Studies on the breeding biology of arctic terns (sterna paradisaea) (=S macrura) with special reference to age

Jean M. Horobin

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Studies on the breeding biology of Arctic terns (Sterna paradisaea) (=S. macrura) with special reference to age

Jean M. Horobin, B.Sc.

St. Mary's College

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ABSTRACT

The breeding biology of Arctic Terns (Sterna paradisaea) (=S.macrura) was studied on the Farne Islands, off the coast of Northumberland, from 1965 to 1968. Clutches of two predominated in 1966 and 1967 but the second eggs were significantly smaller than the first. Starling (Sturnus vulgaris) predation accounted for most of the egg loss, and in 1966 and 1967 approximately 45% of all eggs laid, hatched successfully.

Chicks were weighed daily and showed a steady increase in weight from the third to the fourteenth day. Laboratory rearing of chicks showed that these required 26.2g of fish per day to maintain a daily growth rate of 6.8g. The low chick mortality in 1967 (20.9%) may have been due to an abundance of food. In other years chick mortality was approximately 40%, with a significantly higher mortality of second chicks.

It was only possible to determine the age of individual adult birds from the ringing records of previous years. Ringed adults were caught and from the survival of colour ringed birds, the annual mortality was found to be 13.3%. A life table was constructed and gave an annual mortality of 15.1% with an expectation of life of 4.5 years.

Members of a pair were likely to be of a similar age. Birds over ten years old returned to the colony first and produced more young than any other age group, in spite of having a smaller clutch and egg size than birds of six to eight years. Three year olds were the least successful age group. In 1968 a bloom of dinoflagellates, or red tide, led to the death of approximately 1% of the breeding terns, and breeding success was very low due to increased egg predation by Starlings and chick predation by gulls, which was probably associated with the loss of the advantages of colonial breeding.

CONTENTS

INTRODUCTION

The average life span of different animals shows considerable variation. Within the insects, the may-flies (Ephemeroptera) live for less than a day in the adult stage, while the reproductive forms of some termites (Isoptera) may live between 15 and 20 years (Imms 1964). Summarising the work on the barnacle (Balanus balanoides L.), Deevey (1947) quoted the maximum longevity at about five years. Within the mammals there appears to be a general trend towards the small mammals having a short life span, with a high reproductive rate, while the larger mammals are much longer lived and produce fewer young per year. Southern (1964), however, has noted that the Whiskered Bat (Myotis mystacinus (Kuhl)) has been found to have a life span of 20 years, although much of this time is spent in hibernation. Matthews (1960) has given the average life of shrews (Sorex spp) as 14 to 16 months, and the vole (Microtus agrestis (L.)) and the field mouse (Apodemus sylvaticus (L.)) as less than one year; these animals therefore only experience one breeding season although they produce more than one litter in that year. Red deer stags (Cervus elaphus L.) are stated by Matthews (1960) normally to be at their peak from 7 to 13 years old, after which they start to "go back" with a reduction in the number of points on the antlers, and few wild stags reach an age of over 15 years.

In many cases it is difficult to determine the length of life of an animal because many individuals die without being found and in only a few cases can the age of an individual animal be estimated. Such estimations have been possible by use of the annual rings on the scales and otoliths of bony fish (Actinopterygii), on the horns of Dall Mountain Sheep (*Ovis dalli*) (Scheffer 1950), and on the genital plates of sea urchin tests (Echinoidea) (Moore 1935). The age of some mammals can be estimated by counting the corpora lutea in the ovaries, for example, whales (Cetacea) (Wheeler 1934) and seals (Bertram 1940). Among the birds it is usually possible to identify the immatures from the adults by plumage details, but there is no way of assessing the age of the latter from morphological characters. A long term programme of trapping and ringing nestlings is required, and this has probably limited the number of the studies on the age of long-lived birds.

Average annual mortality rates have, however, been calculated for a number of long-lived birds including the Herring Gull (*Larus argentatus*) (Paynter 1947, Paludan 1951, Kadlec & Drury 1968, Kadlec *et al* 1969), the Common Tern (*Sterna hirundo*) (Austin 1942), the White Stork (*Ciconia ciconia*) (Schüz 1955), the Heron (*Ardea cinerea*) (Lack 1949a), the Common Gull (*Larus canus*) (Onno 1968), the Mallard (*Anas platyrhynchos*) in Great Britain (Höhn 1948) and the Lapwing (*Vanellus vanellus*) (Lack 1954). Coulson & White (1957) estimated the mortality rate of the Shag (*Phalacrocorax aristotelis*) by two independent methods; one from dead recoveries, and the second using Jackson's "live" method of recaptures. Dunnet *et al* (1963) considered the survival of the Fulmar (*Fulmarus glacialis*) nesting on Eynhallow, Orkney. The work on passerine species includes that by Nice (1937) on the Song Sparrow (*Melospiza melodia*) in the United States and that by Lack (1946a) on the Blackbird (*Turdus merula*), the Song Thrush (*T.philomelos*), and the Robin (*Erithacus rubecula*) in Great Britain. Kluijver (1935) has estimated the annual mortality of the Starling (*Sturnus vulgaris*) and the Great Tit (*Parus major*) in Holland. Lack (1954), reviewing the literature on mortality rates, has pointed out that in using ringed birds found dead, to estimate death rates, the estimations may be too high if the birds lose their rings with time. The rings of sea birds are particularly exposed to corrosion and this has been shown to occur in the rings of many birds, including the Manx Shearwater (*Puffinus puffinus*) (Lockley 1942), the Cormorant (*Phalacrocorax carbo*) (Kortlandt 1942) and the Kittiwake (*Rissa tridactyla*) and the Shag (Coulson & White 1955, 1957).

In some cases, as well as estimating mortality, it has been possible to construct a life table (Deevey 1947) for the population. Many of the species studied in this way are those where the animal is of commercial importance for the information in the life table is vital to the proper management of the population to avoid over-exploitation.

Paludan (1951) has produced a life table for Herring Gulls ringed as chicks in Denmark between 1917 and 1942 and Kadlec & Drury (1968) have presented similar information for a population of this species in New England. Austin & Austin (1956) have studied large numbers of Common Terns nesting on Cape Cod, Massachusetts and have compared the mortalities of different year groups, and calculated the age structure of the population.

In two earlier papers (Austin(1938, 1945) considered the effect of age on the breeding success of Common Terns, but he concentrated mainly on the success of the very old birds which were over 13 years old. More extensive studies on the effect of age on the breeding biology of long lived species include those on the Yellow-eyed Penguin (Megadyptes antipodes) by Richdale (1949), the Kittiwake by Coulson & White (1958) and the Shag by Potts (1966). Among the short lived species the majority of studies have compared the success of birds breeding for the first time, usually in these cases one year old birds, with the success of experienced, older breeders. These studies include those on the Song Sparrow by Nice (1937), the Blackbird by Snow (1958), and the Great Tit by Kluijver (1951, 1952) and Perrins (1965).

Apart from the work on the Common Tern at Cape Cod (Austin 1938, 1945; Austin & Austin 1956), there is very little published information on the effect of age on terns, although there are some age records (Andersen 1959, Bergstrom 1952, Grosskopf 1957, and Goethe 1966).

Palmer (1941a) discussed "white-faced" Common Terns and suggested that these were young birds not old enough to breed; he also suggested that some of the very old birds show a plumage similar to that of the winter plumage. His main study (Palmer 1941b), however, was on the behaviour of the Common Tern.

Bullough (1942) considered the Farne Island colonies of the Arctic Tern in 1938 and compared these to the colonies of other sea birds. Cullen (1956, 1957) studied the behaviour of the Arctic Tern on Inner Farne, and during the course of this study undertook some retrapping and colour ringing of adults from which he was able to estimate the annual adult mortality. In a later paper (Cullen 1960), he compared the nesting adaptations of Arctic, Common and Sandwich Terns (<u>Sterna sandvicensis</u>) to different methods of avoiding predation. Springett (1967) has also studied the Arctic Tern on Inner Farne, particularly in relation to chick mortality and he showed that the corpses were an important source of food of the beetle <u>Necrophorus investigator</u> Zett., the reproductive period of the beetles coinciding with the pre-fledging period of the terns. Extensive studies on other Arctic Tern colonies include those of Hawksley (1957), Pettingill (1939), Burton & Thurston (1959) and Belopol'skii (1957), while others consider particular facets of the breeding of Arctic Terns such as incubation period and egg size (Bent 1921), clutch size (Suomailainen 1938, Gullestad & Norderhaug 1967) and dimorphism of young (Bergman 1955).

Among comparative studies with other species of terns are the general survey by Marples & Marples (1934) and the more detailed studies by Ashmole (1961) on Ascension Island and Langham (1968) on Coquet Island, Northumberland. Boecker (1967) made a comparative study of the Arctic and the Common Tern, particularly in relation to their feeding ecology.

It has been possible in the present work, which was carried out between 1965 and 1968, to study the effect of age on the breeding biology of the Arctic Tern by trapping large numbers of adults that had been previously ringed. An extensive ringing programme has been carried out on Inner Farne since 1950 and some nestlings have been ringed in most years before that. There was, therefore, a population of breeding terns whose ages could be determined from ringing details. The general breeding biology of the terns was studied, particularly in relation to different substrates on the island. The effect of age on the breeding biology was studied in detail and an attempt made to assess the age structure of the population and annual adult mortality by the construction of a life table.

To some extent the work on the effect of age was cut short in 1968 by an exceptional bloom of dinoflagellates, hereafter referred to as a red tide, which caused the mortality of many sea birds on the Farne Islands, particularly the Shags. The effects of this outbreak, particularly in relation to the Shags, have been described by Coulson et al (1968). Although only a relatively small proportion of terns were found dead, the breeding of the Arctic Terns in 1968 was considerably upset and the reasons for this are discussed in Section 4.

Note :

1. The species nomenclature for plants mentioned in this thesis is from Clapham et al (1962).
2. The species nomenclature for birds is from Vaurie (1965).
3. The statistical analyses have been based on Bailey (1959) and the following symbols have been used :

   d - a normal variable, with zero mean and unit standard deviation (p.36).

   t - the "Student's" statistic modified for small samples (p.48).
4. All times of the day refer to B.S.T.

Study Area

The field work for this study was carried out on the Farne Islands, 55° 35'N, 1° 35'W, (Grid reference NU 2236) and almost entirely on Inner Farne which is the easternmost island, about 1½ miles from the nearest point on the shore. The Farne Islands are the easterly outcrop of the Whin Sill and show the characteristic north-easterly dip, resulting in cliffs on the south and southwest sides of the island which at their highest point are about 60' above Ordnance Datum. Inner Farne has an area of about 16 acres at low water and approximately two thirds of the island then consists of bare rock or rock covered only by lichen; this is mainly around the coastline, with the greatest extent on the north-eastern side. Part of this area is covered by sand forming St. Cuthbert's Cove. The remainder of the island has a thin layer of soil and supports a mixed vegetation of flowering plants. The dominant plants in the tern nesting areas are nettles (Urtica dioica), docks (Rumex obtusifolius and R.crispus), sea campion (Silene maritima), hemlock (Conium maculatum), ragwort (Senecio jacobaea) and thrift (Armeria maritima).

The Arctic Tern is the most abundant breeding tern on the island (in 1967 the number of breeding pairs was estimated to be 2000), but the Common Tern (100 pairs in 1967) and the Roseate Tern (Sterna dougallii) (20-25 pairs in 1967) also breed regularly. The Arctic Terns breed in the rocky areas around the NW and NE sides of the island, including St. Cuthbert's Cove, and also in parts of the vegetation, particularly near the tower and in the area south of the cove; the Common and Roseate Terns are mainly confined to the vegetation. The extent of the areas used by all three species is indicated in the sketch map of Inner Farne in Figure 1.

The Arctic Tern nests were classified according to the predominant ground cover at the nest site, rocks, sand or vegetation, and the differences in the breeding success of these areas were compared. Rocky sites were usually on a flat rock, often with a vertical face on at least one side of the nest, although sometimes the nest was in a gully, between two vertical faces which were only a few inches apart. The nests in the cove were on fine sand. In the vegetation areas the height of the plants varied from a few inches in the case of thrift up to nearly 6 feet in the case of hemlock.

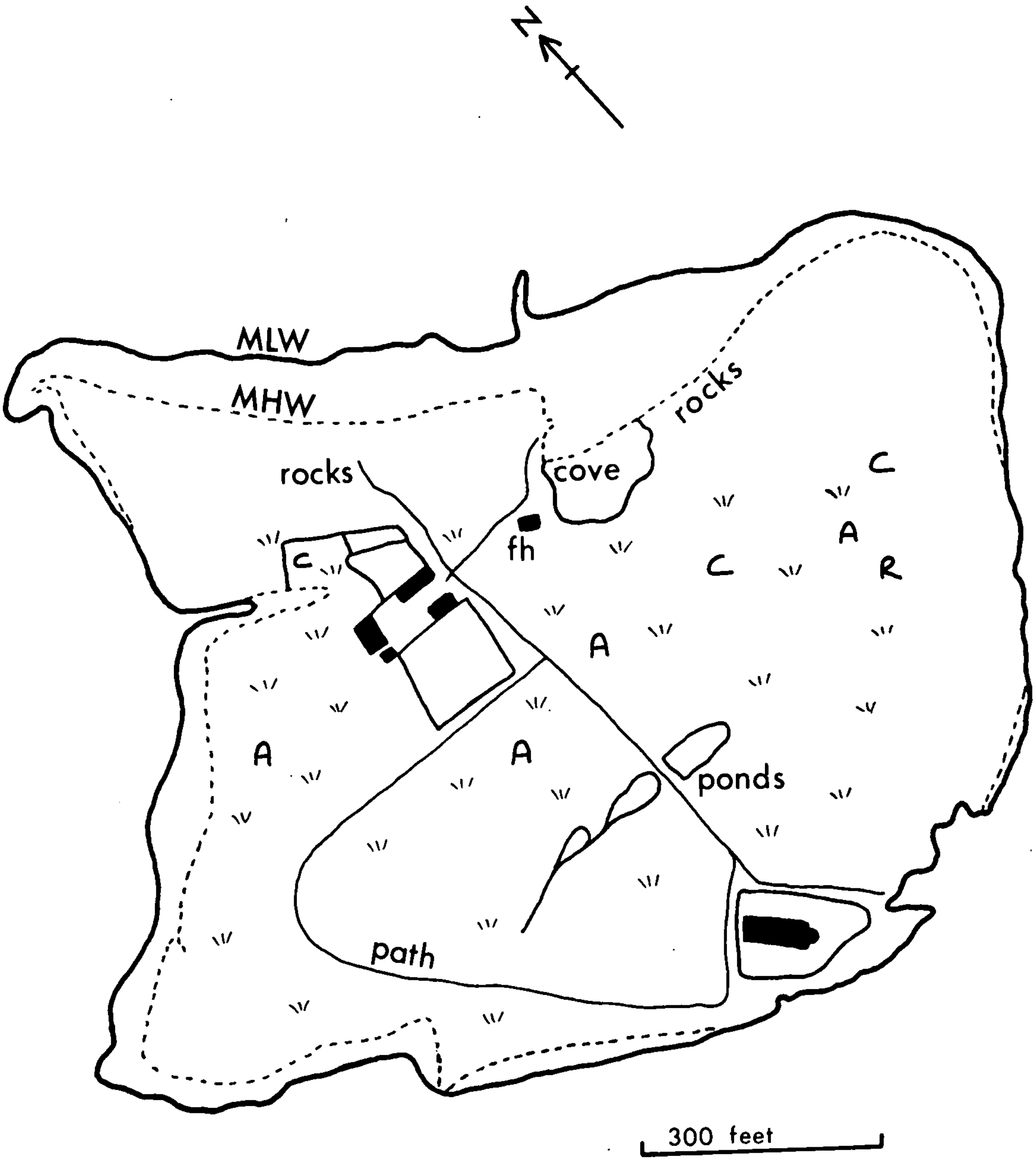
Apart from the comparison between the different areas the main study was concentrated in the cove, particularly the work on birds of known age. There were three main reasons for using the cove extensively :-

(1) Continuous observation of the cove and nearby areas was possible at any time from the top of the derelict building, the Fishe House. Here the observer was hidden from the main path up from the quay, and although some disturbance to the birds was caused by boats landing at the quay bringing day visitors to the island, this was only for a short time each day. The visitors were not allowed access to the nesting areas and were confined to the main paths shown in Figure 1.

(2) Colour-ringing was used to identify birds of known age and it was easier to see the rings on a bird walking over sand than one on rocks or vegetation. In the same way it was found possible to read the ring numbers on some birds using a zoom telescope (magnification x15-x60) and this was much easier in the cove, particularly as the pale sand reflected light on to the rings.

(3) Some re-trapping and colour-ringing of terns in the cove had been undertaken by previous workers, mainly Cullen from 1953 to 1955 and Springett from 1963 to 1965, and some of these colour-ringed birds were still present.

Figure 1. Sketch map of Inner Farne, to show the location of the cove, rock, and vegetation study areas. The Arctic Terns bred predominantly in the cove and rock areas, and in the areas of vegetation indicated by A. The main breeding areas of the Common and Roseate Terns in the vegetation are indicated by C and R respectively. Buildings have been indicated in solid black, including the lighthouse to the SW. of the island, and the fish house (fh) near to the cove.


N
MLW
MHW
rocks
rocks
cove
fh
C
C
C
A
A
A
A
A
R
ponds
path
300 feet

SECTION ONE - GENERAL BREEDING BIOLOGY OF ARCTIC TERNS ON INNER FARNE

Methods

A sample of nests from each of the three main nesting habitats, sand, rocks and vegetation, was studied. This enabled comparisons to be drawn between the effects of the different habitats on the various facets of breeding. As many of the vegetation areas had both Arctic and Common Terns in the same vicinity, the observations on nests in vegetation were confined to those areas used exclusively by Arctic Terns. This avoided the chance of confusing the two species but it reduced the number of vegetation nests which could be studied and therefore this sample was usually lower than those from the other two main habitats.

Each nest was marked with a numbered metal tag and was visited at least once a day when a record was made of its contents. In 1968 the number of nests in the colony at any one time was lower than in other years and it was possible to make twice-daily visits to each nest. This was not attempted in 1966 and 1967 as the number of nests studied was much larger and more time was spent in trapping adult birds at the nest.

The eggs were marked with a chinagraph pencil to record the order in the clutch. The maximum length and breadth of each egg was measured to 0.1mm by use a Vernier caliper. A smaller sample of eggs was weighed at the beginning of incubation and again just before hatching. A sample of young was weighed shortly after hatching and, particularly in 1966 and 1967, a large number of young were weighed every day up to fledging. These were identified by means of a serial numbered metal B.T.O. ring put on a few days after hatching. The young were carried to a torsion balance reading to an accuracy of 0.1g which was kept permanently in a building sheltered from the wind. Some difficulty was experienced in locating young birds more than two weeks of age as by this stage they wandered considerably from the nest site, particularly into dense vegetation. The sample size for the growth rates of older chicks was therefore reduced.

Much of the observation was made from the vantage point overlooking the cove that has already been described. The quantity of experimental rather than observational work was reduced because one was not permitted to enter the nesting areas during the major part of the day when visitors were present on the island.

Return to the colony

Cullen (1956) has given the dates of first sighting of Arctic or Common Terns near the Farne Islands as 3 May in 1953, 7 May in 1954 and 29 April in 1955. Detailed observations on the early arrival were not made in the present study, but single birds were seen in the area of the Farnes from late April onwards in each year. These birds stayed away from the breeding areas at first, spending their time at sea or on areas not normally used for nesting. As the numbers of birds increased at the beginning of May, a few birds came on to the breeding areas, but these usually stayed only for part of the day and were absent overnight. By the middle of May in 1966 and 1968 large numbers of birds were present in the colony, but in 1967 the return to the breeding areas was delayed by nearly a week, possibly by a long spell of very cold, wet weather. At this time of the season, just prior to the onset of laying, the terns were very restless and 'panic' flights (Marples & Marples 1934) were frequent. The behaviour of the terns may have been particularly influenced by the weather until very large numbers of birds appeared when the number of panic flights was reduced, and as the birds settled down to laying their behaviour became more independent of the weather.

Display and nesting territories

When the terns arrived on the breeding areas they very quickly established territories and began to defend these. Springett (1967) suggested that many birds defended a territory during the early phase of the return, which was different from the ultimate territory of the nest site. Of the 35 colour-ringed birds that he studied, 25 changed territories after the initial return and laid their eggs in a different area. For the Black-headed Gull, Larus ridibundus, Tinbergen (1957) postulated that the function of a display territory defended by the male was to ensure the return of the female to the same site, and therefore to the same male. This may have the important function of keeping the pair together before individual recognition is possible, but it does not explain the advantage of changing the territory defended since keeping the same territory all the time could make the pair more familiar with the area and so increase the advantages of having a defended territory. Moore (1957) suggested that these advantages included the prevention of interference with sexual behaviour, the reduction of losses to predators, and less time spent on intra-specific aggression. Tinbergen (1957) further suggested that site attachment was essential as it enabled a bird to return regularly to its brood and, also, that knowing one area very well, the bird could go instantly into cover at the approach of a predator. The latter is inapplicable to adult terns but it is probably of great importance to the chicks.

In 1968 a study was made of the territories taken up on initial arrival in the colony compared with the final nest site. A series of short posts were staked out in the cove, forming a grid where one side of each square was 2 metres long. The grid squares were numbered on a plan of the cove, and the square to which a colour-ringed bird returned initially, and the area in which it was seen displaying, were recorded, together with the area of the nest site. Of the 23 colour-ringed birds under observation, 19 made their initial return to the area in which they finally nested and the majority of the display occurred less than 4 metres from the final nest site. Of the remaining pairs, 2 nested eventually in vegetation and 2 nested very close to a high bank. The display of these pairs took place mainly at the shore line, usually below high tide level when the tide was out. It may have been that display at the nest site was difficult for these pairs because of the nature of the terrain.

It seems likely therefore, that in 1968 at least, the birds returned directly to a particular area of the colony and that most of their pre-laying behaviour took place there, in what would be the ultimate nest site. The only birds which did not display in the nesting area were those which were hindered by vegetation or other physical obstacles, and their display took place mainly in the undefended area below high tide level when the tide was out. The findings of Springett (1967) of a change in territory are not in conflict with the present observations since his results were obtained from birds which were nesting out of the cove, in areas of dense vegetation where display at the nest was physically difficult.

Egg laying

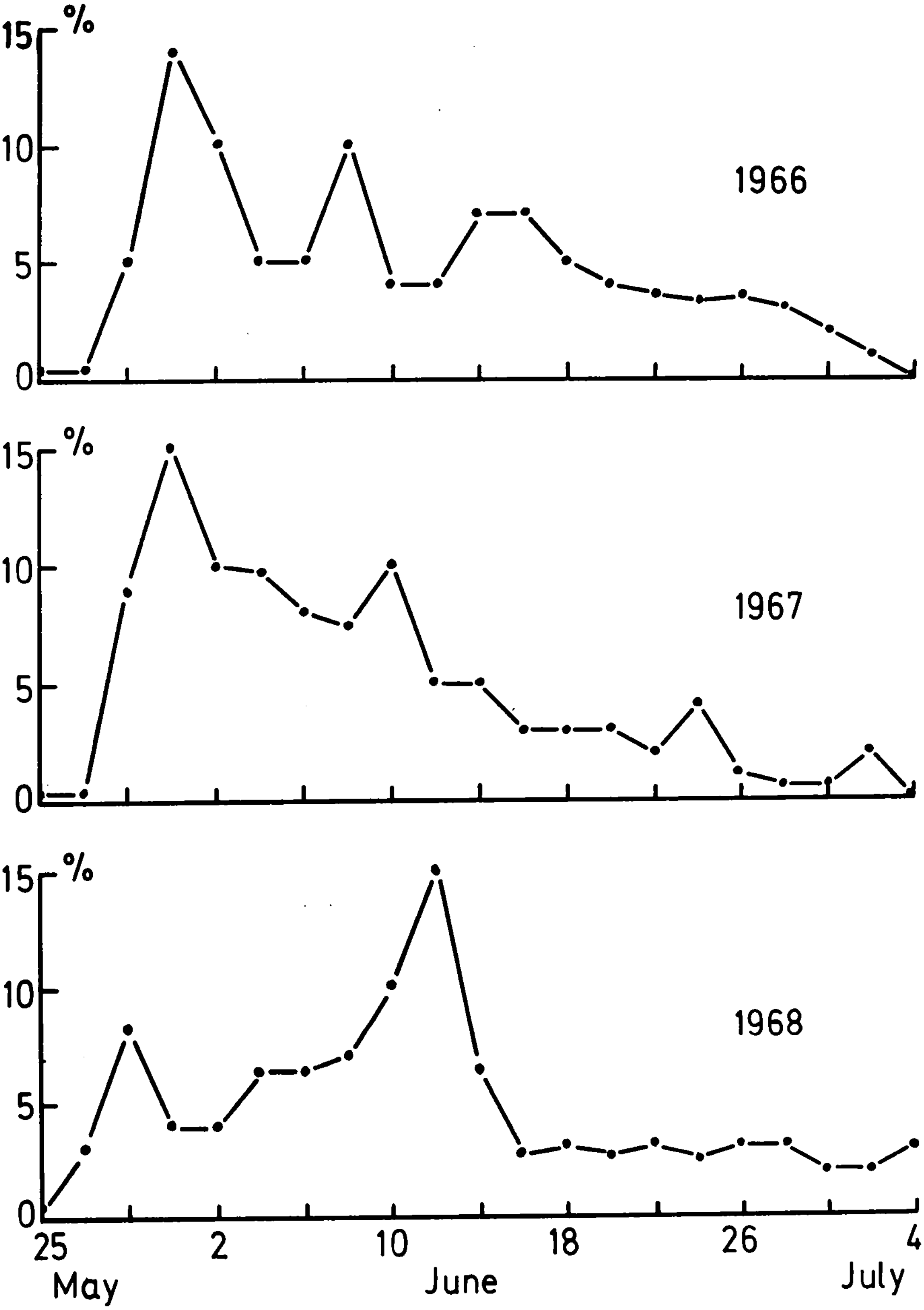
Egg laying normally began a few days after the main return to the breeding areas. The dates when the first eggs were found in each year were 25 May in 1966, 21 May in 1967, and 23 May in 1968, and they correspond closely with the overall mean date of 23 May which has been reported by Springett (1967) for the occurrence of the first egg over the period 1951 to 1964. A more precise comparison between the three years was made by comparing the dates when 25%, 50%, and 75% of the clutches had been started. The data for the three years are presented in Table 1 and show that there was very little difference between the mean dates of the commencement of clutches in the three years, although 1967 was slightly earlier than the other two. This was also reflected in the consideration of 25%, 50%, and 75% of the clutches, the dates for these values being consistently earlier in 1967 than in 1966 and 1968.

Table 1. Dates when 25%, 50%, and 75% of the clutches had been started and the overall mean dates for 1966, 1967, and 1968

Year	25% of clutches started	50% of clutches started (Median date)	75% of clutches started	Mean	No.of clutches
1966	1 June	8 June	17 June	11 June	294
1967	31 May	5 June	12 June	8 June	271
1968	3 June	10 June	16 June	11 June	486

The percentages of clutches started for each 2 day interval for each year are illustrated in Figure 2 which shows that the general pattern of laying was very similar for 1966 and 1967, with a sharp initial increase in the number of clutches started every 2 days, followed by a gradual tailing-off. There is some evidence of a second, smaller peak in these years,which in at least some cases was due to the laying of replacement clutches. In 1968, however, the rate of laying was slow between 29 May and 2 June. This was the main period of the mortality of the adult terns after the red tide and, at this time, many birds were absent from the colony for most of the day until the numbers gradually increased, with the main bulk returning on or after 4 June. These birds spent a few days resuming their courtship and mating, and began laying a few days after their return. This surge of re-laying accounts for the sharp increase

Figure 2. Percentage of total clutches started for every 2 day interval in 1966, 1967 and 1968.



15
%
10
5
0
1966
1967
1968
25
May
2
10
June
18
26
4
July

in the percentage of clutches started between 8 June and 12 June when 25% of the total number of clutches were laid within a 5 day period.

After this the pattern of laying in 1968 was very similar to 1966 and 1967 and the late clutches were again due to the re-laying of clutches destroyed by "normal" mortality which occurred in all three years.

In 1967 a study was carried out to see if there was any diurnal pattern in the time of egg laying. This investigation lasted for 8 consecutive days from 28 May to 4 June. A total of 217 scrapes were each given a large, numbered peg and although the majority of these scrapes were empty, a few contained 1 egg. The scrapes were visited every 2 hours throughout the 8 day period and any new eggs were recorded. In order to minimise disturbance, the scrapes were selected from a concentrated part of the colony, alongside a path. It was thus possible to walk quickly along the path, recording any new eggs without walking through the nesting area. The numbers of all eggs laid in each 2 hour interval over the whole period are shown in Table 2 and Figure 3 and as the total number of eggs laid, 106, is so close to 100, the actual numbers are presented in the figure, rather than percentages, there being little difference between these two parameters.

Figure 3. Total numbers of eggs laid for each 2 hour period of the day between 28 May and 4 June 1967.

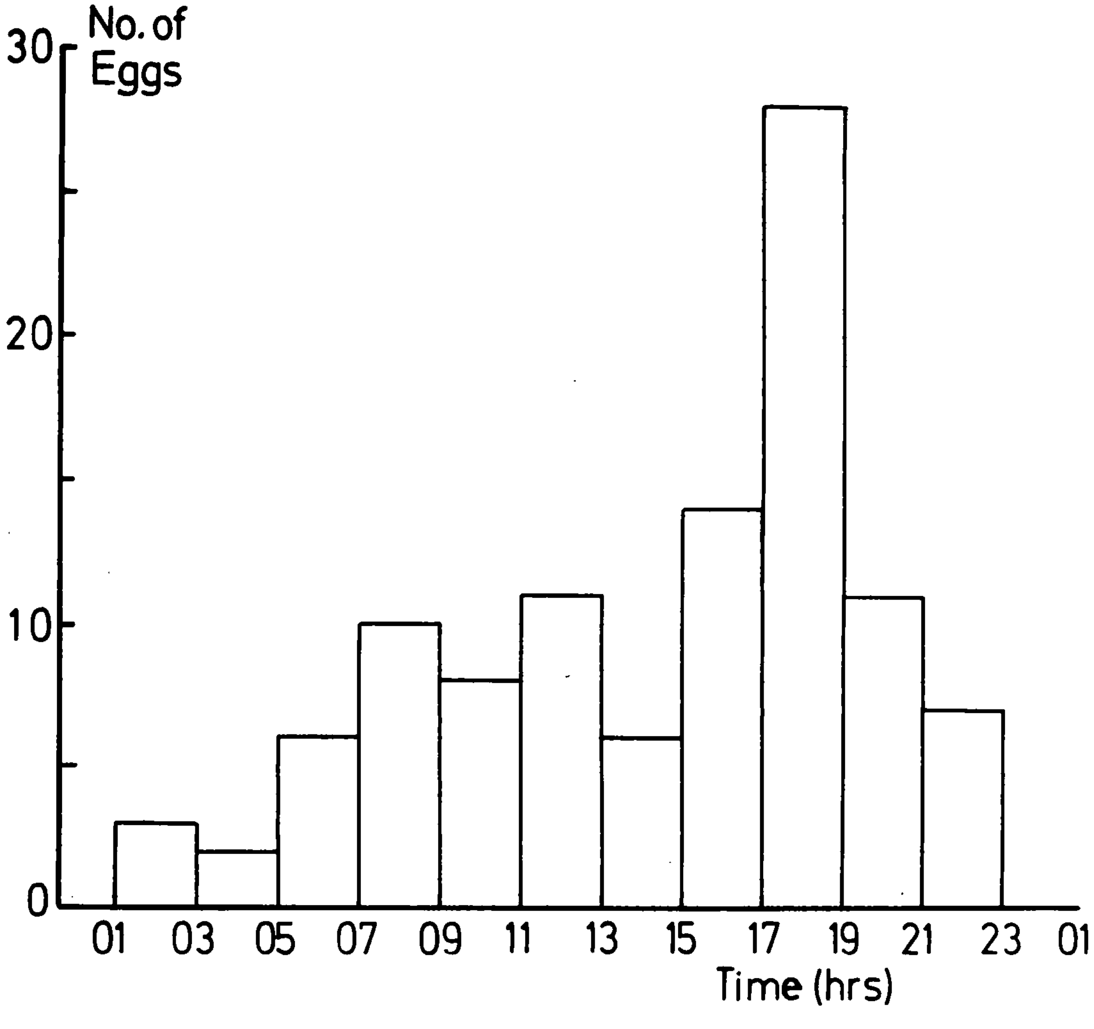

No. of Eggs
30
20
10
0
01
03
05
07
09
11
13
15
17
19
21
23
01
Time (hrs)

Table 2. Total numbers of eggs laid between 28 May and 4 June 1967 in each 2 hour period

Time	Single egg clutch	Clutch of 2 First egg	Clutch of 2 Second egg	Total
0100-0300	1	0	2	3
0301-0500	0	1	1	2
0501-0700	3	2	1	6
0701-0900	3	2	5	10
0901-1100	3	2	3	8
1101-1300	4	4	3	11
1301-1500	0	2	4	6
1501-1700	2	4	8	14
1701-1900	17	3	8	28
1901-2100	6	4	1	11
2101-2300	3	3	1	7
2301-0100	0	0	0	0
Total	42	27	37	106

In comparing the eggs laid during daylight (0501-2100hrs) with those laid during the night, it was found that the mean numbers of eggs laid per two hours (± S.E.) were 11.8 ± 5.0 and 3.0 ± 2.9, respectively. These values are significantly different, $t = 3.02$, df = 10, $P < 0.02$. The higher number of eggs laid during the daylight period was further concentrated into the last six hours, and 50% of all the eggs were laid between 1501 and 2100.

The distribution of the time intervals between the laying of the first and second eggs of clutches of two is given in Table 3.

Table 3. The distribution of the time intervals between the laying of the first and second eggs of a clutch of two in 1967

Time interval (hours)	<10	10-19	20-29	30-39	40-49	50-59	60-69	>69
Number of clutches	0	1	2	5	9	7	3	0

Total number of clutches = 27

The mean time interval (± S.E.) was 46.2 ± 4.6 hours, a finding which shows close agreement with that of Palmer (1941a) who reported that the majority of the second eggs of the Common Tern were laid within two days of the laying of the first egg. It is clear from Table 3 that the second egg may be laid within the same 24 hour period; one egg was laid 18 hours after the first egg, or that it may be laid nearly 3 days later, the three intervals greater than 59 hours being 60, 62, and 64 hours. As the interval between the hatching of the eggs was usually less than two days, it is probable that incubation began sometime after the laying of the first egg. This topic will be considered in more detail later.

Egg measurements

During the three years of the study the maximum lengths and breadths of a large number of eggs were measured, and from these measurements the shape indices, which compare the relative proportions of the lengths and breadths of the eggs and the volumes of the eggs, were calculated. The shape index was calculated from the formula :

$$\text{Shape Index} = \frac{\text{Breadth} \times 100}{\text{Length}}$$

and the volume from the formula and method given by Coulson (1963)

$$\text{Volume} = \text{Breadth}^2 \times \text{Length} \times K$$

where K = 0.000487 and the linear measurements are in mm and the volume is in cc.

A smaller number of eggs were weighed in addition to being measured. The mean values for the lengths, breadths, and calculated volumes for 1966, 1967, and 1968 are presented in Table 4.

It is clear from Table 4 that there was no consistent trend to produce greater lengths and breadths in any one year, and from an inspection of the standard error values it can be seen that there was no significant difference between the mean volumes of the eggs in the three years.

Table 4. Mean lengths, breadths, and volumes (± 2 standard errors) for the eggs in each year

Year	Length	Breadth	Volume	No. in sample
1966	40.35±.24	29.15±.11	16.41±.20	194
1967	40.13±.22	29.00±.09	16.23±.14	246
1968	40.45±.56	29.01±.09	16.36±.13	380
All	40.33±.12	29.01±.06	16.33±.09	820

The overall mean length of these eggs corresponds closely to the value of 40.22mm which is given by Witherby (1941) as the average value for 100 British eggs, but the overall breadth is smaller than Witherby's average value of 29.37mm for this dimension. Both the mean length and the mean breadth of the eggs measured on Inner Farne are smaller than the averages of 41.0mm and 29.5mm respectively, which are given for 123 eggs by Bent (1921). There is no indication in either of these two sources of the time of the season when the measurements were made, and as the dimensions of the eggs were found to vary during the season, it is possible that the discrepancies between the quoted dimensions and those of the present study may be accounted for by seasonal variation. Alternatively, geographical variation in egg size is a possible source of difference, although there is very little indication of variation in the size of the adults.

The values for the overall shape index in 1966 and 1967 were 72.35 and 72.36, indicating almost identically shaped eggs. However, the mean shape index for 1968 was 71.82, indicating longer, narrower shaped eggs, but this value is not significantly different from the other two years.

The eggs from each year have been considered in more detail according to the size of the clutch and the order of laying, and Table 5 shows the mean lengths, breadths, and volumes for three categories of eggs; those from single egg clutches (C1), first eggs from clutches of two (C2/1), and second eggs from clutches of 2 (C2/2) for each of the 3 years.

In 1966 and 1967, there was a tendency for the first eggs of the clutches of two to be larger, both longer and broader, than the single eggs. This trend was reversed in 1968 when the single eggs tended to be larger. Neither of these differences was significant and may have been due to the variation within the years' samples.

