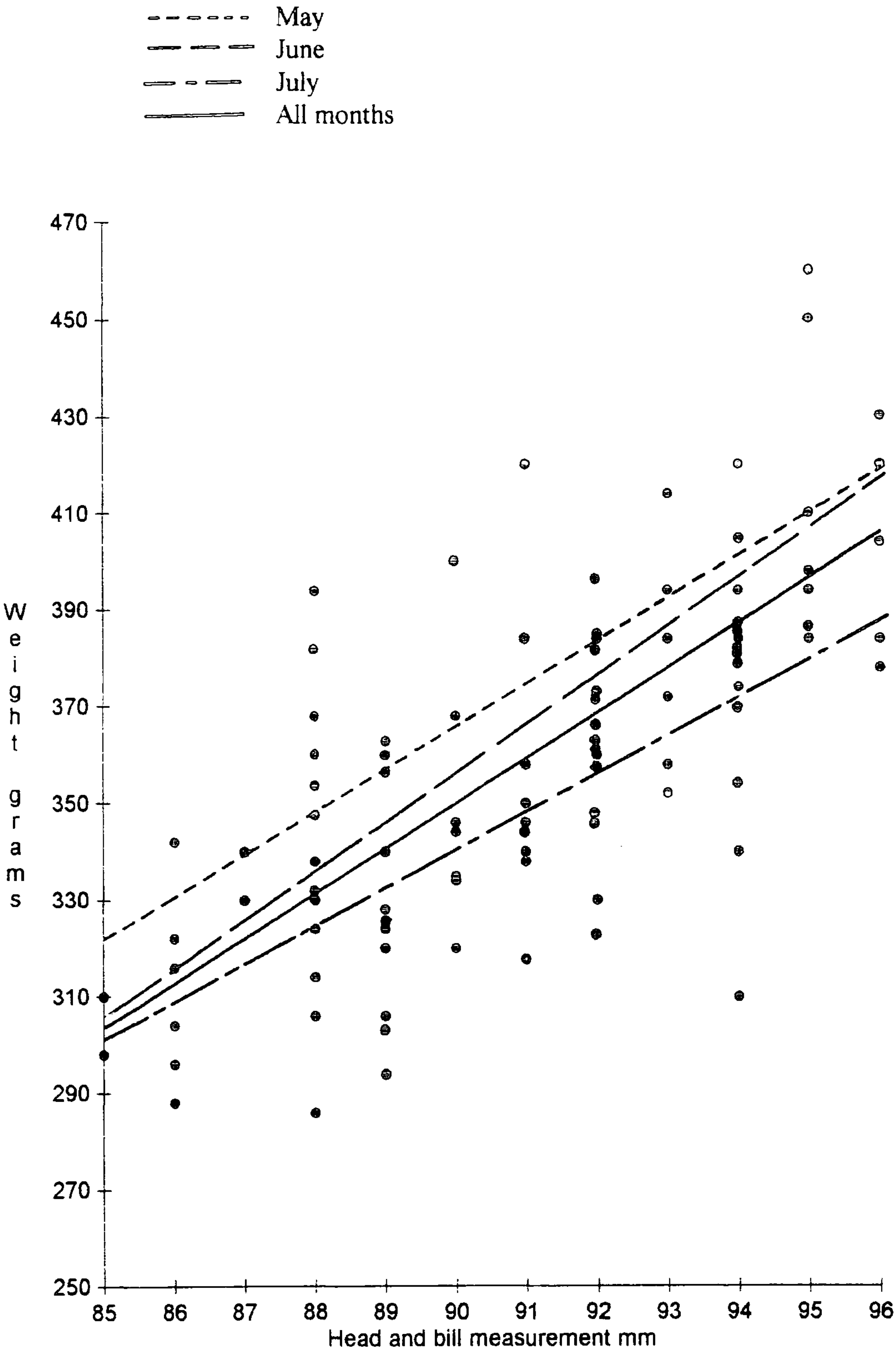


FIGURE 11b

Head and bill measurements, for female (85-89mm) and male (92-97mm) Kittiwakes plotted against weight. The birds were caught for ringing in area F of the Marsden Bay colony in June and July 1990-1992.

— — June

— - — - July

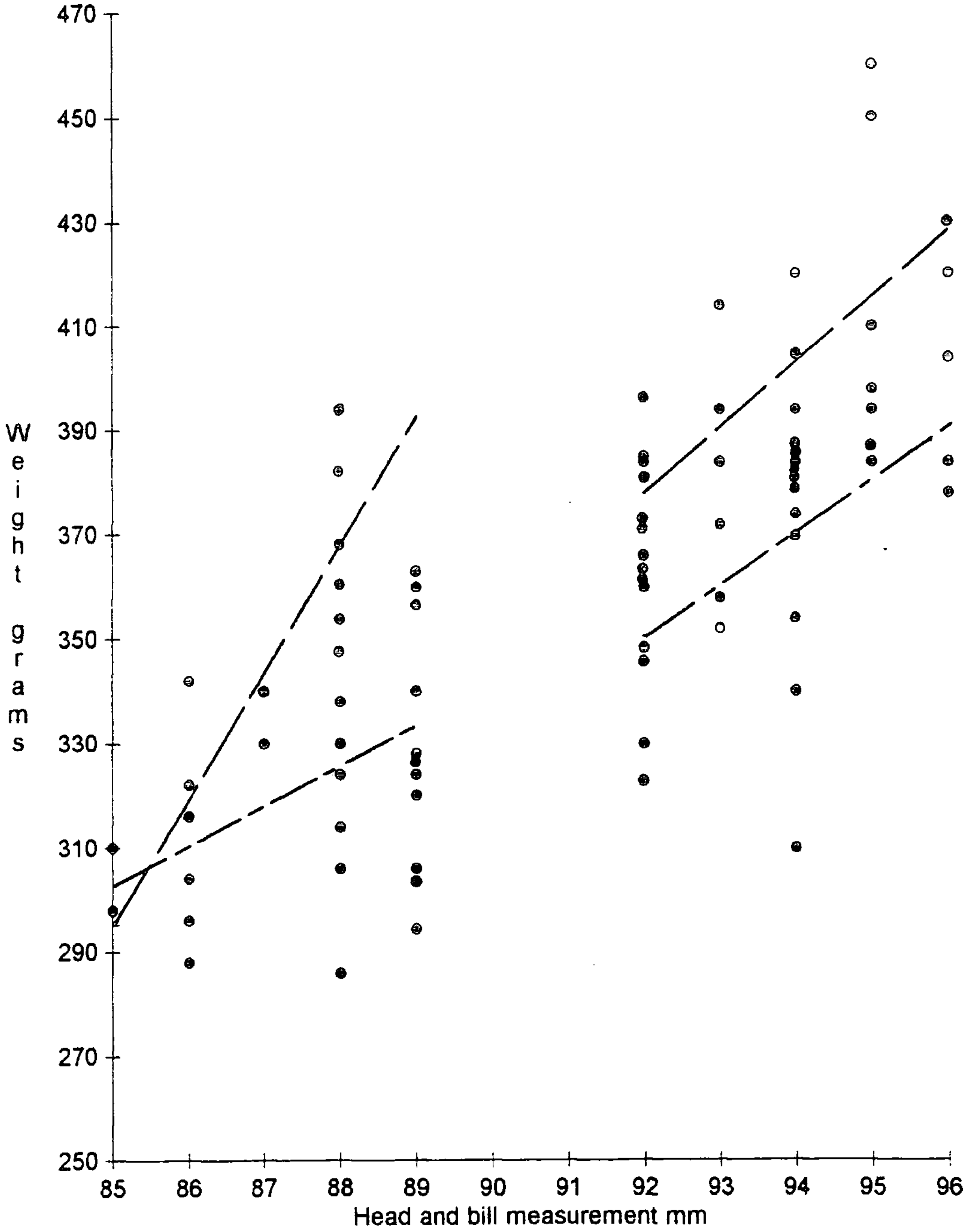


Table 19

Weights, in grams, of adult Kittiwakes in area F of the Marsden Bay colony during 1990 - 1992.

Date	n	mean wt.	SD
03/07/90	16	347	31
12/07/90	31	336	32
11/06/91	8		
18/06/91	10	375	37
25/06/91	8	370	42
02/07/91	5	363	23
13/05/92	3	361	50
20/05/92	3	395	22
10/06/92	9	384	34
17/06/92	8	395	21
01/07/92	9	346	30
08/07/92	3	385	1
15/07/92	2	386	26
Summary			
1990	47	340	32
1991	23	371	36
1992	37	375	33

Mean weights of adults, in grams, arranged by sex and date.

Date	n male	mean wt.	SD	n female	mean wt	SD
03/07/90	4	360	22	8	342	33
12/07/90	7	380	20	21	319	20
	11	372	22	29	325	26
18/06/91	6	401	16	3	341	20
25/06/91	5	393	38	1	330	
02/07/91	3	367	32	1	358	
	14	391	30	5	342	17
13/05/92	2	390	9	1	304	
20/05/92	2	383	3			
10/06/92	3	401	52	4	375	17
17/06/92	8	395	21			
01/07/92	5	362	26	1	298	
08/07/92	2	385	1			
15/07/92	1	382				
	23	386	27	6	350	40

Table 20

Weights of four adult Kittiwakes, in grams, where at least two weights were obtained for the same bird in 1992. Weight loss per day between first and last weighing is shown.

	20/05/92	11/06/92	17/06/92	01/07/92	08/07/92	15/07/92	Weight loss
1	420	376					6.28g/day
2			366			348	0.64g/day
3		460		428		412	1.37g/day
4				382	380		0.29g/day

Table 21

Mean weights, in grams, of adult Kittiwakes from several geographical areas.

Weight	*n*	*Site*	*Source*
360	107	Marsden	this study
354	57	North shields	Coulson and White 1958
368	470	North Shields	Coulson and Thomas 1985
350	23	Farne Islands	Pearson 1968
375		West Norway	Barrett and Runde 1980
375		North Norway	Barrett and Runde 1980
407		Northern Russia	Belopol'skii 1961
437		Newfoundland	Maunde and Threlfall 1972

Sites
Marsden - Marsden Bay, Tyne and Wear
North Shields - North Shields, Tyne and Wear
Farne Islands - Farne Islands, Northumberland.

CHAPTER 8

ADULT ATTENDANCE DURING CHICK REARING

Results

In 1991, non-attendance by both adults at nests with chicks was first noted on 25 June in area G3. During the remainder of June and throughout July there were low levels of non-attendance, but few broods were being left (Table 22, Figure 12a). The mean size of broods left unattended varied erratically between 1.5 and 2.0 chicks up to 21 July. Subsequently the mean unattended brood size was between 1.0 and 1.3 chicks. On only two occasions, 27 and 28 July, was the mean size of attended broods (1.11 and 1.02 chicks respectively) less than the mean brood size of unattended broods (1.19 and 1.11 chicks respectively).

In 1992 non-attendance by adults was first noted on 15 June in colony G3. Few broods were being left until 29 June when larger scale non-attendance was noted in areas A, A1, D, G1 and G3 (Table 22). Differences in the mean size of broods, unattended and attended, were slight (Figure 12b) and not as pronounced as in 1991. Mean attended brood size data were available for all areas on 10 July 1992. The mean sizes of non-attended broods were also available for 10 July 1992 in areas G1 and G3, and for 11 July 1992 in areas A, A1, B and D. Except in the case of area G1, the mean size of unattended broods was in excess of the mean attended brood size. This also suggests that brood size is a factor in influencing attendance by adults at the nest. Additional supporting data are presented in Table 23. On all but a few late July dates, the mean size of unattended broods is in excess of 1.5 chicks. A value of 1.5 chicks is achieved if equal numbers of broods of one and two were involved. If more broods of one were involved, the figure would fall below 1.5, if there are more broods of two, the figure exceeds 1.5.

In only two areas was the difference between unattended brood size and mean attended brood size statistically significant. In area A1, the mean unattended brood size was significantly larger than the mean attended brood size on that day ($z = 2.08$,

$P<0.05$). In area G3, a similar significant relationship existed ($z = 2.89$, $P<0.01$). In the other areas the differences were not statistically significant.

The age of many unattended chicks was recorded in 1992, between 15 June-22 July. A total of 706 chicks, left unattended, were assessed for age, mainly on plumage features (Maunder and Threlfall 1972). The results are shown in Table 25 and Figure 13. Few chicks less than 10 days old were left unattended, less than 5% of those observed.

Discussion

From mid July some chicks are fledging, there is movement of fledged chicks between nests, and adults often stand-off from their nests. The data may therefore reflect the influence of these factors on adult attendance at the nest site. These factors are different from that commonly suspected of influencing adult attendance earlier in the chick-rearing period, ie. availability of food. The data available from Marsden Bay suggests that brood size may be a factor in influencing attendance by adults. Larger broods, ie. broods of two, being more likely to be left than smaller broods, ie. broods of one.

In 1992, there was little difference in mean size of attended and unattended broods. However for most of the observation period the mean size of unattended broods was slightly higher than that for attended broods. Less data were available for 1992 but the period covered was approximately the same.

There is therefore no conclusive evidence from my data that broods of two were being left unattended more often than broods of one, although there is some suggestion that this may be the case.

Wanless and Harris (1992) in an investigation of this behaviour on the Isle of May showed that the frequency of non-attendance in broods of two was significantly higher than for broods of one. The data from Marsden Bay also suggests that larger broods are being left more frequently. The data for 1991 showing this more clearly. Although the abandonment of a brood appears to increase the risk of predation, Wanless and Harris (1992) had little evidence of predation on these un-attended chicks. Similarly, at Marsden, there was no evidence of avian predation of chicks in the nest, although Herring Gulls *Larus argentatus* would readily take chicks which had fallen from the nest or which had left the nest prematurely and were floundering on the beach. In area F, my main study area, there was predation, but not apparently by Herring Gulls . It may be that rats, *Rattus* sp, were involved as they were seen in the vicinity, and some of the nesting ledges appear accessible to them. In a recent analysis of data collected in 1968-1974 at North Shields (Coulson and Johnson 1993, in press) much variation was found between the behaviour of individual adults regarding nest attendance. This was at a time when there was no indication of food shortage and breeding success was high. Relating chick neglect to factors other than differences in adult behaviour and fitness of adults for the task of breeding is very difficult (Coulson and Johnson 1993, in press).