In all 3 years the second eggs of the clutches of 2 were significantly smaller, in length, breadth, and volume than either the single eggs or the first eggs of the clutches of two. For the differences in length, d=3.78 $P < .001$, for the breadth, d=4.80 $P < .001$, and for the volume, d=5.44 $P < .001$. These differences were also reflected in the shape indices; the mean for all single eggs was 71.99, for first eggs of the

Table 5. Mean lengths, breadths, and volumes (± 2 standard errors) for 3 different categories of eggs for all 3 years (the total numbers of eggs measured are shown in Table 6A only, in parentheses)

A - Lengths (mm)

Egg category	1966	1967	1968	All
C1	40.34±.32 (94)	40.30±.32 (105)	40.60±.22 (263)	40.48±.16 (462)
C2/1	40.74±.44 (50)	40.43±.46 (70)	40.30±.40 (69)	40.46±.26 (189)
C2/2	39.97±.54 (50)	39.60±.32 (71)	39.86±.50 (48)	39.78±.26 (169)

B - Breadths (mm)

Egg category	1966	1967	1968	All
C1	29.19±.14	29.09±.16	29.08±.11	29.10±.08
C2/1	29.24±.24	29.17±.16	29.03±.18	29.14±.11
C2/2	28.97±.22	28.70±.17	28.63±.22	28.76±.12

C - Volumes (cc)

Egg category	1966	1967	1968	All
C1	16.51±.22	16.40±.24	16.50±.16	16.48±.12
C2/1	16.74±.36	16.53±.26	16.31±.26	16.50±.16
C2/2	15.90±.58	15.68±.26	15.70±.36	15.75±.22

clutches of two it was 72.13, and for the second eggs of the clutches of two it was 72.39. The single eggs tended to be long and narrow, the first eggs of the clutches of two had a slightly broader shape, whereas the second eggs had a relatively shorter, broader shape than either of the other two groups. This is in contrast to Coulson's findings (1963) for the Kittiwake where the last eggs laid in clutches of two and three were narrow and had a lower shape index than the other eggs in the clutches. However, as in the Arctic Tern, these last eggs had a relatively lower volume than the other eggs laid. This seems a typical feature of the Laridae; Paludan (1951) found a reduction in the volume of the terminal eggs of the Herring and Lesser Black-backed Gulls, Preston & Preston (1953) found a similar reduction in the Laughing Gull, Larus atricilla, as did Gemperle & Preston (1955) in the Common Tern. Gemperle & Preston further suggested that in 90% of the total clutches of three examined, it was possible to pick out the terminal egg without measurement by the differences in shape, but it was not possible in the present study to select the second egg by eye as the differences in the clutches of two in the Arctic Tern were not so great as those found in the clutches of three in the Common Tern.

Variation of egg size with season

The breeding season was divided arbitrarily into 5-day periods and the sizes of the eggs laid during different periods were compared for each year. Where the samples for adjacent periods were both less than 20, these were combined to give an average over a 10 or 15-day period. This occurred particularly towards the end of the laying period. The variations in length, breadth, volume and shape index throughout each season are shown in Figures 4-7 respectively and are considered in greater detail below.

Length

There was very little general pattern in the changes in the lengths of eggs during the season, and while there was an increase towards the end of the season in 1967, this was entirely due to a group of very late clutches laid in an isolated area. The effect of these clutches can be seen in Figure 8 which shows some increase in the standard deviation of the egg lengths throughout the season in 1967, compared with the fairly uniform values of standard deviation throughout 1968. These late clutches in 1967 were laid on an area of the rocks not normally used by the terns and many of the eggs laid were significantly larger than those laid in the rest of the colony at the same time. The laying of these eggs was very well synchronised and may have been due to a group of birds being disturbed from one part of the colony. All the eggs were laid on open rocks and were preyed upon within a few days of being laid. No birds nested in the same area in 1968.

Breadth

The general trend in all 3 years was a decline in the breadth of the eggs during the season; the only exception to this being the increase late in 1967 which was due to the group of birds already mentioned. The variation in the breadths of the eggs was much less

Figure 4. Variation of mean egg length with season in 1966, 1967 and 1968.

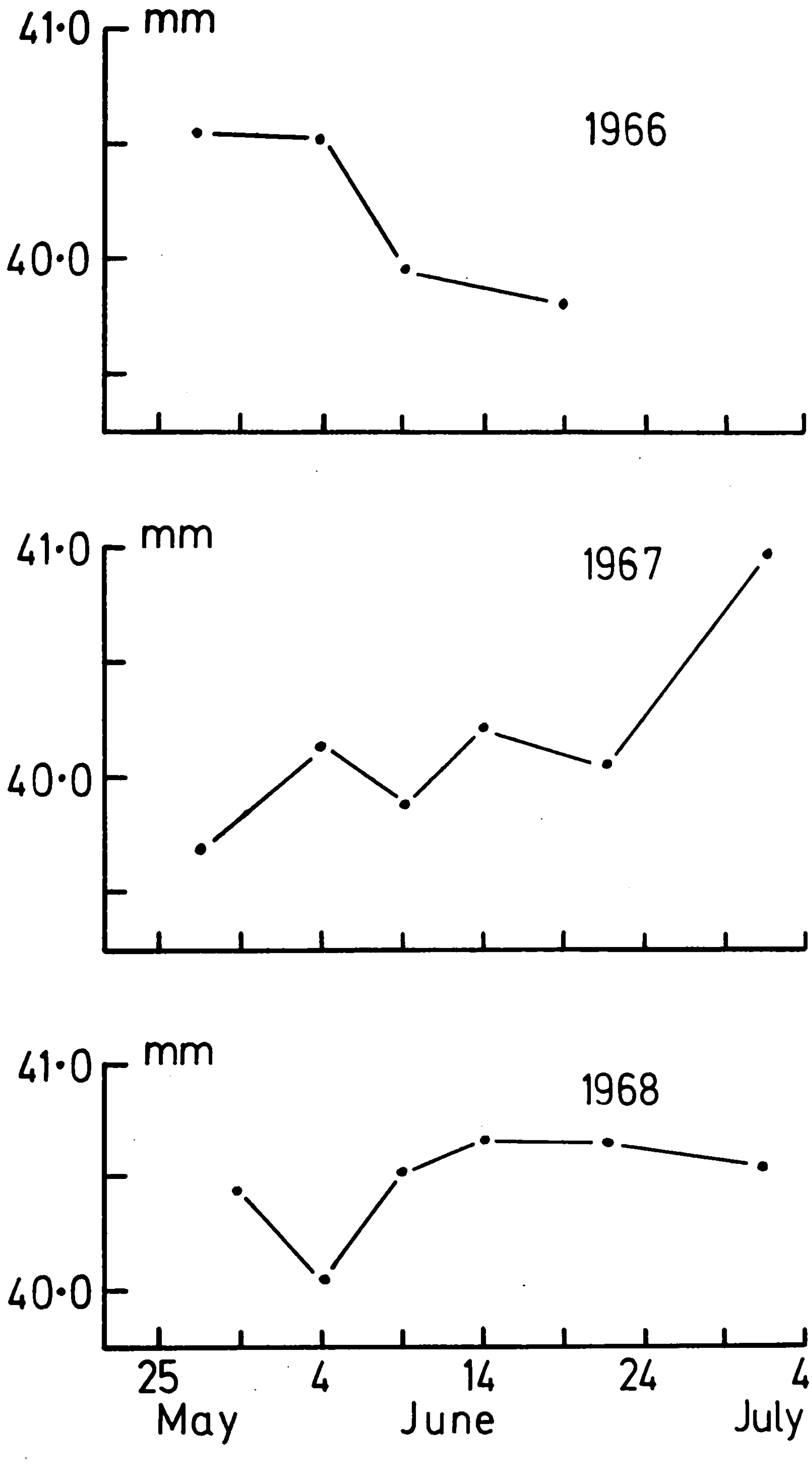
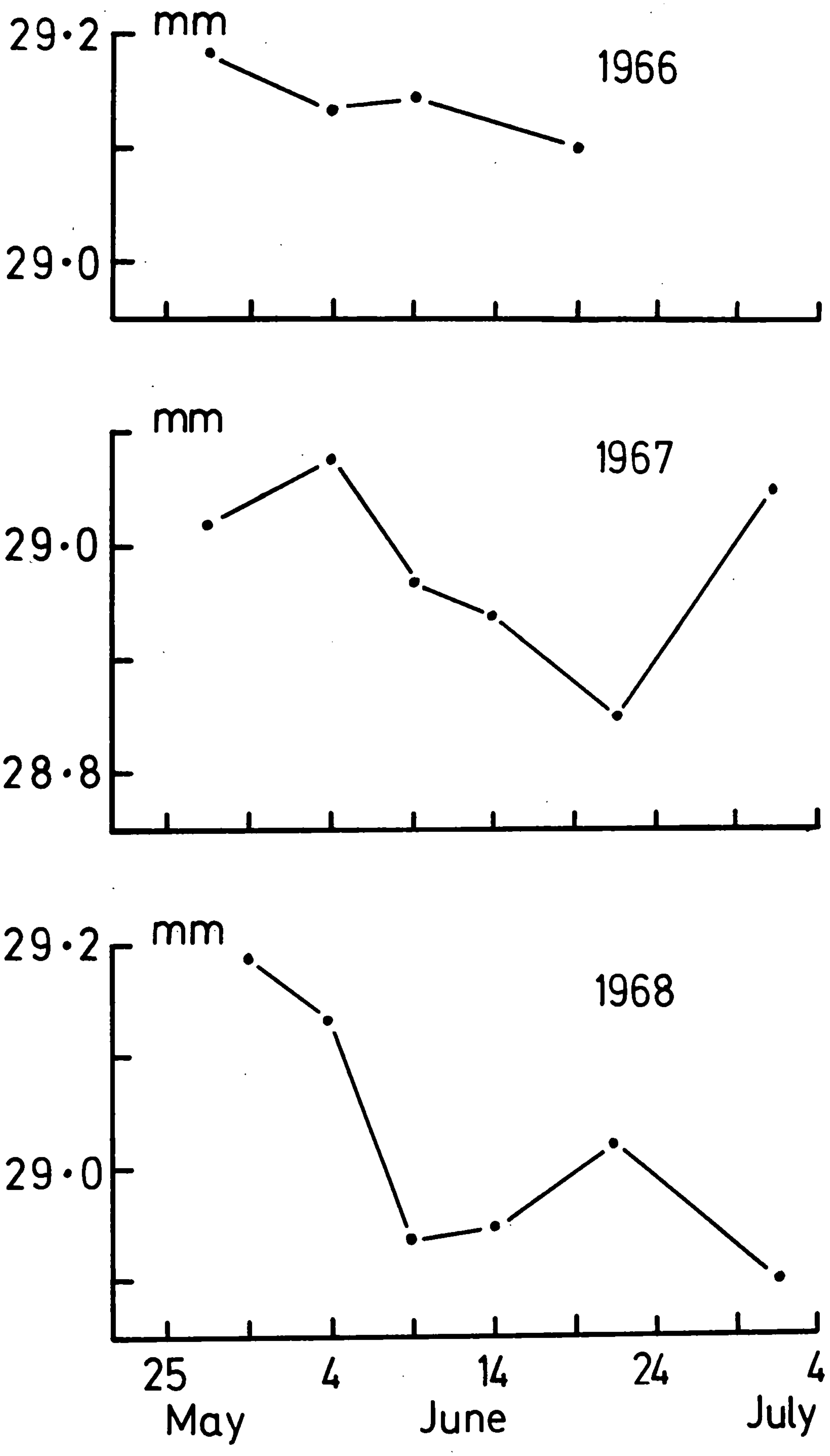

41·0
mm
1966
40·0
41·0
mm
1967
40·0
41·0
mm
1968
40·0
25
May
4
June
14
24
4
July

Figure 5. Variation of mean egg breadth with season in 1966, 1967 and 1968.



29·2
mm
1966
29·0
mm
1967
29·0
28·8
29·2
mm
1968
29·0
25
May
4
14
June
24
4
July

Figure 6. Variation of mean egg volume with season in 1966, 1967 and 1968.

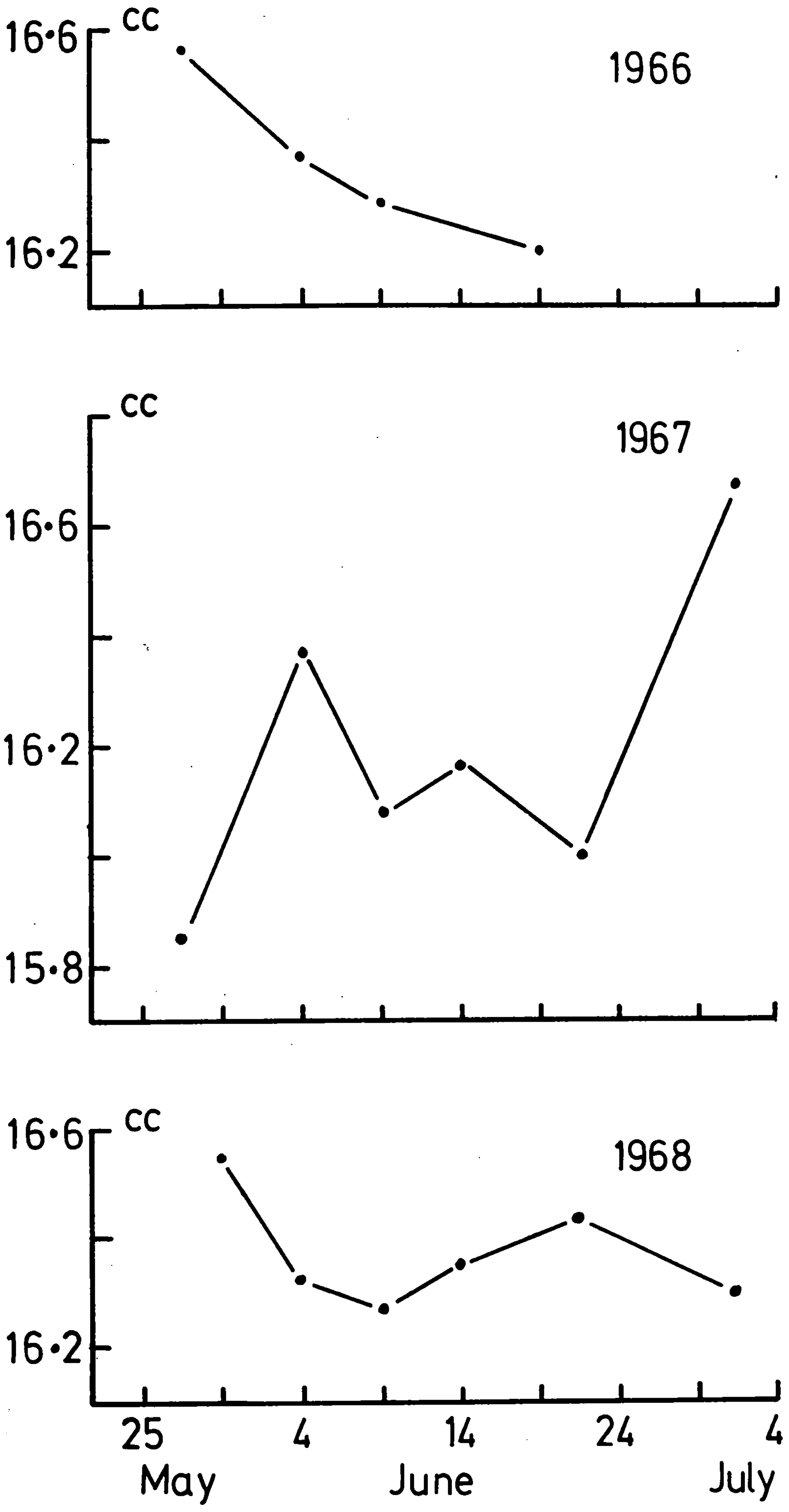

16·6
cc
1966
16·2
cc
1967
16·6
16·2
15·8
16·6
cc
1968
16·2
25
4
14
24
4
May
June
July

Figure 7. Variation of mean egg shape index with season in 1966, 1967 and 1968.

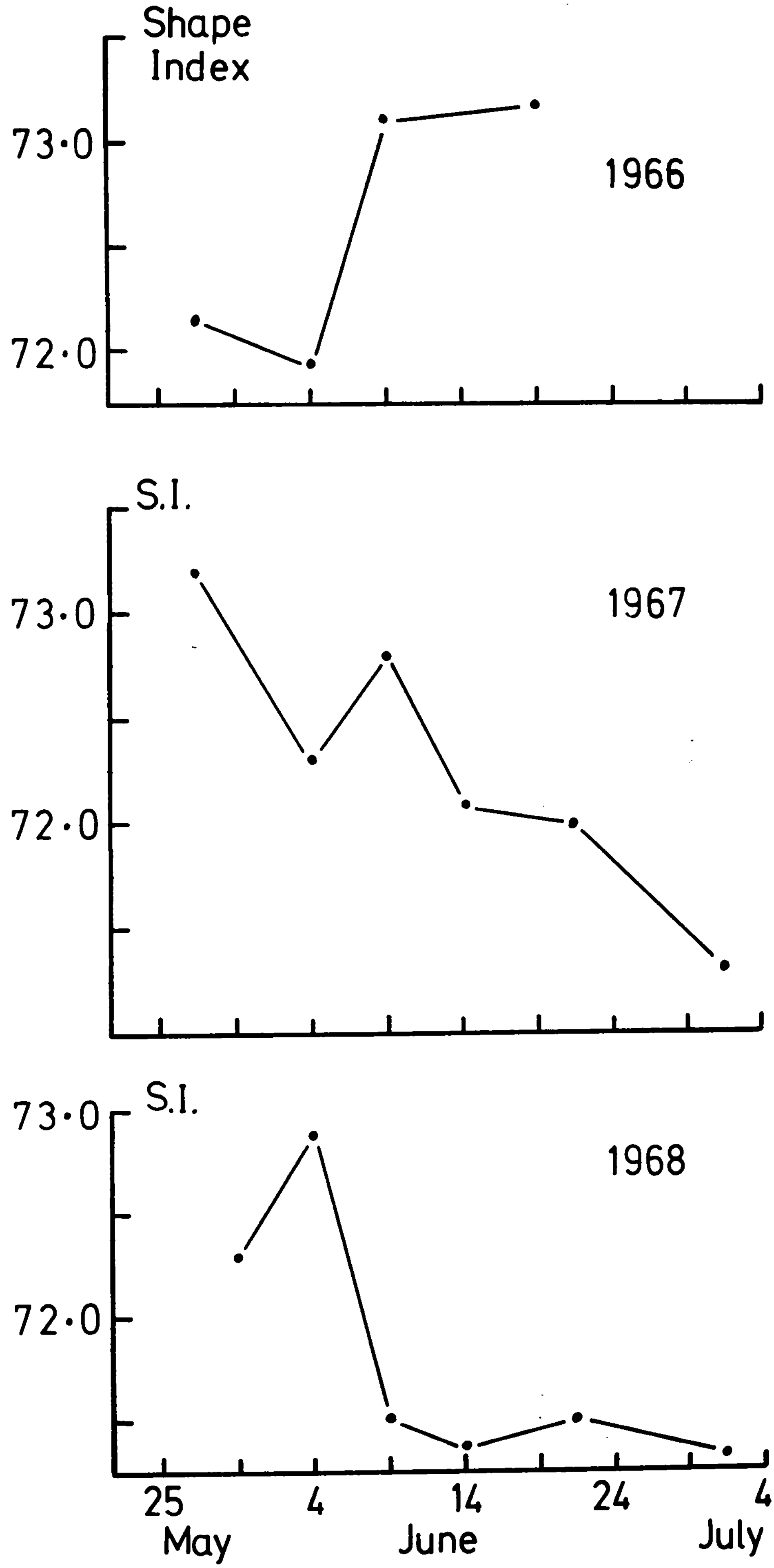
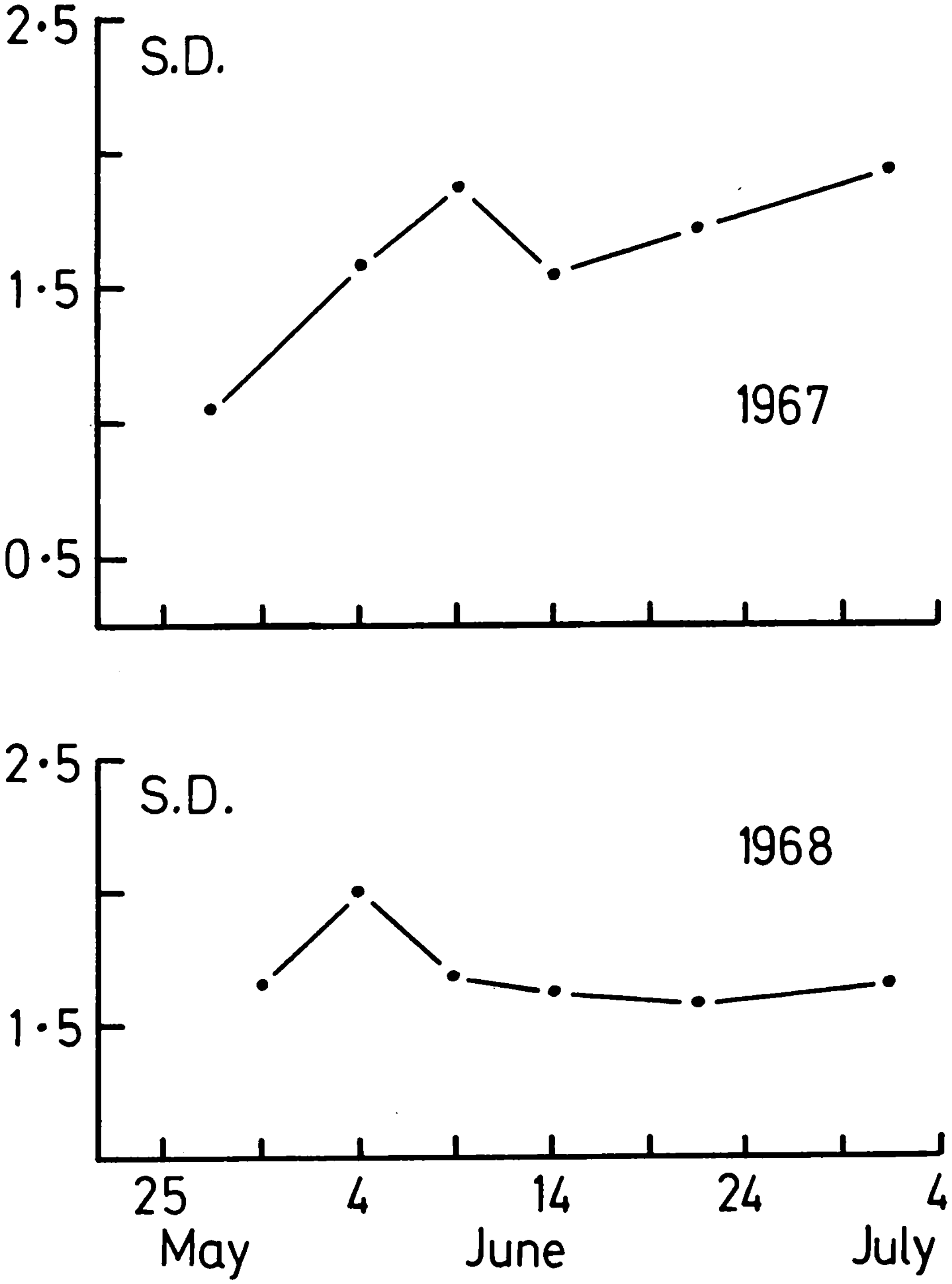

Shape Index
73·0
72·0
1966
S.I.
73·0
72·0
1967
S.I.
73·0
72·0
1968
25
May
4
14
June
24
4
July

Figure 8. Variation of standard deviation of egg length with season in 1967 and 1968.



2·5
S.D.
1·5
1967
0·5
2·5
S.D.
1968
1·5
25
May
4
14
June
24
4
July

than that in the lengths, and in 1966 the full range of the mean breadths lay between 29.1 and 29.2mm.

Volume

As the value of the breadths of the egg was squared during the calculation of the volume, this has a greater influence on the volume than the length. Accordingly it is not surprising to find similar seasonal variation of the volume and of the breadth. In 1966 there was a general decline in the value of the volume throughout the season, and similarly for 1967, apart from the upsurge late in the season due to the group of late-nesters on the rocks. There was very little variation in the volumes of the eggs in 1968.

All the initial eggs laid prior to 28 May were very small; in 1966, four eggs laid during this period had a mean volume of 15.20cc and in the same period in 1967 the mean volume of eight eggs was 15.72cc. No eggs were laid during this period in 1968.

Shape Index

In 1966 the shape index was low initially, indicating relatively long or narrow eggs, but was of a high value later in the season, indicating broader or shorter eggs. As the breadth of the eggs showed a slight decrease throughout 1966, the decrease in the length must have been greater in proportion to the decrease in the breadth. In 1967 and 1968 the shape index gradually declined throughout the season as the eggs acquired a longer, narrower shape. This was due more to a decrease in breadth rather than to an increase in length.

All these trends are rather similar but less marked than those found in the Kittiwake by Coulson (1963) where there was a progressive decrease of the length and shape index throughout the season, an initial increase in volume and length until the middle of the laying season, followed by a rapid decrease in volume and a smaller decrease in length with a suggestion of an increase at the end of the season. Coulson suggested that these trends were partly the result of older females breeding early, but this was unlikely to be the case in the terns as the laying of the birds of all ages was fairly well synchronised and the largest eggs occurred in the middle-aged group rather than in the oldest birds. The effects of age on the time of laying and the size of the eggs are dealt with in more detail in Section 3. In a later paper Coulson et al (1969) showed that for the Shag, within an age class, the early breeding birds laid larger eggs than the late breeders.

Clutch size

In many cases it was impossible to determine the size of the full clutch as predation took place shortly after the laying of the first egg. These clutches were therefore discounted and only those nests which contained the same total number of eggs for 3 consecutive days were included in this analysis. The mean clutch sizes for the 3 years are given in Table 6.

Table 6. The numbers and percentages of one, two, and three egg clutches together with the mean clutch size (± 2 standard errors)

Year	Number(& percentage) of C1	C2	C3	Total clutches	Mean clutch size
1966	99(34.0%)	192(66.0%)	0	291	1.66±0.06
1967	146(34.0%)	275(64.1%)	8(1.9%)	429	1.68±0.05
1968	194(57.9%)	140(41.8%)	1(0.3%)	335	1.42±0.06

The mean clutch sizes, particularly from the "normal" years of 1966 and 1967 are in close agreement with Cullen's comments in Bannerman (1959) stating that clutches of one and two predominate with an average clutch size of 1.5 - 2.0 which varies from year to year. In other regions the clutch size may be quite different. Gullestad (1967), studying two extreme localities in West Spitsbergen, found that 2-egg clutches were more common (69.1%) in the south western locality than in the northern area (57.1%) which had a different climate with later melting of ice and snow. Table 7 gives the clutch size quoted by various authors in different regions. Many of these figures are based on spot checks and may therefore be rather low. Springett (1967) found from a close study of 50 nests, each of which originally had two eggs, giving a clutch size of 2.0, that the mean clutch size was reduced to 1.4 due to egg losses during incubation.

Table 7. Mean clutch size of the Arctic Tern in different regions

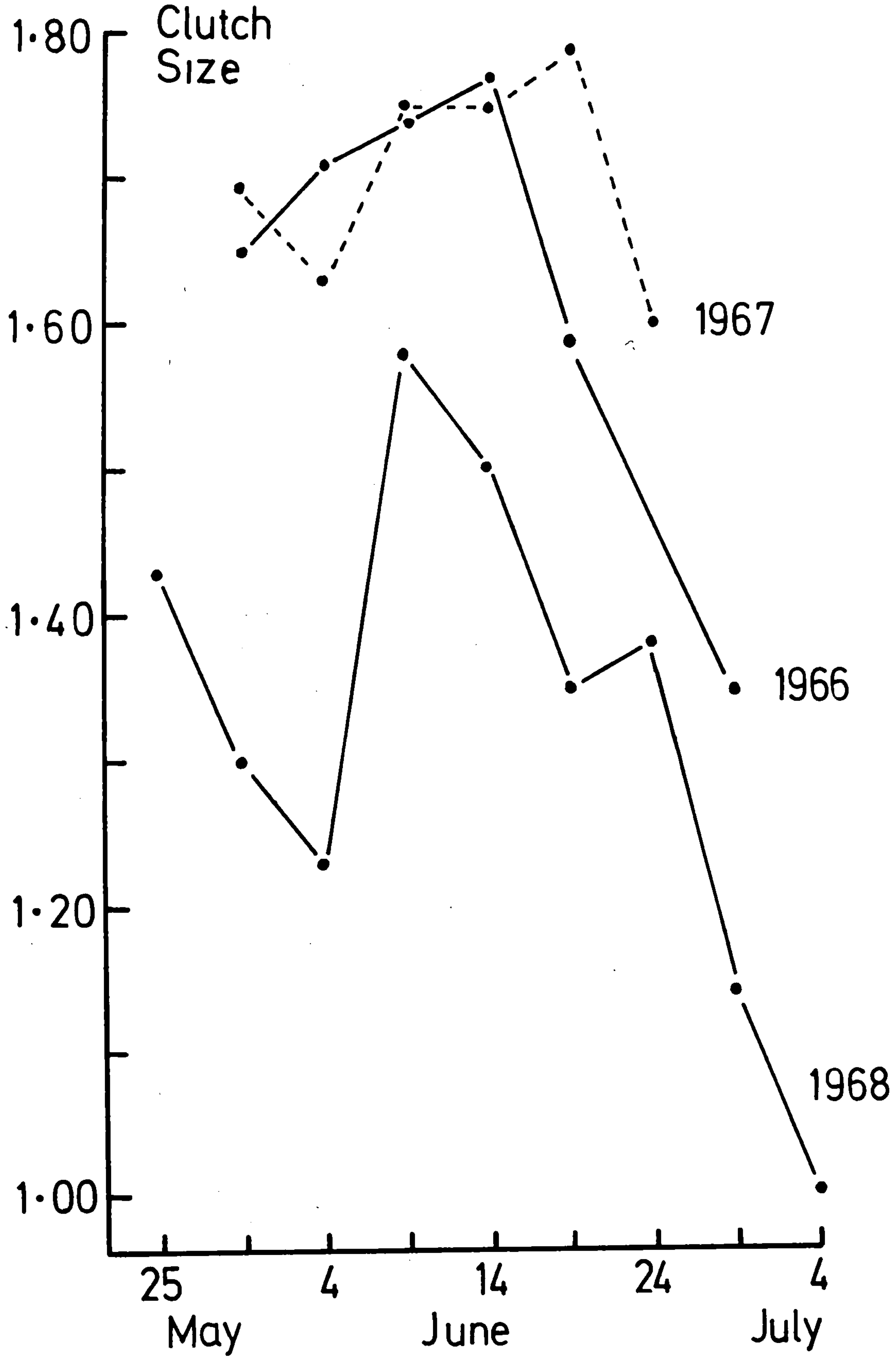
Clutch size	Sample	Locality	Latitude	Authority	Year of observation
1.44	100	Machias Seal Island Canada	45° N	Pettingill (1939)	1939
1.19	130	" "	45° N	Hawksley (1957)	1947
1.73	125	" "	45° N	"	1948
1.62	208	Wangeroog Germany	53° 47'N	Boecker (1967)	1962
2.23	210	"	"	"	1963
2.01	172	"	"	"	1964
1.70	209	Ravenglass, England	54° N	Bickerton(1909)	1909
1.92	82	Norderoog, Germany	55° N	Dircksen(1932)	1932
1.88	92	British Isles	55° N	Marples & Marples (1934)	1934
1.86	55	Coquet Island, England	55° 20'N	Langham (1968)	1965
1.80	45		"	"	1966
1.81	82	"	"	"	1967
1.69	92	Farne Islands England	55° 40'N	Cullen (1957)	1954
1.76	29	"	"	"	1954
1.91	90	"	"	"	1955
1.94	49	"	"	"	1955
1.87	1116	"	"	Springett(1967)	1961
1.61	699	"	"	"	1962
1.75	864	"	"	"	1963
1.76	868	"	"	"	1964
1.66	291	"	"	(pers.obs.)	1966
1.68	429	"	"	"	1967
1.42	335	"	"	"	1968
2.00	45	S.E.Alaska	60° N	Williams(1947)	1947
1.70	279	Greenland	62° N	Eklund (1944)	1944
2.12	60	Finnish coast	63° N	Suomalainen (1938)	1938
1.80	127	Canada	64° N	Sutton (1932)	1932
2.01	82	U.S.S.R.	73° N	Belopol'skii(1961)	1961
1.69	55	Spitsbergen (2 localities)	78° N	Gullestad & Norderhaug(1967)	1965
1.57	42	"	"	"	1965

The difference between the clutch size for 1967 and 1968 is a significant one ($d = 5.66$ $P<0.001$) and may again be explained by the effects of the red tide. Many birds may have started laying before the main dispersal from the colony due to the red tide but may not have completed these initial clutches and the eggs were preyed upon during the birds' absence. When they later returned to the colony and re-laid, the replacement clutches were smaller with a high preponderance of clutches of one. This is shown later in this section to be typical of replacement clutches in a normal year and accounts for the low clutch size in 1968.

The changes in clutch size throughout the season were examined in all years and the results are shown in Figure 9, where in 1966 and 1967 there is a slight increase in clutch size from the beginning of the season until, after reaching a peak with a mean clutch size of 1.77 in 1966 and 1.79 in 1967, the proportion of 2-egg clutches declined, reducing the mean clutch size although this effect was delayed in 1967. In 1968, the clutch size fell during the early part of the season when the main effects of the red tide were seen. After the main mortality of terns, the mean clutch size rose sharply to a peak of 1.58 and then steadily declined during the rest of the season until early July when all the clutches were of single eggs.

During the main period of the red tide some birds did lay but they produced only small clutches. The reasons for this are not obvious, but presumably the

Figure 9. Variation of mean clutch size with season in 1966, 1967 and 1968.


Clutch Size
1·80
1·60
1·40
1·20
1·00
1967
1966
1968
25
4
14
24
4
May
June
July

phenomenon may have had a general depressant effect on the breeding of the colony, possibly by affecting its food supply although there is no direct evidence for this.

Incubation Period

The incubation period may be defined as the time between the onset of continuous incubation of the egg and the hatching of that egg. The onset of continuous incubation was difficult to determine and it was often found that birds which had apparently started incubating would leave the clutch for periods of varying length. It was usually possible to distinguish these clutches by estimating the temperature of the eggs by hand. Eggs which were being continuously incubated felt very warm and retained most of that heat during the period of the routine, twice-daily, round. These eggs were put into the category of 'warm'. Other eggs, where the adults were presumably only incubating at irregular intervals and which did not feel warm, were put into a 'cold' category. In most cases these two categories of continuous and intermittent incubation were confirmed by observation.

On the basis of this information it was found that incubation of a single egg may not begin until one or even two days after laying, which is in general agreement with Cullen (in Bannerman 1959) who stated that incubation began with the first egg but was less continuous than later. Hawksley (1957) also found that in some cases incubation began before the clutch was complete. Of the 32 clutches of two that were examined in the present study, 10 birds (31% of the clutches) began incubating on the same day that the first egg was laid and 19 birds (59% of the clutches) delayed incubation until the second egg was laid. In three cases,(9% of the clutches) incubation began on the day between the laying of the first and second eggs. The mean incubation periods for single eggs, and the first and second eggs of a clutch of two, are given in Table 8.

Table 8. The mean incubation periods for single eggs, and first and second eggs of a clutch of two, together with the overall mean incubation period

Egg category	Mean incubation period (days ± 2 stan.errors)	Number of clutches
Clutch of 1	22.39 ± 0.72	19
Clutch of 2 first egg	22.09 ± 0.44	32
Clutch of 2 second egg	21.87 ± 0.52	32
All eggs	22.07 ± 0.32	83

It is clear that there is no significant difference between the incubation periods of any of the three egg categories. Belopol'skii (1961) found that the average period from the laying of the second egg, which he considered to be the true onset of incubation, to the time the nestlings hatched, was 20.2 days for the first chick, 21.3 days for the second, and 20.5 days for the third, with the maximum time between 20 and 22 days. This apparently shorter incubation time is due to Belopol'skii calculating from the laying of the second egg, and not, as in the present study, from an estimated time of the onset of incubation which in 13 out of 32 clutches was before the second egg was laid.

Role of the sexes in incubation

A continuous watch over a number of days was maintained on a selection of nest sites in order to determine (a) the length of time each bird spent at the nest, and (b) whether there was any difference between the sexes in the length of time spent incubating the eggs. This was possible only on colour-ringed birds where the sex was known, and therefore any detailed analysis of the results is impossible due to the small sample. In 1967, the sex of the incubating bird was found by the observation of colour-rings on 31 occasions, and in 1968, on 34 occasions, and out of this total of 65 observations, the male was found incubating on 30 (46%) occasions, and the female on 35 (54%) occasions. These figures suggest that both parents may share the role of incubation equally and are in agreement with the findings of Dirksen (1932) and Bent (1921). In contrast Palmer (1941a) has reported that females of the Common Tern do 75% of the incubation and Schönert (1961) has suggested that the males of the Little Tern, Sterna albifrons, do no incubating, but bring food for the incubating female.

Hatching success

The hatching success for the three years has been determined by calculating the number of eggs which produced live young as a percentage of the total number of eggs laid. These values are shown in Table 9.

Table 9. Hatching success for 1966, 1967, and 1968

Year	Total number of eggs	Number of young hatched	Hatching success
1966	322	143	44.4%
1967	508	239	47.0%
1968	659	103	15.6%

The results from the first two years were very similar but there is a significant difference between the success of the 1967 and the 1968 eggs ($d=11.67$ $P<0.001$). The reasons for the low hatching success in 1968 were probably related to the red tide and are discussed more fully in Section 4.

The main reason for hatching failure was predation of the eggs by Starlings. This phenomenon was first noted by Springett (pers.comm.) in 1963 and seems to be peculiar to Inner Farne. No reference to its occurrence can be found in any other colony although predation by other species, particularly by gulls of various species, is well documented (Cullen 1960).

A few, usually four or five, pairs of Starlings bred on Inner Farne each year, and these resident birds appeared to constitute the main predators. They were observed flying between nest hole and the tern colony with beaks stained with yolk on a large number of occasions. Small flocks of Starlings occasionally appeared on the island, presumably from the mainland, but these were never observed systematically searching for eggs although they may have taken any eggs discovered accidentally. It seems therefore that this habit of egg predation by Starlings has been acquired on Inner Farne and is confined to the breeding population there.

Although Arctic Terns viciously attacked most intruders entering the colony, even harmless ones like rabbits, Oryctolagus cuniculus (L.) and Eiders, Somateria mollissima, they were less aggressive towards the Starlings. This may be connected with the size and colour of the Starlings. They resemble, in gross appearance, the Rock Pipits, Anthus spinoletta petrosus, which also enter the colony unmolested. Terns seem to react more strongly to larger birds, particularly to light coloured plumages, and their behaviour is, for instance, completely upset by the appearance in the colony of a wandering racing pigeon, which they will mob for hours on end, often leaving clutches unguarded.

The Starlings which had developed the habit of predation were very thorough in their search for eggs. One method of searching was to fly low over the colony and dart straight to an unguarded nest as soon as this was observed. The eggs were broken immediately by one sharp blow with the bill, usually cracking the egg into two pieces. The second method they used particularly when most of the terns had left their eggs during a panic flight. As soon as the terns left the colony on their outward flight, a Starling landed in the nesting area, running quickly through it, darting to either side in its search for eggs. On a few occasions, when Starlings were searching the ground like this, they preyed upon more than one clutch, taking a small amount from each egg.

Starlings sometimes remained at the site of predation for a minute or two, feeding on the egg contents, but they usually left the site fairly quickly, presumably carrying some of the egg contents inside the bill, or perhaps to be later regurgitated if feeding young. They were never observed to carry away the shell with or without any egg contents in it. Sometimes when preying upon a clutch of two eggs Starlings were seen to break both eggs although they only fed from one. They were never seen to return to a clutch to feed on the egg contents on a second occasion.

It was not always possible to determine whether or not an egg of a clutch had been preyed upon. When predation was observed in the cove area, it was sometimes impossible to find any trace of the clutch within two hours of the time of predation. It is possible that some clutches in the study area were started and preyed upon within a few hours of the first egg being laid and as these clutches would be missed by the twice daily round, the true level of predation may have been even higher than estimated. Any eggs which disappeared were assumed to have been preyed upon as this, from direct observation of other clutches, was the most likely explanation. On this basis, in 1967, predation accounted for 85% and in 1968 89% of the total egg loss.

Predation was more likely to occur early in the incubation period than later, and Table 10 shows the number of eggs which were preyed upon, expressed as a percentage of the total number of eggs at risk at that time, for three periods of the incubation time in 1968.

Table 10. Percentage predation during three periods of incubation in 1968 based on 335 clutches

Period of incubation	Percentage predation per day	Significance of the difference
Less than 2 days after laying	8.7	
		d= 3.76 $P < 0.001$
2 - 12 days after laying	5.4	
		d=2.54 $P < 0.02$
More than 12 days after laying	3.8	

There is a significant difference between the percentage of predation in each of the three periods. It is likely that the initial higher level of predation may be explained by the low frequency of incubation, particularly of 2-egg clutches, between the laying of the first and second eggs.

Birds which had been incubating for a few days were less likely to be disturbed than those which were only just starting incubation and their eggs would be less likely to be left exposed to predation.

The other main causes of egg loss were desertion and flooding of nests by high spring tides which, in 1967, accounted for 4.8% and 1.9% of the total egg loss respectively. A few eggs survived the incubation period and started to hatch, but the chick died during hatching. This often seemed to be due to a very thick shell membrane which the embryo found impossible to tear open. A very small number of eggs failed to hatch, less than 0.5%, but the reasons for this are not known; the eggs were incubated apparently normally but failed to hatch. This was a much lower rate of failure to hatch than the 5% observed by Pettingill (1939) and the 10% by Hawksley (1950). It is possible that a much larger proportion of the eggs were infertile or addled, but that they were preyed upon before incubation was completed.

In 1967 an attempt was made to see if human disturbance to the birds increased the chances of predation. It was thought that while the birds left the eggs to attack humans near the colony, the Starlings would find it easier to prey upon these nests than any further away from disturbance.

Two strips of vegetation, 50 x 15 metres, were selected which were as alike as possible, apart from their proximity to the paths used by the general public.

Strip A ran parallel to a well-used public path and the birds, on a busy day, suffered disturbance from between 100 to 200 people passing in an afternoon. Strip B ran parallel and adjacent to the first strip but further away from the path. A total of 94 nests in Strip A and 51 in Strip B were found and examined daily and their nest contents recorded.

The mean clutch size for the disturbed area, based on this daily nest round, was 1.38, and for the undisturbed area the mean clutch size was 1.71. The difference is probably accounted for by the fact that many of the nests in the disturbed area were preyed upon before completion. The mean hatching success for Strip A was 30% and for Strip B 58%. There is a significant difference between these ($d=3.96$ $P < 0.001$) which may be accounted for by the differences in disturbance. Starlings had a much greater chance to prey upon eggs in Strip A while the adults were away from the nest attacking people on the neighbouring path, while Strip B, being further away from the public path, most likely suffered less disturbance.

<u>Re-laying</u>

If the first clutch laid by a pair in the season was preyed upon, then they sometimes laid a replacement clutch. This was usually laid in the same area as the initial clutch and occasionally in the same site. It was possible to determine if re-laying occurred only in colour-ringed birds which nested in the cove. Of 55 pairs which lost their first clutches, 22 pairs (40%) re-laid, and four pairs (7%) laid a second replacement clutch. The first replacement clutches were mainly single eggs, and all the second replacements were single eggs while none of these re-layings resulted in the production of young. Springett (1967) suggested that there was a correlation between the length of time incubation had proceeded and the time interval before re-laying took place. No evidence for or against this was found in the present study but the observations were mainly based on re-layings in 1968 when the breeding of the birds was upset.

Weight of Eggs

A number of eggs were weighed and measured at the onset of incubation and their weights and calculated volumes have been compared and found to be very closely related. The mean values for each category of egg and the values of the correlation coefficient (r), and the regression of volume on weight, are given in Table 11.

In addition to the close relationship between the weight and the volume of the egg, there was also a high correlation (r = +0.83) between the weight of the egg and the weight of the young on hatching, with the regression of the latter on the former being y = 0.49 + 0.75 x (Figure 10). The mean weight of the fresh eggs was 16.8g and the mean weight of the newly hatched young was 13.1. This latter value was 12.2% of the mean adult weight and is identical with the

Figure 10. Comparison of the weights of eggs at the onset of incubation with weights of corresponding chicks within 6 hours of hatching. The regression equation is $y = 0.49 + 0.75x$ and the value of the correlation coefficient $r = + 0.83$.

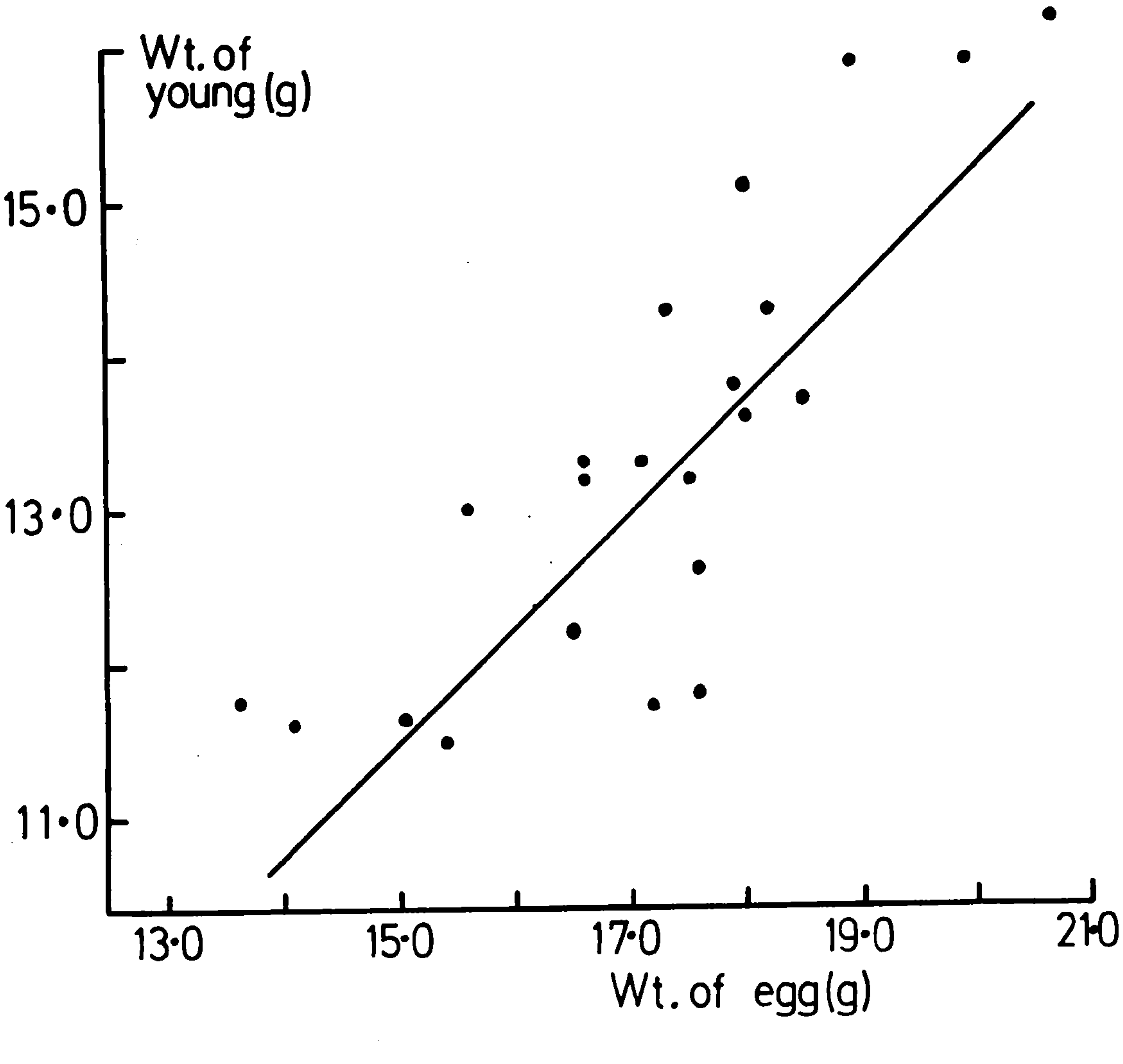

Wt. of young (g)
15·0
13·0
11·0
13·0
15·0
17·0
19·0
21·0
Wt. of egg (g)

Table 11. The mean weights and volumes of eggs in each category together with the number in each sample (n), the correlation coefficient (r), and the regression equation of volume on weight

Egg category	Mean weight (g)	Mean volume (cc)	n	r	Regression equation
C1	17.0	18.0	37	+0.83	$y = 2.57 + 0.91 x$
C2/1	17.0	18.0	13	+0.95	$y = 2.52 + 0.91 x$
C2/2	15.7	16.6	8	+0.93	$y = 2.87 + 0.88 x$
All eggs	16.8	17.8	58	+0.87	$y = 2.71 + 0.90 x$

percentage given by Belopol'skii (1961), although he quotes a mean egg weight, based on 11 measurements, that is higher (17.8g) and a mean weight of newly hatched young that is lower (10.6g), than have been found in the present study.

Weighing the eggs was a rather lengthy process and involved carrying them from the colony to a position where the balance was sheltered from the wind. It caused considerably less disturbance to measure a large number of eggs and from these measurements to calculate the volume, than it did to weigh the same number of eggs. As it has been shown that the volume and the weight of the egg are closely correlated, the volume of the eggs rather than the weight has been considered in relation to chick survival. In 1967 the volumes of a number of eggs in the different categories were obtained and the progress of the chicks which hatched from them was followed. In Table 12 the volumes of the eggs which produced fledged young have been compared with those that produced young which died.

Table 12. The volumes of the eggs, in 1967, which produced fledged young, compared with those producing young which died. The sample sizes are given in parentheses.

Egg category	Mean volume (cc) of eggs where young survived ± 2 S.E.		Mean volume (cc) of eggs where young died ± 2 S.E.	
C1	16.39 ± 0.60	(16)	17.31 ± 0.66	(3)
C2/1	16.37 ± 0.50	(15)	17.19 ± 4.14	(4)
C2/2	16.23 ± 0.72	(8)	15.89 ± 0.04	(15)
All eggs	16.30 ± 0.36	(39)	16.22 ± 0.82	(22)

There was no evidence of any difference between the size of the eggs producing young that survived and those producing young which eventually died, in either the single egg clutches or in the first egg of the clutches of two. However, in the second egg of the clutches of two, there was some evidence that the young hatching from larger eggs were more likely to survive than those hatching from smaller eggs, although the differences in egg size were not significant. The table has included all chick mortality regardless of the age at which this occurred, although it is unlikely that the hatching size of ~~a~~ chick has any effect on its survival after the first few days. However, before this time, the mortality of the chicks is heavy and the size of a chick on hatching may be a critical factor in its survival, particularly in a brood of two where the newly-hatched second chick has to compete with its elder sibling. This first chick may be up to a day older and will also have hatched from a larger egg, giving it a larger size before it started feeding.

The weights of the young on hatching

The distribution of the weights of the young within six hours of hatching, and before they received their first food, is shown in Table 13.

Table 13. The weights of the young within six hours of hatching

Weight (g)	< 10.1	10.1-11.0	11.1-12.0	12.1-13.0
Number of young	0	1	6	3

Weight (g)	13.1-14.0	14.1-15.0	15.1-16.0	>16.0
Number of young	7	2	4	0

Total number of young = 23

Mean weight (±S.E.) = 13.1 ± 0.6 g

The mean weight of the chicks hatching from single egg clutches was 13.5g, from the first egg of clutches of two, 13.1g and from the second egg of a clutch of two, 12.8g, but as these values are based on samples of 8, 8, and 7, respectively, no statistical significance can be attached to the differences between them. However, it seems clear that the second chicks of a brood of two are lighter in weight than their elder siblings, and this, in conjunction with the difference in the time of hatching that is considered later, may have a considerable effect on the relative survival of the two categories of chick.

Interval in hatching between the first and second eggs

In 1968 the hatching time of a number of eggs was recorded to the nearest 12 hours and the distribution of the time intervals is shown in Table 14.

Table 14. Time intervals between the hatching of the first and second eggs in a clutch of two

Time interval (hours)	<12	12-24	24-36	36-48	48-60	60-72	>72
Number of clutches	2	10	7	3	1	2	0

Total number of clutches = 25

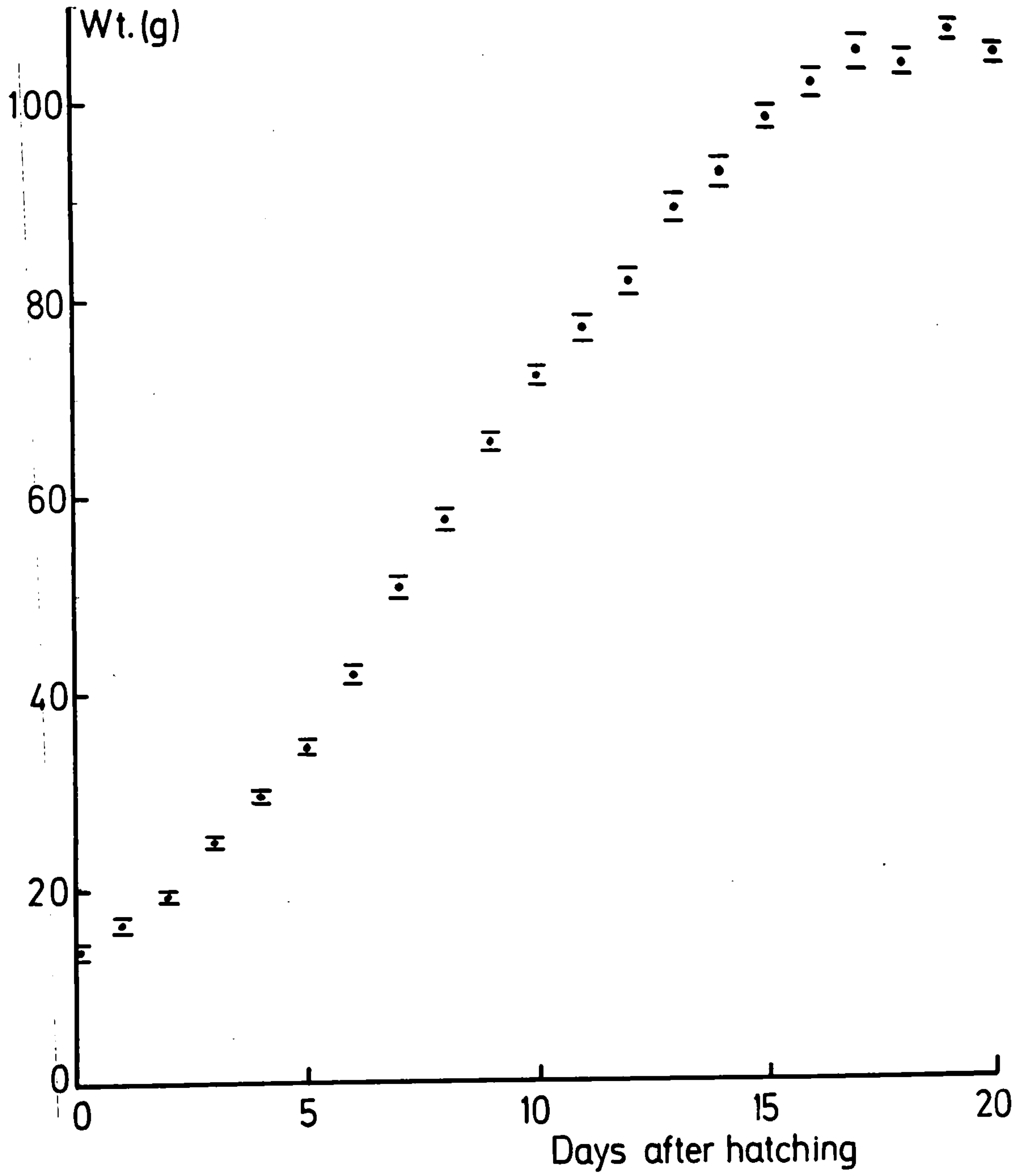
Mean time interval (± S.E.) = 286 ± 64 hours

On average, the second chick hatched just over one day later than the first chick and at a weight approximately 0.5g lighter. Some second chicks hatched on the same day as the first chicks, but in two cases they hatched nearly 3 days later. In 12 cases, both chicks hatched within the same 24 hour period and from this group, one of the first chicks died (8%) and three of the second chicks (25%). There were 6 cases when the interval between hatching was greater than 36 hours and one of these first chicks died (17%) but five of the second chicks (83%). Although the numbers were small, they showed a tendency towards a higher survival rate for those second chicks which hatched within the same 24 hour period as the first chicks compared with those which hatched after an interval of more than 36 hours of the first chick hatching. As the interval between hatching of the eggs showed a close relationship with the laying interval, it was an advantage for the survival of the second chick for the two eggs to be laid within a short time interval or for full incubation to be delayed until the laying of the second egg. It has been shown already that there was a tendency for incubation to be delayed until after the laying of the second egg; 59% delayed incubation until after the second egg had been laid, 9% began incubating on the day between the laying of the two eggs and only 31% began incubating on the day the first egg was laid.

Growth rates of young

In 1965, 1966 and 1967, a large sample of young were weighed at the same time each day, from a few days after hatching onwards. After the young had reached 2-3 weeks, difficulty was experienced in finding them at a regular time each day, as they could then wander considerable distances from the original nest site. The mean growth rate for the young was calculated for each year for the first three weeks of life, and as the differences between the years were very slight, only the growth curve for 1967 is shown in Figure 11. After initial small increases, there was

Figure 11. Mean growth curve of chicks up to 20 days old ± 2 standard errors, in 1967. Day 0 is the day of hatching. The sample size is always greater than 30.


Wt. (g)
100
80
60
40
20
0
0
5
10
15
20
Days after hatching

a constant daily increase in weight from the third to the fourteenth day which in 1967 was 6.8g. After this time chicks had reached adult weight and showed large fluctuations in their daily weights, probably due to differing amounts of exercise and irregular feeding.

The growth rates of chicks which had come from different brood sizes have been compared by placing them into four categories; single-brooded, first chick of a brood of two where both survived, second chick of a brood of two where both survived, and the surviving chick of a brood of two where one died. The mean growth rates for chicks from each of these four categories in 1967 are shown in Figure 12. Although the rate of increase for each of the four categories was very similar, there is a significant difference between the mean weights at each age for first and second chicks of a brood of two where both young survived. The second chick was always significantly smaller than the first at any given age ($t = 7.60$ $df = 16$ $P < 0.001$). This was approximately equal to one day's delay in development but after this delay there was no difference in the development rate.

The growth curves of single chicks and the surviving young of a brood of two where one young died were very similar but both these categories of chicks attained a smaller average weight at any age than the first chick of a brood of two, where both young survived.

Studies on the feeding of the young

In 1967 observations were made on a total of 14 colour-ringed young in the cove. The time when each young was fed was recorded, together with an estimate of the type and size of the fish. All the food brought in during this time

Figure 12a Mean growth curves of 2 categories of chicks in 1967

1) Brood of one from clutch of one

2) Brood of one from clutch of two

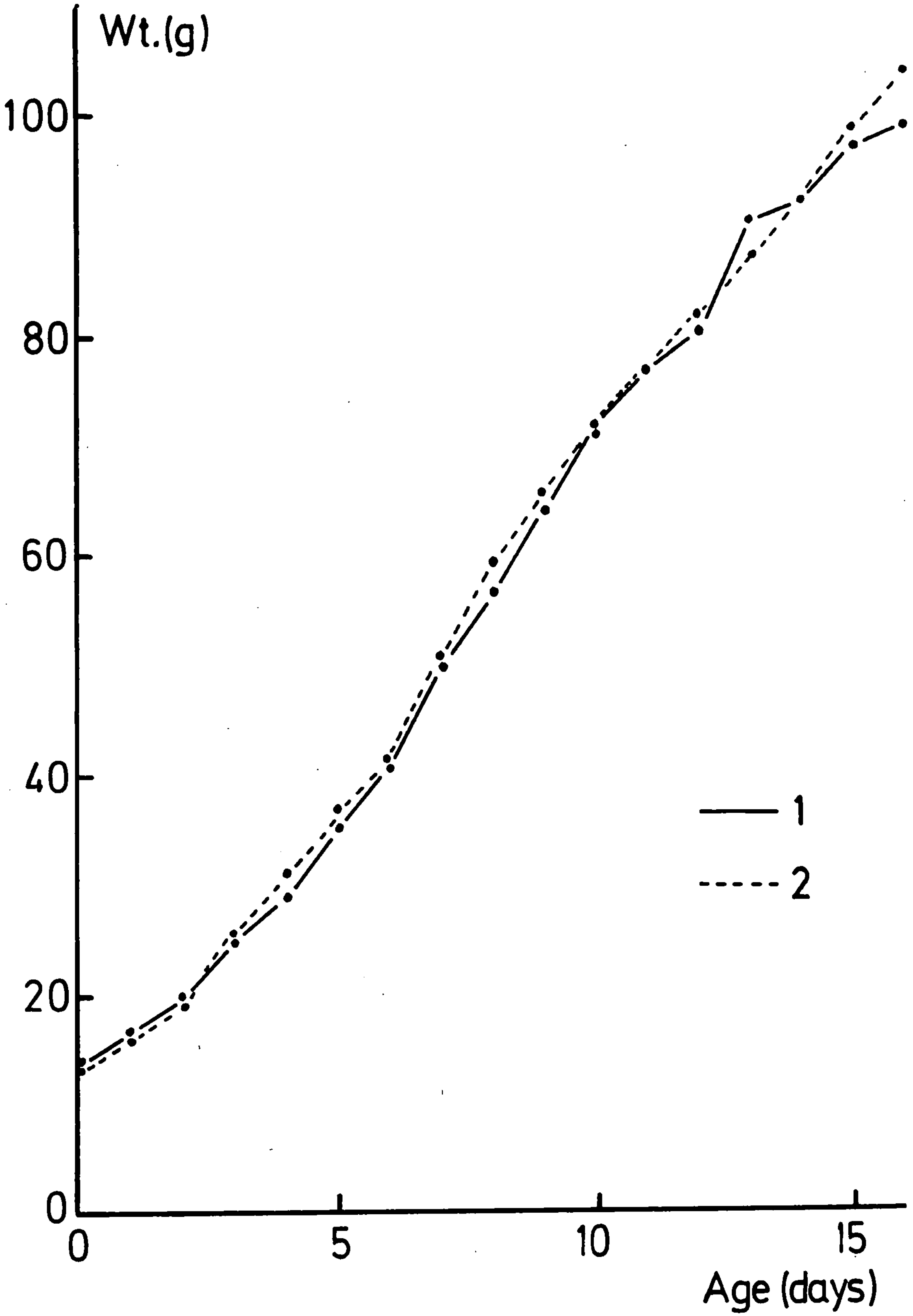
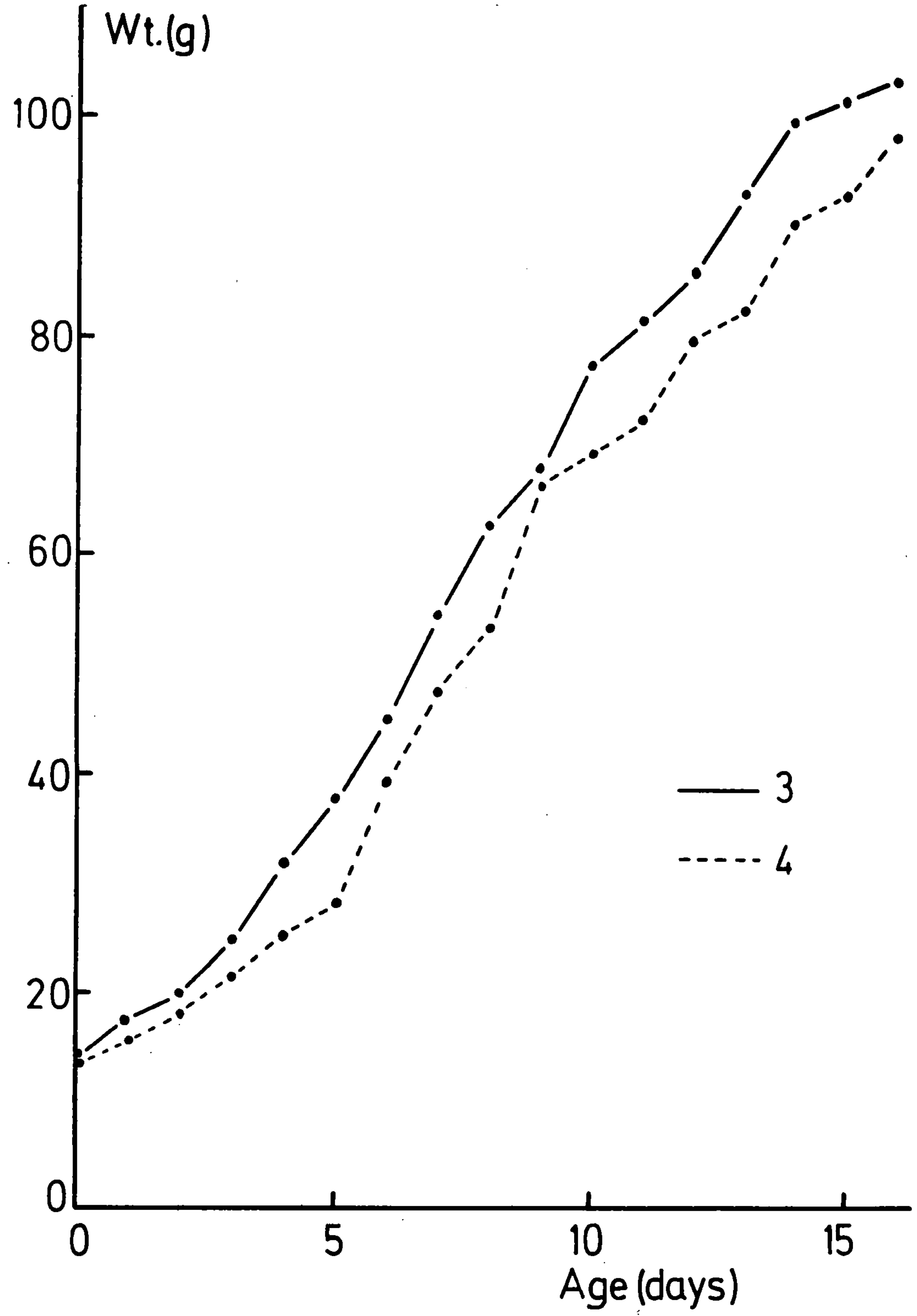

Wt.(g)
100
80
60
40
20
0
0
5
10
15
Age (days)
1
2

Figure 12b Mean growth curves of 2 further categories of chicks

3) Brood of two, first chick

4) Brood of two, second chick


Wt.(g)
100
80
60
40
20
0
0
5
10
15
Age (days)
3
4

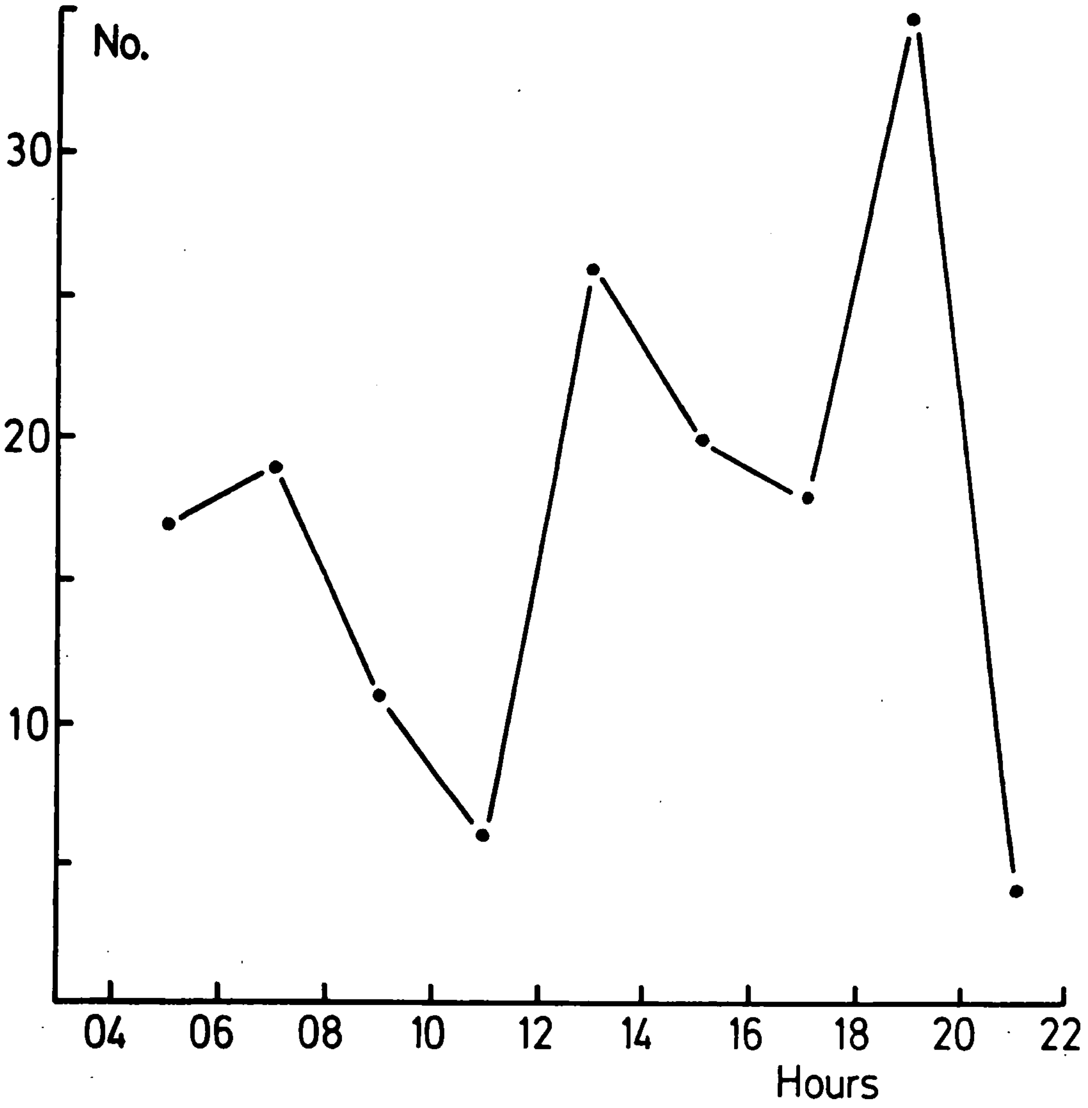
consisted of sand eels (*Ammodytes* spp.) although at other times Clupeids and Euphausiids were eaten. The numbers of fish supplied to the 14 young under observation at different times of the day are illustrated in Figure 13 and show an intensive period of fishing activity in the late evening which has also been noted from casual observation on other days. It is unlikely that any fishing occurs during the hours of darkness, although on a clear night, particularly in late June and early July, the actual period of darkness could be of less than four hours duration and some fishing may occasionally have commenced before 0400 hours.

The average number of feeds to the young over the whole 24 hour period was 0.67 feeds per hour. Over the main period when the chicks were fed, during the hours of daylight (0400-2100), this produced an average of 11.4 feeds per chick per day. The feeding has been considered in more detail in relation to age in Table 15.

Table 15. The mean number of feeds per hour over a 24 hour period together with the mean length of the fish supplied to chicks of different ages

Age of chick	Mean number of feeds per hour	Mean length of fish (inches)	No.of young under observation
Less than 1 week	0.45	2.2	4
1 to 2 weeks	0.74	2.3	5
More than 2 weeks	0.61	2.5	5
Mean and Total	0.67	2.4	14

Figure 13. The numbers of fish supplied to 14 chicks in every two hour period of the day. Data from two days' observations in the cove, in June 1967.


No.
30
20
10
04
06
08
10
12
14
16
18
20
22
Hours

These results may be interpreted with reference to the growth curve, from which the average growth rate for chicks of less than a week old was calculated as 5.25g per day, and that for chicks between one and two weeks old 6.06g per day. After two weeks the chicks showed considerable fluctuations in weight and many were the same weight as the adults. The size of the fish brought to the chicks showed a tendency to increase with the age of the chicks, but during the period of maximum growth it was the number of feeds which was increased to provide the necessary food for the young and the slight increase in fish size was probably less important.

The lengths of the fish were estimated to the nearest half inch as they were brought in by the adult birds and when any of the fish were dropped they were collected and measured. In all cases where this occurred, the original estimate of the size of the fish was correct to the nearest half inch. The mean length of fish brought to the young during the period of observation was 2.4ins (6.1cm).

In addition to measuring their lengths, the dropped fish were also weighed whilst they were still fresh. This gave an estimate of the weight of a known length of fish and from this the average weight of fish taken per day by chicks of all ages was found to be 26.6g.

Rearing chicks in the laboratory

In 1967 an attempt was made to rear chicks in the laboratory for a comparison of the weight of food taken per day with their growth rates. A total of seven chicks of various ages were removed under licence at the end of the season.

The chicks were divided into two groups for the analysis of data; four younger chicks with initial weights of 27.0, 27.0, 35.2, and 35.5g, and three older chicks whose initial weights were 84.5, 86.0, and 98.3g.

The chicks were fed every 1-2 hours between 0700 and 2300 each day on pieces of raw herring cut from the whole fish, and of a size approximating to that of the average sand eel. The fish pieces were offered to the chicks with a pair of forceps and at first the smaller chicks begged and took food from the forceps. The older chicks and, after a few days, the younger ones too would not take food in this way and were force-fed. Sometimes they regurgitated the food after feeding but usually accepted it when it was fed to them a second time. A model cardboard head and a stuffed head of an adult tern were both used in conjunction with the forceps in an attempt to provide the necessary stimulation for begging. These had limited success with the smaller chicks at first but provoked no reaction after a few days; the older chicks hardly responded to them at all.

The chicks were kept in an open tray of sand with a wire-netting guard round the edge. They were provided with water but took little interest in this. At first they seemed to suffer from cold, particularly the smaller chicks which probably missed the warming effect of a brooding adult, and an infra-red lamp was set up over the tray to raise the temperature. This was apparently successful in providing conditions close to those which prevailed in the cove on a hot day when the temperature in the sheltered areas reached 25-30°C and the parents spent very little time brooding.

All the food which was given to the chicks was weighed and they were weighed before and after feeding to obtain an accurate measure of the weight of food they had ingested. The total amount of food taken in 24 hours was calculated together with the net change in weight of the chick over the same period. The mean net weight changes for different weights of food taken in are shown in Table 16 and Figure 14.

Table 16. The mean changes in weight (g/day) in relation to the different weights of fish ingested (g/day) for the two groups of chicks in the laboratory. The number of occasions that food within any weight range was ingested is shown in parentheses.

	Younger, lighter chicks		Older, heavier chicks	
Range of food weights (g/day)	Mean food intake	Mean weight change	Mean food intake	Mean weight change
0 - 5	2.5 (3)	-2.1	..	..
5-10	8.4 (15)	-1.2	..	..
10 - 15	12.2 (14)	+1.2	13.8 (5)	-4.4
15 - 20	17.9 (5)	+3.3	..	..
20 - 25	21.5 (5)	+4.8	21.6 (1)	-4.5
25 - 30	26.0 (4)	+7.0	..	..
30 - 35	..	..	32.8 (4)	-2.2
35 - 40	..	..	..	..
40 - 45	..	..	42.3 (2)	+7.0
45 - 50	..	..	46.8 (2)	+12.3

The amount of fish that any one chick could be induced to ingest permanently has been divided into a series of weight ranges that are indicated in the table, and within each range the mean weight of fish ingested per day is given, together with the resulting mean change in weight over the same period, and the number of occasions that this happened. This number of occasions that a chick consumed food within a given weight range was determined entirely by how much the chicks would ingest, though it is clear that the larger group of chicks tended to consume proportionately more food per day.