At Marsden in 1992, among older chicks, chick size and hence overcrowding may have been a factor in adults leaving the nest unattended. However, in this case one would assume that the adult would be on a nearby ledge for much of the time and not away foraging for food at sea. There was no evidence that adults were nearby but this may have been the case. In the 36-40 day group, the chicks would be at an age when fledging would have been possible and may have occurred. Adult attendance would then become more erratic, as it is not unusual for large chicks, nearing fledging, to be occasionally left unattended (Barrett 1978). Again adults may be standing on a nearby ledge, but with care these birds can be identified when making observations.

Coulson and Johnson (1993, in press) have calculated that a single spot observation per day leads to a delay of 10.54 days in observing the first desertion by both adults. This would suggest that many of the chicks in the 11-20 day range, which were observed unattended at Marsden, would in reality have been left at an earlier age. Few chicks in the age range, 0-10 days recorded as being left unattended at Marsden Bay, less than 5% of the total number of unattended chicks observed. Coulson and Johnson (1993, in press) recorded no chicks younger than about 8 days being left by both parents. As chicks are not homeothermic until at least 6-8 days after hatching (Barrett 1978), it is particularly important that an adult should be present at all times. At this age they would also be particularly vulnerable to predation. Wanless and

Harris (1989) in a three year study on the Isle of May found that chick neglect coincided with the majority of young reaching 21-28 days of age. But Wanless and Harris (1992) first noted unattended broods in 1989 and 1990 about 14-21 days after the main hatching period, although they do not give chick ages. They state that this, plus the fact that broods of two were almost twice as likely to be left as single chicks, suggests strongly that chick neglect was related to the increased energy demands of the chicks. Wanless and Harris (1989) suggest neglect commences when chicks are 3-4 weeks old and nearing fledging. The demand for food by chicks increases with their age (Coulson and Pearson 1985, in Coulson and Porter 1985) so the effect of food shortage on adult attendance would manifest itself later rather than sooner in the chick rearing period. Barrett and Runde (1980) in their Norwegian study area, observed high levels of non-attendance midway through the nesting period in 1977 when breeding success was low. In addition, Wanless and Harris (1992) state that the incidence of unattended broods has also been a feature of the recent Kittiwake breeding failures in Shetland. The younger age of neglect at Marsden in 1992 suggests that problems with food supply occurred earlier in the breeding season than on the Isle of May. Wanless and Harris (1992) suggest that the level of non-attendance in 1990 on the Isle of May, was a contributory factor in the poor number of chicks fledged per nest, 0.17 + 0.04, the lowest value for at least 10 years. If the adults were experiencing difficulty in obtaining food at Marsden, they apparently managed to overcome the problem and continued to supply the energy requirements of their chicks and themselves. Growth rates of chicks at Marsden were about 20% lower than those reported by Coulson and White (1958) and Coulson and Porter (1985) for the nearby colony at North Shields, covering periods when there was no evidence of food shortage. At Marsden this may reflect a less than adequte food supply to the chicks. However there was little difference in growth rates between 1991 and 1992, although chick neglect was more pronounced in 1992. Breeding success between years was the same. Chicks, although fledged, may subsequently have a reduced chance of survival in their first autumn and winter if the fledging weight and body condition are below normal (Coulson and Porter 1985).

Galbraith (1983) found that broods which were left overnight received more feeds as compensation the following morning compared with those broods where an adult had been in attendance throughout. It does not follow therefore that low attendance by adults at the nest, invariably means reduced food supply for the chicks. There is no evidence from Marsden to contradict this conclusion.

Table 22

Numbers of broods of one, two and three chicks left un-attended by both adults and those attended by at least one adult in areas G1 and G3 combined, in the Marsden Bay colony between 25 June-28 July 1991 and 26 June-22 July 1992. The total number of broods in each category and mean brood sizes on each day are also shown

Date	Un-attended					Attended				
1991	B/1	B/2	B/3	Total	Mean	B/1	B/2	B/3	Total	Mean
25/06	1	4	0	5	1.80					
26/06	2	2	0	4	1.50					
27/06	0	3	0	3	2.00					
01/07	6	10	0	16	1.75	84	81	0	165	1.49
03/07	2	5	0	7	1.71	89	90	1	180	1.51
05/07	5	9	0	14	1.64	84	92	1	177	1.53
06/07	2	3	0	5	1.60	94	93	3	190	1.52
07/07	1	4	0	5	1.80	97	90	3	190	1.50
08/07	1	8	1	10	2.00	97	86	2	185	1.49
09/07	3	9	9	21	1.75	95	85	3	183	1.50
10/07	3	4	0	7	1.57	96	89	3	188	1.50
11/07	1	2	0	3	1.66	97	93	3	193	1.51
12/07	0	1	0	1	2.00	63	53	3	119	1.49
16/07	0	3	0	3	2.00	102	84	3	189	1.48
17/07	2	3	0	5	1.60	95	83	3	181	1.49
18/07	4	4	0	8	1.50	94	87	3	184	1.51
19/07	1	7	1	9	2.00	100	78	2	180	1.46
20/07	11	11	0	22	1.50	94	67	3	164	1.45
21/07	2	5	0	7	1.71	105	60	2	167	1.38
23/07	2	1	0	3	1.33	123	41	1	165	1.26
24/07	1	0	0	1	1.00	113	28	1	142	1.21
26/07	5	0	0	5	1.00	98	16	0	114	1.14
27/07	13	3	0	16	1.19	78	10	0	88	1.11
28/07	8	1	0	9	1.11	51	1	0	52	1.02
Date 1992										
26/06	3	7	0	10	1.70	37	90	3	130	1.74
03/07	13	12	1	26	1.54	68	97	3	168	1.61
05/07	19	30	2	51	1.66	59	75	3	137	1.59
10/07	37	38	2	77	1.55	92	82	3	177	1.45
17/07	50	36	3	89	1.47	102	68	3	173	1.43
22/07	96	37	2	135	1.30	110	41	2	153	1.29

Table 23
Mean number of chicks in broods left un-attended by both adults in areas of the Marsden Bay colony in 1992.

			Area				
Date	A	A1	B	D	G1	G3	G1 & G3
15/06					0.00	1.50	1.50
17/01					0.00		
21/06	2.00	2.00	2.00	1.62	1.90		
26/06	2.10		1.33		1.60	1.80	1.70
29/06	1.64	1.64		1.74	1.63	1.72	1.67
30/06		1.57			1.79	1.78	1.84
03/07	1.79	1.68	1.47	1.62	1.50	1.56	1.54
04/07	1.77	1.62	1.80	1.76	1.54	1.77	1.66
05/07	1.69	1.55	1.78	1.76	1.64	1.69	1.66
06/07					1.74	1.56	1.61
10/07					1.46	1.62	1.55
11/07	1.66	1.65	1.64	1.71			
16/07					1.61		
17/07						1.37	1.47
22/07					1.29	1.32	1.30

Mean number of chicks in attended broods on 10 July 1992 (data in Table 24).

1.56	1.45	1.43	1.47	1.49	1.49	1.49

Table 24

Brood sizes in a selection of randomly chosen nests in areas of the Marsden Bay colony on 10 July 1992

Area	AOS	AOS with chicks	No. of chicks	Brood size				Chicks per		% AOS with chicks
				0	1	2	3	AOS	AOS with chicks	
A	81	57	89	24	26	30	1	1.10	1.56	69
A1	63	49	71	14	27	22	0	1.13	1.45	78
B	53	44	63	9	26	17	1	1.19	1.43	81
D1	59	50	78	9	22	28	0	1.34	1.56	85
D2	70	54	75	16	35	17	2	1.07	1.39	77
D3	72	58	87	14	30	27	1	1.21	1.50	81
D4	36	26	39	10	13	13	0	1.08	1.50	69
D5	60	45	70	15	21	23	1	1.17	1.55	75
D6	49	38	55	11	21	17	0	1.12	1.48	78
D7	60	43	64	17	22	21	0	1.07	1.49	72
D8	30	22	26	8	18	4	0	0.87	1.18	73
F	59	34	49	25	19	15	0	0.83	1.44	58
F1	39	24	38	15	10	14	0	0.97	1.58	61
G1	112	86	128	25	42	44	0	1.14	1.49	77
G3	115	94	140	21	51	40	3	1.28	1.49	82

Table 25

Age of chicks (in days) which were observed as being un-attended by both adults at Marsden Bay in1992.
***A total of 706 instances of chicks being temporarily abandoned* were recorded between 15 June - 22 July.**

Age	No.	Percentage of total.
1-10	34	4.8
11-20	240	34.0
21-30	184	26.1
31-40	248	35.1
All	706	100

FIGURES 12a and b

Mean brood sizes for attended and un-attended broods in areas G1 and G3 combined in the Marsden Bay colony.