Of the three larger chicks, two showed little overall weight increase, and although the third gained 25.0g in three days, it died the following day. These chicks have therefore been considered separately in Table 16 and Figure 14, and none of them survived for long; two died on the 7th day after collection, and the third after 10 days. The direct cause of death was probably starvation as all the birds were very thin when they died, and weighed respectively 108.0g, 86.6g, and 76.3g; the latter two weights were 20-30g less than the average weights for 3-4 week old chicks that have been reported earlier. It was likely that although adequate food was available, they lacked the necessary stimulation to beg for food or to accept it. It seemed unlikely that herrings lack any essential food items which are possessed by sand eels, as herrings have been used successfully in the laboratory in the rearing of Shag and Kittiwake chicks (Brazendale pers.comm.), both of which are normally fed on sand eels on the Farne Islands.

The four smaller chicks survived for longer, two for 11 days and two for 15 days, and they showed some weight increases during this time. These increases were at a very low rate, on

Figure 14. The relationship between the mean food intake (g/day) in the laboratory, and the resulting mean change in weight (g/day) for two groups of chicks :

A Four young, small chicks all weighing less than 40g initially

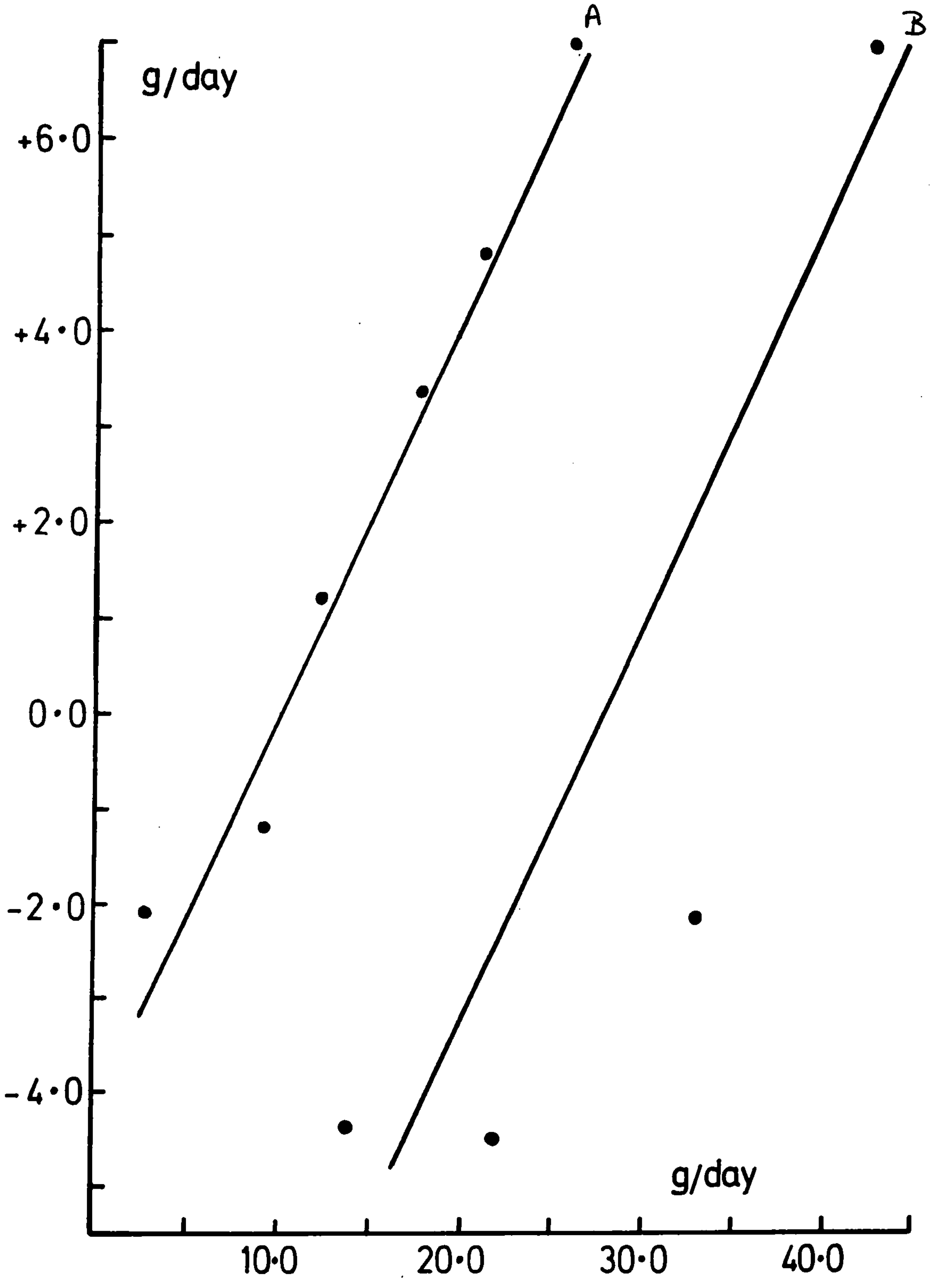
$r = + 0.93$

$y = - 4.22 + 0.42 x$

B Three older, larger chicks all weighing more than 40g initially

$r = + 0.71$

$y = - 11.9 + 0.42 x$


A
B
g/day
+6·0
+4·0
+2·0
0·0
-2·0
-4·0
g/day
10·0
20·0
30·0
40·0

average less than 1g per day, as opposed to 6-7g per day for chicks of the same age in the wild. They were offered food as frequently as in the wild, 10-11 times a day, and although at first they begged for this, they were easily satisfied and accepted less than 15g of fish a day, rejecting more when this was offered to them, although this amount was inadequate to sustain normal growth. The only way their daily intake could be increased was by force-feeding and this was resorted to after the first few days of feeding.

The weight changes for the older chicks were rather erratic, but they showed that the chicks were capable of consuming very large amounts of food in one day, often over 50% of the weight of the chick, and that this could result in a very large net weight increase. The largest recorded increase was 18.3g after consuming 46.1g of fish. Some of the younger chicks also regularly ingested over 50% of their own weight in fish in a day. The maximum recorded was a chick weighing 34.1g which ingested 27.8g of fish, 81.5% of its own weight, producing a net weight increase over 24 hours of 7.0g.

It is clear from Figure 14 that both groups show a reasonably linear relationship between mean food intake per day and mean weight change per day. The correlation coefficients for the two groups are : young, $r = +0.93$ and old, $r = +0.71$, both of which are significantly different from zero. The equations of the two regression lines are, $y = -4.22 + 0.42\,x$, for the young group and $y = -11.49 + 0.42\,x$ for the older group. The identical slopes indicate that the same amount of fish produces the same change in weight in the two groups, although the different intercepts on the horizontal axis indicate that, while the younger chicks required only 10g of fish to produce no change in the weight, the older group required slightly more than 27g to produce the same effect.

From the earlier section on the measurements of daily growth rates of chicks in the field, it was shown that the mean daily growth rate in 1967 was 6.8g and it was estimated that a chick was supplied with approximately 26.6g of fish each day. From the graph of the young chicks fed in the laboratory, it was found that to maintain a growth rate of 6.8g per day required 26.2g of fish, which was very similar to the estimate obtained from field observations.

Cymborowski & Szulc-Olechowa (1967) reared 15 Common Tern nestlings successfully in the laboratory and compared their development with 8 chicks reared in the wild. They found that similar weight increases occurred in both groups, but the hand-reared birds reached maximum weight a few days later. The weight of the hand-reared birds did not exceed the adult weight which normally occurs under natural circumstances and they showed greater fluctuations from the mean values.

Mortality of the chicks up to the time of fledging

Methods

Chick mortality was estimated in two ways, (a) by the recording of all dead chicks in the study area, both ringed and unringed, and (b) by recording all surviving chicks and assuming that any which disappeared before an age when fledging would be likely, had died. These two methods were used in conjunction with each other for all the nests in the study areas. At every nest round, the corpses of any young were recorded and removed, so that the time of death was known to within 12 hours.

The ring numbers of the surviving young were also noted or, if they were too small to be ringed, the number of the nest from which they came. This gave a good cover of the area as all the chicks which were known to have hatched in the area were either seen alive at least once every five days or were found dead. If they were not observed for a period of five days, prior to fledging age, they were assumed to have died. If they were observed within a few days of fledging and in a healthy condition, but not subsequently found, these were assumed to have fledged successfully.

As a further check on survival, mist nets were used later in the season to catch flying juveniles, partly to obtain weights for birds of this age, but also to provide a check on the chicks which had fledged from the study area. Most of the juvenile birds were caught in this way and all were in the previously "assumed survived" category; none in the "assumed died" category.

These methods depended on the fact that Arctic Tern chicks spent their first few weeks of development near the natal site. A few days after hatching they wandered for short distances, particularly into cover, but always returned to the original nest site to be fed. Even after fledging, when the birds are still being fed by their parents, they often returned to the natal site for this food and it was therefore possible to net flying juveniles over the original study area although they were not confined to this area and were not spending all their time there.

Causes of mortality

The main causes of mortality were exposure, predation, attack by adult terns and possibly starvation. It was difficult to assess the differing contribution of all these to the mortality, particularly when the chick was assumed dead on the negative evidence that it was not found alive. It was also likely that in some cases more than one factor contributed to the death of a chick and so a detailed evaluation of the different causes of mortality could be misleading.

1. Exposure

Very young chicks, those up to 3-4 days old, were brooded almost continuously by their parents. If this brooding did not take place, the heat losses from small chicks would be very great and they would suffer from exposure, particularly during periods of strong winds or rain. Belopol'skii (1961) stated that the thermo-regulatory powers of tern chicks are not fully developed until the chicks are a few days old. As the tern chicks increased in size, brooding became less continuous and finally ceased by the time the chicks were about a week old, except during heavy rain. Heat loss from these older chicks was reduced as their surface area to volume ratio was less. They also had greater mobility and moved away from exposed areas into the shelter of rocks or vegetation.

Exposure was probably a more important factor in the mortality of very young chicks than in the deaths of older ones, although it had an effect on all chicks in poor weather conditions. The effects of poor weather were enhanced if the colony was suffering disturbance, which on Inner Farne usually took the form of the general public walking on the paths around the edges of the colony. The reasons why this disturbance added to the effects of bad weather were (a) that the amount of time spent brooding was reduced as the adults spent more time attacking the intruders into the colony than looking after their young and (b) that when the adults left the nest, the chicks made for the nearest cover.

In the vegetation areas this usually consisted of a small tunnel into the vegetation, sometimes up to a foot long, and after heavy rain the walls of these tunnels became very wet so that the chicks, on pushing their way into the vegetation, became soaked. Their subsequent heat losses were much greater and they were more likely to suffer from exposure. This probably contributed to the higher mortality in the vegetation areas which is discussed later.

Nye (1964) investigated the heat loss in wet ducklings and chicks and found that wet birds had considerably lower temperatures than dry birds. She further found that week old chicks that had been wetted by half immersing them in water for three minutes suffered a much greater reduction in their body temperatures after removal from the water than did four week old birds after the same treatment. A tern chick on the Farnes during rain, although unlikely to be immersed in water, suffered considerable wetting, particularly if it was pushing its way through wet vegetation. When the adults were disturbed from the nest site, the chicks were also exposed to the cooling effect of the wind. The effects would be particularly marked in small chicks, as apart from their poorly developed thermo-regulatory mechanism and high surface area to volume ratio, these chicks were more liable to wetting as they lacked the waterproofing contour feathers of older chicks. The down feathers possessed by the young chicks quickly became soaked and the birds soon suffered from hypothermia.

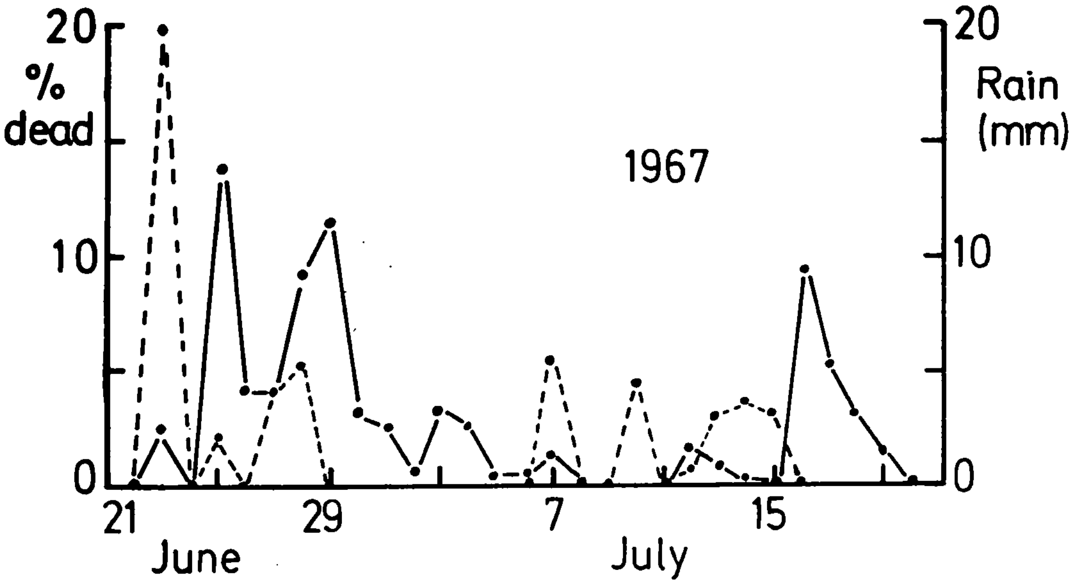
Chicks which were suffering from exposure could usually be identified before they succumbed. Typically they stood still with drooping wings and with their eyes closed, and called at regular intervals, although not apparently in response to any external factor. In the more extreme stages the chicks were apparently unable to stand, but lifted their heads, with eyes still closed, to call occasionally. They were sometimes found shivering. All the chicks which showed any of these symptoms were later found dead. The reactions of the parents to these chicks varied considerably but they rarely brooded them. If there was a surviving chick still in the nest, particularly if this was begging for food, the feeding urge was much stronger than the brooding urge, and the dying chick was abandoned for the healthy one. This has obvious selective advantages where the parents attempted to rear two chicks.

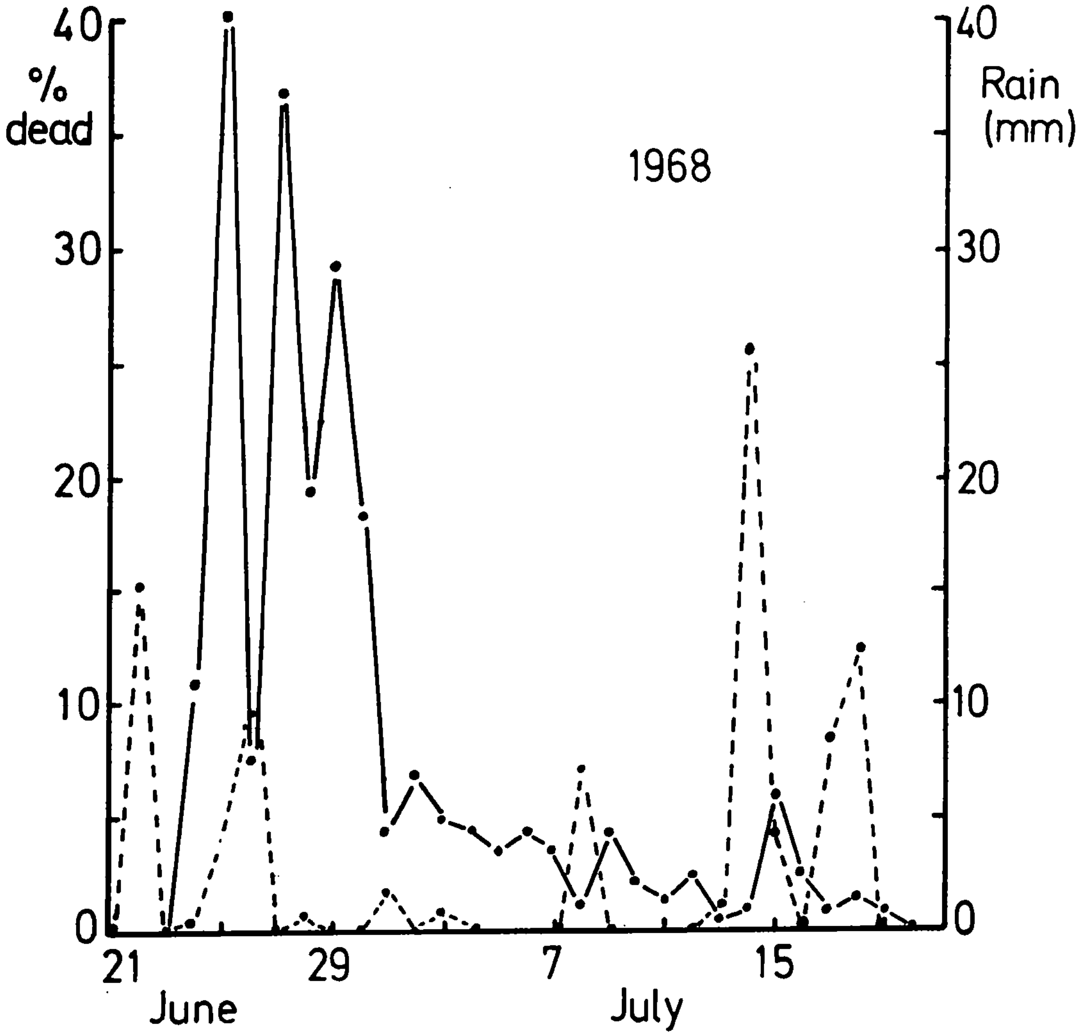
Figure 15 shows the numbers of chicks found dead each day in 1966 and 1967 for the main period of the breeding season, together with the mean daily rainfall. In each year, after a period of heavy rain, the numbers of chicks found dead increased. This was particuarly marked at the beginning of the season when there were a very large number of chicks about. In 1967, a spell of heavy rain lasted only for a short time, less than 12 hours, and although this resulted in some mortality, this was not as great as that earlier in the season due to the predominance of older chicks in the colony at this time. Springett (1967) found severe hypothermia resulting from exposure in the vegetation areas that here caused 44 out of a total of 64 deaths (68%) in 1963 and 1964. In the cove he found no deaths through exposure in 1963 and only 5 out of a total of 23 (21%) in 1964.

2. Predation

Springett (1967) does not mention predation as being a cause of chick mortality on the Farne Islands and it is likely that this has increased since his observations from 1963 to 1965.

Figure 15. The numbers of Arctic Tern chicks found dead during the main part of the breeding season in 1966 and 1967, expressed as percentages of the total number of chicks at risk. The daily rainfall is shown for the same period. (•----•)


20
%
dead
10
0
20
Rain
(mm)
10
0
1967
21
29
7
15
June
July


40
%
dead
30
20
10
0
40
Rain
(mm)
30
20
10
0
1968
21
29
7
15
June
July

In 1966 and 1967 very little predation of chicks was observed, but this was greatly increased in 1968. Casual observations by N. Brown (pers.comm.) in 1969 and 1970 suggest that predation was at a fairly high level in those years, particularly towards the end of the seasons. The predation was caused by Herring and Lesser Black-backed Gulls *Larus fuscus* which do not nest on Inner Farne but breed in large numbers on the neighbouring islands of Knoxes Reef, and East and West Wideopens. The reasons for the increase in predation in 1968 are discussed fully in Section 4. No accurate estimate could be made of the percentage of chicks preyed upon as only rarely was this known by observation to have occurred to a particular chick, and many chicks which came into the "disappeared" category may have been preyed upon. This category also included chicks which had wandered away from the study area and probably died either of starvation because their parents could not find them, or of attacks from other adults into whose territory they had wandered.

Predation has been found to be a major factor in chick mortality in other colonies; for instance Burton & Thurston (1959) found the Glaucous Gull *Larus hyperboreus* an important predator in Spitsbergen. Cullen (1960), referring to the terns breeding on the Farnes, found evidence of gull predation and suggested that this was reduced by the mobbing attacks of the adult terns. These attacks also had the effect of making the gulls move quickly through the colony so that they had the chance of seeing and picking up only poorly camouflaged young. Colonial attacks on predators were also seen in the Wideawake Tern *Sterna fuscata* on Ascension Island by Ashmole (1963) where the synchronisation of hatching was an important protection against the marauding cats and frigate birds. Any young which hatched later than the majority stood a much greater chance of being preyed upon due to the reduced or minimal attacks on the predators by the few adult terns that remained.

3. Attack by adult terns

During the first week of their life, chicks often wandered short distances away from the original nest site. If they strayed into the neighbourhood of another nest site, the adult attacked them by pecking sharply at the chicks' heads. Unless the chicks could move out of the area quickly, this usually resulted eventually in death. The attacks by the adults continued while the chicks were trespassing until they lay still. Older chicks were much more skilful at avoiding these attacks and moved quickly either back to their own nest site or to neutral ground. The attacks were mainly confined to open areas of the cove or rocks where the chicks were much more likely to stray into the wrong area and accounted for only a small percentage of the mortality in each year, approximately 5% of all chicks found dead in the open areas were found to have been attacked in this way. Pettingill (1939) found that internal factors in the colony accounted for the greatest loss of young and Springett (1967) calculated that attack by adults accounted for 39% of all deaths in the cove but only 3% in the vegetation areas. In the latter, the chicks were usually confined to the area around the nest site and their "escape tunnels", by the physical height of the vegetation until they were at least three weeks old. The amount of mortality from attack by adult terns was therefore considerably reduced in the vegetation areas.

4. Starvation

It was difficult to assess when a chick had died from starvation as the weights of chicks found dead varied considerably according to the length of time since death and the rate of drying of the corpses. It was difficult to separate starvation and exposure as distinct causes of death, particularly when the young had died during heavy rain. It was likely that these two factors operated together. Starvation was the likely cause of death in many of the second-hatched chicks in broods of two as these chicks hatched on average just over one day later than the first chicks and, having come from smaller eggs, had an average weight on hatching 0.5g less than that of the first chicks. It was unlikely that they were able to compete with the older chicks for food, particularly if this was at all limited. Even when food was plentiful, the adults returning to the nest site with food gave this to the chick which begged most greedily or which grabbed the fish. As the first chick had a head start in development and would be more vigorous in begging for fish, it usually obtained this in competition with the second chick. Only when the first chick was satiated would the second chick obtain food. If it became weak, the pecking of the adult's bill which Quine & Cullen (1964) found to be essential to stimulate the adult to further fishing became less, until the adult received insufficient stimulation and failed to feed the chick. The resultant starvation was probably the main cause of death in the second chicks of broods of two where these died in the first week of life.

Comparison of the total annual chick mortality during 1965-1968

The total mortality for 4 years from 1965-1968 was estimated from limited study areas and this is shown in Table 17. In 1968 the minimum chick mortality is shown; the actual chick mortality may have been much higher, but this is discussed in detail in Section 4.

Table 17. Total chick mortality for 1965-1968

Year	Total young hatched	Total young found dead	Percentage mortality ± S.E.
1965	258	104	40.3 ± 3.1
1966	404	179	44.3 ± 2.5
1967	239	50	20.9 ± 2.6
1968	103	39	37.9 ± 4.8

Although considerably fewer young hatched in 1968, the minimum mortality of those which did hatch was similar to that in 1965 and 1966. In 1967, however, the mortality was significantly lower than that in other years ($d = 5.98$ $P < 0.001$). There was very little difference in the total rainfall of the four years and each year suffered some very heavy rain with over 20mm in 12 hours. In 1967, most of the rain fell at night when the colony was undisturbed and the adults were not away at sea fishing. They had greater opportunity to brood the chicks and this may have contributed to the increased survival. Casual notes on the weather were made on Inner Farne and in 1967 there was some very hot weather in late June and early July, the time when the majority of chicks were hatching, and it is suggested that this, combined with the rainfall mainly occurring at night, accounted for the lower chick mortality observed in this year.

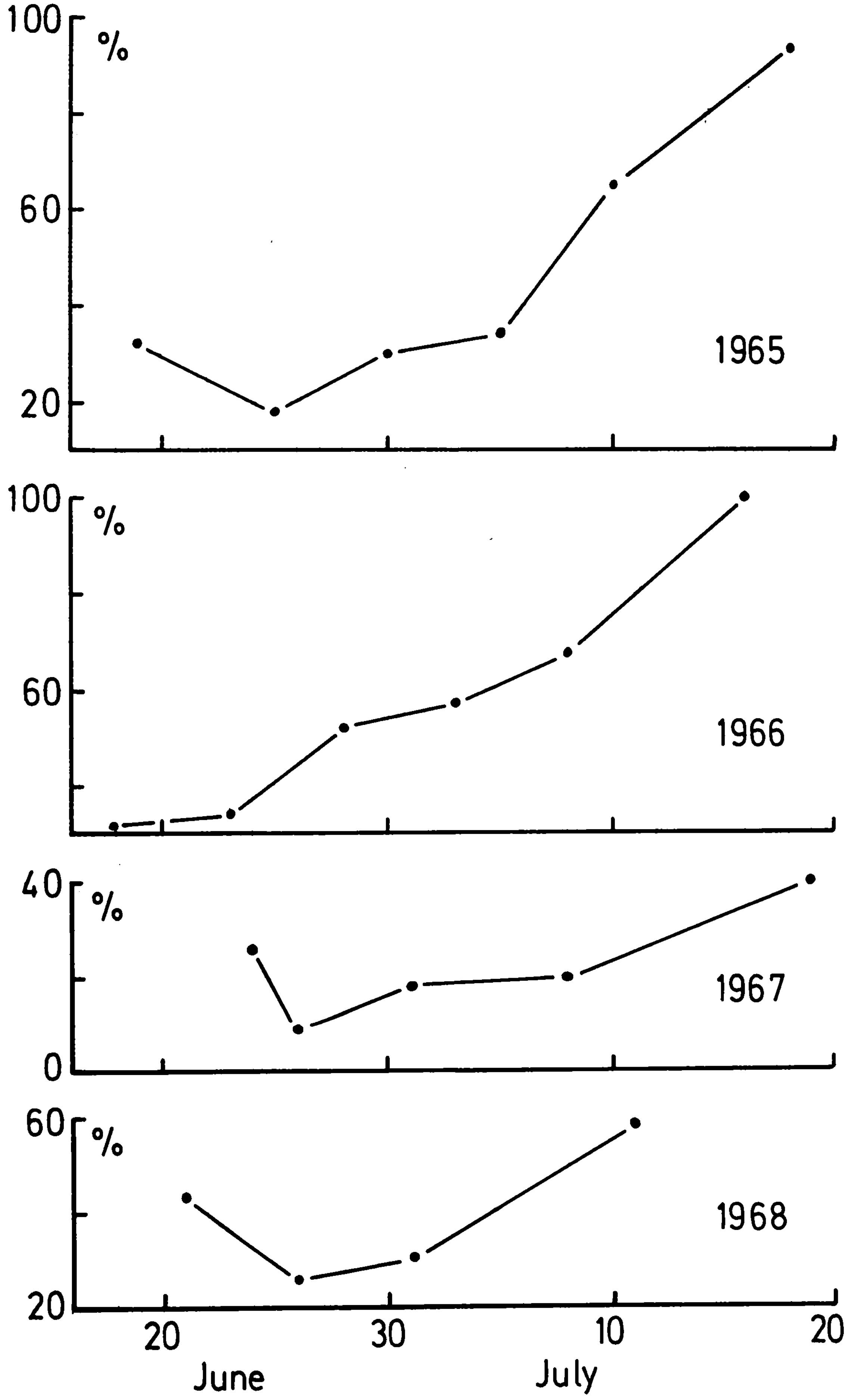
Further observations around the Farne Islands in 1967 suggested that there was an abundance of plankton and that small fish, feeding on the plankton, were also plentiful. On several occasions, when it was possible to look down from a small boat into a calm sea, this was seen to have a 'soupy' appearance and planktonic animals visible to the naked eye were very abundant. The terns were bringing in more clupeoids than sand eels which was unusual as normally sand eels form the major part of their diet. Pearson (1968) found that on average sand eels accounted for 65% of the Arctic Terns' diet when the numbers of fish were considered. Clupeoids normally only accounted for 22% by number, although this was 63% by weight. It is possible that the clupeoids were in greater abundance around the islands due to the abundance of plankton, and this may have been the northern end of a large scale concentration of sprats recorded by Johnson (pers.comm.) which mainly occurred 10-15 miles north-east and south-east of Tynemouth during the early part of 1967. Johnson said that this concentration broke up to some extent early in 1967 but that stocks of fish throughout the summer of 1967 were at a very high level. A similar situation was recorded off the coast of North Yorkshire near Robin Hood's Bay by Feare (pers.comm.) who found that the inshore waters in July 1967 were teeming with sprats and thousands of fish were left stranded in the rock pools at low tide.

All this evidence suggests that in 1967, during the period June to July, there was an abundance of food around the Farnes. The main effect of this may have been that the adult terns found food very easily and could spend more time brooding the chicks than in other years when fish were less abundant. It is rather surprising that this did not give rise to increased growth rates of the chicks, but it may have been an important indirect factor in the increased survival of the chicks in 1967.

Chick mortality in relation to time of breeding season

The differences in chick mortality throughout the season were examined by comparing the percentage mortality of chicks which hatched at various periods throughout the season. The seasonal changes in mortality are shown in Figure 16 for the four years 1965-1968. In each year the mortality showed a general increase towards the end of the season and reached very high levels, 94% and 100% in 1965 and 1966 respectively for the last period. In all years except 1966, the mortality at the beginning of the season was fairly high, the value then dropped to the lowest level, and finally showed a slow increase to the end of the season. In 1966, although the mortality in the early part of the season was lower than any other value in 1966, it was still higher than the early value in 1967 and approximately the same as that in 1965. In other years the highest mortality occurred in the very early and the very late part of the season and this may have been due to the smaller numbers of breeding birds in the colony at these times. When the number of birds in the colony was reduced, the attacks on predators were much less intensive and the increased mortality may be partly accounted for by an increase in predation. In 1966 particularly, and to a lesser extent in 1967, a few nights of very

Figure 16. The numbers of chicks dying, expressed as percentages of the total at risk, in relation to the date of hatching 1965 to 1968.


100
%
60
20
1965
100
%
60
1966
40
%
0
1967
60
%
20
1968
20
30
10
20
June
July

heavy rain in mid-July may have contributed to the late mortality of chicks.

Comparison of chick mortality in different areas

The numbers and percentages of chicks which died in three different areas were examined in the three years 1966-1968 and the figures are shown in Table 18. The totals for the years were not combined as the total mortality in 1967 was significantly lower than in the two other years.

The discrepancy between the total number of chicks in 1966 studied for seasonal mortality and the lower totals in Table 24 was due to the smaller sample of nests studied in 1966. The main effort in 1966 was concentrated on the weighing of a large sample of chicks; the ages of these were known but in many cases neither the brood size nor, in the cases of older chicks, the precise areas in which they had hatched were known.

There was little difference between the mortality on the rocks area or in the cove in any year. In 1966 the mortality in the vegetation was much higher than in the other areas, but not significantly so, and in 1967 and 1968 it was only slightly higher. This was probably due to the wetting effect of the vegetation which has already been discussed. In 1967, when the general mortality was much lower, possibly partly due to the drier season and partly due to the fact that the rainfall which did occur fell mainly at night when the effect on chick mortality was much less, the mortality in the vegetation was only slightly higher than in the other areas. In 1968, when one of the main causes of mortality was probably gull predation, the mortality of chicks in the vegetation was similar to that in other areas as the chicks in the vegetation were more protected from predation than chicks in the more open areas.

Table 18. Chick mortality in three different nesting areas 1966-1968

	Cove			Rocks			Vegetation		
Year	No. hatched	No. died	% died	No. hatched	No. died	% died	No. hatched	No. died	% died
1966	83	41	49	44	17	39	16	10	63
1967	92	17	19	101	22	22	46	11	24
1968	48	17	35	15	5	33	40	17	43

Table 19. Mortality of young from different brood categories (not including young which died during hatching)

	B1			B2/1			B 2/2		
Year	No. at risk	No. died	% died	No. at risk	No. died	% died	No. at risk	No. died	% died
1966	87	39	45	129	32	25	83	62	75
1967	48	4	9	34	4	12	37	20	54
1968	34	13	38	18	6	33	15	10	67

Comparison of mortality of chicks from different brood sizes

The numbers of chicks dying from broods of one (B1), first chicks from broods of two (B2/1), and second chicks from broods of two (B2/2) in each year were compared and are shown in Table 19.

In 1966 the mean mortality of single-brooded chicks was significantly higher than that of first chicks of a brood of two ($d = 3.08 \quad P < .01$). This may have been due to the decline in clutch size throughout the season with a greater proportion of single-egg clutches towards the end of the season. Mortality has been shown to be higher at this time, for reasons discussed earlier, and the single brooded chicks were subject to an increased risk from mortality due indirectly to the time of hatching. This difference was not seen in 1967 or 1968, but the figures for these years were based on much smaller numbers of chicks.

In 1966 and 1967 there was a significant difference between the mortality of the first and second chicks from a brood of two (1966 - $d = 7.97 \quad P < 0.001$; 1967 - $d = 3.36 \quad P < 0.001$). In 1968 the figures were too small to show significance but reflected the same general trend. The majority of the second chick mortality, over 95%, occurred during the first week and was probably due to two main factors (1) the first chicks hatched from larger eggs and as has been estimated earlier, had a greater mean weight on hatching than the second chicks and (2) the first chicks hatched on average over one day before the second chicks (mean interval between hatching 28.6 ± 6.4 hours).

During the first few days of life, the second chicks were therefore competing with a much larger chick and in many cases could not survive the competition. Figure 17 shows the mean weights of second chicks for the first week of life, taken from the growth curve, together with the corresponding weights of the first chicks, at an age when they would be competing, i.e. slightly over a day older. The mean difference in the weights of the competing chicks for the first week of competition was 15.0g; the greatest difference, 21.1g, occurred when the first chick was just over 6 days old, competing with its 5 day old sibling. After that the difference between the chicks lessened and the mortality of the second chick was reduced. This was very similar to the effect found by Hawksley (1957) who said that most of the mortality in the first week of life was that of second chicks and that this was due to competition from older chicks, which were disproportionately larger due to their earlier start.

Age at which mortality occurred

The ages of all chicks which were found dead were known to within one day from the ringing and the nest records. The numbers of dead chicks of different ages from the three categories are shown in Table 20 and in Figure 18, these are expressed as percentages of the total number found dead in any one category.

The majority (66%) of the mortality of all chicks took place within three days of hatching and 92% of the total number of deaths occurred during the first week of life.

Figure 17. The mean weights (g) of second chicks during the first week of life compared with the corresponding weights of the first chicks.