a during 25 June-28 July 1991

b during 26 June-22 July 1992

Figure 12a

1991

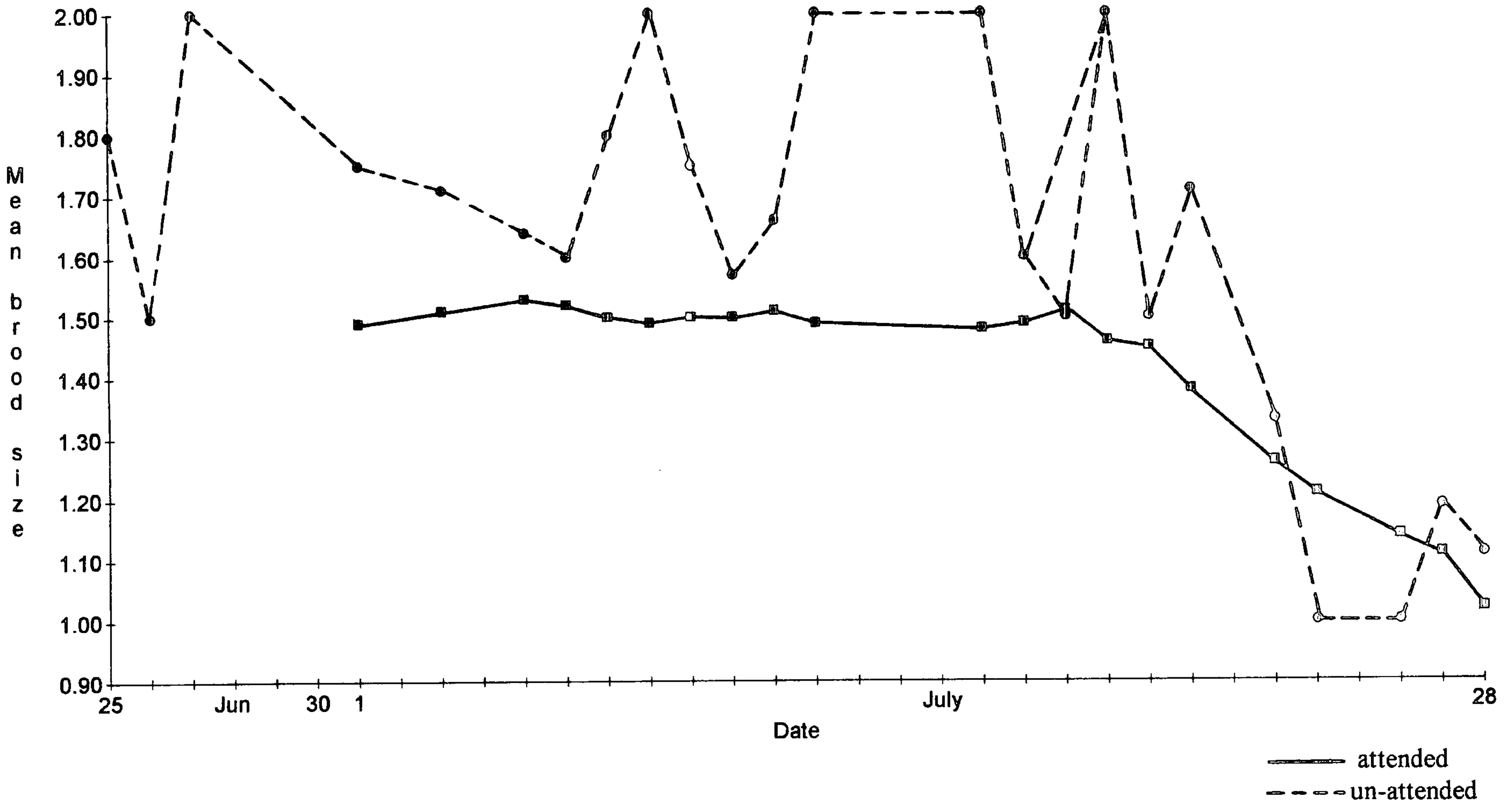


Figure 12b

1992

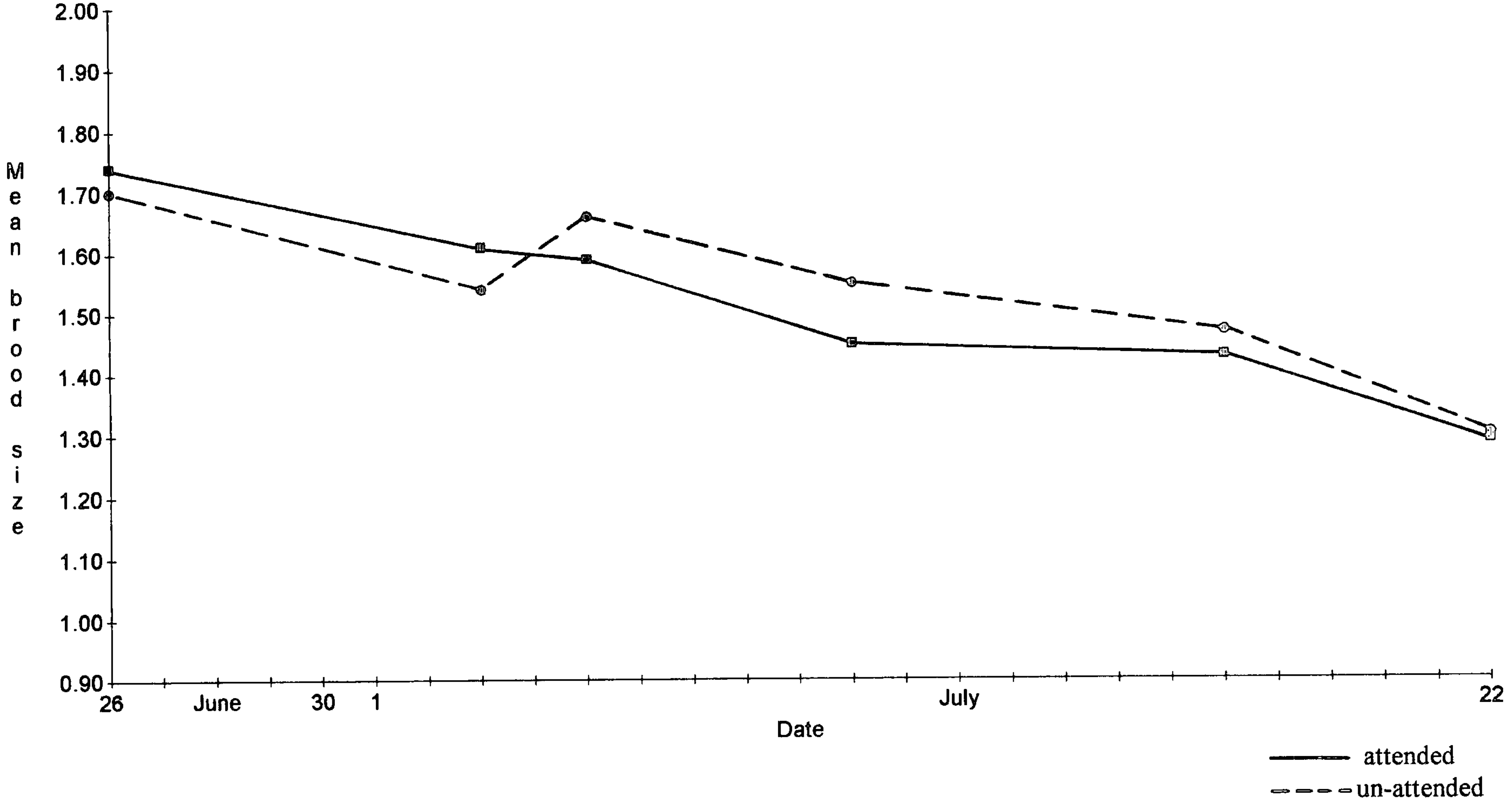
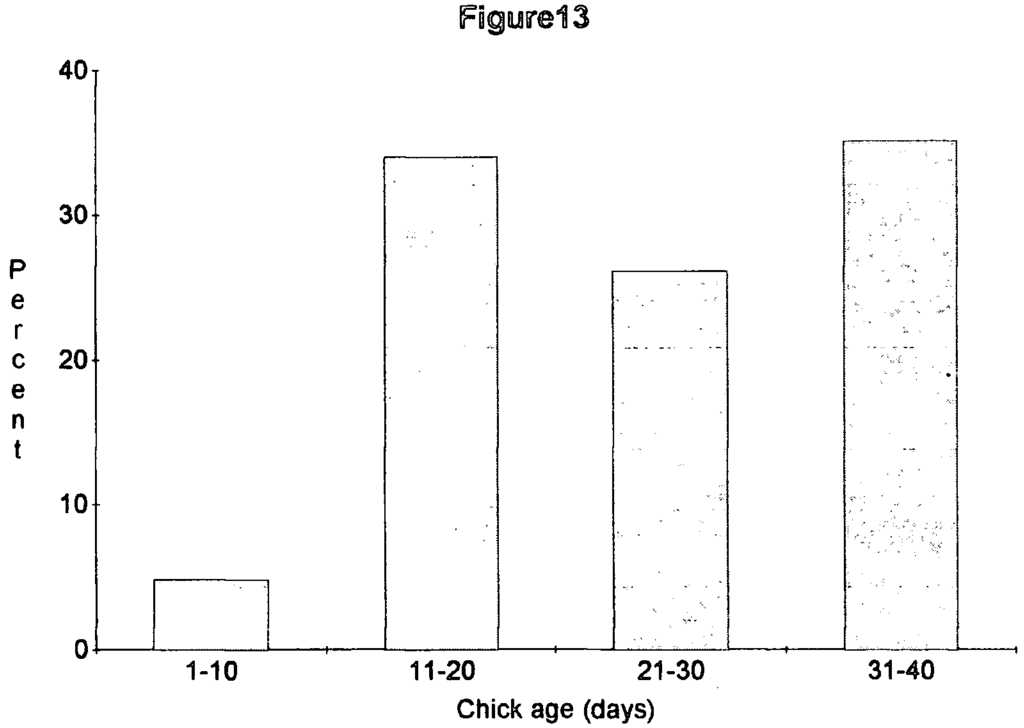


FIGURE 13

The number of chicks, in 10 day age bands, left un-attended by both adults, expressed as a percentage of the total number of chicks observed as being un-attended, during the period of 15 June - 22 July 1992. Observations were made variously in areas A, A1, B, D, G1 and G3.



CHAPTER 9

DISCUSSION OF THE PAST AND PRESENT BREEDING BIOLOGY OF THE KITTIWAKE AT MARSDEN.

The breeding biology of the Kittiwake at Marsden during 1953-1992 is summarized in Table 26. Additional data from the nearby North Shields colony have been included and are indicated, where data from Marsden were not available. The extra data are used in the following discussion.

Changes in the breeding biology during 1953-1992 are :-

1. A later date for annual return of adults to the colony.
2. A shorter period during which initial annual recolonisation occurs compared to the 1950s, but longer than in the 1970s.
3. 50% occupancy of nest sites by adults was later than in the 1970s and slightly later than in the 1950s.
4. 50% of nests (area F) with eggs 15 days earlier than in the 1950s.
5. Chick growth rates less than in the 1950s and 1970s at North Shields.
6. The number of chicks fledged per brood is less than in the 1970s.
7. Chick neglect much more frequent in 1992 than in the 1950s and 1970s.
8. Adult annual survival rate higher.
9. Adults and newly fledged young, separately, have an earlier and more synchronous departure in the autumn.

Little or no change has occurred during 1953-1992 in :-

1. Mean date of laying.
2. Mean clutch size.
3. Hatching success.

The Kittiwake colony at Marsden Bay was formed in 1931 (Temperley 1951). The first nest count recorded was 308 in 1937 (Grey 1937). Over the next 56 years the number of nests increased to 5768. The rapid increase in the number of nests continued until the early 1970s (Coulson and White 1960, Dixon 1979). The increase in nest numbers then slowed, the number remaining relatively constant in the years 1974-1977

(Dixon 1979). Since the late 1970s the number of nests increased by 27% to the 1992 total. Another period of relative stability may now be occurring (Chapter 3).

However, the total nest count for the colony masks changes taking place on a smaller scale within the colony. The areas colonised in the 1930s and 1940s are now showing a decrease in the number of nests probably for geological reasons. Areas colonised in the 1950s are still showing signs of increase, in part due to a favourable cliff structure. It is important, when investigating population size, even in colonies occupying a relatively small area, to look at these small scale changes and the reasons for them, if one is to attempt an understanding of factors affecting the breeding biology of birds (Chapter 3).

Changes have occurred since the 1950s in both the timing of the adults return to the colony each year and the departure of adults and fledged chicks in the post breeding autumn dispersal. They now arrive later and leave earlier. The effect of these changes is to reduce the length of time that the adults spend at the colony. In the 1950s the attendance by some birds was as long as 8 months and in some cases up to 10 months, currently it is about 6 months. The Kittiwakes therefore have a longer pelagic period each year, away from the colony. This contrasts with the Fulmar, which now spends large proportion of the year at the breeding site.

The time of initial annual recolonisation of each area of the Marsden colony varies much less now than in the 1950s (Coulson and White 1956), but a little more now than in the 1970s (Dixon 1979). The process extended over 5 or 6 weeks forty years ago, now it is compressed into less than half that time. In the 1970s, no more than one week separated the different areas of the colony. Similar changes have occurred in the achievement of 50% occupancy, in individual areas of the colony. In the 1950s, the period, after initial annual recolonisation, required to achieve 50% occupancy, varied from 4-8 weeks, in the 1970s it was less than 3 weeks and in the 1990s, less than 4 weeks. The sequence in which different areas of the colony were reoccupied each year varied during 1991-1992, but was less regular and ordered than that recorded in the 1950s (Coulson and White 1960) and 1970s (Dixon 1979). Kittiwakes, although initially arriving later in the spring, reoccupy all areas over a shorter period of time than in the 1950s and achieve 50% occupancy of the whole colony more quickly. The result is that

50% occupancy is achieved at about the same time now, early March, as it was in the 1950s. By contrast, in the 1970s, birds arrived early in January, all areas were initially recolonised within a few days, and 50% occupancy had been achieved before the end of January. There appears to have been a much greater sense of urgency in that period to establish possession of nest sites. Although the adult survival rate at the time was high, at up to 85% (Coulson and Thomas 1985), it is comparable with the current level. A large number of birds surviving the winter and subsequently returning to the colony would not seem therefore to be an explanation for this marked difference. Coulson and Thomas (1985) drew attention to the changes which had occurred in North Sea Herring stocks and how these could be tentatively linked with the changes they observed in the breeding biology of the Kittiwake at North Shields. The mid-1970s marked the low point in the stocks of Herring and this coincides with the early return of Kittiwakes to Marsden. The Herring is an important food fish for the Kittiwake during the winter and early spring. Shortage of food, offshore from the colony, may have encouraged a return to inshore waters, to either seek an alternative food supply, in the form of early Sandeels *Ammodytes*, or to establish themselves in the colony before the effects of food shortage reduced their ability to do this effectively. An equally early return to the colony in the 1950s, when Herring stocks were high, may not be too contradictory, as the period of return was very much longer than that in the 1970s. A later return in the 1990s, may be compensated for by the relatively quick recolonisation process, resulting in achievement of 50% occupancy by a time comparable with that in the 1950s,

Over the years, the Marsden Bay colony has become more homogenous and differences between areas of the colony, for example in terms of nest density, are less marked than those observed by Coulson and White (1956) and Dixon (1979). Area F, was shown by Coulson and White (1960) to be a low density area, in which the achievement of 10% and 50% of nests with eggs lagged, on average, 15.5 days behind the highest density area, area A. These milestones, in area A, were achieved by 10 May and 23 May respectively. Area F, in 1992, had a similar nest density to that of area A in the 1950s. In 1992, 10% of nests in area F had completed clutches by 13 May and 50% had clutches by 20 May. The similarity in these dates also reflects the change towards a more uniform pattern of breeding in the colony, as the differences in nest density and time of annual reoccupation between areas has been reduced.

In the 1990s, the earlier a nest site was attended by adults during annual reoccupation and the more often it is occupied subsequently, the later the time of evening departure by the adults from the nest site in the pre-egg laying period. Evening vacation of nest sites by adults, in the pre-egg laying period, does not occur simultaneously in all areas of the colony. Overnight occupation of the nest sites, by adults, is apparently not occurring until about two weeks before egg laying, except on the isolated stack of Marsden Rock, where it was suspected that at least some birds were staying overnight by early April.

Wooller (1973) stated that overnight occupation of the nest site, at the North Shields colony, started when the pair first came together each season. In seven out of twelve pairs considered, the first overnight of the year took place on the same day that the pair were re-united. Dixon (1979) observed that by the time 50% of nest sites were regularly occupied, Kittiwakes were remaining at the colony until several hours after sunset, although the colonies were eventually vacated each night until about two weeks before egg laying. Experienced birds, returning in February and early March in the 1990s, were paired soon after arrival and yet widespread overnight occupancy at Marsden was not indicated until early May.

The mean date of clutch completion is now slightly later, leading to greater synchrony in egg laying. Mean dates, except for 1953 when it was 15 May, fall into the period 19-22 May, the latter date being that for 1992, three days later than in the 1970s. Currently the mean clutch size is slightly less than that recorded in the two earlier periods, now being less than 2.00 eggs per clutch. The reduction in mean clutch size is due in part to the smaller percentage of 3 egg clutches, 5%, compared with 13% in the 1950s. Also an increase in 2 egg clutches, from 77% to 87% of the total. Clutch size and time of laying are also linked with the previous breeding experience of females (Coulson and White 1959b). More experienced birds lay earlier and are more likely to lay clutches of three eggs. The slightly later mean laying date in 1992 could indicate less experienced birds laying later and smaller clutches. The annual adult survival rate is however high, but could relate to relatively young birds breeding for only the second or third time. The lack of early returning birds in the spring would also contribute to the later laying date.

The daily growth rates of chicks in 1991-1992 was 12%-18% less than those at North Shields during the 1950s and 1970s. Fledging success was also higher in the two preceding periods. This may result from the lower growth rate of chicks recorded at Marsden. Fledging success in the 1970s was at a low level, having peaked at about 95% in the early 1960s. Due to the closeness of the two colonies it would seem reasonable to assume that the adults were all feeding in essentially the same offshore area and exploiting the same food supply. Differences in quality of breeding birds may exert an influence. There is evidence, that some of the adults in the main Marsden study area are of poorer quality and hence raise fewer young (Chapter 5). Data involving these chicks may exert a disproportionate influence on the figures for hatching success and growth rates. The number of chicks fledged per brood is intermediate between the values for the 1950s and 1970s.

Non-attendance by both adults at the nest site during chick rearing was minimal during 1991. In 1992, it occurred on a much larger scale although this did not appear to affect the ability of chicks to fledge. Broods of two chicks were more likely to be neglected through non-attendance of both adults, than broods of one, in 1991. This distinction was much less clear in 1992. Young chicks in 1992 were most likely to be neglected, through non-attendance of adults, when 11-20 days old. Chick neglect was not reported locally during the 1950s and 1970s in the literature of the time. A retrospective analysis of data for North Shields, between 1968-1974 by Coulson and Johnson (1993, in press), showed that adult attendance was very variable, as was the onset of neglect.

Current adult annual survival rates are comparable with those at North Shields at the moment and slightly higher than those in 1954 and 1976 (Coulson and Thomas 1985). The longer pelagic phase of the yearly cycle, in the early 1990s, may be contributory, birds being physically fitter in the spring on return to the colony. In addition, the reduced time at the colony, during the breeding season, leaves birds fitter in August at the commencement of the next pelagic phase.

The changes in the breeding biology of the Kittiwake at Marsden therefore manifest themselves in a shorter period spent by adults and young birds at the colony and a greater synchrony in timing of the breeding effort while maintaining a level of breeding success similar to that in the previous study periods.