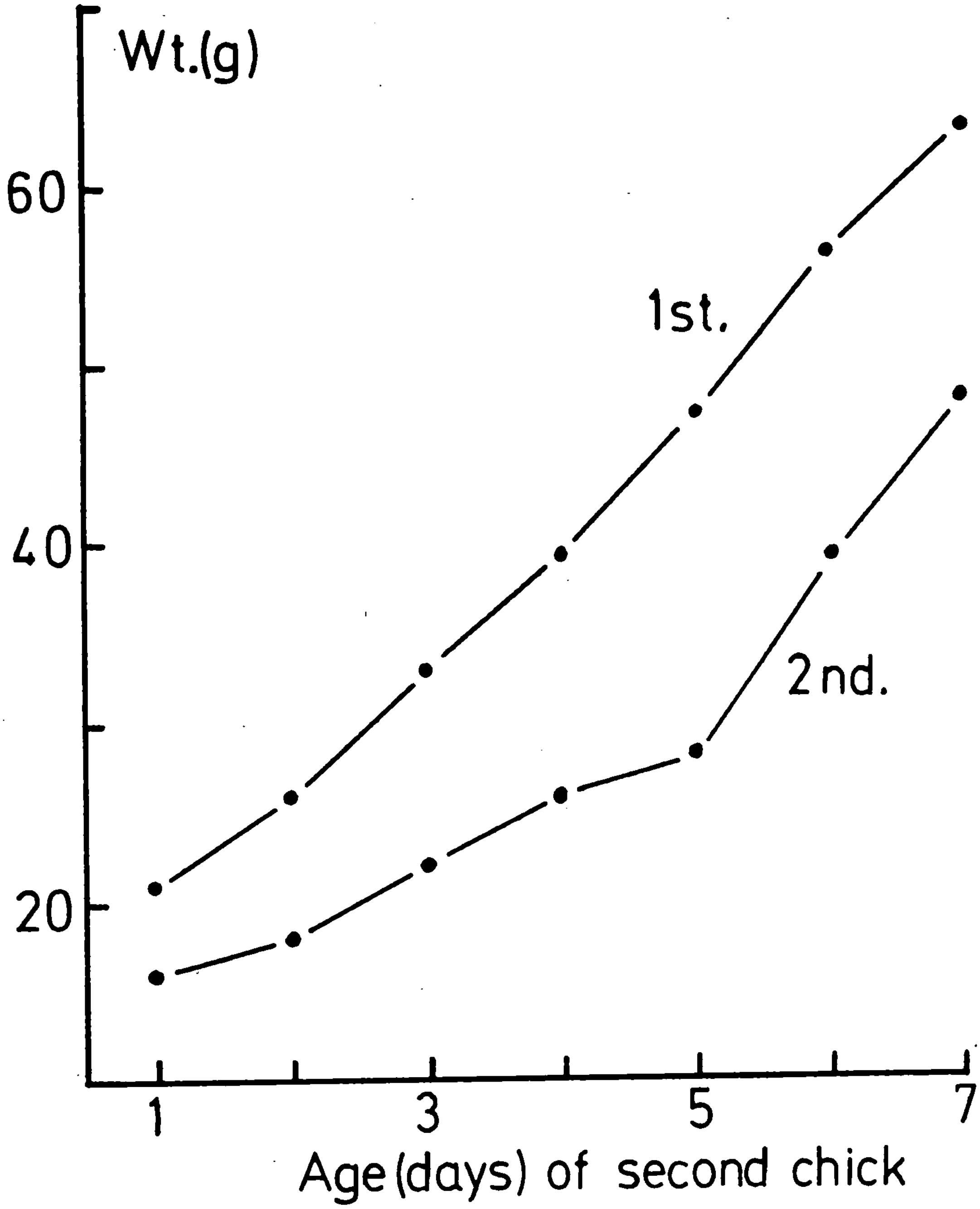

Wt.(g)
60
40
20
1st.
2nd.
1
3
5
7
Age (days) of second chick

Figure 18. The numbers of chicks dying at different ages, expressed as percentages of the total which died in each category :

A Broods of two, i first chicks
ii second chicks

B Broods of one

C All chicks

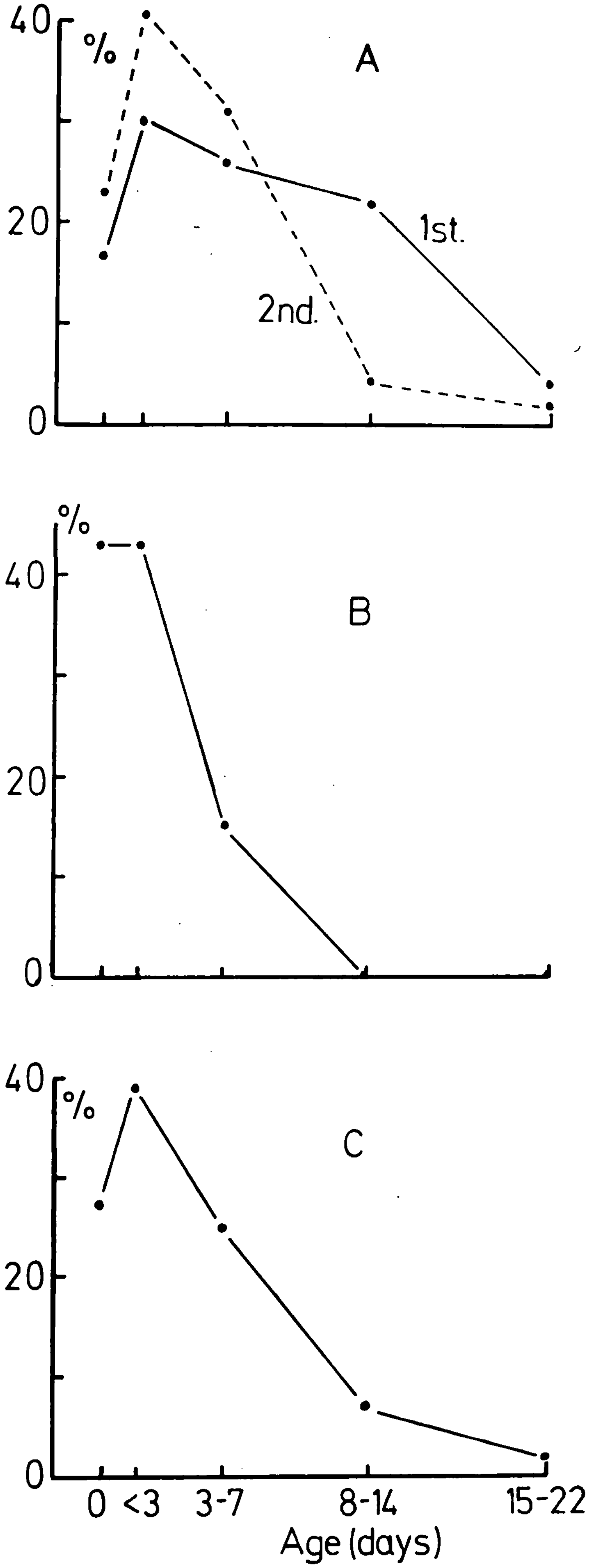

40
%
A
20
1st.
2nd.
0
%
40
B
20
0
40
%
C
20
0
0
<3
3-7
8-14
15-22
Age (days)

Table 20. Numbers and percentages off the total number at risk of dead chicks of different ages from the three brood categories

	B2/1		B2/2		B1		All	
Age	No.	%	No.	%	No.	%	No.	%
Hatching	4	17	13	23	12	43	29	27
Less than 3 days	7	30	23	41	12	43	42	39
3 - 7 days	6	26	17	31	4	15	27	25
8 - 14 days	5	22	2	4	0	0	7	7
15- 22 days	1	4	1	2	0	0	2	2
Total	23		56		28		107	

Hawksley (1957) found that 76% of all chick mortality occurred within the first week of life. This effect was particularly marked in single-brooded chicks. The reason for this early mortality was the effect of exposure on small chicks that has been discussed earlier. The increased effect of this on the single-brooded chicks was probably due to the predominance of these later in the season. At this time disturbance in the colony increased and parents of young chicks spent more time away from the nest than adults with chicks of the same age earlier in the season. If this wass at the very early stages of development, during the first few days of life, when the chicks required almost continuous brooding, there was an increased risk of chick mortality.

Within the broods of two, the mortality of the second chick was higher for the first few days when this was competing with a disproportionately larger first chick. After the first week the surviving second chick was more capable of competing successfully with its elder sibling and the mortality decreased to less than 5% of the total deaths of the second chicks. The mortality of the first chicks apparently increased in the second and third week of development, but these percentages were based on totals of only five and one dead chicks respectively and were not significant.

Fledging success and weights of juveniles

The age at which a bird was said to have fledged was defined as the age at which it could fly, but in practice a bird was assumed to have fledged, that is, to be capable of flight when the primaries were fully developed in length. Belopol'skii (1961) stated that Arctic Terns flew from the nest site after 20-24 days, but he quoted differences between the Northern Regions given by Pleske (1928) as 20 days, and the Southern regions given by Horthig (1929-31) as 28 days. Palmer (1941) said that Common Terns fly at an average of 30 days but Boecker (1967) suggested that they may require more time to fledge than Arctic Terns. Cullen (in Bannerman 1959) said that Arctic Terns took their first flight of a few yards at between 3 and 4 weeks.

In 1966 a large number of chicks were weighed daily and their plumage was examined. The development of the primaries was recorded and the mean time (± S.E.) for the full development of the primaries in 77 birds was 17.7 ± 0.6 days. There was a significant difference between the mean for the first chicks, 17.0 ± 0.5 days and the second chicks of a brood of two, 19.3 ± 1.1 days ($t = 2.11$ df 57 $P < 0.05$). The mean time for thirteen single brooded chicks to reach fledging age was 17.5 ± 1.0 days.

The majority of young birds were probably flying at least short distances by the time they were 21 days old. Mist nets were used in the later part of the season to catch these flying juveniles and all birds caught were weighed and their plumage examined. By the time the birds were 4 weeks old, all traces of down feathers had disappeared, and in 1966 when the use of mist nets was most intensive, the youngest juveniles caught were 17 days old; only four birds were caught in the cover over 4 weeks old. By this age, the birds were still being fed by the parents but this mainly took place in the open rocky areas or on the 'club' areas at low tide, rather than in the nesting area. The mean weight (± S.E.) of 44 flying juveniles caught in 1966 was 95.05 ± 2.66g and the range of weights was from 73 - 112g. This was slightly but not significantly lower than the mean weight, 99.34 ± 1.12g, of 17 adults weighed in 1966 when the range of weights was from 93 - 108g. There was however a significant difference between the mean weight of the adults in 1966 and the mean weight, 108.05 ± 1.70g (range 92 - 124g), of 57 adults weighed during a similar period in 1967 ($d = 6.09$ $P < 0.001$). The difference between the mean weights was nearly 10g and this may have been due to the abundance of food in 1967 which has already been discussed. The significantly higher weights of adults in 1967 may account for the increased breeding success in that year. Belopol'skii (1961) found that the mean weight of 67 males to be 107.3g (range 93 - 134), and of 31 females 106.1g (range 89 - 129) and these means are nearer the weights of 1967 on the Farne Islands. Belopol'skii also suggested that the mean weight of the adults dropped by 8 - 10g from May to August, but he had only small samples to support this. No evidence for this was found and it cannot explain the differences observed between the mean weights in 1966 and 1967 as the birds were weighed throughout the same period.

Breeding success

Total breeding success was calculated in each year by expressing the number of young which fledged successfully from the study area as a percentage of the number of eggs laid in that area. The figures for the three years are shown in Table 21. In 1966, the number of chicks under consideration in the chick mortality section was large; 179 chicks died out of a total of 404, giving a mortality rate of 44.3% and a survival rate of 55.7%, but the number of chicks from 1966 under consideration in Table 21 is reduced, as the chicks here include only those where the clutch size of the nest from which they came was known. This information was not available for many of the chicks in 1966 as they were primarily studied to provide data for the daily growth rate section.

Table 21. Hatching, fledging and total breeding success 1966 - 1968

Year	No.of eggs laid	No.of young hatched	% hatch	No.of young fledged	% fledged	% total breeding success
1966	322	143	44.4	75	52.4	23.3
1967	508	239	47.0	189	79.1	37.2
1968	659	103	15.6	64	62.1	9.7

The total breeding success in 1966 (23.3%) was lower than that in 1967 when 37.2% of all eggs laid produced fledged young. The hatching success for the two years was very similar and the differences in breeding success were mainly due to the increased chick survival in 1967, which has already been discussed. The breeding success in 1968 was significantly lower than the breeding success in 1966 or 1967 ($d = 11.7$ $P<0.001$), and this was due to the considerably lower hatching success (15.6%) in 1968 compared to 44.4% in 1966 and 47.0% in 1967. The reasons for this are discussed in Section 4. Those chicks which did hatch in 1968 had a fairly good chance of fledging; 62.1% fledged compared to 79.1% in 1967 and 52.4% in 1966.

The figures for the total breeding success include any clutches which were re-laid after the loss of the first clutch. As the incidence of re-laying may have been different in the three years, the breeding success was also calculated as the number of young fledged per breeding pair. Unfortunately this could be known only for colour-ringed pairs and therefore the samples which are shown in Table 22 are rather small.

Table 22. Number of young fledged per pair of breeding birds

Year	No. of pairs	No. of fledged young	Observed No. of fledged Young/pair ± S.E.	Expected no. of young/pair	% increase between observed and expected
1966	72	34	0.47±.12	0.39	+ 20%
1967	93	61	0.66±.10	0.63	+ 5%
1968	111	23	0.21±.08	0.14	+ 50%

Knowing the mean clutch size and the breeding success for each year, it was possible to calculate an expected number of young per pair, assuming that each pair only laid one clutch. These expected values are shown in Table 22 and they are all smaller than the observed values; the percentage increases between the figures are shown in the final column. These differences between the observed and expected values were not significant in 1966 ($d = 1.39$) or 1967 ($d = 0.60$) but the difference in 1968, an increase of 50.1%, was a real one ($d = 2.12$ $P < 0.05$) and was probably due to the re-laying of clutches lost during the main period of the red tide.

Dimorphism of young

In each year a dimorphism in the colour of the young Arctic Terns was observed; one form having predominantly brown and the other grey down plumage for the first week of life. As soon as the primary feathers began to develop, this ground colour was no longer obvious. A few chicks were found with very yellow down feathers, but as these accounted for less than 1% of all chicks, they were ignored in the present analysis. Approximately

5% of all chicks had a plumage which was intermediate between grey and brown, and these were also disregarded.

In 1967 and 1968 a total of 95 chicks was investigated; 67 of these, i.e. 71% were brown and 28 (30%) were grey. The proportion of brown to grey chicks was similar in each year, 74% of brown chicks in 1967 and 67% in 1968. There was no difference in the proportion of the two forms in different areas in either year.

Table 23. The mortality of grey and brown chicks in 1967 and 1968

	1967			1968			1967 and 1968		
Chick colour	No. at risk	No. dead	Mortality	No. at risk	No. dead	Mortality	No. at risk	No. dead	Mortality
Brown	33	10	30%	34	7	21%	67	17	25%
Grey	16	9	56%	12	3	25%	28	12	43%

The values for the mortality of the brown and grey young are given in Table 23, and although there is no significant difference between these mortalities, there appears to be a tendency for the brown young to suffer less mortality than the grey young. There was no evidence of a seasonal trend in the proportions of the two colours of young and the mean hatching dates in each year were very similar with no significant differences between them.

There is a possibility that the dimorphism may have evolved originally as a camouflage adaptation for different ground colours. Cullen (1960) has mentioned the importance of camouflage in Arctic Tern chicks when the adults mob marauding gulls, forcing them to fly quickly through the colony so that they are able to see only the most obvious chicks. As no differences were found between the proportions of brown and grey chicks in the different areas on Inner Farne, it seems unlikely that colour has any selective advantage at the present, although a more detailed and longer term study would be necessary to confirm this.

Preliminary discussion of Section One

The breeding biology of Arctic Tern on Inner Farne was considered in detail for the years 1966 to 1968, with some information from the latter part of 1965. The terns normally laid a clutch of one or two eggs, but it was found that in a brood of two, the second chick had a considerably higher mortality than the first. This was probably due to a smaller second egg resulting in the second chick having a lower hatching weight than the first and being unable to compete with the first chick which had hatched just over a day earlier. The second chick may quickly have become so weak that it was unable to provide the parent with sufficient stimulation to feed it and eventually succumbed. It is unlikely that the young brood was limited by the amount of food the parents were physically able to bring to the nest site as other pairs, at the same time would be successfully feeding two chicks of much greater size when the second chick did survive. It seems possible that the high mortality of the second chick is caused mainly by a behavioural failure rather than directly by food shortage. As the mortality of the first chicks of a brood of two was not significantly higher than single brooded chicks, it is clearly an advantage overall for the adult to lay two eggs as, in spite of the high mortality of second chicks, this results eventually in an increased total production of young.

In both 1966 and 1967, when the breeding was uninterrupted by the red tide, there was considerable evidence of a short initial increase followed by a general decline in reproductive success throughout the season. This was shown in the clutch size and egg volume, and particularly in the survival of chicks; in all years, the later hatched chicks had a much higher mortality than any other group and in 1965 and 1966, the mortality of chicks hatched after 10 July was nearly 95% and 100% respectively. This decline in reproductive success towards the end of the season may have been due to one or more of the factors which are discussed below, decline in food supply, increase in disturbance, reduced density of the colony, or the age of the breeding adults.

It is possible that the supply of sand eels, the main food item of the Arctic Tern on Inner Farne, may decline towards July and August, although no sampling has been carried out in this area of the North Sea. Macer (1966) said that in the south-western North Sea, the peak of the sand eel fishery was in June and that this normally extended from April to July, exceptionally from March to August. Cameron worked on sand eels in the waters near the Isle of Man and found they were shoaling heavily near the shore from March to the end of August, but after this time they moved further offshore and changed to a more sedentary habit of lying on the bottom. If this happens near the Farne Islands, there could be a reduction in the number of fish available to the terns towards the end of the season but at the moment there is no evidence for this.

There is, however, positive evidence that the number of human visitors to the islands increases during the season, particularly in the main holiday period of July and August. The effect of disturbance on the breeding success of the terns has been shown in this section and it is probable that this is one factor contributing to the low success of the late nesters. Similarly, the reduction in the density of the colony as the early breeders move away with fledged young may reduce the success by removing the advantages of colonial breeding. These are considered in greater detail in the general discussion.

The age composition of the late breeders may have an important effect on the reproductive success; this is discussed further in Section 3 where it is shown that the younger birds return later to the colony but apparently synchronise their laying with the older birds which have returned earlier. It is probable that a proportion of these late nesters are birds which have already laid one clutch and are attempting to breed for the second time. It has been shown already that replacement clutches have a very limited chance of success and this could be the direct result of reduced reproductive drive and lower capacity for egg production of the adults because they were re-laying or could be a consequence of the lateness of these clutches which would be affected, like all late clutches, by the factors considered above. It is difficult in this case to separate cause and effect, as, by definition, replacement clutches must always occur later in the season than initial clutches.

SECTION TWO - ESTIMATES OF THE AGE COMPOSITION OF THE COLONY AND ADULT MORTALITY

Introduction

Austin & Austin (1956), working on a population of Common Terns breeding at Cape Cod, Massachusetts, found that 75% of the breeding birds were 3 - 7 years old inclusive and that 90% were 3 - 10 years old. Only 3.4% were under three years and less than 7.0% were older than ten years, although they estimated the maximum reproductive life span to be about 20 years, based on the presence of a few older birds in the colony. Grosskopf (1957) found the average age of 46 Arctic Terns which had originally been ringed as nestlings and were found breeding on Wangerooge to be 11.7 years, and of 56 birds originally ringed as adults of unknown age (x years) to be x + 6.5 years. All these birds were caught on the nest apart from nine found dead. Andersen (1959) records three Arctic Terns ringed as young at Tipperne in Denmark which were later re-trapped as adults at 10, 10, and 14 years old. The oldest Arctic Tern appears to be a 29 year old recorded by Goethe (1966), although Bergstrom (1952) quoted a record of a 27 year old Arctic Tern, a 26 year old Caspian Tern, and a 21 year old Little Tern. The oldest Arctic Tern caught on the Farne Islands was a 27 year old in 1965, but the ring number of a 29 year old was read by telescope in 1968. It seems likely that the average life span for Arctic and Common Terns is up to ten years, with a few individuals surviving to a much greater age.

Methods of estimating the age composition of the colony

1. Plumage

All birds which were known to be one year old from ringing details possessed the 'Portlandica' plumage which was described by Cullen (1957). This plumage was identical with the eclipse plumage and had the following characteristics, white forehead, dark carpal bars, light underparts, dark beak, and dark legs. These birds were easily distinguishable in the field and none attempted to breed. They arrived later than the other birds and spent very little time in the actual breeding area, staying on the edge of the shore line with the 'club' of other non-breeders or failed breeders. Although these birds were easily identified as one year olds, it was difficult to assess their numbers as none of them was colour ringed. No accurate counts were possible, but the general impression gained was that there were far fewer one year old birds on the island at any time during the breeding season than any other age group. It seems unlikely that many Arctic Terns return to their natal area during the first summer after hatching.

Cullen (1957) found that some, but not all, of the two year olds had a plumage intermediate between the Portlandica and the full adult plumage. This was typified by the presence of white speckling on the forehead, dark carpal bar, whitish face, and a black marking on the inner edge of the primaries which Cullen referred to as the 'Pikei' plumage. Several birds which were known to be two years old were seen with some or all of these characters, but other two year olds were indistinguishable in plumage details from older, breeding adults. One in particular, found dead on Brownsman in 1967, was examined carefully and showed all the adult characteristics and none of the Portlandica ones. Palmer (1941b) suggested that in the Common Tern, the eclipse plumage was worn in the summer by all birds which were not old enough to breed and that these birds had rudimentary gonads, but it is not clear whether he is referring to the one year old birds only. In the Arctic Tern the 'Pikei' plumage characteristics did not apply to all the two year old birds, although there was no evidence of breeding in those two years old birds that did possess the full adult plumage.

Palmer (loc.cit.) further suggested, for the Common Tern, the existence of an 'old-age' plumage in birds 13 years and older that was intermediate between that of the eclipse and the normal plumage of younger breeding birds. Cullen (loc.cit.), however, found that in the Arctic Tern some characters of this 'old-age' plumage could be distinguished in any age group and that many birds wore this plumage for one year only. He suggested that there was a whole range of plumages intermediate between the adult and eclipse (or Portlandica) plumage and that they were not age-specific, although some characters of this 'Pikei' plumage were more likely to be worn by two year old birds than by any other age group.

In the present study the plumage details of a large number of adults whose age was known from ringing were recorded. The majority of these possessed the full breeding plumage, but a few had some characters of the 'Pikei' plumage, mainly speckling on the head. This was very variable in its extent, from an almost pure white forehead and crown to a few feathers of the crown having white tips. The numbers of birds of different ages showing one or more of the 'Pikei' plumage characteristics are given in Table 24. There was a significantly higher proportion of 'Pikei' birds among the two year olds (69%) and the birds over nine years old (18%) than among the remainder of the breeding population (mean for 3 - 8 years, 5%) (the values for χ^2 respectively were 131.8 and 17.8; $P < .001$ in both cases). Some birds, which were observed for three consecutive years, were seen to wear the plumage in one year and not in the succeeding years, while others were without it for one or two years, but appeared later with some 'Pikei' characters. There was no evidence to suggest that, apart from the two year old birds, these 'Pikei' birds abstained from breeding or that they bred either more or less successfully than adults in full breeding plumage. Plumage differences could not therefore be used to age individual Artic Terns apart from the one year old birds.

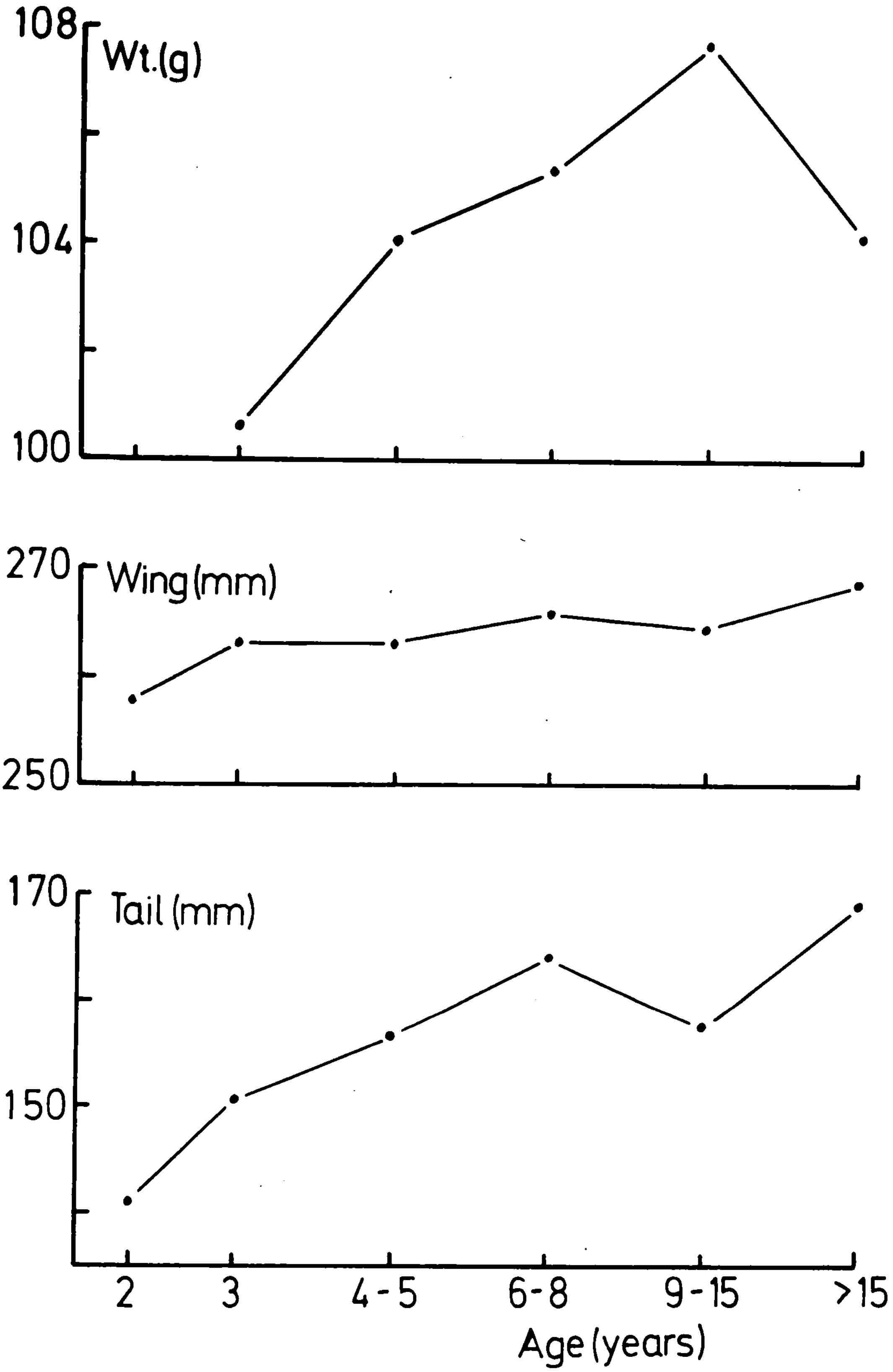
Table 24. Numbers of birds of different ages which possessed at least one characteristic of 'Pikei' plumage

Age in years	2	3	4	5	6	7	8	9	10-15	>15	Total
Numbers with 'Pikei' plumage	25	5	4	4	3	0	0	5	8	5	59
Number examined	36	37	88	69	64	40	37	35	42	20	468
Percentage of birds caught with 'Pikei' plumage	69	13	4	6	5	0	0	14	19	25	126

2. Measurements and weights of adults

Many of the adults caught were weighed and measurements made of their wing and tail length. The wing length was measured from the shoulder of the wing to the end of the longest primary feather and the tail length from the base of the tail to the end of the longest tail feather. The mean weights, wing and tail lengths, for different age groups are shown in Figure 19. There was a correlation between age and wing length ($r = + .22$ $df = 92$ $P < 0.05$) and between age and tail length ($r = + .23$ $df = 83$ $P < 0.05$) but there was no significant correlation between the age and weight of the birds, although older birds tended to be heavier, and it was impossible accurately to estimate the age of an individual bird from its weight or measurements. The sex of some of the birds was known and the differences between the weights and measurements for the sexes are

Figure 19. The mean weights (g) and the mean wing and tail lengths (mm), for adults in different age groups.



108
Wt.(g)
104
100
270
Wing (mm)
250
170
Tail (mm)
150
2
3
4-5
6-8
9-15
>15
Age (years)

shown in Table 25 together with figures quoted by Witherby _et al_ (1940) and Belopol'skii (1961). In the present study none of the differences between the sexes was significant and they were insufficient to allow an individual bird to be sexed on the basis of measurement alone. They reflect the general trends suggested by Cullen (1956) who said that on average the females are slightly smaller than the males. The figures given by Belopol'skii (loc.cit.) show the same trends although, on average, the birds he measured were all larger than the birds nesting in Britain.

Table 25. Mean weights and mean wing and tail lengths of male and female Arctic Terns. The sample sizes are given in parentheses

	Weights (g)		Wing length (mm) ± S.E.		Tail length (mm) ± S.E.	
	♂	♀	♂	♀	♂	♀
Inner Farne (1966-1968)	102.5 (5)	101.6 (11)	267.1±3.8 (20)	265.4±2.6 (20)	162.0±5.4 (19)	158.7±6.2 (20)
Belopolskii (1961)	107.3 (67)	106.1 (31)	274.2 (61)	264.3 (25)		
Witherby (1940)			265-282	260-275	170-200	158-185

3. Ringing details

It was found that the only reliable method of accurately ageing the birds was by marking as nestlings. Approximately 20% of all the adult terns on Inner Farne have been ringed, but some of them were ringed as adults and were therefore of limited use in age studies. The majority of ringed adults, however, were originally ringed as chicks and their age was therefore known to the nearest year. Some of those ringed as adults over 12 years before the study began were assumed to belong to the oldest age group (>15 years) as there was a high probability that they were ringed as breeding adults, when they were at least three years old.

The methods of trapping birds and reading ring numbers are discussed below :

a) Mist netting

The use of mist nets was confined to the early (pre-laying) and late parts of the season as this might have caused too much disturbance to incubating adults or to adults looking after very young chicks in the main part of the season. Large numbers of terns were caught in the net if it was placed in the line of a normal panic flight and, as the terns were fairly easy to extract from the net, they could be removed very quickly. The main disadvantage of this method of trapping was that it was unselective and large numbers of unringed adults were caught which were of no particular use for age studies. Any ringed birds which were caught were colour ringed, weighed, measured, and released. Observations were then made in the colony in an attempt to locate the nesting site of these colour ringed birds and to estimate their breeding success. If the birds had chosen to nest in vegetation the chances of finding the nest were low; a much higher success rate was achieved with the birds nesting on the sand in the cove or on the rocks. The trapping of adults using mist nets therefore had limitations in providing colour ringed birds for individual studies of breeding success, but was useful in obtaining a random sample of adults for assessing the age composition of the colony.

b) Sight records of year-ringed birds

In 1962, 1963, and 1964, all the chicks ringed on Inner Farne were, in addition to the B.T.O. ring, also given a colour ring according to the year in which they hatched. These rings were visible from the edge of the study areas using 8 x 30 binoculars only and were useful for ageing some individual birds. They eliminated the need for catching birds, except to put on individual sets of colour rings, and considerably increased the sample size for breeding birds of known age. It was found difficult to assess the numbers of year-ringed birds around the colony or on the 'club' areas and therefore the sight records were not used to estimate the numbers of birds of one age group in the colony unless their nest site was known.

c) Telescope readings of ring numbers

It was possible to read the ring numbers of many birds using the prismatic telescope with a magnification range of x15 to x60, but as there was a possibility of error, a ring number was assumed to be correct only if each digit had been checked at least once. Many birds whose ring numbers were read in this way were later caught and the ring numbers verified. This method was time-consuming but had the advantage of keeping disturbance to a minimum. The numbers of telescope readings in each year were 55 in 1967 and 90 in 1968; none was read in 1966. The effort on telescope reading was concentrated in 1968 as very few birds were caught at the nest.

d) Trapping of incubating birds using cage traps

Experiments were carried out with various types of trap, placed over the nest, including those incorporating a trap door operated either by a trip wire or by a string pulled by the observer. These latter two types were found to cause some disturbance to the bird when the door fell. The bird sometimes panicked inside the trap and there was a danger of it breaking its eggs before it could be removed. Observations on the nest after trapping showed that birds caught in this way took longer to return to the nest to continue incubation than birds caught in simple cage traps. This left the eggs unguarded and increased the chances of predation.

The most useful type of trap was found to be a simple cage trap with an open, but funnelled entrance. These were made out of wire-netting and were easily put into place over the eggs. Most birds entered the traps within ten minutes of their being positioned and continued incubation inside the traps. As the observer approached a trap from the open end, the bird moved away from the eggs towards the closed end of the trap and was then lifted out. As the bird moved away from its eggs, the chances of breakage were considerably reduced. After being ringed, weighed, and measured, the birds were released and most returned to continue incubation within 15 minutes. The birds were colour ringed so that observations could be made in subsequent years without re-trapping.

This method was found very useful as it enabled the selection of nests for trapping where at least one adult was known to be ringed. In 1968 very little trapping was carried out, so that apart from the twice-daily nest round, disturbance was at a minimum. The numbers of adults caught in each year and observations of colour ringing from previous years were respectively in 1966, 94 and 28, in 1967, 39 and 58, and in 1968, 25 and 159.

Of the four methods used, the last three were found to be the most useful. Most effort was concentrated in the cove or the open rocky areas as it was easier to observe colour ringed birds there in subsequent years. Some cage trapping was carried out at random in other areas, particularly in the high vegetation, where observation of rings was impossible, to see if there was any difference between the age structure of the cove and other parts of the colony. As no significant differences were found, the main study on age structure was concentrated in the cove.

Results of adult trapping

In each year, large numbers of birds were recorded by being physically caught, by telescope readings of ring numbers or by records of colour combinations of birds caught in previous years. The majority of these birds were breeding birds, although a few telescope readings of ring numbers were obtained from non-breeders. None of the breeding birds was less than three years old and it seems unlikely that Arctic Terns attempt to breed until their fourth summer. Cullen (1956) also found no evidence of breeding in two year olds, and consideration of re-trapped birds in this section has been limited to those where breeding was confirmed. The numbers of breeding birds of each age which were recorded in 1966, 1967, and 1968 are shown in Table 26. Figure 20 shows the total for each age recorded in all three years expressed as percentages of the total number recorded. Birds which were seen in more than one year are included each time they were seen as there was an equal chance in each year of observing or catching a bird of any age.

Figure 20. The numbers of breeding birds in each age group that were caught in the three year period 1966 to 1968, expressed as percentages of the total number of birds caught.

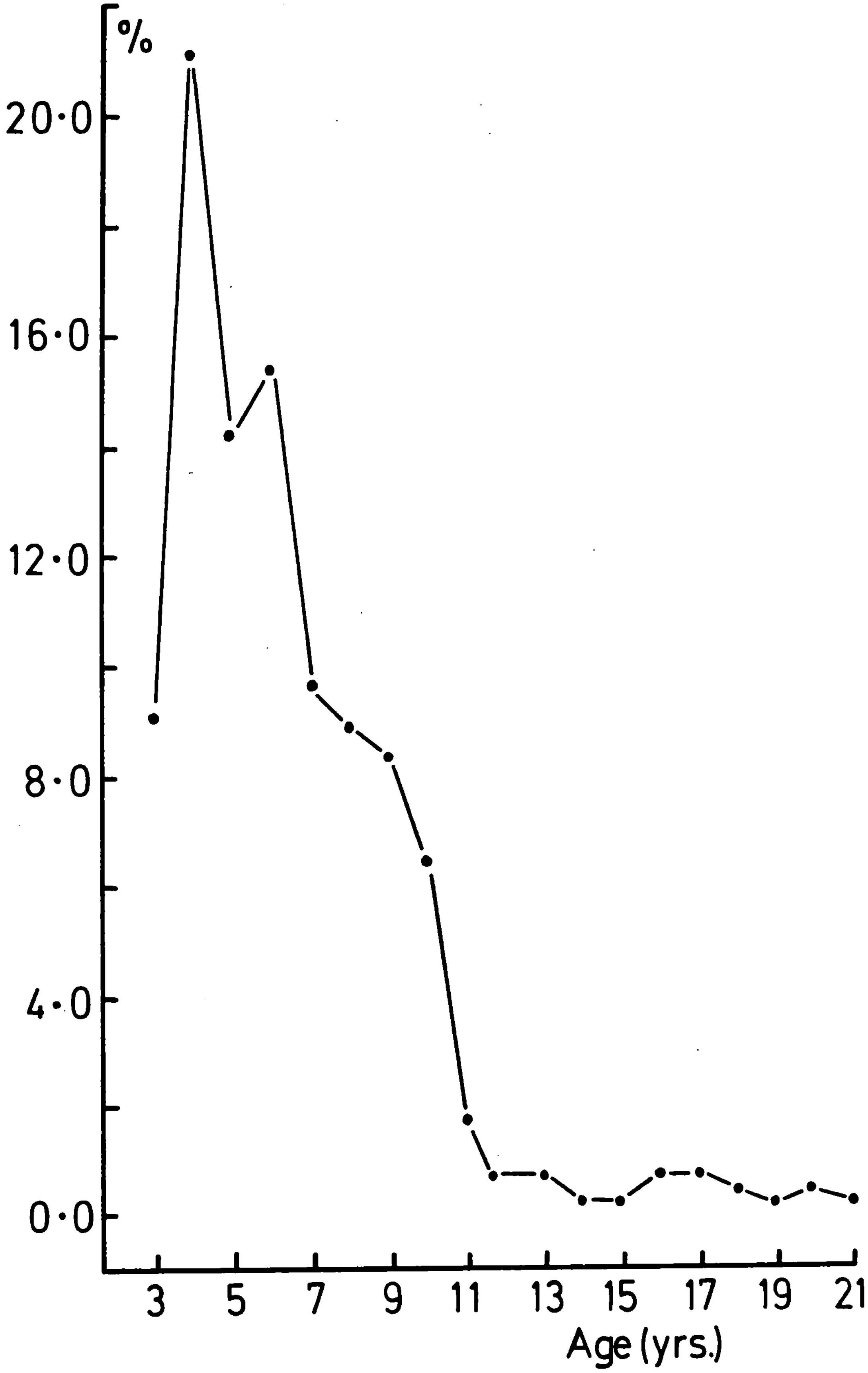

%
20·0
16·0
12·0
8·0
4·0
0·0
3
5
7
9
11
13
15
17
19
21
Age (yrs.)

Table 26. Numbers (and percentages of total) of breeding birds of known age re-trapped or observed in each year

	1966		1967		1968		ALL	
Age	No.of birds	% of total	No. of birds	% of total	No.of birds	% of total	No.of birds	% of total
3	11	12.7	25	16.9	2	1.1	38	9.1
4	24	27.6	27	18.2	37	20.4	88	21.1
5	5	5.7	23	15.5	31	17.1	59	14.2
6	13	14.9	14	9.5	37	20.4	64	15.4
7	7	8.0	19	12.8	14	7.7	40	9.6
8	15	17.2	9	6.1	13	7.2	37	8.9
9	7	8.0	15	10.1	13	7.2	35	8.4
10	0	0	6	4.0	21	11.6	27	6.5
11	2	2.3	0	0	5	2.8	7	1.7
12	0	0	3	2.0	0	0	3	0.7
13	0	0	0	0	3	1.7	3	0.7
14	1	1.1	0	0	0	0	1	0.2
15	0	0	1	0.7	0	0	1	0.2
16	2	2.3	0	0	1	0.6	3	0.7
17	0	0	3	2.0	0	0	3	0.7
18	0	0	0	0	2	1.1	2	0.4
19	0	0	1	0.7	0	0	1	0.2
20	0	0	2	1.3	0	0	2	0.4
21	0	0	0	0	1	0.6	1	0.2
29	0	0	0	0	1	0.6	1	0.2

These figures give only an indication of the age structure of the breeding population as they do not take into account the different totals of birds originally ringed. The chances of re-trapping birds from some years was higher than from other years due to the higher ringing totals and this is dealt with more fully later in this section.

In the cove, the ages of approximately 50% of all the breeding birds were known and in each year the mean age of these birds was calculated. In 1966 the mean age (± S.E.) was 7.90 ± 1.18 years, in 1967, 7.39 ± 1.10 years, and in 1968, 8.47 ± 1.04 years. The differences between the years were not significant.

The sex of some of the birds of known age was known and in each year the mean ages of breeding males and females were calculated. These are shown in Table 27. As there was no significant difference between the total mean breeding ages of 1966, 1967, and 1968, the values were combined to give an overall mean breeding age for males of 8.1±1.1 years, and for females, 7.9±1.1 years. There was no significant difference between these means either and the range for both sexes was from 3 to at least 19 years. The maximum ages were not known as some birds which had originally been ringed as adults were assumed to be the minimum possible age. Thus, if a bird was known to be at least 12 years old, it was counted as 12 years old in the calculation, and both means are probably therefore too low.

Table 27. Mean ages of males and females in each year, from 1966 to 1968. The sample sizes are given in parentheses

	1966	1967	1968	All years
♂	7.8(9)	7.6(16)	8.6(27)	8.1±1.1(52)
♀	8.4(10)	7.2(21)	8.4(23)	7.9±1.1(54)

Estimation of Mean Annual Adult Mortality

The survival rate of adults in each year, and hence the mean annual mortality rate was calculated from re-traps or sightings of birds colour ringed in the previous year. This was confined to birds which nested in the cove as observations were made in this area every day and it was unlikely that any colour ringed birds were missed. The numbers of adults colour ringed in each year, the numbers observed in subsequent years, and the annual survival rates are shown in Table 28 which includes only birds which were breeding and were therefore at least three years old. Survival of the younger adults could not be estimated as very few of these were caught.

Table 28. Survival rate of adults colour ringed in 1966 and 1967

Number originally colour ringed		Number observed following year		Number observed third year	
1966	94	1967	85 (90.4%)	1968	73 (85.9%)
1967	39	1968	31 (79.5%)		
Total	218		189		

$$\text{Mean survival rate} = \frac{189}{218} \times 100 = 86.7\%$$

The figures in the table gave a mean annual survival rate (± S.E.) of 86.7 ± 4.6% or a mortality rate of 13.3 ± 4.6%. Cullen (1956), working with smaller numbers of Arctic Terns in the same colony from 1952-1954 found a mean annual mortality rate of 13.6% whilst Springett (pers.comm.) found the mortality rate to be 15.7% between 1963 and 1965. It seems likely therefore that the annual mortality of breeding Arctic Terns is about 13%. Birds which were colour ringed at the end of one breeding season and observed at the beginning of the next season had not been subject to a whole year's potential mortality and it was possible therefore that the estimate of annual mortality was slightly too low. Austin & Austin (1956) found that the annual mortality rate for the Common Tern was constant from the 4th to the 18th year at 25%, and that after this there was a steady increase in mortality. Coulson & White (1959) found the annual adult mortality rate of the Kittiwake to be 12.4% which was then the lowest mortality recorded for any British bird.

Construction of a life table for the Arctic Tern

Deevey (1947) stated that the sources of information for the construction of a life table fell into three groups : (1) cases where the age at death was directly observed for a large, random sample of the population; (2) cases where the survival of a large cohort, born more or less simultaneously was followed

at fairly close intervals throughout its existence;
(3) cases where the age structure was obtained from a sample, assumed to be taken at random from the whole population. Deevey considered that only information obtained by the second method was statistically respectable but, unfortunately, in the present study information was available in any quantity only from the third method. The numbers of adults found dead, whose ages were known from ringing, was very small in each year and provided insufficient information for the construction of a life table. In the present study, therefore, only information on the age structure of the population, based on the ages of live recoveries from trapping and reading ring numbers, has been used in the life table.

A further limitation was imposed by the lack of information on the pre-breeding birds. No birds were found to be breeding before three years old and very few of the one and two year old birds entered the colony. These were not therefore available for trapping and no estimate of their annual mortality was obtained, although it is likely that this was higher than that of the older birds. Austin & Austin (1956) estimated that first year mortality of the Common Tern was between 60 and 70% although the annual mortality for the second and third year birds was less than for the other breeding birds. Lack (1946) suggested that in many species the juveniles had a higher mortality than older birds due to their inexperience. As no precise figures were available for the Arctic Tern, only the breeding birds were considered in the construction of the life table and this therefore begins with the three year old birds.

The numbers of birds of any age (x years) recovered alive in a later year depended on two factors; (1) the mortality rate of the birds and (2) the numbers of birds originally ringed as pulli x years previously. As the total number of pulli ringed on Inner Farne varied considerably from year to year, particularly in the 1940s and early 1950s, this was corrected for by expressing the total number of birds of x years recovered live in one year as a percentage of the number of pulli ringed x years previously. These percentages, together with the ringing totals and the numbers of birds recovered, are shown in Table 29. There are a few anomalies in the table which are discussed in detail below.

In 1968 only two three-year old birds were recovered (0.18%) and this was considerably lower than the twenty-five three-year old birds recovered in 1967 (1.83%) and the eleven birds recovered in 1966 (0.81%). It is possible that the low recovery rate in 1968 was due to the effects of the red tide. In 1966 and 1967 the three year old birds returned to the colony on average five days later than the four year old birds. It was possible that in 1968 the return of the three year old birds coincided with the main period of the red tide and that these birds delayed their breeding due to the lack of stimulation from other birds in the colony, which might be particularly necessary

Table 29. Recoveries of ringed birds in each year

Year	Number pulli ringed	Age in 1966	Number retraps 1966	Number retraps as % of number ringed	Age in 1967	Number retraps 1967	Number retraps as % of number ringed	Age in 1968	Number retraps 1968	Number retraps as % of number ringed
1965	1093	1	0	0	2	2	0.18	3	2	0.18
1964	1369	2	5	0.37	3	25	1.83	4	37	2.70
1963	1358	3	11	0.81	4	27	1.99	5	31	2.28
1962	(615)	4	24	2.00	5	23	2.75	6	37	3.08
1961	1043	5	5	(3.90) 0.48	6	14	(3.74) 1.34	7	14	(6.02) 1.34
1960	910	6	13	1.43	7	19	2.09	8	13	1.43
1959	603	7	7	1.16	8	9	1.49	9	13	2.16
1958	963	8	15	1.56	9	15	1.56	10	21	2.18
1957	965	9	7	0.73	10	6	0.62	11	5	0.52
1956	211	10	0	0	11	0	0	12	0	0
1955	255	11	2	0.78	12	3	1.18	13	3	1.18
1954	64	12	0	0	13	0	0	14	0	0
1953	26	13	0	0	14	0	0	15	0	0
1952	411	14	1	0.24	15	1	0.24	16	1	0.24
1951	319	15	0	0	16	0	0	17	0	0
1950	373	16	2	0.54	17	3	0.80	18	2	0.54
1949	190	17	0	0	18	0	0	19	0	0
1948	(200)	18	0	0	19	1	0.50	20	0	0
1947	(200)	19	0	0	20	2	1.00	21	1	0.50
1939	(?50)	27	0	0	28	0	0	29	1	2.00

to birds attempting to breed for the first time. After the red tide, the number of birds in the colony was considerably reduced and the amount of courtship and display by the older birds may have been insufficient to stimulate the three year old birds to commence breeding. Lacking this stimulation, they may have moved out of the breeding areas as only two ringed birds were recorded in these areas in 1968.

The number of pulli ringed in 1962 (615) was low compared to the number ringed in 1961 (1043) and in 1963 (1358). The recovery rate of the 1962 birds in 1966 (3.9%) was significantly higher ($d = 2.48$ $P < 0.02$) than for birds of the same age in 1967 (2.0%). It is possible that this may be accounted for in conjunction with the low ringing total for 1962, for although the total ringing effort was less in 1962 than in other years, it may have been concentrated on older pulli. In subsequent years chicks of all ages were ringed and these suffered heavy mortality, particularly those less than a week old. If older chicks or flying juveniles were ringed in 1962, they would have a better chance of survival, and this would explain the differences between the return of four year old birds in 1966 (hatched in 1962) and the return of four year old birds in 1967 (hatched in 1963). As the recoveries from 1962 were significantly different from the other years, these were re-calculated using an estimated total of birds ringed in 1962, based on the average ringing total of 1961 and 1963, assuming that this would have been the total in 1962 if chicks of all ages had been ringed. The estimated percentages of recoveries obtained by this method are underlined in Table 29 and the actual percentages are given in brackets.

In many cases the number of retraps in 1968 was higher than the number in 1966 and 1967, and yet all the birds retrapped in 1968 must have been alive during the two preceding years. However, if these birds were not caught or observed in 1966 or 1967 they were not included in the total retraps. This meant that the age structure for each year was based solely on the random sample for that particular year and these figures could then be summed to calculate the mean age structure as described below.

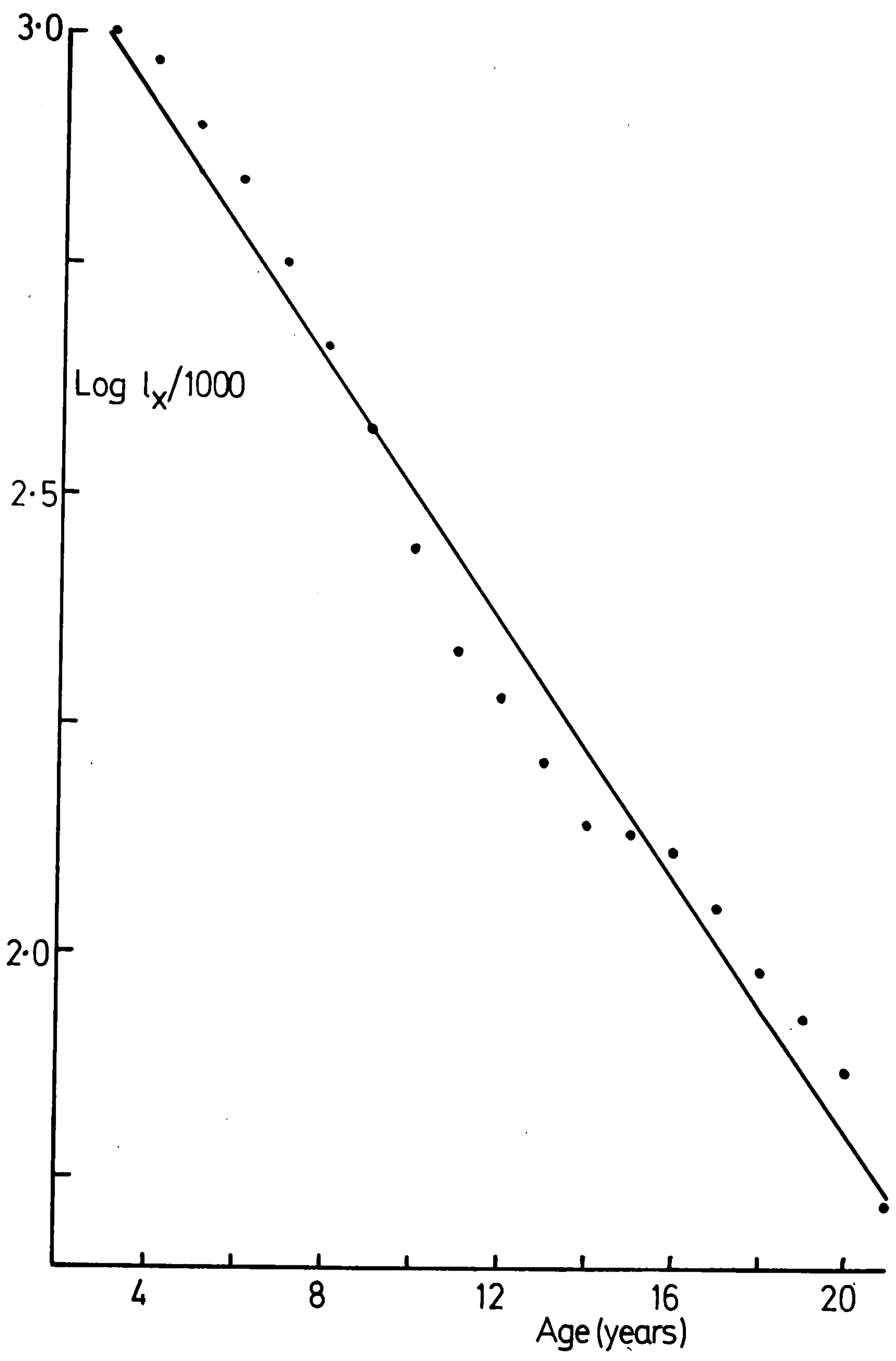
The percentages of ringed birds recovered at a particular age were summed for the three years to give the first column of Table 30 which represents the numbers of birds of age x years alive at one time. Nice (1937) quoted in Deevey (1947) argued that the ratio of the living at any age to the total number of the living must equal the ratio of the dead at any age to the total number of deaths, that is :

$$\frac{l_x}{\Sigma l_x} = \frac{d_x}{\Sigma d_x}$$

As Σd_x by convention is 1000, $d_x = \frac{l_x}{\Sigma l_x} \cdot 1000$

By use of this formula, the second column of Table 30 has been calculated and, from this, the value of $l_x/1000$. These values have been plotted on a logarithmic scale in Figure 21 to give a survivorship curve for the Arctic Tern. The value for 29 years was omitted from the calculation of the regression as only one bird of this age was recovered.

Figure 21. The survivorship curve for the Arctic Tern; log lx/100 is plotted against age, the equation of the line is $y = 3.20 - 0.07\ x$.


3·0
2·5
2·0
Log l_x/1000
4
8
12
16
20
Age (years)

The equation of the line is $y = 3.20 - 0.07x$ and the close linear relationship is indicated by the slope being very significantly different from zero ($t = 29.68$ $df = 17$ $P < 0.001$).

This suggests that a constant proportion of Arctic Terns die within each age group although there is some evidence from the graph of slightly increased survival in the 4 - 8 year old birds and the birds over 15 years old; while between 9 and 15 years there is some evidence of slightly decreased survival. It is suggested later in Section 3 that birds of 4 - 8 years old are at the best physiological age for breeding and this may explain their better survival. Austin (pers.comm.) found in both the Common and the Sooty Tern a comparatively high mortality in the first year of life followed by a lower mortality that remained steady over the adult years until the onset of old age, starting at about age 18 in the Common Tern and at 25-27 in the Sooty Tern.

Table 30. Initial figures used in the calculation of the life table

Age in years	Total of percentage retraps l_x	Calculated value of d_x $\frac{l_x}{\lesssim l_x} .1000$
3	2.82	59
4	6.69	141
5	5.51	116
6	5.85	123
7	4.59	98
8	4.48	94
9	4.45	94
10	2.80	59
11	1.30	27
12	1.18	25
13	1.18	25
14	0.24	5
15	0.24	5
16	0.78	16
17	0.80	17
18	0.54	11
19	0.50	11
20	1.00	21
21	0.50	11
29	2.00	42
	$\lesssim l_x = 47.45$	$\lesssim d_x = 1000$

The life table for the Arctic Tern from three years old has been calculated from the formulae given by Deevey (1947) and this is shown in Table 31. The mean mortality rate (± S.E.) from 3-21 years was calculated as 15.1 ± 3.0% which is similar to the value of 13.3 ± 4.6% obtained from the observations of colour-ringed birds.

From Table 31, the average expectation of further life (± S.E.) for an adult Arctic Tern of three years or more on Inner Farne was calculated as 4.48 ± 0.36 years. Austin (1942) gave the average expectation of further life of the Common Tern as 2.8 years with an adult mortality of 30%. Lack (1954) gave figures for the expectation of further life in many birds calculated from different sources and he compared the small life span of many Passerines, having an expectation of life of only one to two years, and an adult mortality of 40 to 60%, with that of many larger birds. He used Richdale's figures (1952) for a small population of the Royal Albatross (Diomedea epomophora) to calculate the expectation of further life as about 36 years and for the Yellow-eyed Penguin (Richdale 1949a), 9.5 years. Lack quoted Paynter's figure (1947) for the Herring Gull as 2.8 years and calculated the expectation of life in the Heron as 2.7 and the Lapwing 2.4 years. He expected the highest average to be in the larger petrels or eagles, with a clutch of only one egg and several years of immaturity.

Table 31. Life Table for Arctic Terns from 3 years old

Age in years	d_x Number dying in age interval out of 1000 alive	l_x/1000 Number surviving at beginning of age interval	$1000q_x$ Mortality rate/1000 alive at beginning of age interval	e_x Expectation of further life to those attaining age interval
3	59	1000	59.0	6.01
4	141	941	149.8	5.36
5	116	800	145.0	5.21
6	123	684	179.8	5.01
7	98	561	174.7	5.00
8	94	463	203.0	4.95
9	94	369	254.7	5.09
10	59	275	214.5	5.65
11	27	216	125.0	6.06
12	25	189	132.3	5.85
13	25	164	152.4	5.66
14	5	139	36.0	5.59
15	5	134	37.3	4.78
16	16	129	124.0	3.94
17	17	113	150.4	3.42
18	11	96	114.6	2.94
19	11	85	129.4	2.25
20	21	74	283.8	1.51
21	11	53	207.5	0.91
29	42	42	1000	0.50

Preliminary Discussion of Section Two

As the only accurate way of determining the age of individual Arctic Terns was from ringing, this limited the study to a certain extent. Although terns have been ringed on the Farnes for a long time, the numbers of birds which were ringed 20-30 years before the study began, i.e. 1930s and 1940s, were very small, particularly as this period included the war years. The chances of an adult being recovered from this early period were therefore very slight, particularly in view of the fact that ring wear and loss is known to occur to some considerable extent in sea-birds. Austin & Austin (1956) found that some series of rings put on to Common Terns only lasted 5-6 years although a few remained readable after 20 years. They found great variation in the durability of different series of rings and between individual terns, but on average, the older series of rings lasted between eight and twelve years. In the present study very few signs of wear were seen in Arctic Tern rings, even in some of the very old aluminium rings which were over 15 years old, and it is possible that this is not such an important cause of ring loss in Arctic Terns as in other sea-birds. Corrosion of rings was found to occur in a few cases, particularly in the earlier Monel series, sometimes making the ring illegible after only a few years.

Some retrapping and re-ringing of adult terns has been carried out on Inner Farne, but this has been at infrequent intervals. The chances, therefore, of very old birds being retrapped on Inner Farne were fairly small and yet, in spite of this, a few very old birds were caught. This suggested that the Arctic Tern may be a longer-lived species than was previously thought. The oldest definite record of a retrapped bird was a tern of 27 years, caught in the year before the present study began, although there was a telescope reading of a ring number of a bird 29 years old. As this was recorded at the time without any doubt, and each digit was checked at least once, it seemed likely that this was a correct record. If larger numbers of birds had been ringed in the 20-30 years before the study, and an intensive programme of retrapping and re-ringing of adults had been followed consistently, it is likely that larger numbers of older birds would have been caught, and the age structure might have had a slightly older bias.

However, on the information available at the present time, it can be assumed that although individual birds may survive to considerable ages, the majority of the breeding population is less than 10 years old. This is a fairly typical age structure for sea-birds; Austin & Austin (1956) found 90% of the Common Tern on Cape Cod were 3-10 years old. Although they also found that the mortality rate increased after the 18th year, with the onset of old age, no evidence for this was found in the present study. The survival rate of the very old birds was not significantly different from the younger birds; nor, as is shown in Section 3, was their total breeding success reduced. It is possible that the Arctic Tern, like the Sooty Tern, may normally be a longer-lived bird than the Common Tern and may not go through a period of senility and increased mortality, or that this occurs at a later age than was possible to measure in the present study.

SECTION THREE - THE BREEDING BIOLOGY OF ARCTIC TERNS OF KNOWN AGE

Introduction

It has been shown already that the Arctic Tern is a relatively long-lived bird. The majority of the birds in the breeding population were between three and fifteen years old, with individuals surviving and breeding at a much greater age. There have been few studies on the effect of age on the breeding biology of long-lived birds, other than those of Coulson & White (1958) on the Kittiwake, and Richdale (1949) on the Yellow Eyed Penguin. Austin (1945) studied the Common Tern but concentrated mainly on the demographic aspects of the colony, although he did give some information about breeding success in relation to age.

There are, however, many references to the age at which birds commence breeding. This can vary from a few months old in the Estrildine Firefinch (*Lagonostica senegala*) (Morel 1964) to the eight, nine and eleven year old individuals recorded for the Royal Albatross (Richdale 1952). This deferred maturity of the Procellariiformes has been well documented and is typical of long-lived birds. In the Arctic Tern it has been fairly well established that the birds do not breed until they are at least three years old. Neither Cullen (1957) nor the present study found any evidence of birds breeding at two years of age. Hawksley (1957) cited one instance of a two year old Arctic Tern breeding, but Cullen suggested that this might have been the result of a triangular marriage where the non-breeding two year old was tolerated by the older breeding pair, and even allowed to sit on the eggs. Triangular marriages were occasionally recorded in the present study where three birds were seen consistently at the same nest site, with very little animosity between them. Unfortunately it was not possible to determine the ages of any of these birds as many of them were not ringed.

The three year period, from 1966 - 1968, was a short enough time to study age effects on long-lived birds, and the original plan for the study was to concentrate on trapping and colour-ringing the adults in 1966 and 1967 whilst also studying their breeding biology. Thus, by 1968 it was hoped that there would have been a large number of colour ringed birds, whose ages were known, breeding in the study area. The breeding biology of these known aged birds could then have been studied mainly by observation, with very little trapping of adults necessary, but unfortunately the breeding of all the birds was so disrupted in 1968 by the red tide that discussion of any age effects is mainly confined to the results from 1966 and 1967.

That the numbers of adults in each group was fairly small was due to the practical difficulties of working on Inner Farne where, as has been stated earlier, work in the colony was only permitted during times when the general public were not on the island. This limited the hours of work in the colony to a period before

10.00 hours when the first visitors arrived and a period after 17.00 hours when the last boat usually left. On fine days, particularly at the weekends, the visiting period was much longer and work, apart from observation, was even more limited.

In order to compensate for these small groups, some of the age classes have been combined in some parts of the study to give groups of approximately the same sample size. For the same reasons where no significant difference exists between 1966 and 1967, results from these two years have often been combined.

Methods

The ages of the birds were estimated by retrapping ringed birds, observations of colour-ringed birds, or by telescope readings of ring numbers as described in Section 2. In some cases, where both members of a pair had been ringed as pulli in previous years, it was possible to determine the mean age of the pair. From observations on courtship and mating made early in each season, the sex of many colour-ringed birds was also known.

In many cases only one bird in a pair had been ringed, and it was possible to know the age of only this bird. This was assumed to be the mean age of the pair and is considered as such in this section. From studies on pairs where the ages of both birds were known there was found to be a high correlation (r = + 0.92) between the ages of the two members of a pair.

When the nest of a bird of known age was found this was marked with a numbered metal tag and observations were made on the nest and eggs until the young hatched. The young were ringed within a few days of hatching and were given a numbered British Trust for Ornithology ring and a single colour-ring on the other leg to distinguish the chicks from parents of known age. When the chicks were older and had wandered from the immediate nest site the colour-ring enabled quick identification of young which were to be weighed. In all three seasons a sample of these chicks was weighed at daily intervals to compare the growth rates of chicks from parents of different ages.

Date of return to the colony

The dates when colour-ringed birds were first seen in the study area were recorded, provided that they were seen on at least two subsequent occasions. This eliminated the chance of including birds which had failed to breed in other areas and later wandered into the main study area. The results obtained are not true dates of return, as it was not possible to record with certainty the first dates on which the birds returned to the breeding colony, but at any time during the early part of the season there was an equal chance that a bird of any age might be observed and therefore these dates can be compared for different age groups.

There was no significant difference between the mean dates for 1966 and 1967 ($t = 2.03$ $df = 9$ $P > 0.05$) and these have therefore been combined in Table 32 and in

Figure 22. The return in 1968 was probably upset by the red tide when the behaviour of the birds returning at the normal time was unsettled, rendering them more liable to early observation. This may have been responsible for the earlier mean date in all age groups in 1968.

Table 32. Mean dates of first sighting for birds of known age - 1966/1967 and 1968. (All dates are June unless otherwise stated)

Age (years)	Mean date ± S.E. 1966/1967	No.	Mean date ± S.E. 1968	No.
2	13 July ± 4 days	7	-	-
3	29 ± 4 days	24	13 ± 3	2
4	25 ± 3	43	29 May ± 3	30
5/6	21 ± 4	42	3 ± 3	66
7/8	18 ± 3	45	9 ± 4	28
>8	12 ± 4	64	5 ± 3	74

The mean dates for the first sighting of the two year old birds were considerably later in both 1966 and 1967 (mean 13 July ± 4) than the youngest breeding birds, that is, the three year olds (mean 29 June ± 4). There was no evidence of any of the two year old birds attempting to breed. It was possible, but not meaningful, to calculate this date in 1968 as the return of the two year old birds probably occurred in the middle of the red tide.

Figure 22. The mean dates of first sighting birds of known age. The data for 1966 and 1967 have been combined.

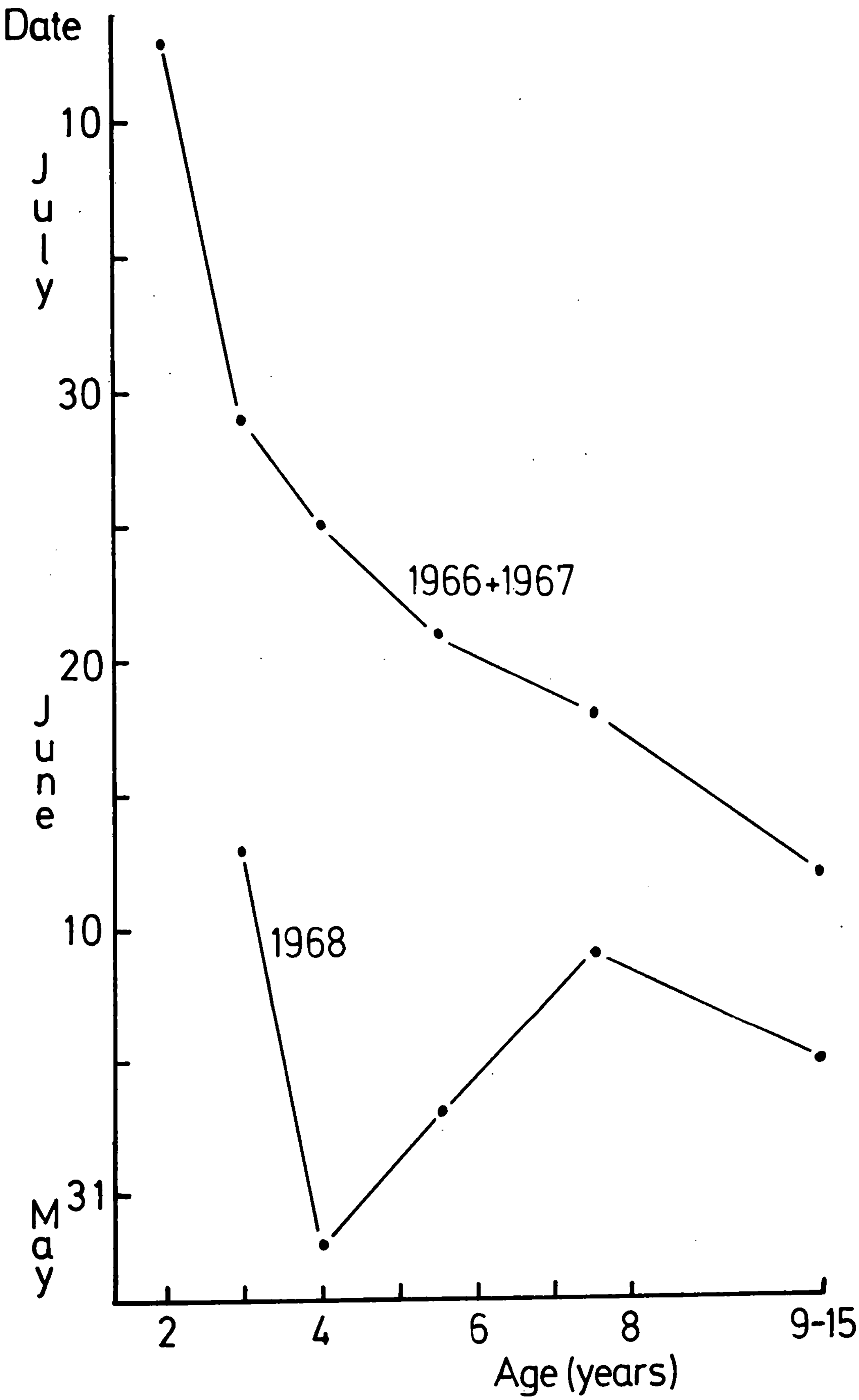

Date
10
July
30
20
June
10
May 31
1966+1967
1968
2
4
6
8
9-15
Age (years)

Table 33. Analysis of variance for mean dates of return to the colony in each age class

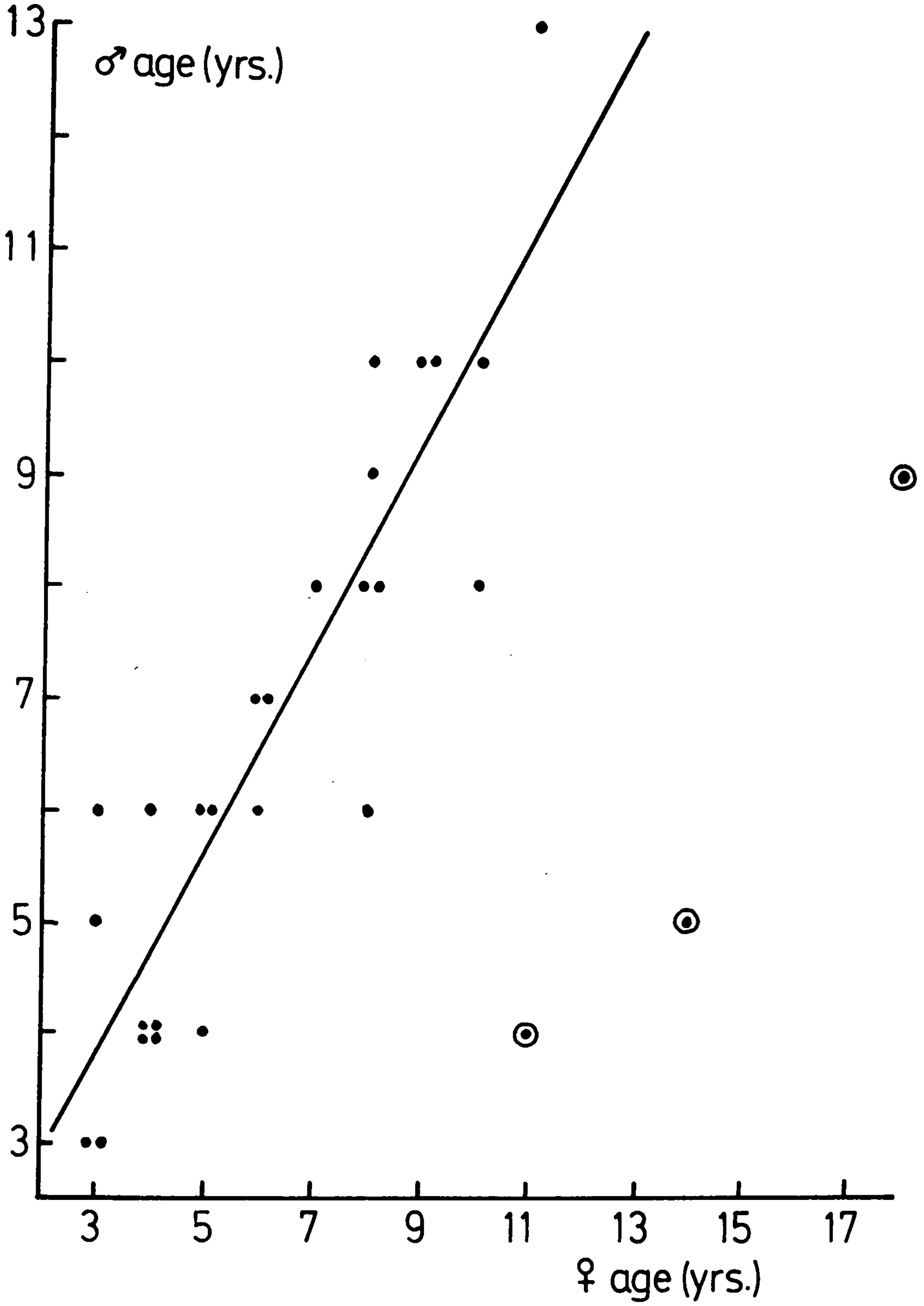
Source of variation	Sum of squares	D.F.	Mean squares	Var. Ratio	P
Between age classes	9338	8	1167.3	2.84	<0.01
Residual	85791	209	410.5		
Total	95129	217			

The analysis of variance given in Table 33 shows that there is a significant difference ($P < 0.01$) between the mean dates of return for each age class using the combined data for 1966 and 1967. The older birds returned to the colony first and there is a high correlation between the age of the birds and the mean date of return : $r = -0.93$, $df = 7$, $P < 0.001$. This may give the older birds a chance to secure a better nest site than those younger birds returning later. There is some evidence to suggest that the younger birds nest in the less densely occupied areas, particularly at the edge of the colony. The younger birds, especially those returning to breed for the first time, may not choose to nest at the edge of the colony, but as a consequence of a late return, these areas may be the only ones not already occupied. Coulson & White (1958) found a similar effect in the Kittiwake, where birds that had bred at least once before, returned to the colony approximately a month earlier than those returning to breed for the first time. It was difficult to estimate the mean date of arrival of the young Arctic Terns as none of them were individually colour ringed, but general observation showed a similarity with the findings of Cullen (1957) that the Portlandica birds arrived three to four weeks after the adults had first appeared and certainly after the main bulk of the adults had arrived.

Age of the pair

An attempt was made to determine the age of both members of a pair but this was only possible where both birds had been originally ringed as pulli, or as adults, if they were known to be at least nine years old and could be put into the 'old' category. The birds were sexed by observation of courtship and mating. The details for twenty-nine pairs where the age and sex of both birds was determined are shown in Figure 23. The regression of the line is $y = 1.0 + 0.92x$, showing a close relationship between the ages of the two parents although, as might be expected, this is less so in the older birds. If the long-standing partner of an old bird dies, then the survivor is more likely to choose a mate from younger age classes. With this in mind, three very wide values have been omitted from the regression calculation, but they are shown on the graph. As the ages of the pairs are overall so equal : the slope of the regression does not differ significantly from unity ($t = 0.83$ $df = 24$ $P < 0.10$), where the age of only one partner was known, this has been assumed to be the mean age of the pair.

Figure 23. The relationship between the ages of paired birds, the equation of the line is : $y = 1.0 + 0.92\,x$. The three values marked ⊙ have not been used in the regression (see text).



♂ age (yrs.)
13
11
9
7
5
3
3
5
7
9
11
13
15
17
♀ age (yrs.)

Observations on colour ringed pairs suggested that the pair bond is strong in the Arctic Tern and birds may retain the same mate until one partner dies. Birds returning to the colony to breed for the first time are therefore more likely to find a mate of similar age as, apart from the surviving member of a pair where one bird has died, there will be few other unmated birds around. Cullen (1957), however, suggested that there may be a shortage of younger females as the males of three years old have a stronger urge to return to the breeding grounds than females of the same age.

Nest Site

The choice of nest site may affect the ultimate breeding success of the pair. An attempt was made to see if the choice of different types of nest site was related to the age of the pair.

Where both members of a pair survived the winter, there was considerable evidence to show that they returned to nest in precisely the same place as the previous year. This has been noted elsewhere in Arctic Tern (Andersen 1959), and also in Common Tern (Austin 1956). Austin also suggested that in the Common Tern, this site tenacity increased with age and was largely responsible for keeping the group together and returning it to the same place. In the present study, general observations on colour-ringed birds confirmed this site tenacity in the Arctic Tern.

In any one year the only birds which will be choosing a nest-site rather than returning to a familiar one are those returning to breed for the first time and perhaps the birds whose mates have not survived the winter. As the average annual mortality of adults is 13-15%, the latter group will be fairly small. However, this group and the young birds are the only ones which are likely to breed in new areas.

In order to quantify the density at which birds of different ages were nesting, a 2 metre square grid was staked out in the study area before the onset of breeding. The position of each nest was recorded according to the square of the grid it occupied. Knowing the dates at which all the eggs in the study area were laid, an estimate was made of the numbers of nests in any one square at a particular time in the breeding season. Knowing the laying dates of birds of known age, it was possible to determine how many other nesting sites in the same grid square were occupied at the time when a bird commenced laying. This does not give a true value for density as it takes into account only the particular grid square in which the bird has nested and not the neighbouring squares. It does, however, give some indication of the number of other nests in the proximity of a particular bird. These "densities" were calculated in relation to age and are shown in Table 34.

Table 34. Relative density of nest sites in relation to age

Age of breeding birds (years)	Mean Density	Number of pairs
3	6.0	2
4	6.4	23
5-6	9.5	34
7-9	8.1	17
10-15	8.9	27
>15	10.3	7

The figures obtained for the densities of the nests show that there was a marked tendency for older birds to nest more closely together than the younger birds, particularly those returning to breed for the first or second time.

Another aspect of the nest site was considered by comparing the nests which were in a corner of the study area, sheltered by a bank, with the nests which were in the more exposed central parts of the cove. The mean age of birds (± S.E.) breeding in the sheltered areas was found to be 9.47 ± 0.12 and in the exposed areas 6.35 ± 0.24 years. These values are significantly different ($d = 12.73$ $P < 0.001$).

It seems likely that the older birds, returning to the colony first, either return straight to their breeding place of the previous season or deliberately choose a favourable nest site. They also apparently choose to crowd into a particular area where presumably the greater proximity of other breeding birds may have a selective advantage.

Darling (1938) concluded "that colonial nesting birds furnish each other with the necessary visual and auditory stimulation for the reproductive cycle" and Salomønsen (1943) showed that small groups of Kittiwakes, Guillemots, Little and Lesser Black-backed Gulls failed to breed, presumably because of lack of stimulation. It is possible that the older Arctic Terns on the Farne Islands chose to nest at a very high density in order to obtain the maximum stimulation from their neighbours. This crowding may also result in the birds being more aggressive towards predators, for it has been shown in many species that birds nesting in small groups are much less aggressive than those nesting in large, dense colonies. Isolated Arctic Tern nests may be more prone to attacks by predators due to this lack of aggression.

The older birds, returning earlier to the colony and having first choice of nest site, probably benefit in two ways by choosing to nest close together; first, the increased stimulation on the sexual cycle by other breeding pairs, and, second, the protection from predation gained by the increased aggression of the sub-colony.