Table 26

Summary of changes in the colony and breeding biology of the kittiwake at Marsden Bay during 1953-1992. Additional data from the nearby North Shields colony has been included where data from Marsden was not available. The data from North Shields is shown in italics. An asterisk (*) indicates data, not for a specific year, but for a period of time, ie 1950s,1970s or 1991-1992.

	YEAR					
	1953	1954	1975	1976	1991	1992
No.of nests	1661	1905	4534	4561	4700	5768
Date of return	mid-Jan	mid-Jan	early Jan	early Jan	late Feb	early Feb
Period of return(days)	44	33	7	1	13	17
50% occup	mid-Feb	early March	late Jan	mid-Jan	early March	early March
Mean date of laying (May)	_15_	_21_	_19_	_19_		22
10% of nests with eggs (area F)		29 May				by 13 May
50% of nests with eggs (area F)		04 June				by 20 May
Mean clutch size	_2.27_	_2.05_	_2.02_	_2.05_	1.87	1.95
Clutch size c1/c2/c3.	_10:77:13*_				8:87:5*	
Hatching success	_69%*_		_62%_	_61%_	62%	78%
Chick growth rate g/day		_15.5_		_15.5_	13.6	12.7
Fledging success	_86%*_		_84%*_		79%*	
Chicks fledged per brood	_1.16*_		1.58-1.78*		1.26*	
Chick neglect		_rare*_		_rare*_	rare	frequent
Date of departure	late Aug/ early Sept*		late Aug/ early Sept*		mid/late Aug*	
Annual adult survival rate		_78%_	_85%_	_76%_	82%	92%

Explanation of terms used in Table 26

No. of nests - the number of apparently occupied nests in the Marsden Bay colony. Data for 1953-1954 fom Coulson and White (1960) and for 1975-1976 fom Dixon (1979).

Date of return - the approximate time of annual return of Kittiwakes to the colony. Data for 1953-1954 from Coulson and White (1956) and for 1975-1976 from Dixon (1979).

Period of return - the number of days between the first and last areas of the colony being reoccupied for the first time that year Data for 1953-1954 from Coulson and White (1956) and for 1975-1976 from Dixon (1979).

50% occupancy - the approximate time, when any area of the colony first achieves 50% occupancy, during a spot count, based on the number of nests counted in June of that year. Data for 1953-1954 from Coulson and White (1956) and for 1975-1976 from Dixon (1979).

Mean date of laying - the mean date of egg laying in May. Data for 1953-1954 and 1975-1976 from Coulson and Thomas (1985).

10% of nests with eggs (F) - the date when 10% of nests contained eggs in area F of the colony. The "1950s" data are for the year 1958, from Coulson and White (1960). The date for 1992 is the date by which completed clutches were in 15% of nests, clutch sizes only being checked every 7 days..

50% of nests with eggs (F) - the date when 50% of nests contained eggs in area F of the colony. The "1950s" data are for the year 1958, from Coulson and White (1960). The date for 1992 is the date by which completed clutches were in 60% of nests, clutch sizes only being checked every 7 days.

Mean clutch size - the mean size of all clutches recorded. Data for 1953-1954 from Coulson and White (1958a) and for 1975-1976 from Coulson and Thomas (1985).

Clutch size - the percentage of clutches with 1, 2 and 3 eggs. Data for 1954 from Coulson and White (1958a).

Hatching success - the percentage of eggs laid which hatch. Data for 1950s from Coulson and White (1958a) and for 1975-1976 based on 5 year running mean (Coulson and Thomas 1985).

Chick growth rate - mean daily chick growth rate in grams between 60-300 g chick weight. Data for 1954 and 1976 from Coulson and Thomas (1985).

Chicks fledged per brood - the mean number of chicks fledged from each successful nest. Data for 1950s from Coulson and Thomas (1985) and for 1975 from Dixon (1979).

Fledging success - the percentage of chicks which fledge. Data for 1950s from Coulson and White (1958a) and for 1970s from Coulson and Thomas (1985).

Chick neglect - the presence of unfledged chicks on the nest, without either adult being present.

Date of departure - the approximate time of post breeding departure of Kittiwakes from the colony. Data for 1950s from Coulson and for 1970s from Dixon (1979).

Adult survival - the annual adult survival rate. Data for 1954, 1975 and 1976 from Coulson and Fairweather (unpublished).

CHAPTER 10

SUMMARY

1. Some aspects of the breeding biology of the Kittiwake were investigated at the colony in Marsden Bay, Tyne and Wear during 1991 and 1992. The current status and breeding biology were considered in relation to published data from the 1950s and 1970s, relating to the same or nearby colonies,

2. The main study areas were the same as those used by Coulson et al in the 1950s. The numbers of nesting pairs in these areas were counted and the nesting density (number of nests in a 1.52 m, 5 feet, radius) was calculated. A total nest count for the whole colony was also obtained in each year. A count for 1990 had previously been made.

3. Adults and chicks in one area of the colony were captured and colour-ringed allowing biometrics and growth rates to be obtained and observations requiring individual recognition of birds to be made.

4. Marsden Bay was colonised in the 1930s and the number of nesting pairs increased steadily before levelling off in the mid-1970s. Over the next 15 years the number of nesting pairs increased by 28%.

5. Those areas within the colony which were the first to be occupied during 1931-1937 are showing signs of a decrease in the number of nesting pairs. Those areas established during 1947-1953 are still showing an increase in the number of nesting pairs. These changes are considered to be largely due to alterations in the cliff structure and the availability of sites for nests. Although the colony as a whole is increasing in size, in terms of the number of nests, some areas are showing a decrease, indicating the need to examine in detail the colony structure when studying population trends.

6. Annual recolonisation by adults occurs later now than in the 1950s and 1970s. Although the adult annual survival rate was high in the early 1990s, the expected earlier return of adults to the colony did not occur.

7. The relationship between annual reoccupation and wind speed and direction appeared to be variable.

8. Evening vacation of the colony continued until late in the pre-laying period. The last areas of the colony to be vacated each evening were located on isolated stacks.

In the study area, containing colour-ringed adults, for every attendance recorded at a nest site, after the first nest site was occupied that year, the nest site was vacated on average 3 minutes later each evening in 1991 and 2.8 minutes later in 1992.

9. The mean clutch size was 1.92 (n=97) during 1991-1992. This is less than that recorded in the two earlier study periods at North Shields due in part to the smaller number of 3 egg clutches.

Hatching success of 72% and fledging success of 79% in 1991-1992 were less than values recorded in the 1950s and 1970s at North Shields. In one of the main study areas, area F, predation by Herring Gulls was suspected of reducing the fledging success.

10. The mean daily growth rates of chicks were 13.6 g in 1991 and 12.7 g in 1992 when chicks were in the 60-300 g weight range. The growth rates are similar to those of chicks in the nearby colonies in the River Tyne during June of each year. During July 1992 the mean daily growth rate was less. Chicks from clutches which hatched earliest had the highest initial growth rates and fledging success.

11. Weights and head and bill measurements were recorded for the majority of adults caught in area F for ringing during 1990-1992. A positive relationship, which was statistically significant, existed between head and bill measurement and weight, for all months combined. Similar positive relationships exist for the data from May, June and July separately, although the relationship for May was not statistically significant.

The weight of any bird would be expected to decrease from May to June to July. Small birds of both sexes are affected less than larger birds.

For males and females considered separately, June weights exceed July weights for a given head and bill measurement, except at the lower end of the female head and bill range.

On the basis that adult male Kittiwakes have head and bill measurements greater than those of females, it can be concluded that adult males have a tendency to be heavier.

12. Low levels of non-attendance by adults of chicks occurred in 1991. The levels of non-attendance were much higher in 1992 but this had little effect on chick fledging

success and chick growth rates were similar in both years. In 1992 the mean size of unattended broods was higher than that for attended broods but there was no conclusive evidence that broods of two were left more than broods of one. Chick neglect was not reported locally during the 1950s and 1970s in the literature of the time.

13. Current adult annual survival rates are high, slightly above those at North Shields in 1954 and 1976 and comparable with that site in 1991-1992.

14. The changes in the breeding biology of the Kittiwake at Marsden manifest themselves in a shorter period spent by adults and young birds at the colony and a greater synchrony in timing of the breeding effort, while maintaining a level of breeding success similar to that in previous study periods.

REFERENCES

Aebischer, N. J., Coulson, J. C. & Colebrook, J. M. (1990) Parallel long-term trends across four marine trophic levels and weather. Nature, 347, 753-755.

Barrett, R. T. (1978). Adult body temperature in the development of endothermy in the Kittiwake *Rissa tridactyla*. Astarte, 11, 113-116.

Barrett, R. T. & Runde, O. J. (1980). Growth and survival of nestling Kittiwakes *Rissa tridactyla* in Norway. Ornis Scandinavica, 11, 228-235.

Belopol'skii, L. O. (1961). Ecology of sea colony birds of the Barents Sea. Jerusalem. Israel Program for Scientific Translations.

Brown, B. J. (1984) A history of the Kittiwake in Suffolk. Suffolk Birds, 1984, 66-71.

Calvo, B. & Furness, R. W. (1992) A review of the use and the effects of marks and devices on birds. Ringing and Migration , 13, 129-151.

Coulson, J. C. (1963) The status of the Kittiwake in the British Isles. Bird Study, 10, 147-179.

Coulson, J. C. (1966) The movements of the Kittiwake. Bird Study, 13, 107-115.

Coulson, J. C. (1972) The significance of the pair bond in the Kittiwake. Proceedings of the 15th International Ornithological Congress, 424-433, Leiden.

Coulson, J. C. (1974) Kittiwake *Rissa tridactyla*, Pp. 134-141 in: Cramp, Bourne and Saunders, *The Seabirds of Britain and Ireland*. London (Collins).

Coulson, J. C. (1983) The changing status of the Kittiwake *Rissa tridactyla* in the British Isles 1969-1979. Bird Study, 30, 9-16.

Coulson, J. C. & Johnson, M. P. (1993 in press). The attendance and absence of adult Kittiwakes *Rissa tridactyla* from the nest site during the chick stage. Ibis.

Coulson, J. C. & Neve de Mevergnies, G. (1992) Where do young Kittiwakes *Rissa tridactyla* breed; philopatry or dispersal? Ardea, 80, 187-197.

Coulson, J. C. & Porter, J. M. (1985) Reproductive success of the Kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. Ibis, 127, 450-466.

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Coulson, J. C. & Thomas, C. (1980) A study of the factors influencing the duration of the pair bond in the Kittiwake Gull *Rissa tridactyla* . Proceedings of the 17th International Ornithological Congress, 822-833. Berlin.

Coulson, J. C. & Thomas, C. S., Butterfield, J. E. L., Duncan, N., Monaghan, P. & Sheddon, C. (1983) The use of head and bill length to sex live gulls Laridae. Ibis, 125, 549-557.

Coulson, J. C. & Thomas, C. (1985) Changes in the biology of the Kittiwake *Rissa tridactyla;* a 31 year study of a breeding colony. Journal of Animal Ecology, 54, 9-26.

Coulson, J. C. & White, E. (1956) A study of colonies of the Kittiwake *Rissa tridactyla*. Ibis, 98, 63-79.

Coulson, J. C. & White, E. (1958a) Observations on the breeding of the Kittiwake. Bird Study, 5, 74-83.

Coulson, J. C. & White, E. (1958b) The effect of age on the breeding biology of the Kittiwake *Rissa tridactyla.* Ibis, 100, 40-51.

Coulson, J. C. & White, E. (1960) The effect of age and density of breeding birds on the time of breeding of the Kittiwake *Rissa tridactyla.* Ibis, 102, 71-86.

Coulson, J. C. & White, E. (1961) An analysis of the factors influencing the clutch size of the Kittiwake. Proc. Zool. Soc. Lond. 136: 207-217.

Coulson, J. C. & Wooller, R. D. (1976) Differential survival rates among breeding Kittiwake Gulls *Rissa tridactyla* (L). Journal of Animal Ecology, 45, 205-213.

Coulson, J. C. & Wooller, R. D. (1984) Incubation under natural conditions in the Kittiwake Gull *Rissa tridactyla.* Animal Behaviour, 32, 4, 1204-1215.

Cullen, E. (1957) Adaptations of the Kittiwake to cliff-nesting. Ibis, 99, 275-302.

Dixon, F. (1979) A study of some factors influencing breeding of the Kittiwake Gull *Rissa tridactyla.* Unpublished Ph.D. Thesis, Durham University.

Fisher, J. & Waterston, G. (1941) The breeding distribution, history and population of the Fulmar *Fulmarus glacialis* in the British Isles. Journal of Animal Ecology 10: 204-272.

Galbraith, H. (1983) The diet and feeding ecology of breeding Kittiwakes *Rissa tridactyla*. Bird Study, 30, 109-120.

Grey, F. G. (1937) Sea-birds at Marsden Bay. Vasculum, 23, 95-96.

Harris, M. P. & Wanless, S. (1990) Breeding success of British Kittiwakes in 1986-1988: Evidence for changing conditions in the Northern North Sea. Journal of Applied Ecology, 27, 172-187.

Heubeck, M., Harvey, P. V. & Robinson, I. S. (1987) Chick production at Kittiwake *Rissa tridactyla* colonies in Shetland, 1986. Seabird, 10, 34-42.

Hodges, A. F. (1974) A study of the biology of the Kittiwake *Rissa tridactyla*. Unpublished Ph.D Thesis, Durham University..

Maunder, J. E. & Threlfall, W. (1972) The breeding biology of the Black-legged Kittiwake in Newfoundland. Auk, 89, 789-816.

Pearson, T. H. (1968) The feeding biology of the seabird species breeding on the Farne Islands, Northumberland. Journal of Animal Ecology, 37, 521-552.

Temperley, G. W. (1951) A History of the Birds of Durham. Trans. of the Nat. Hist. Soc. of Northumberland, Durham and Newcastle upon Tyne, IX, 267-269.

Wanless, S. & Harris, M. P. (1989) Kittiwake attendance during chick rearing. Scottish Birds, 15, 156-161.

Wanless, S. & Harris, M. P. (1992) Activity budgets, diet and breeding success of Kittiwakes *Rissa tridactyla* on the Isle of May. Bird Study, 39, 145-154.