Date of laying

In some cases the date when the first egg was laid was known accurately, but for many birds of known age the laying date was estimated by an extrapolation back from the hatching date. This occurred in cases where the colour-rings on the bird were not seen until after it had started incubating. As stated earlier, the mean incubation period from the laying of the first egg is twenty-two days, and there is no indication of any appreciable variation in this with age. Therefore the laying date was assumed to be twenty-two days earlier than the hatching date, and these calculated dates have been used in this analysis together with the known laying dates.

The mean laying dates (± S.E.) for each age group in 1966, 1967 and 1968 are shown in the first part of Table 35a where it should be noted that the absence of a standard error value in this and subsequent tables indicates that the mean was derived from identical numbers. As there is a significant difference between 1966 and 1967 ($t = 4.5$ df = 8 $P < 0.01$), a correction factor (mean difference = + 9.1 days) was applied to the 1966 results before they were combined with those from 1967. These combined results are shown in Table 35b and have been subjected to an analysis of variance with respect to age. The analysis is presented in Table 36 and shows that no significant difference exists between the mean laying dates for the different age classes. An analysis performed on the 1968 data gave a similar result.

Table 35a. Mean laying date in relation to age (all dates in June unless otherwise stated)

	1966		1967		1968	
Age (Yrs.)	MEAN L.D.± S.E.	N	MEAN L.D.± S.E.	N	MEAN L.D.± S.E.	N
3	7 ± 5	3	11 ± 3	13	4	1
4	6 ± 2	12	9 ± 3	9	16 ± 3	12
5	3	1	14 ± 3	14	11 ± 2	11
6	2 ± 1	8	14 ± 3	9	12 ± 2	9
7	3 ± 2	3	17 ± 6	5	10 ± 2	2
8	3 ± 1	13	24 ± 3	4	11 ± 3	5
9	6 ± 2	8	9 ± 5	7	13 ± 6	6
10-15	31 May ± 2	3	6 ± 3	11	9 ± 2	28
>15	4 ± 2	5	12 ± 7	5	13 ± 4	7
All	4 ± 2	56	12 ± 3	77	11 ± 2	81

Table 35b. Mean laying date in relation to age. Corrected data from 1966 and 1967 combined (all dates in June)

Age years	Mean laying date ± S.E. 1966/1967		N
3	12 ± 3		16
4	12 ± 2		21
5	14 ± 4		15
6	13 ± 3		17
7	15 ± 4		8
8	15 ± 2		17
9	12 ± 4		15
10-15	7 ± 3	10 ± 4	14
>15	13 ± 6		10
All	12 ± 4		133

Table 36. Analysis of variance between the mean laying dates for each age class, using the combined and corrected data of 1966 and 1967

Source of variation	Sum of squares	D.F.	Mean squares	Var. Ratio	P
Between dates	796	8	99.6	1.13	0.05
Residual	10946	124	88.3		
Total	11742	132			

It has been suggested from the dates when first observations were made on colour-ringed birds that the older birds return to the colony first. The advantage of an earlier return was probably mainly in the greater choice of breeding site. The younger birds, returning later, had a more limited choice of nest site, but they spent less time in pre-laying activities than the older birds. The presence of birds already involved in breeding activities probably stimulated the younger birds to commence breeding fairly quickly and this resulted in a synchronisation of the time of laying of birds of all ages.

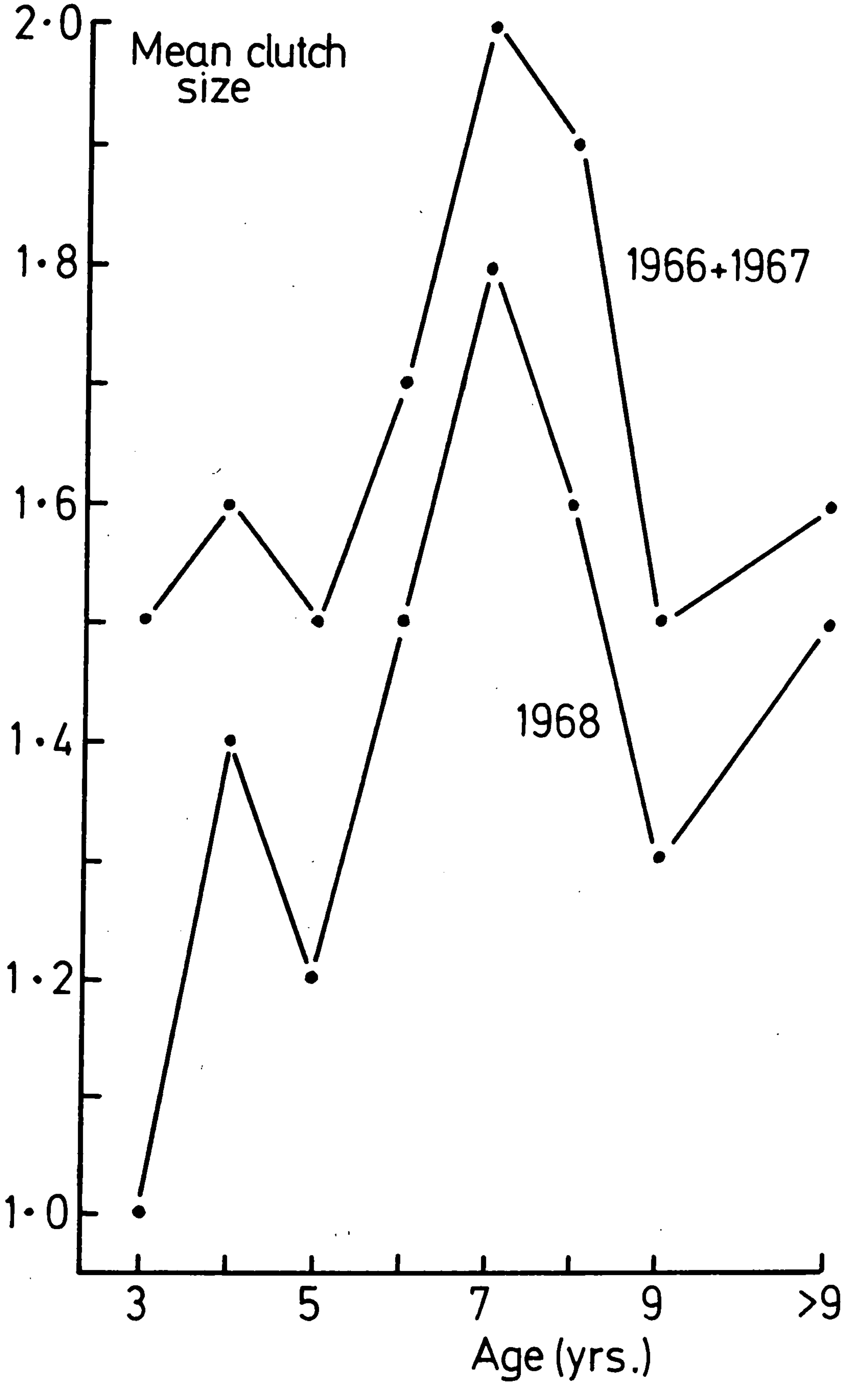
Clutch size

The difficulties of determining the clutch size accurately when the birds were suffering egg predation have already been discussed in Section 1. The same criterion for clutch size is used here, namely that the clutch must have had the same number of eggs for at least three days. This eliminates the chance of including clutches which are preyed upon before completion. In many cases birds which had their first clutch preyed upon laid a second and sometimes even a third. Only the size of the first clutch is included in this analysis. The mean clutch sizes for each age group in 1966, 1967 and 1968 are shown in Table 37 and Figure 24.

Table 37. Mean clutch size in relation to age

			Mean Clutch sizes			
Age	1966 ± S.E.	N	1967 ± S.E.	N	1968 ± S.E.	N
3	1.6 ± 0.3	5	1.5 ± 0.2	12	1.0	1
4	1.7 ± 0.1	13	1.5 ± 0.2	11	1.4 ± 0.1	14
5	1.5 ± 0.5	2	1.5 ± 0.1	20	1.2 ± 0.2	9
6	1.9 ± 0.1	11	1.3 ± 0.2	7	1.5 ± 0.2	11
7	2.0	3	2.0	7	1.8 ± 0.3	4
8	1.9 ± 0.1	10	2.0	4	1.6 ± 0.3	5
9	1.6 ± 0.2	7	1.4 ± 0.3	5	1.3 ± 0.3	4
10-15	1.5 ± 0.2	2	1.0	1	1.5 ± 0.1	34
>15	1.7 ± 0.2	2	1.8 ± 0.3	4	1.5 ± 0.2	6
All	1.8 ± 0.2	55	1.6 ± 0.1	71	1.5 ± 0.2	88

Figure 24. The mean clutch size in relation to age.



2·0
1·8
1·6
1·4
1·2
1·0
Mean clutch size
1966+1967
1968
3
5
7
9
>9
Age (yrs.)

There was no significant difference between the clutch sizes in 1966 and 1967 and 1968 but the results from the latter year tended to be lower and have not been included in the combined data that are presented in Table 37b.

Table 37b. Mean clutch size in relation to age. 1966 and 1967 data combined

Age	Mean clutch size ± S.E.	N
3	1.5 ± 0.1	17
4	1.6 ± 0.1	24
5	1.5 ± 0.1	22
6	1.7 ± 0.1	18
7	2.0	10
8	1.9 ± 0.1	14
9	1.5 ± 0.2	12
>9	1.6 ± 0.2	10

An analysis of variance was carried out on the combined data and the results in Table 38 show that there was more variation between the age classes than would be expected by chance. The largest clutches were laid by the seven and eight year old birds, while birds of less than seven years and greater than eight years were less likely to lay clutches of two than the intermediate aged birds. A similar effect with inexperienced birds was found in the Kittiwake by Coulson & White (1958) where the clutch size of females breeding for the first time was lower than those breeding on the second and subsequent occasions. They found no evidence of a decline in the clutch size of the older birds.

Table 38. Analysis of variance between the mean clutch sizes for each age class, using the combined data of 1966 and 1967

Source of Variation	Sum of squares	D.F.	Mean squares	Var. Ratio	P
Between age classes	4.0	8	0.50	2.32	0.05
Residual	25.3	118	0.21		
Total	29.3	126			

Egg measurements

The maximum length and breadth of all eggs laid by adults of known age was measured in mm using a vernier caliper. From these measurements the shape index and volume were calculated as has been described in Section 1. A number of eggs were weighed within a day or two of being laid and the weights were very closely correlated with the volumes (see Section 1) and in this study the volumes of the eggs are considered rather than the weights for the reasons given earlier.

The mean lengths and breadths (± S.E.) of eggs measured in 1966 and 1967 from birds of different ages are presented in Table 39.

Table 39. Mean length and breadth of eggs for each age group in 1966 and 1967. Dimensions in mm

	1966			1967		
Age (yrs)	Length ± S.E.	Breadth ± S.E.	N	Length ± S.E.	Breadth ± S.E.	N
3	40.1 ± 0.8	28.8 ± 0.2	3	39.6 ± 0.5	28.7 ± 0.2	12
4	40.3 ± 0.4	29.1 ± 0.2	13	40.0 ± 1.2	29.4 ± 0.6	3
5	-	-	-	41.3 ± 0.7	29.1 ± 0.2	12
6	41.3 ± 0.5	29.2 ± 0.4	6	40.5 ± 0.6	29.5 ± 0.3	8
7	40.4 ± 0.4	29.5 ± 0.2	4	40.8 ± 0.5	29.4 ± 0.1	6
8	40.5 ± 0.4	29.2 ± 0.2	10	42.1 ± 0.8	29.4 ± 0.1	6
9-15	40.7 ± 0.2	29.4 ± 0.2	10	40.6 ± 0.4	29.3 ± 0.3	11
>15	40.6 ± 0.8	29.3 ± 0.3	5	40.3 ± 0.5	29.3 ± 0.2	3

Length

There is very little difference between the lengths of the eggs laid by birds of different ages, and although there is a slight possibility that birds breeding for the first time may lay a somewhat shorter egg, the differences are not significant.

Breadth

The mean breadth of eggs laid by three year old birds is somewhat less than the mean breadth laid by any other age group, but the differences again are not significant.

There is, therefore, a tendency for young birds to lay narrow eggs and for the breadth to increase after the first year of breeding. Richdale (1955) found a similar effect in the Yellow-eyed Penguin, where two year old females which were breeding for the first time laid significantly lighter and narrower eggs than the older birds.

Volume

As there is little difference between the lengths and breadths for the different age classes in either 1966 or 1967, these data have been combined to give the mean volumes (± S.E.) shown in Table 40. It is important to stress that these means have been calculated from the individual volumes for each age class, and not from the mean length and breadth values.

Table 40. Mean egg volumes, 1966 and 1967 combined data

Age (years)	1966 and 1967 Mean Vol. (cc)	± S.E.	N
3	15.7	± 0.2	15
4	16.5	± 0.3	16
5	16.7	± 0.2	12
6	17.0	± 0.3	14
7	16.9	± 0.2	10
8	16.9	± 0.2	16
9-15	16.8	± 0.2	21
>15	16.7	± 0.3	8

It has been shown in Section 1 that the volume of the egg is closely correlated with the weight of the chick on hatching ($r = +0.83 \quad y = 0.49 + 0.75x$), and this factor is probably the most important one ultimately influencing breeding success. Although there is only a statistically significant difference between the egg volumes of three and four year old birds ($t = 2.22$ $df = 29$ $P < 0.05$), there is, nonetheless, a definite trend of increasing volume with age. Six year old birds show a maximum egg volume of 17.0cc and after this there is a slight decline to 16.7cc for birds older than fifteen years. Romanoff & Romanoff (1949) found in the domestic hen that their eggs were smallest during the first year and then increased in volume until the third or fourth year. Subsequently the volume of the egg decreased as the age of the fowl advanced.

The mean lengths and breadths for 1968 are presented separately in Table 41 together with the mean volumes. These latter, together with those from 1966-1967, are illustrated in Figure 25.

Reference to Figure 25 shows that although the egg volumes in 1968 for the two age groups, four years and greater than fifteen years, are close to those for 1966-1967, the trend of increasing volume up to six years old does not occur. These latter birds in 1968 have the lowest egg volume of 15.8cc. Although the majority of the egg volumes for 1968 are lower than those for 1966-67, only the volumes for the five and six year old birds are significantly so :

5 years : $t = 2.10$ $df = 19$ $P < 0.05$

6 years : $t = 4.14$ $df = 31$ $P < 0.001$

Figure 25. The mean egg volume (cc) in relation to age.

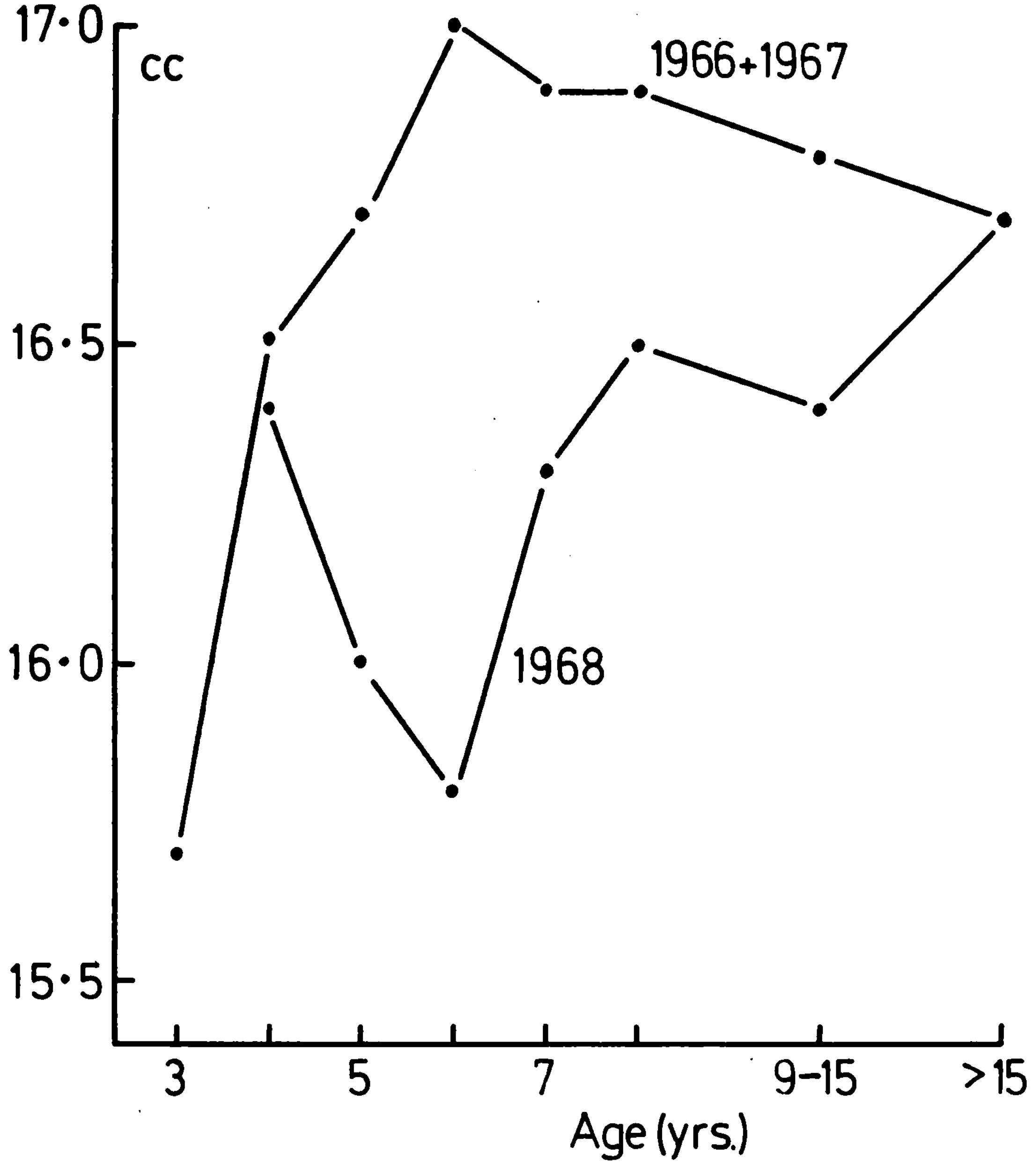

17·0
cc
16·5
16·0
15·5
1966+1967
1968
3
5
7
9–15
>15
Age (yrs.)

Table 41. Mean length, breadth, and volume for 1968 in relation to age

Age (years)	Mean length (mm)	± S.E.	Mean breadth (mm)	± S.E.	Mean volume (cc)	± S.E.	N
4	41.2	± 0.4	28.8	± 0.1	16.4	± 0.2	20
5	40.5	± 0.7	28.7	± 0.1	16.0	± 0.3	9
6	40.6	± 0.4	28.5	± 0.4	15.8	± 0.4	19
7	40.2	± 0.5	29.1	± 0.3	16.3	± 0.5	9
8	40.8	± 0.3	29.0	± 0.3	16.5	± 0.4	11
9-15	40.2	± 0.3	29.1	± 0.1	16.4	± 0.2	55
>15	40.3	± 0.3	29.3	± 0.3	16.7	± 0.4	9

The reduction in egg volume in 1968 may have been due to a general effect of the red tide on the birds' abilities to produce large eggs. Part of the reduction may be accounted for by the active selection for smaller eggs, in that in 1968 many birds were found dead in an egg bound condition and if the latter was the primary cause of death, then possibly those birds laying smaller eggs would be more likely to survive. It is interesting that the volumes laid in 1968, while lower, are within a range of two standard deviations from the 1966 and 1967 volumes.

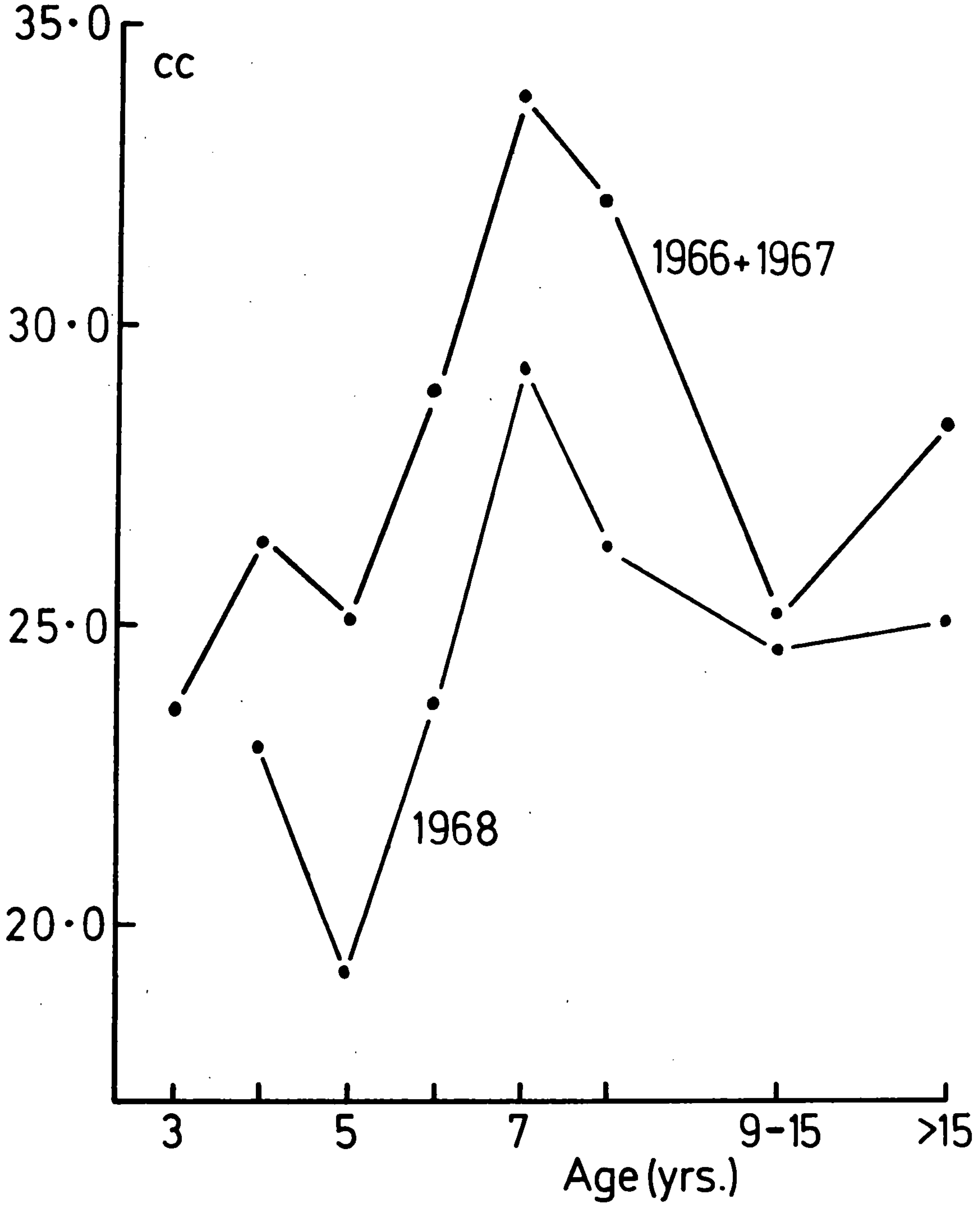
Clutch volume

The mean clutch volume for each age group in 1966-1967 and in 1968 has been calculated by multiplying the respective mean clutch sizes and the mean egg volumes. The mean clutch volumes obtained in this way are given in Table 42 and illustrated in Figure 26.

Table 47. Mean clutch volume (mean clutch size x mean egg volume) in relation to age, 1966-1967 and 1968

Age (year)	Mean clutch volume 1966-67 (cc)	Mean clutch volume 1968 (cc)
3	23.6	-
4	26.4	23.0
5	25.1	19.2
6	28.9	23.7
7	33.8	29.3
8	32.1	26.4
9-15	25.2	24.6
>15	28.4	25.1

Figure 26. The mean clutch volume (cc) in relation to age.


35·0
cc
30·0
25·0
20·0
1966+1967
1968
3
5
7
9–15
>15
Age (yrs.)

The clutch volumes for 1966-1967 show a general increase up to the seven year old group, with some evidence of a slight decline after this. The lowest value for clutch volume occurred in the three year old birds. The values for 1968 are all lower, with the largest clutch volumes in the six, seven and eight year age groups.

Shape Index

The values of the shape index for each age class in 1966, 1967, and 1968 are given in Table 43 and have been calculated from the individual shape indices for each group. The table shows very little relationship between shape index and age for any of the years. Given the possible relationship between egg volume and age, discussed earlier, this must mean that increases in egg volume are brought about by equally proportional increases in length and breadth together.

Table 43. Mean shape index (± S.E.) for each age class in 1966, 1967, and 1968

Age (yrs)	1966 Mean S.I. ± S.E.	1967 Mean S.I. ± S.E.	1968 Mean S.I. ± S.E.
3	71.8 ± 1.8	72.5 ± 0.9	---------
4	72.3 ± 0.7	73.5 ± 2.9	70.2 ± 0.6
5	----------	70.8 ± 1.5	71.0 ± 1.5
6	70.6 ± 0.9	72.9 ± 0.9	70.2 ± 1.2
7	72.9 ± 0.5	72.2 ± 0.9	72.3 ± 0.6
8	72.3 ± 0.5	70.1 ± 1.7	71.1 ± 1.7
9-15	72.2 ± 0.7	72.1 ± 1.0	72.7 ± 0.5
>15	72.3 ± 1.4	72.9 ± 1.4	72.8 ± 0.6

The differences in egg size for different age groups are reflected in the change in egg size laid by individual females in successive years. In this short term study it was possible to follow individuals only for two or at the most three years, but they show a reflection of the general trends. The mean volumes of all eggs laid by individual females in each year are shown in Table 44.

Table 44. Mean volume of all eggs laid by individual females of known age in 1966, 1967, and 1968

Ring number	Age in 1966 (years)	Mean egg volume (cc) 1966	Mean eggvol. (cc) 1967	Mean egg vol. (cc) 1968
CK36695	2	-	14.42	15.32
CK34198	2	-	14.86	15.73
CK23164	3	16.14	-	17.32
CK10959	4	16.29	-	16.13
CK25358	4	-	15.20	16.14
CK02481	5	-	17.89	15.70
705055	6	15.91	-	15.67
727593	6	15.48	-	14.75
CK63528	9	17.16	15.94	17.93
727112	>10	16.22	-	15.13
CK02108	>10	16.87	15.44	16.15

When considering these individual measurements, it must be borne in mind that the total mean egg volume for 1968 was considerably less than the mean for either 1966 or 1967, the reasons for which are discussed in Section 4. Where an increase is seen from 1967 to 1968 in the size of the eggs from a normal individual, this would probably have been a larger increase in a normal year; where no increase or a slight decrease has occurred, there would probably have been a slight increase in a normal year.

Hatching Success

The hatching success of birds of known age was calculated by expressing the number of eggs which hatched as a percentage of the total number of eggs laid by a particular age group. The results for 1966/1967 have been combined and are given in Table 45a together with those from 1968. Table 45b shows the hatching success for clutches of one and two for different age groups, using the combined data from 1966 and 1967.

Table 45a. Hatching success in relation to age of the adults, 1966 and 1967 combined and 1968

Age (years)	1966/1967	No. of clutches	1968	No. of clutches
3	30.9%	28	-	0
4-5	37.6%	55	40.7%	27
6-8	48.2%	50	31.1%	29
>8	53.2%	42	26.9%	54

Table 45b. Hatching success for 1966 and 1967 combined in relation to clutch size and age of adults

Age (years)	Clutches of 1	No. of clutches	Clutches of 2	No. of clutches
3	42.8%	14	25.0%	14
4-5	64.0%	25	26.7%	30
6-8	41.2%	17	50.0%	33
>8	50.0%	22	55.0%	20

There was some evidence of an increased hatching success from the older birds in 1966/1967. Table 45b shows that this was mainly due to the greater success of clutches of two; there is a significant difference between the hatching success for clutches of two in 1966/67 from four and five year olds (26.7% and from 6-8 year olds (50%) ($d = 2.68$ $P < 0.01$). This could reflect a greater ability of the older birds to look after two eggs, particularly in the critical period early in incubation when it was shown in Section 1 that this was the time when clutches of two were most likely to be preyed upon.

Reasons for hatching failure

These have been discussed in detail in Section 1 and are dealt with here only in relation to age.

1. Starling predation

Starling predation accounted for most of the hatching failure in each year and showed some variation with the age of the adult terns. The percentage of clutches laid by birds of known age, which were presumably preyed upon by Starlings, is shown in Table 46. These figures are for 1966 and 1967 only.

Table 46. The percentage of the total number of clutches laid which were preyed upon by Starlings in relation to age; data from 1966 and 1967

Age (year)	Total clutches	No.preyed upon	% preyed upon
3, 4, & 5	74	28	38
6, 7, & 8	50	22	44
Greater than 8	41	25	61

Although Starlings may sometimes take only one egg from a clutch of two, this incomplete predation never occurred where the age of the parents was known. The results are therefore related to the number of clutches, rather than eggs laid, to be consistent with other data presented under this heading. Although there is an apparently higher level of predation in the older group, the difference between this and the 6, 7, and 8 year groups is not significant.

2. Exposure

It has been shown earlier in this section that there is a correlation between the age of the bird and the date of return to the colony. This may give the early arrivals, the older birds, an advantage in the choice of nest site. Within the cove the most important variable in the different sites was the amount of shelter. The cove was protected from the north-west to the south by a fairly steep bank and to a lesser extent to the south-east by a low ridge of rocks. Parts of the cove were thus fairly sheltered from the main westerly winds, other areas were much more exposed. There is some evidence to suggest that birds which return early to the cove, having a free choice of nest site and no attachment to a particular site, select the more sheltered areas, and it has been shown earlier that there is a significant difference between the mean age of birds breeding in the sheltered areas and those breeding in the more exposed areas.

The significance of the shelter may be related to the density at which birds are nesting in these areas.

It may also be related to the rate of cooling of an unattended clutch. If there was some delay during change-over or if a bird left a clutch for any time, this would cool much more quickly in the exposed areas than in those sheltered from the prevailing wind.

3. Flooding

Some nests were in a position below the High Spring Tide level and if a Spring Tide occurred during the incubation period then the eggs were washed away. This accounted only for a very small percentage of the total egg loss. The percentage of clutches from birds of known age lost this way in 1966 and 1967 are shown in Table 47.

Table 47. The percentage of clutches lost through flooding in relation to the age of the parents; combined data from 1966 and 1967

Age (year)	Total clutches	No.flooded	Percentage flooded
3, 4, and 5	74	7	10
6, 7, and 8	50	2	4
Greater than 8	41	0	0

The flooding of nests accounted overall for a very small percentage of the hatching failures, and was confined to the younger birds. This suggests that a bird may become more experienced in its choice of nest site and that birds breeding for the first time are more likely to choose unsuitable nest sites. There is considerable evidence to show that older birds return to the same nest site every year, but insufficient to show that if young birds are consistently unsuccessful at one site they will move on to a new one, although this seems very likely.

4. Other causes of egg loss

As discussed in Section 1, other reasons for hatching failure accounted for only a very small percentage of clutches and the data are insufficient to show any age specificity.

Re-laying replacement clutches

The ability of a bird to lay a second clutch if it loses the first is obviously an important factor in its ultimate breeding success and an attempt was made to see if there was any difference in the re-laying ability of birds of different ages.

This study was confined to colour-ringed birds nesting in the cove area. As observations were made by telescope for at least two hours on almost every day of the breeding seasons of 1967 and 1968, the chances of identifying a colour-ringed bird at its nest site were fairly high. Those birds which re-laid always did so in the same immediate area, although not always at the exact site as the first clutch. None was seen to re-lay in other areas and observations of some of these colour-ringed "failed" breeders in the "club" areas provided further confirmation that they had not laid a replacement clutch. Table 48 shows the numbers and percentages of birds of different age groups which laid a replacement clutch when the initial clutch failed.

Table 48. Percentage of lost clutches that resulted in re-laying in relation to age

Age (years)	Number of failed clutches	Number of replacement clutches	Percentage of replacement clutches
3	10	2	20
4-5	9	4	44
6-8	14	3	21
>8	22	13	59

The differences between the age groups are rather varied, but there is a possibility that the older birds may have a greater ability or inclination to re-lay a clutch if the first one fails.

Growth rates of young from parents of known age

A sample of chicks from parents of known age was weighed at the same time each day in all three years. The chicks were ringed with a single colour ring on the day after hatching and later with a numbered British Trust for Ornithology ring. The colour ring enabled quick identification of chicks which were to be weighed every day. These rings were removed before fledging and replaced with the normal year colour ring.

The growth curve of Arctic Tern chicks has been discussed in Section 1 where it was shown to have a constant daily increase in weight between the fourth and the fourteenth day. Only chicks of this age are included in this study and the mean growth rates between the fourth and fourteenth day for chicks from parents of known age are shown in Table 49.

Table 49. Mean growth rates of chicks from parents of known age, 1966 and 1967 data combined

Age of parents (year)	Mean growth rate of chick (g./day)	± S.E.	N
3	6.7	± 0.7	10
4	5.5	± 0.4	10
5	6.6	± 0.5	12
6	6.1	± 0.4	9
7	6.3	± 0.9	4
8	6.1	± 0.5	11
9	6.4	± 0.3	7
>9	7.5	± 0.4	12

The growth rates of young from parents of over nine years old were over one gram per day more than those from younger parents. This increase in the growth rate is presumably a reflection of the parents' greater efficiency at fishing or of a greater concentration on the task of feeding the young or of a combination of both these factors. Coulson & White (1958) found that in the Kittiwake, the growth rates of chicks from parents breeding for the first time were significantly lower than those where the parents had bred before.

It is important to remember that the growth rate only represents a proportion of the amount of food brought to a chick. Chicks were reared in the laboratory as described in Section 1 and their total intake of food and daily growth rate were measured. These were compared with observations in the field on the number and estimated length of fish brought to chicks. By weighing sand eels of various lengths, it was possible to estimate the weight of the mean daily intake of fish. The two sets of data showed a great similarity and suggested that in order to maintain a daily increase in weight of seven grams a chick must receive between twenty-five and thirty grams of fish each day.

As the increase in the growth rate of the chicks from older parents is maintained for the whole of the linear section of the growth curve, the chicks from these parents will be approximately 10g heavier when they are 14 days old than the chicks from younger parents. This difference in weight may well have an effect on their survival through the fledging period.

Fledging success

The fledging success has been calculated as the percentage number of young which fledged, compared with the number of young which hatched. In Table 50a the fledging success is presented for the young of parents in the different age groups using combined data from 1966 and 1967, while Table 50b gives a breakdown of fledging success for broods of one and two. The numbers of young that were fledged from each parental age group in 1968 were very small and are not considered here.

Although there is no significant difference between the results for the different ages, there is some evidence of a slight increase in fledging success among the older parents. The causes of chick mortality have been discussed in Section 1 and no evidence is available to indicate that any particular mortality of the chicks is specific to the age of the parents.

Table 50a. Fledging success, using combined data from 1966 and 1967, in relation to age

Age of parents (years)	No. of young hatched	No. of young survived to fledging	Percentage fledged
3	13	7	54
4-5	32	25	66
6-8	40	25	63
>8	33	23	70

Table 50b. Fledging success in relation to age and brood size, 1966 and 1967 combined

	Brood of one			Brood of two		
Age of parents (years)	No.of young hatched	No.of young fledged	Percentage fledged	No.of young hatched	No.of young fledged	Percentage fledged
3	6	3	50	7	4	57
4-5	16	9	56	16	12	75
6-8	7	5	71	33	20	61
>8	11	9	82	22	14	64

Breeding success

The total breeding success for each age group has been calculated as the percentage of eggs which produced fledged young. As has been discussed earlier, it was not possible to assess post fledging survival in this short term study. The breeding success of the different age groups is given in Table 51 which illustrated the very slight tendency for breeding success to increase with age, although the differences are not statistically significant.