Wooller, R. D. (1973) Studies on the breeding biology of the Kittiwake *Rissa tridactyla* using marked individuals. Unpublished Ph.D. Thesis, Durham University.

APPENDIX 1

The reoccupation of the areas in 1991 of the Marsden Bay colony described by Coulson and White (1956). The number of sites occupied in any area of the colony is expressed as a percentage of the final nest count in that area in June 1991.

a reoccupation of area A

b reoccupation of area B

c reoccupation of area C

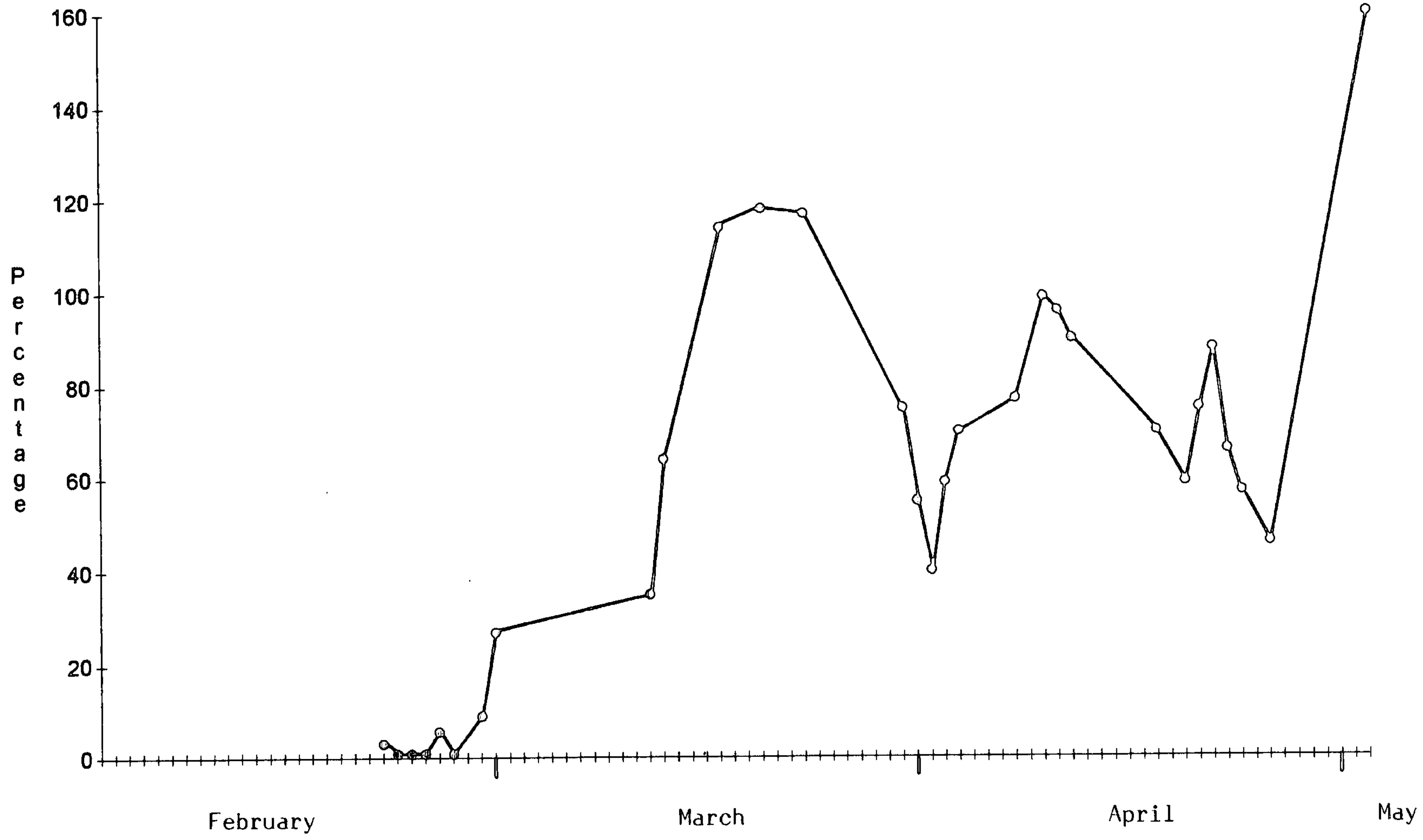
d reoccupation of area D

e reoccupation of area E

f reoccupation of area F

g reoccupation of area G1

Appendix 1a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140
120
100
80
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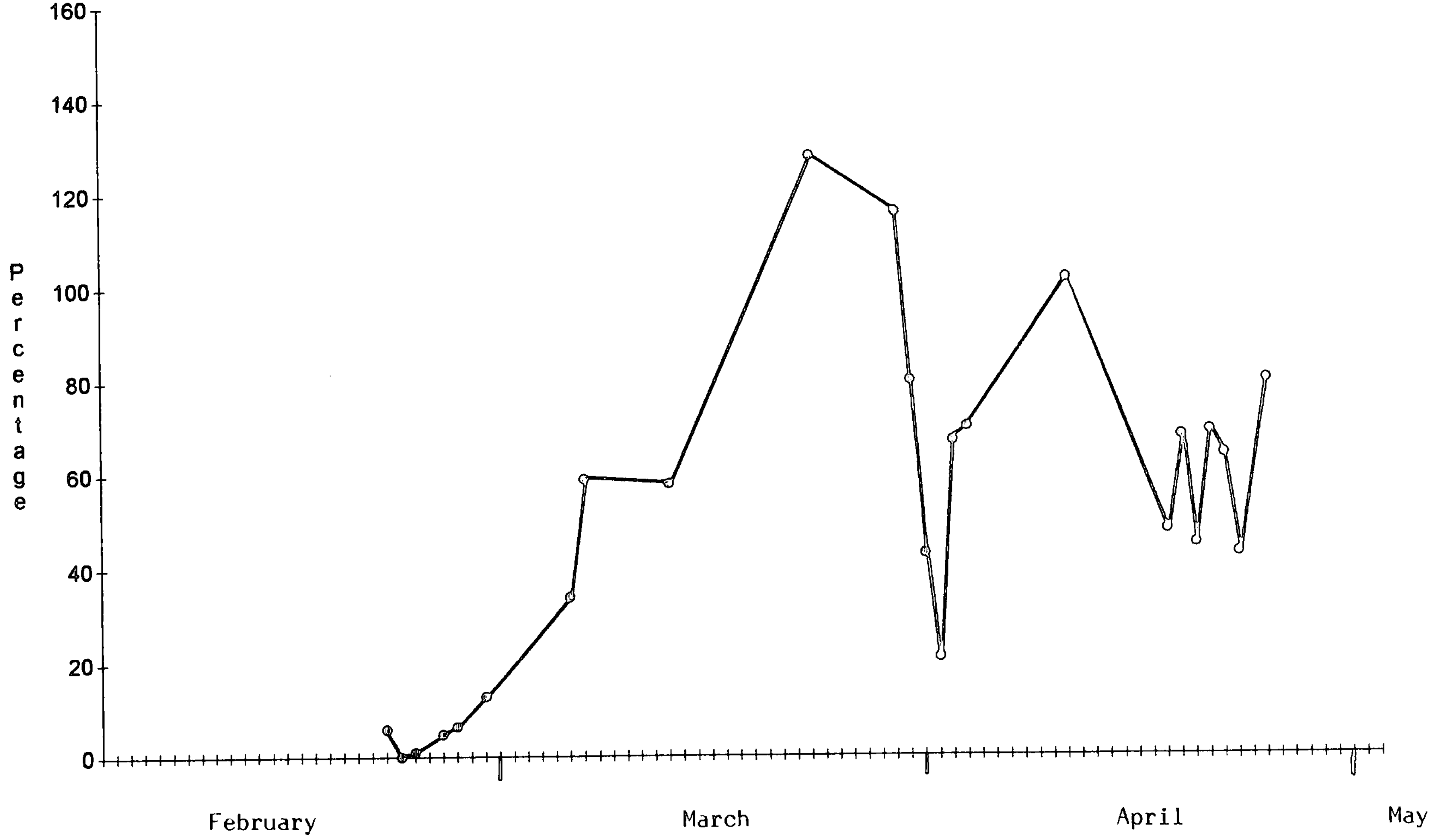
40
20
0
Percentage
February
March
April
May

Appendix 1b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20
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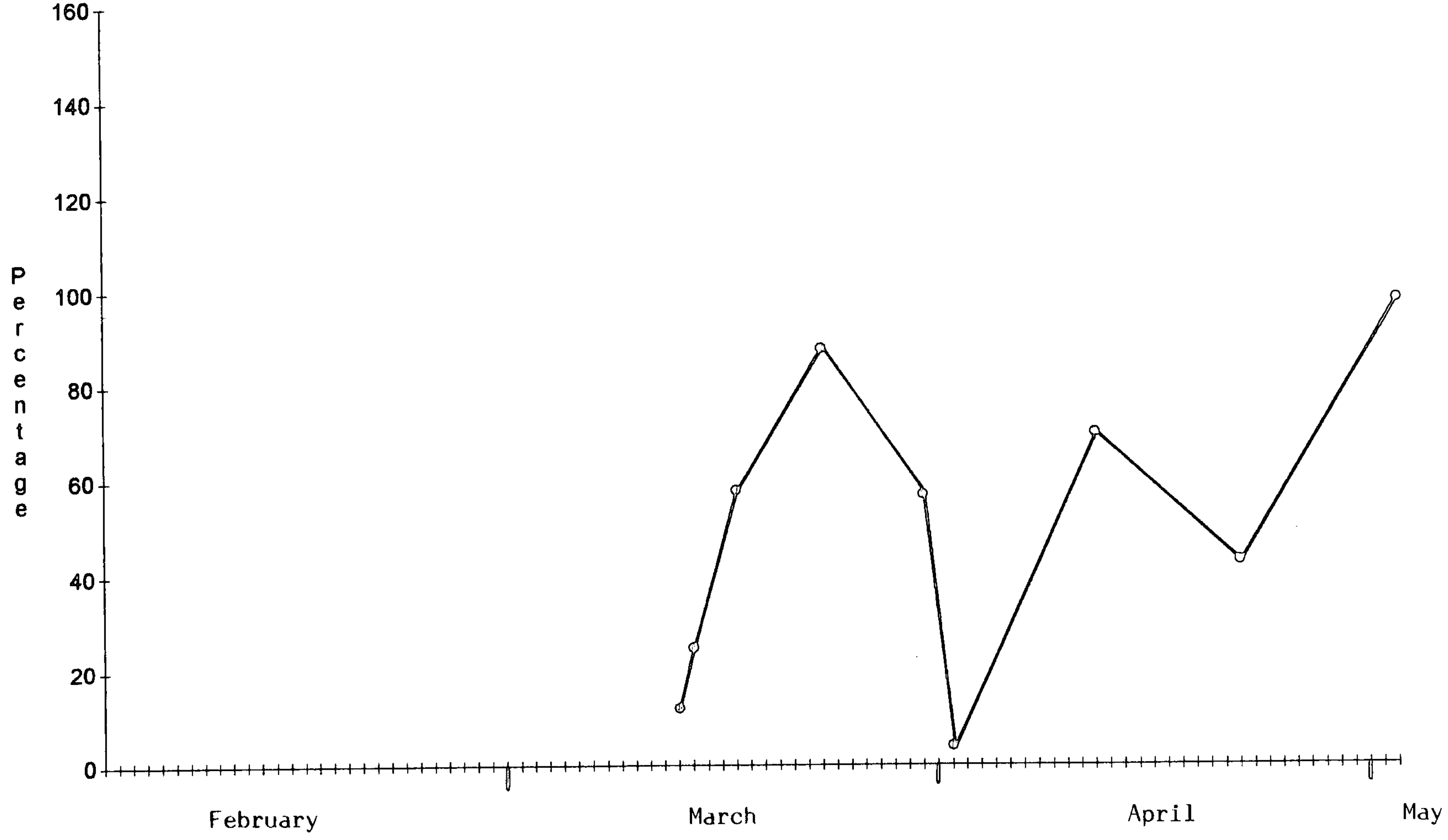
Percentage
February
March
April
May

Appendix 1c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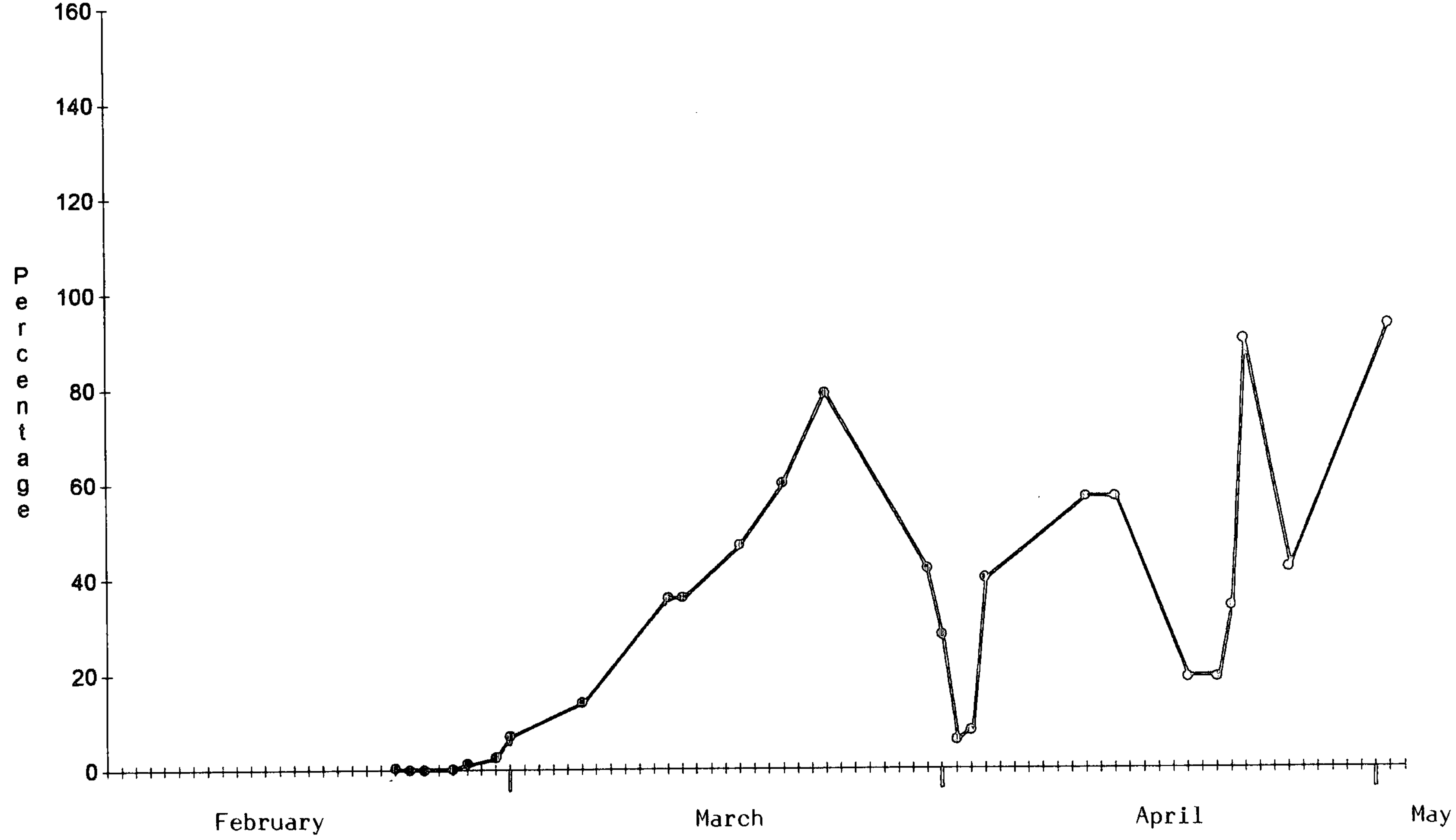
Percentage
February
March
April
May

Appendix 1d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February
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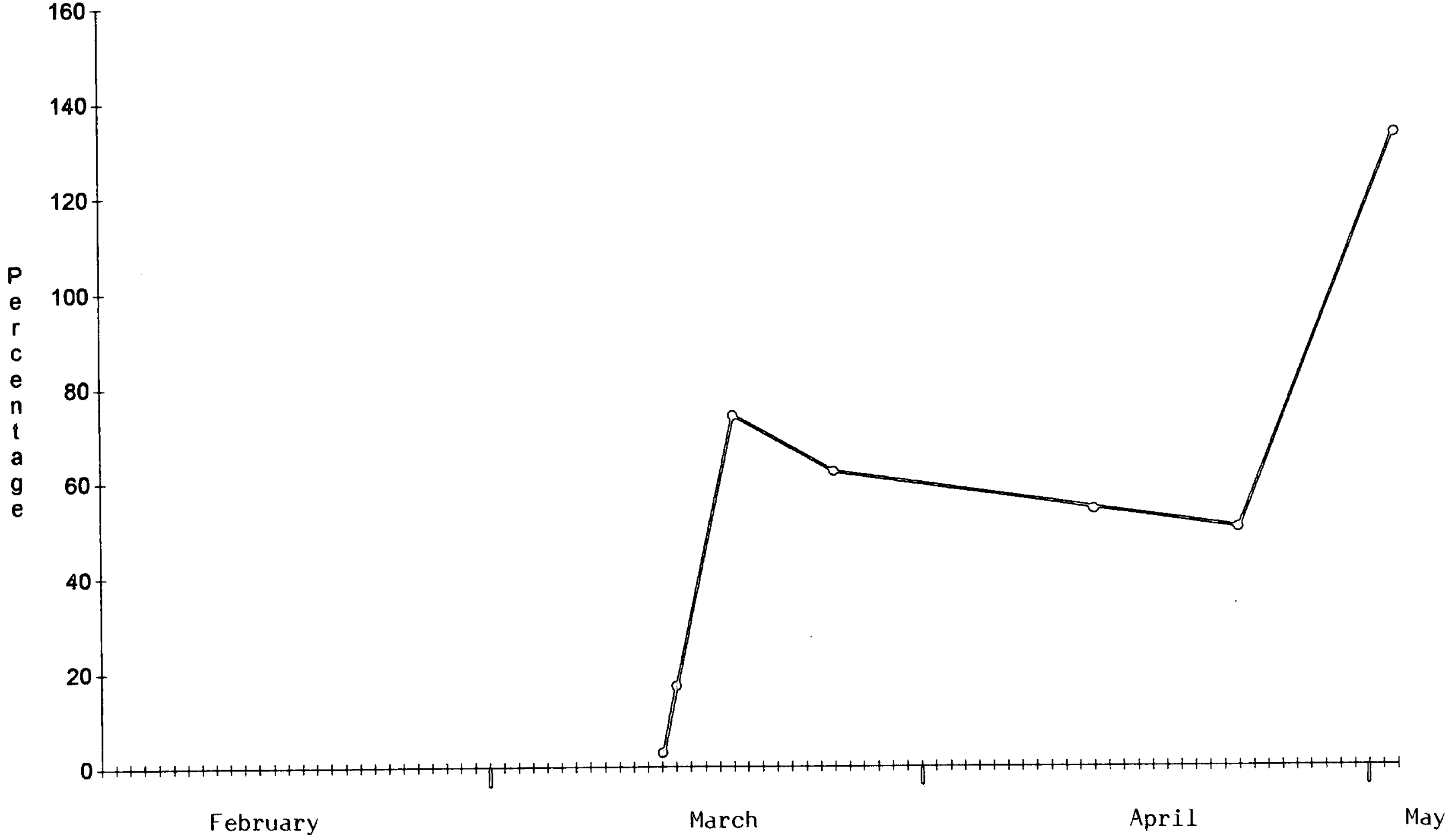
April
May

Appendix 1e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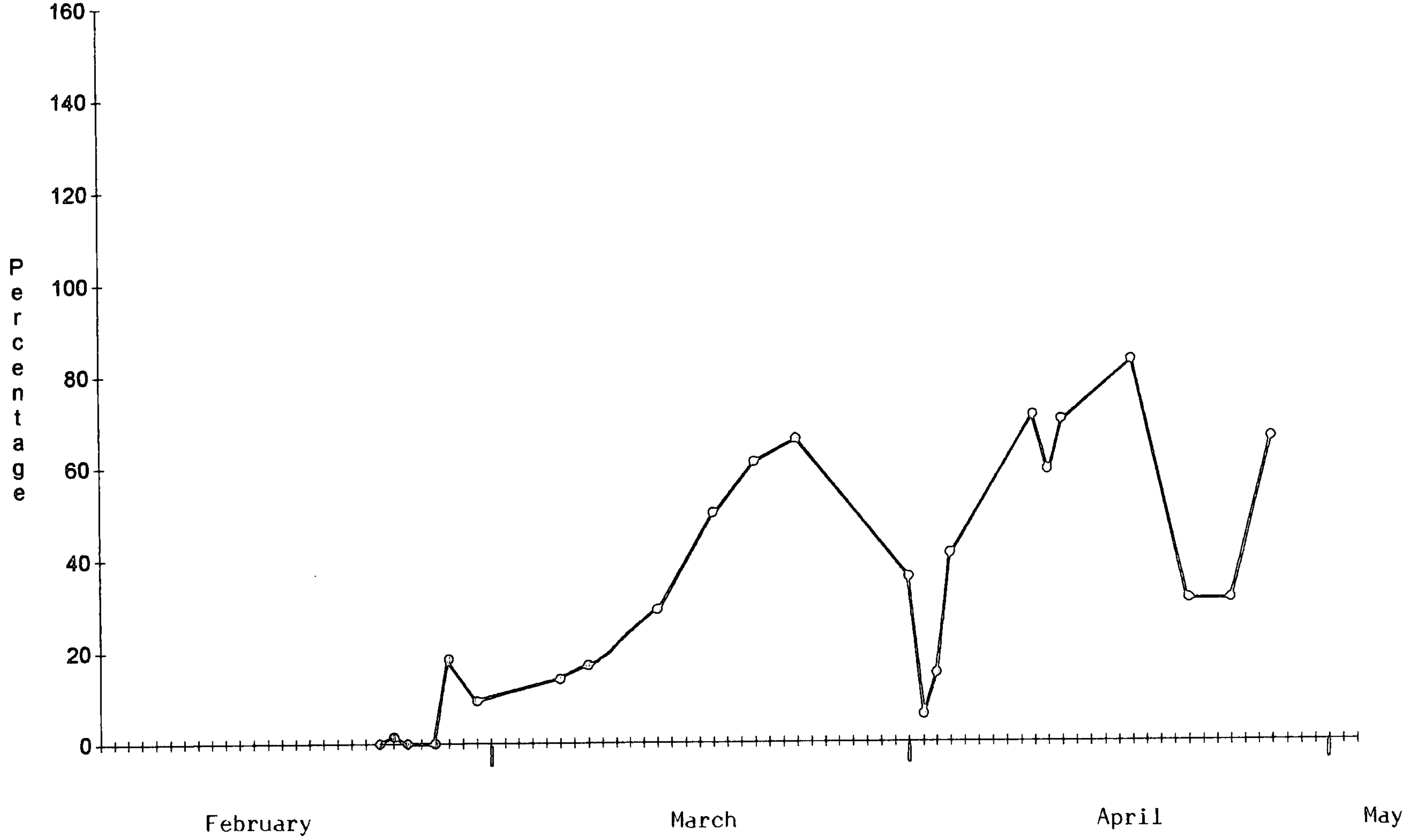
Percentage
February
March
April
May

Appendix 1f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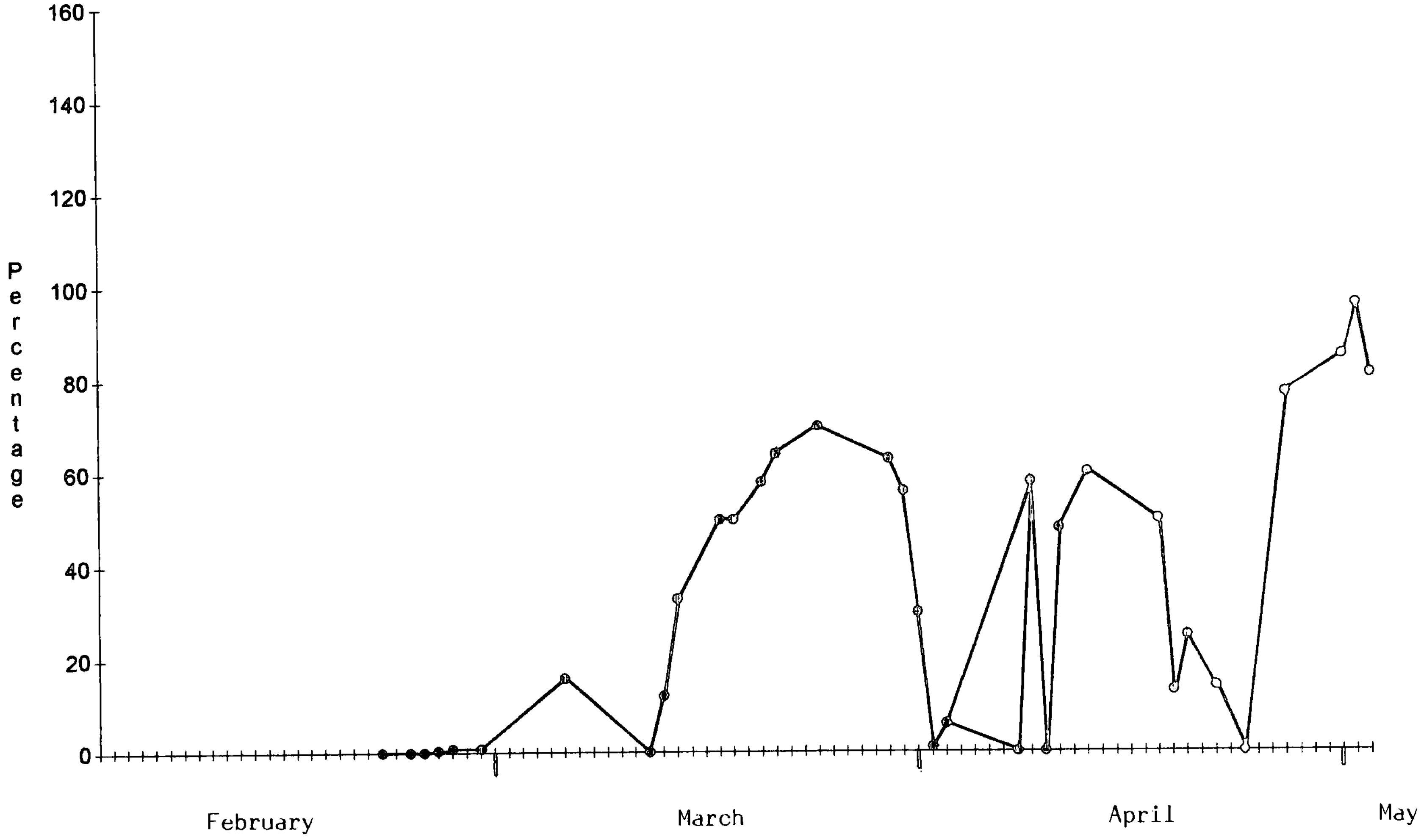
Percentage
February
March
April
May

Appendix 1g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February
March
April
May

APPENDIX 2

The 1992 reoccupation of areas described by Coulson and White (1956) in Marsden Bay. The number of sites occupied is expressed as a percentage of the final nest count and is plotted against date.

a reoccupation of area A

b reoccupation of area B

c reoccupation of area C

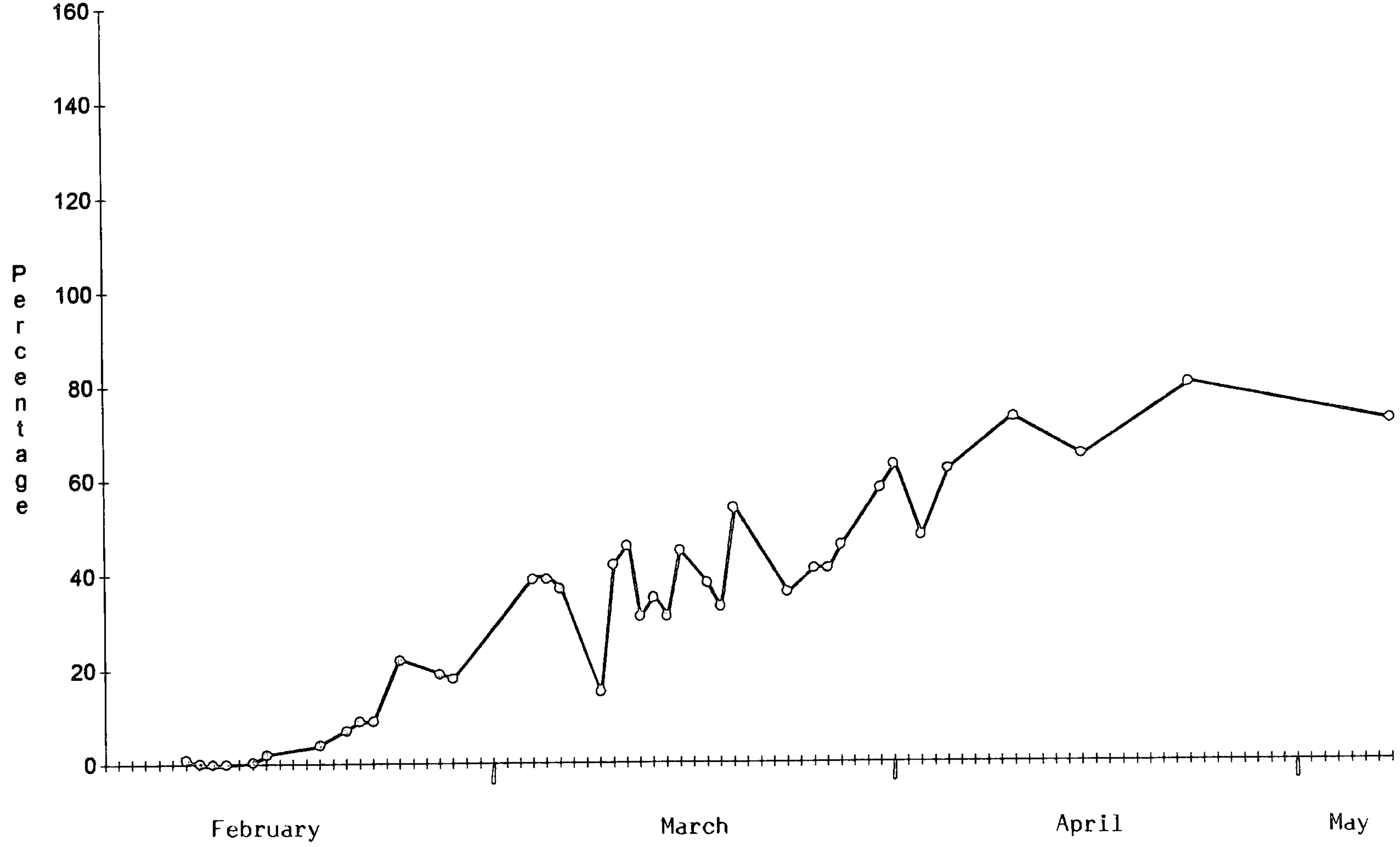
d reoccupation of area D

e reoccupation of area E

f reoccupation of area F

g reoccupation of area G1

Appendix 2a



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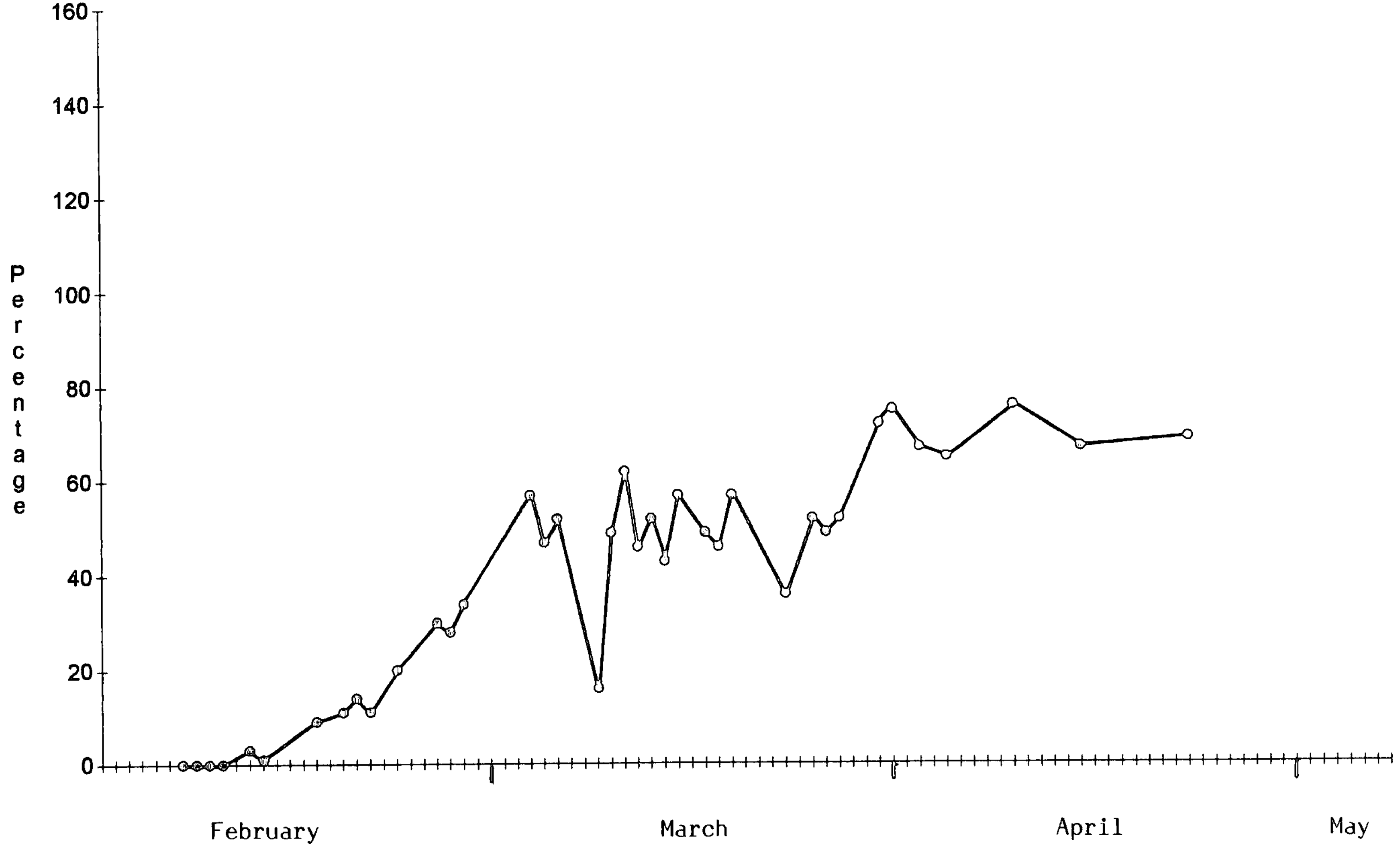
February
March
April
May

Appendix 2b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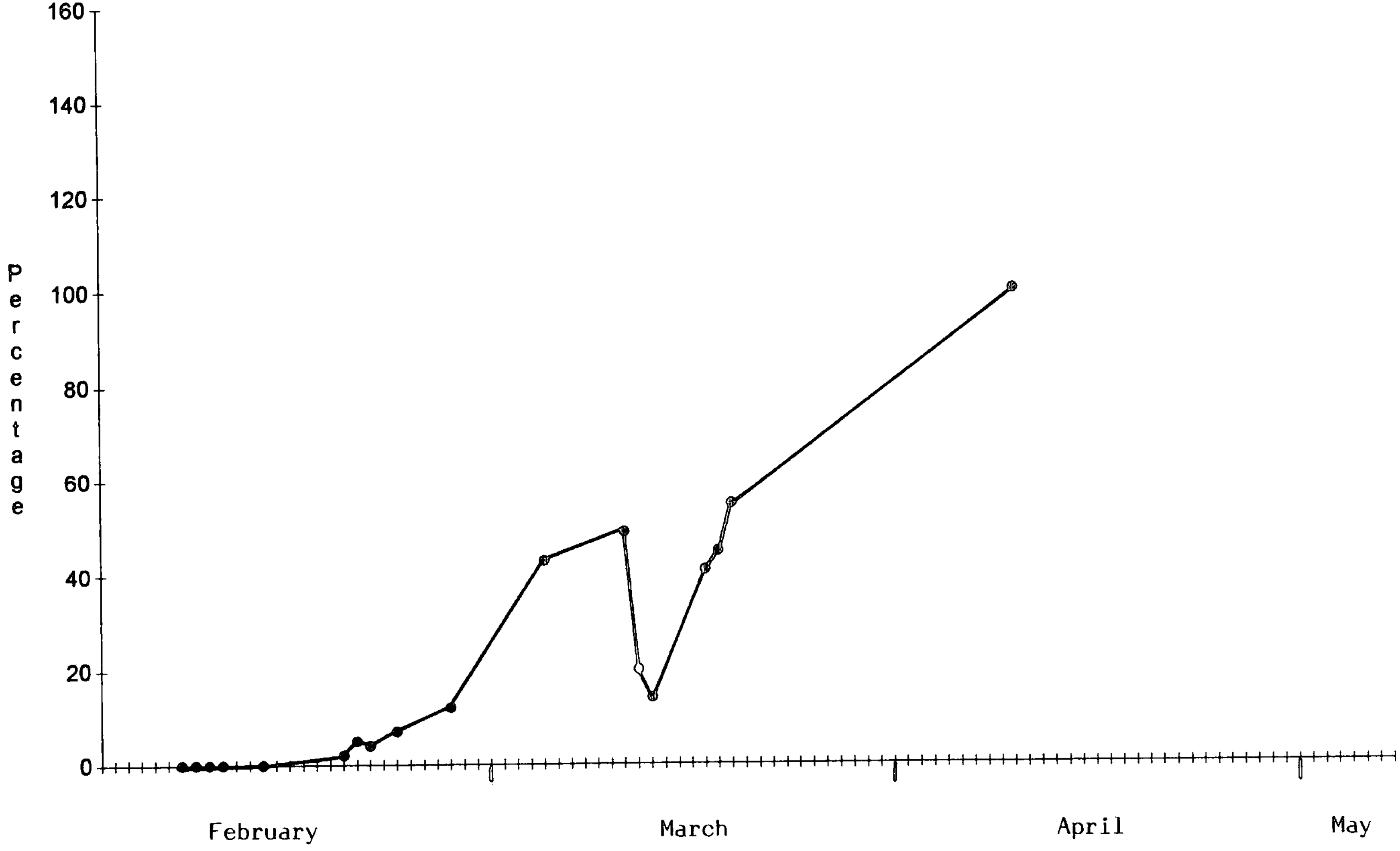
February
March
April
May

Appendix 2c


Percentage
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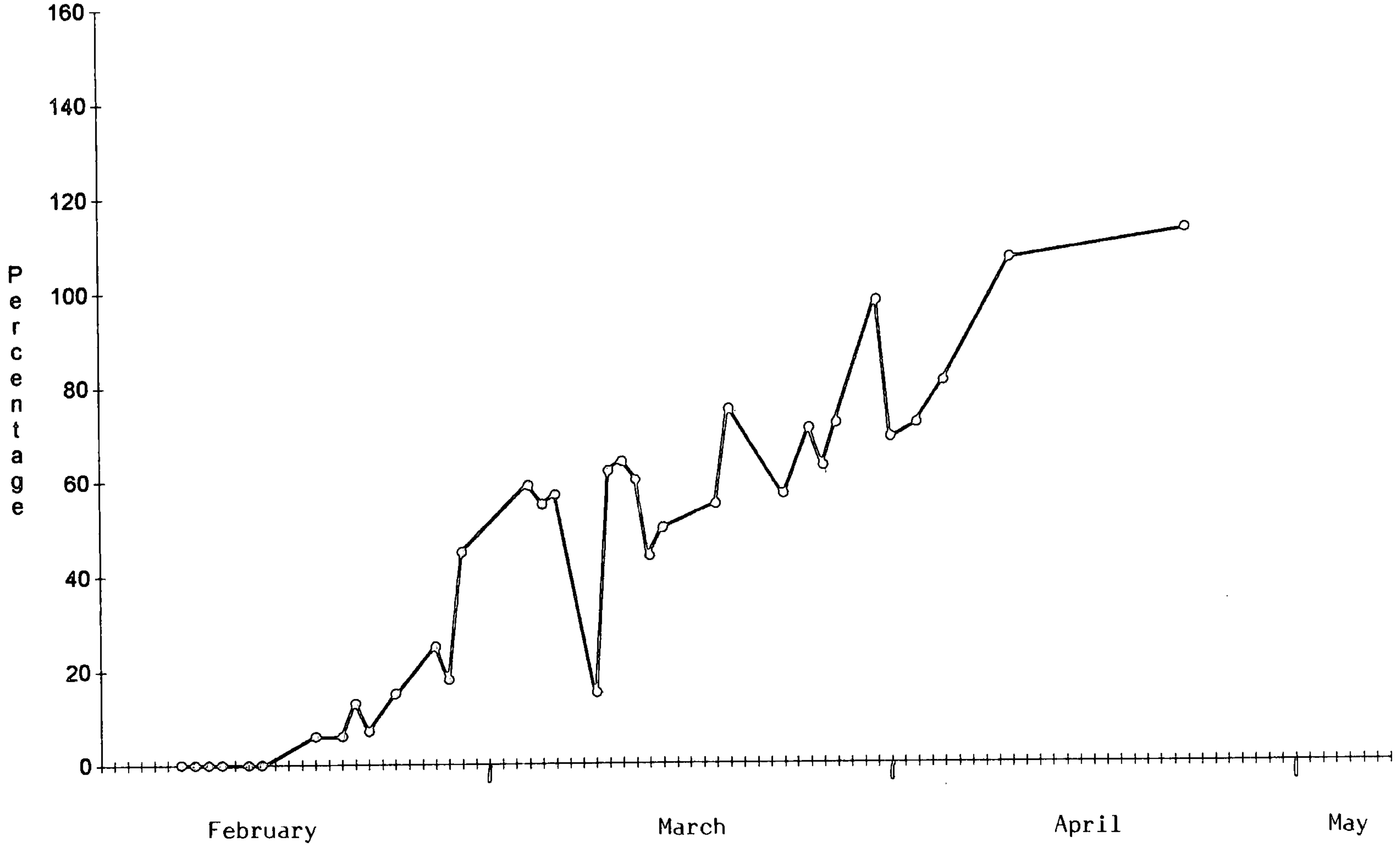
February
March
April
May

Appendix 2d



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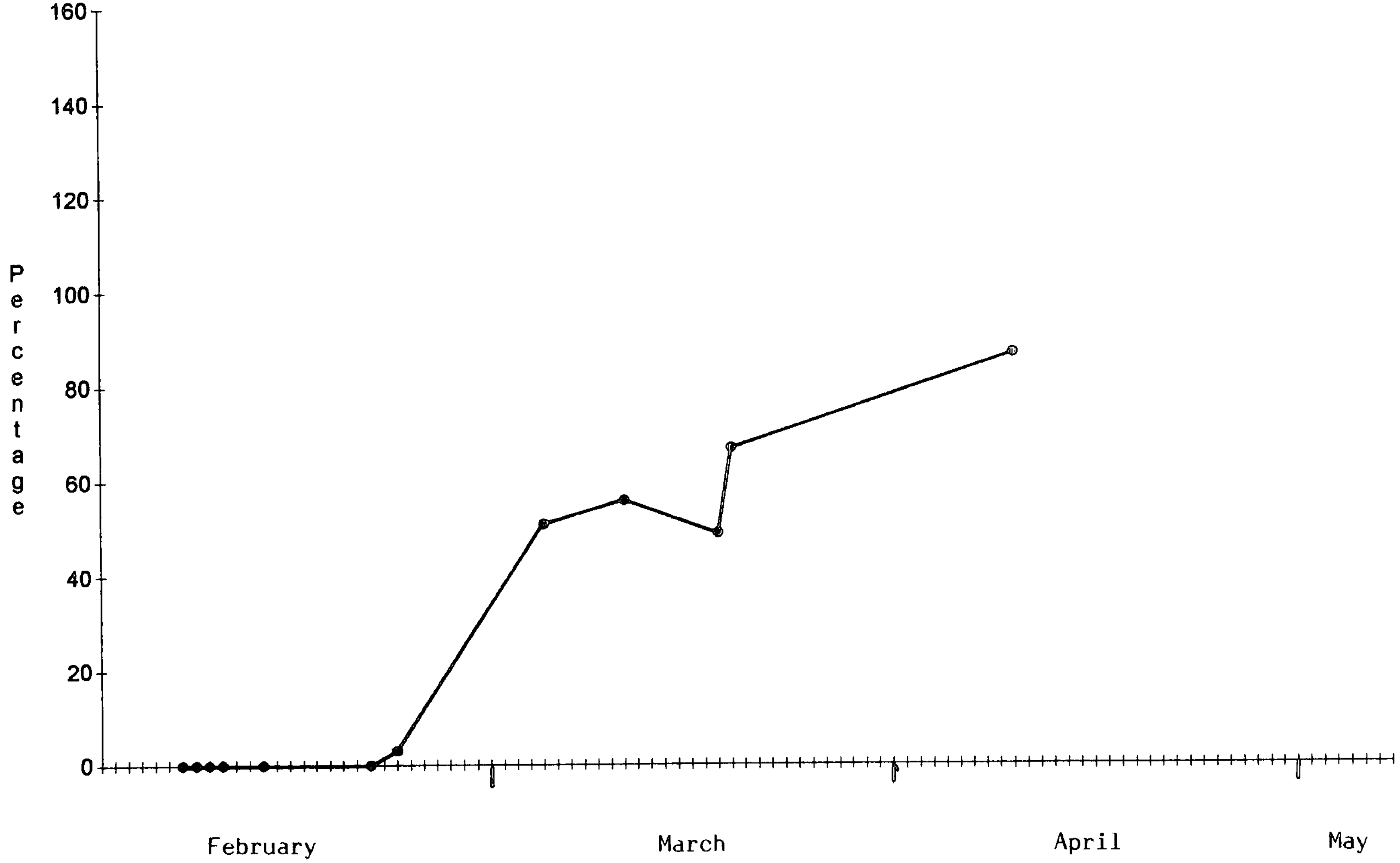
Percentage
February
March
April
May

Appendix 2e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February
March
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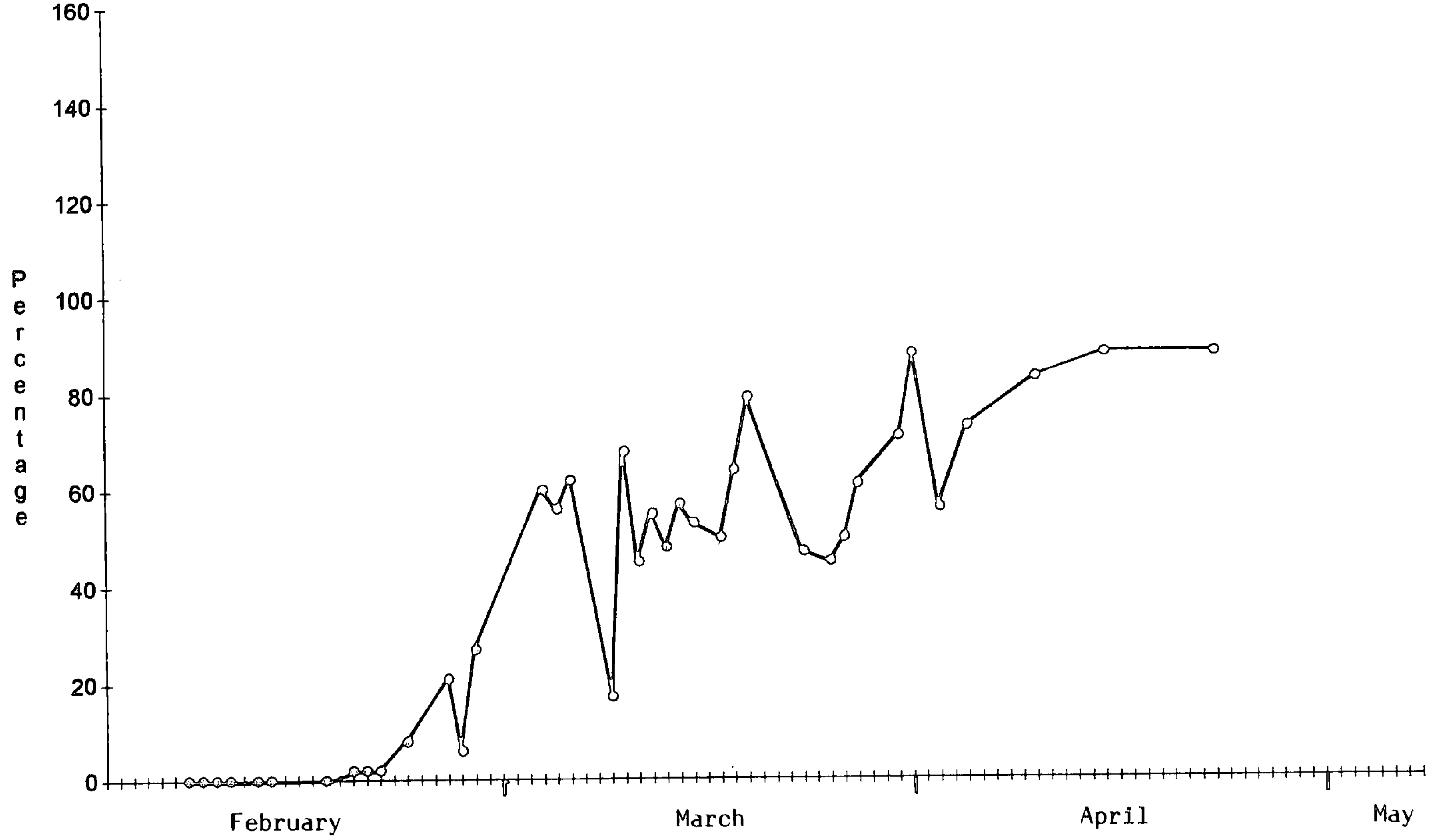
May

Appendix 2f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February
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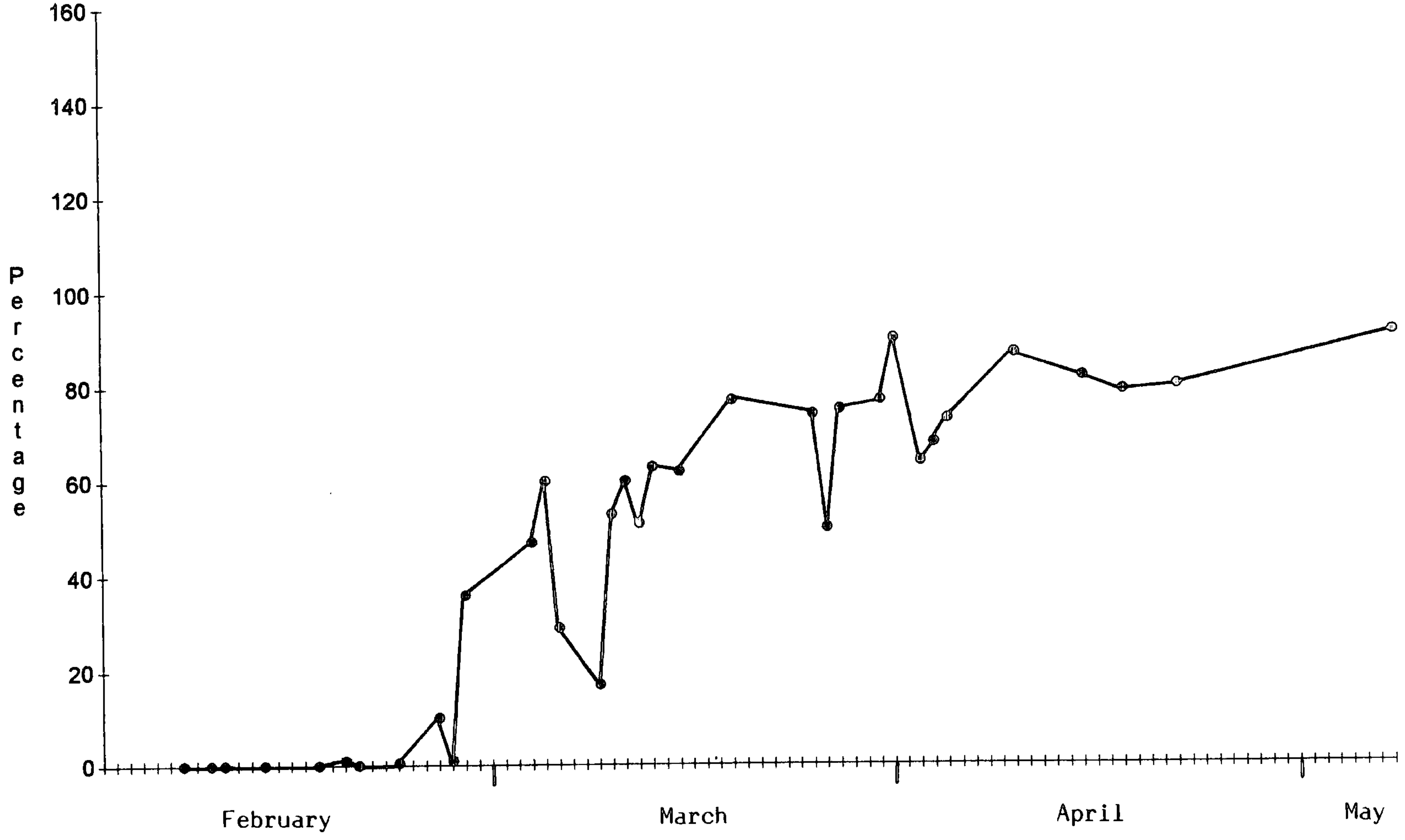
May

Appendix 2g


Percentage
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February
March
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May

APPENDIX 3

Weights of chicks, in grams, from area F of the Marsden Bay colony in 1991. The growth rates derived from these weights are listed in Table 15a (page 64).

APPENDIX 4

Weights of chicks, in grams, from area F of the Marsden Bay colony in 1992. The growth rates derived from these weights are listed in Table 15b (page 64)

APPENDIX 3

Ring no.	Date		
	18.6.91	25.6.91	2.7.91
A1	168		
K7	140	180	258
A6	208	298	404
A2	221	276	374
A7	169	330	364
A3	133	292	336
A8	131	286	356
A5	167	286	378
A9	151	278	366
J6		260	348
J7		180	244
J8		88	
K1		160	266
J9		142	252
C7		59	82
C5		68	182
K0		154	290
K2		131	242
K3		175	262
K4		269	410
K5		185	240
K6		234	374
L2		144	226
L3		100	
P3			
K8		184	296
K9		86	132
L0		70	168
L1		98	194
J4		196	296
J5		142	248
C9		172	304
C6		132	172
L4		114	208
L5		104	176
L7		152	220
L6		138	256
L8		208	320
L9		138	
C0		240	334
C3		192	246
C1		118	250

APPENDIX 4

Ring no.	Date					
	10.6.92	17.6.92	24.6.92	1.7.92	8.7.92	15.7.92
AL	66	180	300			
AK	55	178	274			
AX	100	236	268			
AT	80	180	240	294		
AB	42	152	242			
AC	52	172	230			
AS	76	222	330			
AU	90	200	340			
AW	76	202	302			
AF		110				
AM		68	182			
AD		60				
AP		134	218	292		336
AZ		76	108	190		338
AN		66	180	290		378
AG		47				
AA		76	204	250	292	
AY		64	172	222	230	
48		102	164	266	204	
42		116	222	312	346	280
46		118	160	226		
47		144	250	336		
43		118	204	366		
41		150	274	334		
44		178				
45		186				
49		66	160			
96		51				
91		108	214			
93		94	188	242		
99		68	120	234		
BA		55	158			
DZ		44	142			
BB		104	220	276	336	
BC		92	202	272	286	
BD		96	224	298	336	
AE		152	258			
AH		92	138	262	262	370
AR		114	178	288	276	336
CS			70	126		
BH			114	234	304	
BG			63	132	240	
BE			102	184		
BF			104	226	304	352
DT			176	228		
DN			120	180		
DV			168	322	360	
BY			114	186		
BW			200			
BN			146			
CX				78		
CG				94		326
CR				110	210	
CA				88		
CF				230	326	288
CC				210		
CL				254		

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