Table 51. The percentage of eggs which produced fledged young in relation to age in 1966 and 1967 combined and in 1968

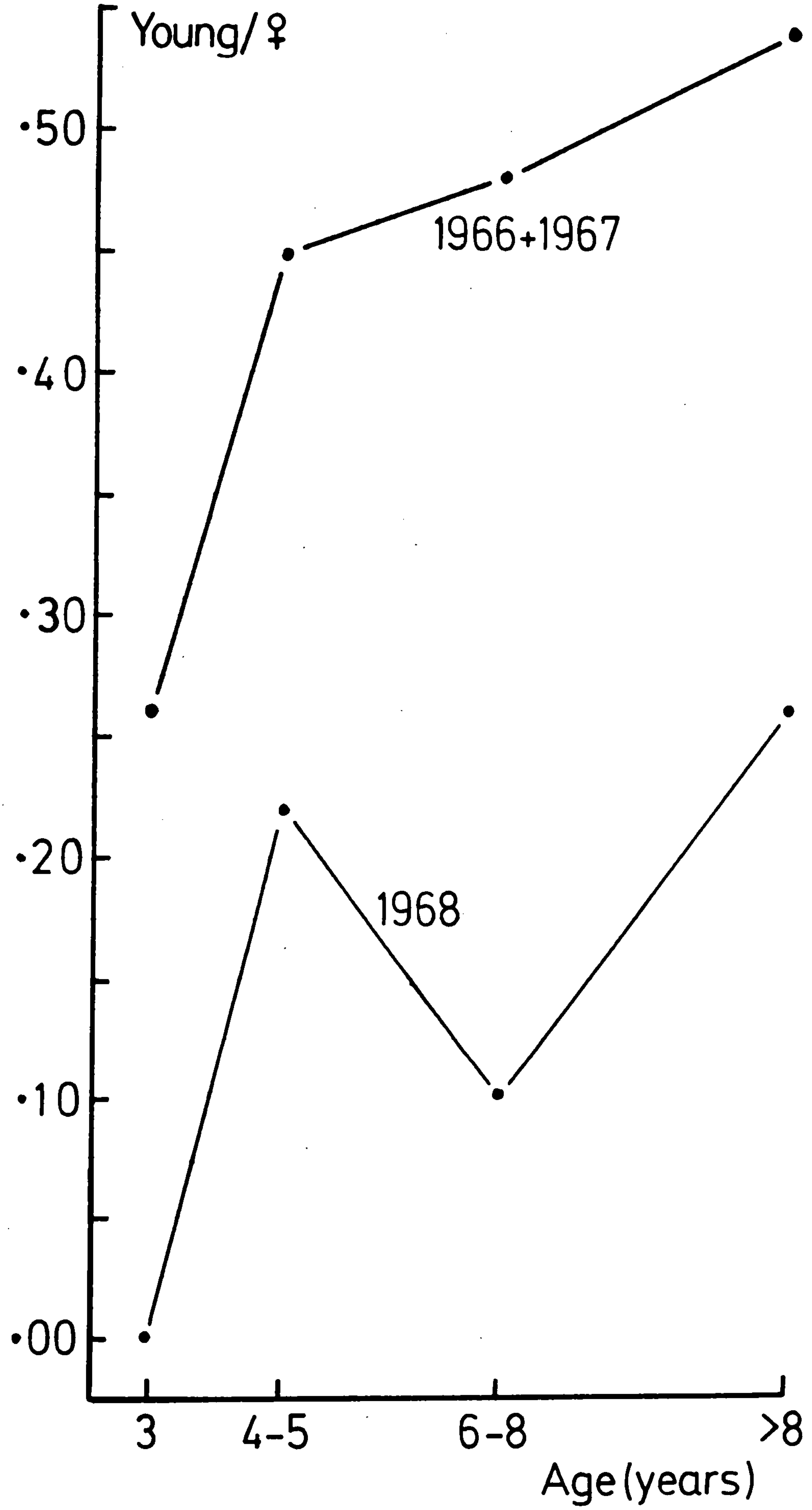
	1966 and 1967			1968		
Age (yr)	No. eggs	No. fledged	Percentage fledged	No. eggs	No. fledged	Percentage fledged
3	42	7	17	1	0	0
4-5	85	21	25	34	6	18
6-7	51	11	22	34	3	9
8-9	49	20	41	15	1	7
>9	45	17	38	70	13	19

This value of the breeding success is not, however, a true representation of the breeding success of the age groups as it does not take into account either the clutch size or the ability of the birds to re-lay. The true success of the population has therefore been expressed as the number of young reared per female parent and these values are given in Table 52 and illustrated in Figure 27.

Table 52. The number of young reared to fledging per adult female, in relation to age; combined data 1966 and 1967, 1968 separately

	1966 and 1967			1968		
Age (yr)	No. Adult ♀	No. young	No. young/♀	No. adult ♀	No. young	No. young/♀
3	27	7	0.26	1	0	0
4-5	47	21	0.45	27	6	0.22
6-8	50	24	0.48	29	3	0.10
>8	37	20	0.54	54	14	0.26

Figure 27. The number of young reared to fledging per adult female, in relation to age.


Young/♀
·50
·40
·30
·20
·10
·00
1966+1967
1968
3
4-5
6-8
>8
Age (years)

In 1966 and 1967 there was clear evidence that the older birds were more successful than the younger ones although the data have had to be grouped into rather large categories in order to maintain a reasonable sample size. The 1968 results once again manifest the effect of the red tide which will be dealt with in the next section. The results from 1966 and 1967 are similar to those reported by Coulson & White (1958) who, in their study on the Kittiwake, found that birds breeding for at least the third time had the greatest breeding success, those breeding for the second time a reduced success, whilst the lowest breeding success occured amongst birds breeding for the first time.

Preliminary discussion of the breeding biology of Arctic Terns in relation to age

Arctic Terns of all ages returned to the breeding colony, but the time of their return depended on age. The older birds returned on average a week or two earlier than the younger birds which in turn arrived a week or two earlier than the non-breeding birds. This latter group consisted mainly of the first year or "Portlandica" birds which spent very little time in the nesting areas and were not seen in large numbers until the breeding season was almost over, together with two year old birds. It has been suggested that the two year old birds may play a part in triangular 'marriages', but no evidence has been found of their breeding. Even though they spent more time in the nesting areas than the "Portlandica" birds, they did not arrive until the breeding season was well established, and it is concluded that three year old Arctic Terns comprised the youngest group of breeding birds.

This deferred maturity has already been mentioned and is typical of long-lived birds. Lack (1966a) suggested that breeding, being difficult, was not attempted until the birds were older, because they would then be more likely to succeed and overall raise more young. There may be some evidence for this from the present study where young parents are less effective at raising chicks than older parents, but it is difficult here to separate a true age effect from that of the lack of experience by birds breeding for the first time. The alternative explanation of deferred maturity was offered by Wynne Edwards (1955, 1962) who suggested that it might have been evolved by group selection to reduce the number of young and so prevent over-population. The implications of this are dealt with in greater detail in the General Discussion.

Throughout this study it was found that birds breeding for the first time were considerably less successful than any other age group. Much of this lack of success may have been related to inexperience or as a consequence of a late return. The late arrival of the three year old birds may mean that their choice of nest site is limited to the edge of the colony where they may lack the stimulation of other birds nearby. Their inexperience would make them less likely to avoid areas below Spring Tide level where flooding of the nest might occur. Similar reduced reproductive success in birds breeding for the first time has been recorded in many other long-lived species, for example, the Kittiwake (Coulson & White 1958) and is also typical of many short-lived species, for example, the Great Tit (Perrins 1965).

After the first attempt at breeding, the total breeding success showed a general increase with age, so that the oldest birds produced the largest number of young. This occurred in spite of the fact that this group showed a reduced clutch size and egg volume when compared with the six, seven, and eight year old birds, but these latter ages may represent the best physiological ages for breeding. However, it may be that the older birds have an overall higher breeding success because they make up for a possible physiological deficiency of their reproductive capacity by being more experienced. This may give them an advantage when selecting a nest site and this initial choice may affect their whole reproductive success. Although there is a suggestion that they may be more liable to predation, they may compensate for this by having a greater ability to re-lay. The growth rates for the chicks from older parents were higher than those from the other groups and indicate that older birds are more efficient at fishing than the other groups or are more responsible in caring for their young. It is possible that younger parents, although equally capable of catching fish, may not be so single-minded in taking the food to the young and may be more easily distracted from this purpose. Again, it is likely that this is also influenced by the position of the nest site in relation to other nest areas and access to the sea.

It seems likely therefore that, physiologically, the middle age groups are better adapted for reproductive success in that they are likely to produce the largest eggs by volume, and hence the largest chicks on hatching, and that they are more likely to have a clutch of two eggs. In spite of this, the overall breeding success of the older birds is greater and this is probably because, although they may be physiologically less capable of breeding, their greater experience leads to behaviour which results in an increased production of young.

SECTION FOUR THE EFFECTS OF AN EXCEPTIONAL BLOOM OF DINOFLAGELLATES ON THE BREEDING OF THE ARCTIC TERNS IN 1968

Introduction

At the beginning of the 1968 breeding season, there was an exceptionally high mortality of sea-birds on the Farne Islands and many of the surviving birds had their breeding so seriously upset that they were unsuccessful in raising young in 1968. This was probably caused by the exceptional 'bloom' of dinoflagellates, mentioned earlier, which released toxins into the sea and has been documented by Coulson et al (1968). The birds most affected were Shags and, although only 199 corpses were found (17% of the birds at risk) the loss of colour-marked birds indicated that 80% of the breeding population died. Fewer corpses of Arctic Terns were found, namely a total of 71 (1% of the birds at risk). This difference may have been a real one in that Shags were more likely to succumb to the effects of the toxins or it may have been influenced by the smaller chance of finding the corpse of an Arctic Tern compared to that of a Shag. There was some evidence from the return of colour ringed terns that the mortality was less than 5% of the birds at risk. The main effect on the terns was that the breeding was considerably upset, resulting in the production of less than 10% of the normal number of young, and the reasons for this are discussed in this section.

Number of adult Arctic Terns found dead in 1968

The numbers of adult Arctic Terns found dead on Inner Farne each day in May and June 1968 are illustrated in Figure 28 which shows the main peak of mortality to be between 25 May and 3 June. This was slightly later than the main Shag mortality, 21-28 May, and coincided with the commencement of the main tern laying period. It was possible to sex 48 of the tern corpses recovered and 38 (79%) of these were females. Many of the birds were in the process of egg laying and either had a fully formed egg in the cloaca or had obviously just laid an egg; one bird was found freshly dead on top of a new egg. It seems likely that the toxins produced by the dinoflagellates did not in general adversely affect the Arctic Terns to the point of mortality until the females had the extra muscular strain and co-ordination of egg-laying. This was not the case in the Shag where the mortality occurred equally in both sexes.

Ages of dead Arctic Terns

A total of 18 of the Arctic Terns found dead were ringed birds whose ages were known accurately, and the numbers of dead terns from different age groups are shown in Figure 29. There was no evidence of age specific mortality; the lack of any dead one or two year old birds was due to the mortality occurring early in the season, before the younger non-breeding birds arrived in the colony.

Figure 28. The numbers of adult Arctic Terns found dead each day on Inner Farne in May and June 1968.

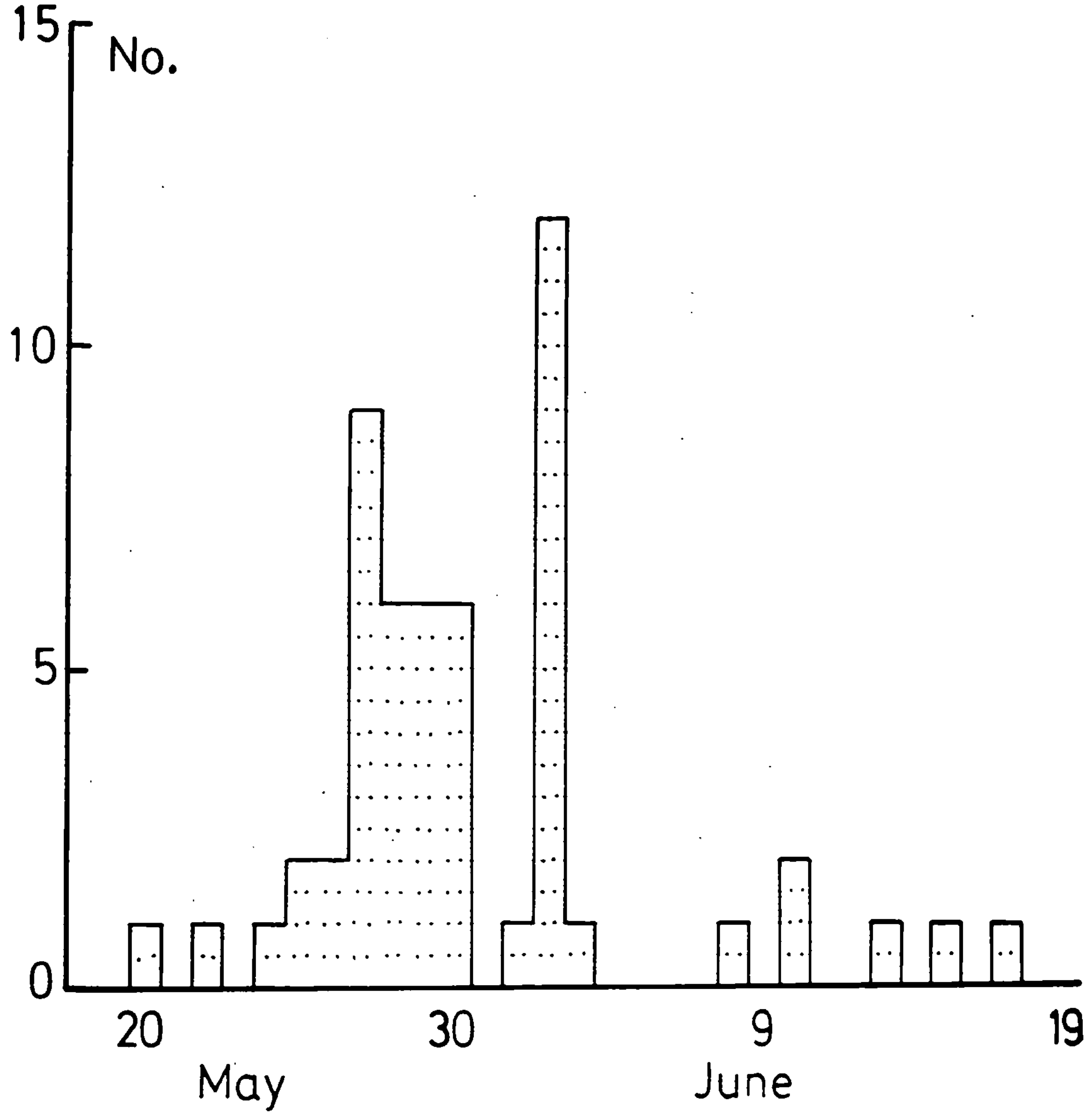
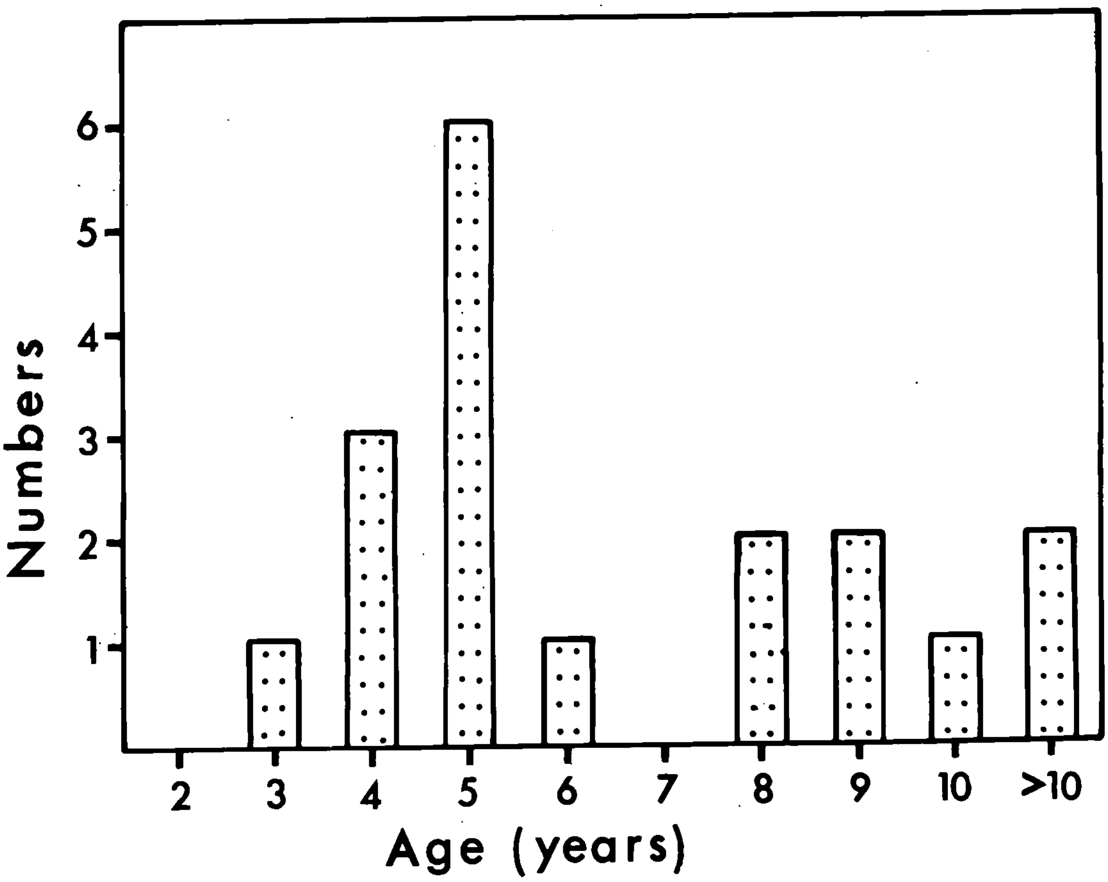

15
No.
10
5
0
20
30
9
19
May
June

Figure 29. The numbers of adult Arctic Terns of known age found dead in May and June 1968.



Numbers of Arctic Terns found dead 1968

Hatching success in 1968

It has been shown in Section 1 that the hatching success for 1968 (15.6%) was significantly lower than that in 1967 (47.0%) and 1966 (44.4%) (d = 11.7 $P < 0.001$). In 1968 the causes of egg failure were investigated in detail for different areas and these are shown in Table 53. The majority of the eggs which were lost came into the 'disappeared' category, that is, they were present on one nest round but no trace of them could be found on the next round 12 hours later. The most likely reason for their disappearance was predation by Starlings; eggs pierced and damaged by Starlings disappeared completely within six hours, presumably removed by the terns. The eggs in the 'disappeared' category were therefore combined with those which were known to be preyed upon and this gave an overall level of predation that represented 93.9% of all eggs which failed to hatch. The amount of predation in the cove and on the rocks was very high (95.1%) and (96.8%) respectively, but was significantly less in the vegetation (83.5%) (d = 4.3 $P < 0.001$). The main reason for the high level of predation was that during and immediately after the period of main mortality due to the red tide, many of the clutches were left unguarded and many breeding areas were sometimes completely devoid of terns for parts of each day. For the remainder of the breeding season, the numbers of terns in the breeding areas at any one time were considerably less than normal. Marauding Starlings were therefore able to work their way through the eggs with little interruption, particularly as the incubation of many clutches was sporadic. The lower level of predation in the vegetation was probably because many eggs were hidden by the plants compared to the eggs exposed on the rocks and sandy areas of the cove.

Eggs which were being incubated for more than 22 days and failed to hatch were assumed to be infertile, but it is probable that the overall percentage of infertility is an under-estimate, due to the high level of predation.

Spot checks were carried out to quantify the intensity of incubation during and immediately after the main mortality, from 25 May to 3 June. Only nests where the eggs had been laid for more than 12 hours were included in these checks as it has already been shown that incubation is normally rather erratic immediately after egg laying. A total of 140 observations were made on 34 clutches and on only 108 occasions (77%) were the clutches incubated, while experience from 1966 and 1967 indicated that almost 100% incubation was usual at this time.

Table 53. Causes of egg failure in different areas, 1968

	Cove		Rocks		Vegetation		All	
	No.	%	No.	%	No.	%	No.	%
'Disappeared'	183		127		44		354	
Predation known	88		53		27		168	
Predation assumed	271	95.1	180	96.8	71	83.5	522	93.9
Flooded	6	2.1	4	2.2	0	0	10	1.8
Deserted	2	0.7	0	0	7	8.2	9	1.6
Died during hatching	4	1.4	2	1.1	3	3.5	9	1.6
Infertile	0	0	0	0	4	4.7	4	0.7
Others	2	0.7	0	0	0	0	2	0.4
Total eggs lost	285		186		85		556	

The proportion of clutches being incubated in 1968 was almost 100% at times, but at others was less than 10%. This was shown by notebook comments, as on 2 June at 1800hrs when there were no birds at all in the breeding areas apart from the cove and a small area of the rocks nearby. A similar comment on 3 June at 1900hrs recorded 23 birds in the cove and 1 in the vegetation, all sitting on clutches, but no other birds in the nesting areas at all and very few around the island, although there were a large number of clutches in other areas. The detailed notebook comments, together with the timetable of the red tide are shown in Table 54. From these the general pattern of activity of the surviving terns during and immediately after the red tide was a return to the island each day in the very early morning at about 0300hrs with apparently normal activity, including incubation, followed by a slow drift away from the island during the day. At first, 2 June, this was almost complete by 0900hrs, but on 3 June the majority of the birds stayed until 1300hrs, and on 4 June until 1800hrs. By 7 June there were birds present in all breeding areas for the majority of the day but the numbers present at any one time were still less than 50% of the normal numbers seen in previous years. This situation continued until the end of the season with a steady decline in total numbers.

Although there was no definite evidence for the reason for the birds' absences from the islands for long periods, immediately after the main mortality, it seems likely that it was due to a shortage of food near the Farne Islands. The evidence for this, although rather subjective, is presented below.

1. In the period 25 May to 10 June very few terns were observed fishing from the island. This was unusual as normally,large numbers of terns, particularly in concentrated groups over shoals of fish, could be seen at all times from the island.

2. Large numbers of dead sand eels were washed up on the shore of the island and were reported from the mainland coast by the local fishermen.

3. Very few of the terns flying around the island carried fish. Several hour-long observations of birds flying into the cove at different periods of the day were made and a total of 15 fish were brought in

Table 54. Timetable of the red tide based on Coulson *et al* (1968) and daily notebook comments

13 May	4 Shags died at Amble
14 May	1 Shag died Farne Islands. Phosphorescence seen from Inner Farne. 1 Sandwich Tern dead at Amble.
15 May	2 Sandwich Tern found dead on Northumberland coast.
16 May	Reduced number of Shag nests occupied on Farne Islands.
17 May	About half the expected number of Arctic Terns in Inner Farne colony.
18 May	Few Shags around apart from incubating birds.
19 May	Normal activity among Arctic Terns on Inner Farne. No mention of reduced numbers.
21 May	1 Arctic Tern died overnight - Inner Farne.
23 May	Only 9 out of 298 Shag nests occupied on Farnes. First Arctic Tern egg laid. Fewer terns in cove than on 22 May.
24 May	Dead sand eels (*Ammodytes*) washed ashore.
25 May	Arctic Tern seen with Earthworm.
26 May	Dead Arctic Tern with fully formed egg in cloaca.
27 May	Vast numbers of sand eels washed up on Northumberland coast. Large numbers of Arctic Terns found dead. 14 Arctic Tern clutches commenced.
28 May	35 Arctic Tern clutches commenced.
30 May	Arctic Tern seen in cove with symptoms of poisoning - inability to stand.
2 June	10 Arctic Terns seen with sand eels all day. 0900 - no terns in enclosure. 2000 - no terns in colony apart from a few in the cove and on rocks nearby.
3 June	0300 - large numbers of terns in vegetation. 1300 - no terns in enclosure. 1800 - no birds in vegetation. 1900 - 19 nests under observation in cove, 9 being incubated, 10 not. 2100 - 19 nests, 5 being incubated, 14 not being incubated.
4 June	0700 - large numbers of terns in cove and on rocks. Only one small group seen fishing during whole day. 10 terns seen with sand eels all day. 1800 - a few terns in cove, on nearby rocks, and in vegetation on top of island. None elsewhere.
5 June	Large amount of activity in all tern nesting areas throughout the day.
6 June	Terns very active. Large numbers of panic flights. 1800 - very few terns in any areas apart from cove and nearby rocks. 2-hour watch - 2 terns returned to cove carrying sand eels.

during 12 hours of observation between 29 May and 7 June; 11 of these were Ammodytidae, 3 Clupeidae, and 1 Syngnathidae (pipe-fish).

4. There was some evidence of terns using rather unusual food, for example, the pipe-fish quoted in (3), while one bird was seen during this period carrying an earthworm, and one with a dead sand eel which was covered in sand.

It is likely therefore that the reason for the absence of the terns from Inner Farne immediately after the red tide was due to a shortage of their main food, sand eels, in the vicinity of the Farne Islands. The birds were spending longer looking for fish and were travelling much further than usual from the islands. Later in the season there was more fishing activity within sight of Inner Farne, and although only six chicks were weighed regularly, their mean growth rate of 6.7g/day was the same as that in 1967 which suggests that there was no food shortage from the middle of June onwards.

Chick mortality

It was difficult to determine chick mortality accurately in 1968 for a number of reasons. The rearing of chicks in the laboratory on the mainland caused the routine twice-daily nest round to be discontinued after 6 July, and observations were restricted to those made on four separate day visits to the island, the last being on 29 July. This also meant that no daily weighings of

chicks could be made, and in previous years these had provided a useful check on the survival of chicks.
In 1966 and 1967 it was possible to estimate chick mortality accurately due to the intensity of observations and in addition to finding corpses, mortality was also assumed where a chick was not seen alive for five days before an age at which it could be assumed to have fledged. It could also be assumed that if a chick of nearly fledging age disappeared, then this had successfully fledged, as many of these birds were later caught in mist nets.
This was not possible in 1968 as the main cause of chick mortality was predation by Herring and Lesser Black-backed Gulls and many chicks disappeared at an age of 1-2 weeks before they could be assumed to have fledged. Predation was observed on a number of occasions and one gull pellet was found with the ringed leg of a chick inside. Very few corpses were found, except on the visit of 19 July, immediately after a period of heavy rain. The minimum chick mortality has been calculated on the basis of direct evidence but this is likely to be a considerable underestimate, and on the basis of the known survival of ringed chicks it is possible that chick mortality could have been as high as 85%. The minimum chick mortality has assumed that if a chick had survived the first week of life, then it survived to fledging, unless its corpse was found, and was based on the assumption that the amount of observation on the day visits was too low to find all surviving chicks. Minimum chick mortality in 1968 as shown in Section 1 was 38% and was not significantly

different from the known mortality in 1966 (44%) or in 1965 (40%). The reasons for the very low chick mortality in 1967 have already been discussed in Section 1. The mortality values for 1968 are given in Table 55 and on an area basis, the 1968 mortality in the vegetation (43%) was not significantly higher than that in the cove (35%) or on the rocks (33%). The significantly higher mortality in the vegetation in 1966 over other areas was probably due to the greater wetting effect of the vegetation, but in 1968, although this factor still operated, the mortality in the vegetation was relatively lower, probably because of the protective cover it provided against gull predation.

Table 55. Minimum chick mortality, 1968

	Cove	Rocks	Vegetation	All
Number of chicks hatched	48	15	40	103
Number of chicks assumed died during first week of life or found dead later	17	5	17	39
Minimum mortality	35%	33%	43%	38%

The reasons for the deaths of chicks whose corpses were found in 1968 were probably, as in previous years, a combination of exposure and food shortage, the latter particularly applying to the second chick in a brood of two. No chicks were found which showed signs of attack by adult terns, and this is probably related to the small numbers of adults in the colony in 1968. The main reason for the increase in chick mortality was gull predation which was not seen to occur in 1966 or 1967. There was little direct evidence of gull predation apart from observation on a few occasions, but a number of chicks disappeared and despite intensive searching, their corpses were not found. At no time during the breeding season of 1968 were there large numbers of terns on the nesting areas and gulls were frequently seen flying over these areas, unmolested by adult terns. In previous years, small groups of terns were seen to attack gulls which came close to the nesting areas, but in 1968 the low density and small numbers of terns probably resulted in a lack of aggression which enabled the gulls to search for and prey upon large numbers of chicks.

Total production of young in 1968

It has been shown in Section 1 that the proportion of re-laying in 1968 was much higher than in previous years, but the success of each pair considerably lower. Over the whole of Inner Farne, as has been stated earlier, a total of only 112 young were ringed in 1968, while in 1967 and 1966 the totals were respectively 1243 and 1189, with approximately the same amount of effort in searching for the chicks. Of the birds that were ringed in 1968, only 13 are known to have died, but as 63 of them were not seen after ringing, it is possible that only 36 of the ringed birds survived. Spot checks of fledged terns standing on rocks showed that approximately 50% of these birds were ringed and it is likely therefore that the total production of fledged Arctic Terns from Inner Farne in 1968 was about 70-100 birds. The breeding of Common and Roseate Terns on Inner Farne was not studied in detail in 1968, but from general observations and the ringing totals, it is likely that their breeding was affected in a similar way to that of the Arctic Terns. The numbers of Common Tern pulli ringed in 1967 and 1968 were respectively 186 and 8, and for the Roseate Tern, the totals were 30 and 8.

Preliminary discussion of Section 4

From the recoveries of corpses and the return of colour-ringed birds, it is unlikely that the mortality of adult Arctic Terns exceeded 5% during the main period of the red tide. The breeding was, however, considerably disrupted, resulting in a total production of young which was probably less than 10% of that in a normal year, the main reason for which was a shortage of food caused by the red tide coinciding with the main laying period. The terns were away from the breeding areas for long periods and therefore unable to defend their eggs against Starling predation. It has been shown in Section 1 that both the clutch size and egg dimensions were small in 1968. This latter may have been due to a selection for small eggs, in that the birds producing larger eggs were more likely to die during the process of egg laying. Alternatively, both these factors may have been the direct result of the food shortage rendering the terns unable to lay more or larger eggs.

An indirect effect of the food shortage was that breeding was unsynchronised and the birds were nesting in scattered pairs rather than in a dense colony. They may thus have lost the advantages of colonial nesting and were unable to drive away predators, particularly gulls, for in the vegetation areas where predation is thought to be less important, these effects were less marked.

GENERAL DISCUSSION

In 1966, 1967, and 1968, at the age of 16, 17, and 18 years respectively, an individual Arctic Tern returned to breed at the same nest site on Inner Farne. In each year, this bird, which was probably a female, with its mate of unknown age, successfully reared one young to fledging. This occurrence is probably by no means an unique event; during the relatively short duration of the present study it has become obvious that some Arctic Terns may live to a considerable age and that their ability to produce young is not impaired by age and may be increased by their greater experience.

In many long-lived species, it has been well established that birds which have acquired adult plumage and are apparently mature, may delay their time of first breeding for a few years. Austin & Austin (1956) stated that very few Common Terns nest in their second or third summers and some not until their fifth. The age of first breeding in the Common Gull is given by Onno (1968) as 2-4 years, in the Gannet (<u>Sula bassana</u> L.), 4-5 years (Wynne Edwards 1954) the Fulmar up to 7 years (Bannerman 1959), and in the Yellow-eyed Penguin up to 8 years (Richdale 1949). Richdale further suggested that of the two year old birds, females were more likely to breed than males as there was probably an excess of males in the population. Palmer (1941a) said that Common Terns which were not old enough to breed, possessed the eclipse (or winter) plumage in the summer, had rudimentary gonads and were not truly migratory; some of them arrived in the northern colonies ~~as~~ only because they are social and followed the flocks of breeding birds. He does not give the age of these non-breeders, but it is likely that they are one year old birds as, similarly in the Arctic Tern, the first year birds possess the "Portlandica plumage". Only small numbers appear in the breeding areas late in the season and they do not attempt to breed. Many of the two year old birds are apparently fully adult, although a higher proportion than any other age group possess some characteristics of the "Pikei plumage", but there is no evidence that any of them breed (Cullen 1956, pers.obs.).

The reasons for this deferred maturity in long-lived birds have been discussed by Wynne-Edwards (1962) and Skutch (1967). Wynne-Edwards considers that it has been evolved by group selection to prevent overpopulation and overexploitation of the food resources and Skutch similarly regards it as an adaptation to adjust the rate of reproduction to mortality. He finds it difficult to accept that birds which learn in a few weeks how to find sufficient food to keep themselves alive, require a matter of years to develop sufficient skill in foraging to maintain, with a mate, one or two young. Skutch believes that the greater proficiency of older birds comes from practice at rearing young rather than an increased skill in foraging. However, Schüz (1957) used Hornberger's figures (1954) for the White Stork to show that in birds breeding for the first time, older birds (5 years) were more successful in rearing young than younger birds (3 years). As Lack (1966a) points out, this does not show a selective advantage for deferring first breeding as, although the three year old birds produce fewer young, they do produce some and therefore, unless breeding at this earlier age increases the risk of mortality, there is a selective advantage in breeding earlier as this adds to the eventual total production of young by these birds. Lack suggests that young birds do not in many cases attempt to breed as this would be dangerous for them, although he admits there is no evidence for this.

Even in species where deferred maturity occurs, birds breeding for the first time are considerably less successful than those breeding for the second and subsequent occasions. Coulson & White (1958) found that Kittiwakes breeding for the first time reared less than half the number of young produced by birds breeding for the third time. Richdale (1949) found that the fertility of the eggs in the Yellow-eyed Penguin was very low in the two year old birds but increased considerably in the three year old birds, particularly in those which had bred at two years. After reaching a peak at four years, when 91% of the eggs were fertile, there was some evidence of a decline with age. In the present study, the number of young reared to fledging by three year old Arctic Terns (0.26/adult female) was considerably less than that of the four year old birds (0.50/adult female).

A number of reasons have been suggested for the low reproductive success of inexperienced birds. It has been established in many cases that birds breeding for the first time have a smaller clutch size; this has been shown among others in the Kittiwake (Coulson & White 1958), Yellow-eyed Penguin (Richdale 1949), Great Tit (Perrins 1965) and in the Blackbird (Snow 1958). Klomp (1970) considered that this had adaptive significance as females laying for the first time are less likely to be able to provide food for a larger brood than older birds. This is similar to Lack's thesis (1966a) that the clutch size corresponds to the brood size from which most young survive.

However, not only do inexperienced birds produce fewer eggs, but these eggs are usually smaller than those from older birds. Romanoff & Romanoff (1949) showed that hens' eggs are always smallest during the first year and this has been found to be true for many wild birds, including the Kittiwake (Coulson & White 1958) and the Shag (Coulson et al 1969). Heinroth (1922) showed that the size of the newly hatched chick is proportional to the size of the egg and a chick hatching from a larger egg has a greater food reserve. The newly hatched chicks from inexperienced females may therefore be a disadvantage from the time of hatching due to their small size. Coulson et al (1969) further showed that the size of eggs laid by a particular year class of Shags declined through the season. This seasonal effect may be common in other sea-birds and may adversely affect the size of eggs laid by inexperienced birds, as it has been shown that they tend to nest later in the season, Coulson & White (1958), Perrins (1965) and Snow (1958).

A further reason for the reduced success of inexperienced birds may be that they are less able to look after chicks than older birds. It is difficult to measure directly the ability of adults to find food, but this can be estimated indirectly from the growth rates of chicks. Coulson & White (1958) showed that the growth rates of Kittiwake chicks from inexperienced birds was reduced in broods of two but not in single-brooded chicks. In the Arctic Tern, the highest growth rates occurred in chicks from experienced birds, over nine years old.

After the first attempt at breeding, the reproductive success increases considerably with age. In some cases it is considered that this reaches a peak and then declines in the very old birds. Richdale (1949) suggested a tendency for very old penguins to produce single eggs, for these to be on average smaller in weight and length, and for them to have a lower fertility than eggs laid by younger birds. Austin (1938) considered that Common Tern attained maximum fertility in the fourth year, retained this for three years, and then showed a decline, until after about ten years they were not reproducing effectively. However, in a later paper, Austin (1945) considered that older birds, that is, those over 13 years, were more successful in breeding than the younger birds because of a more 'propitious behaviour pattern' which was presumably the result of greater experience. Similarly, in the present study it has been found that Arctic Terns of nine years and older produce on average more young per pair than younger birds. As these older birds have reduced clutch sizes and smaller eggs, it is suggested that they may be physiologically at a disadvantage compared to the younger birds, but their greater experience and ability to look after the young, shown by higher growth rates of chicks, more than compensates for this. In the Arctic Tern, as in the Common Tern and the Kittiwake, there seems to be no evidence of a decline in reproductive success with age, and birds which do survive for a long time seem to gain greater experience and produce more young per pair than younger birds.

It is possible that older birds may, by their choice of nest site, benefit more from the effects of colonial breeding than the younger birds. The older birds return earlier to the colony and their nests are at a high density. Many sea-birds nest colonially and it has been found that, in general, the productivity increases with the size of the colony. Fisher (1952) showed that in Order 1 Fulmar colonies, with fewer than 10 eggs, only 18.5% of the sites occupied produced young, whereas in Order 3 colonies, over 50% of the occupied sites produced fledged young. Hall (1970) found that small colonies of the Black-headed Weaver <u>Ploceus cucullatus</u> were less successful than larger ones, apparently because the process of pair formation failed due to a lack of social stimulation. This was first suggested by Darling (1938) as being important in colonial nesting birds where the display and peripheral activities provided stimulation for reproduction. Palmer (1941) found that scattered pairs of Arctic Terns, nesting up to half a mile away from the main group, gathered with the others for social flights early in the season. This may have been important in providing the necessary stimulus to breed but also in synchronising the laying of the eggs with the laying in the main colony. Belopol'skii (1961) considered that this synchronisation was important in maintaining the sexual cycle, and that at the beginning and end of the season, when synchronisation was less effective, he found higher proportions of unfertilised eggs. Salomonsen (1943) supported Darling's argument that the larger the colony, the earlier and the more successful the breeding. He found that breeding was unsuccessful in very small groups of Kittiwakes, Guillemots and Little and Lesser Black-backed Gulls.

In terns, in addition to social stimulation and synchronisation of breeding, one of the important functions of the colony is to provide co-operative attacks on predators. These may have the effect of directly chasing away the predator or as Cullen (1960) found, they may make the predator move more quickly through the colony and less likely to spot any but the very poorly camouflaged eggs or chicks. Palmer (1941) found that in the Common Tern these attacks were very well organised with two or three birds plunging at a time so that the predator suffered a constant succession of diving birds. Tinbergen (1951) suggested that the attacks on the predators probably conditioned them to avoid places where such attacks had recently occurred.

These colonial attacks on predators may be one important reason for the synchronisation of the breeding season in the tropics, where there is no seasonal change in weather and breeding would be potentially possible all the year round. Ashmole (1963), working on the Wideawake Tern which breeds every nine and a half months on Ascension Island, found that the synchronisation was important in reducing attacks from cats and frigate birds; any early eggs or late young were much more likely to be preyed upon than those in the main part of the season. However, Harris (1969), working on the breeding cycle of the Red-billed Tropic bird *Phaethon aethereus* on the Galapagos Islands suggested that in this and some other non-annual breeders, the availability of food was the main factor controlling the synchronisation of breeding.

Tinbergen (1953) suggested that one of the problems of colonial nesting was that too dense a concentration of prey makes the predator specialise on them and therefore the nests must be spaced out to some extent. This is also important in avoiding aggression between neighbouring pairs; Palmer (1941) found that this increased as the size of the territories within the colony decreased. He found that in the Common Tern, the lower limit of tolerance was achieved when the nests were about 17 inches apart. The boundaries were not rigidly defended; defence increased towards the centre of the territory. Austin (1929, 1932) found that the average home circle of Common Tern nests was about 6 feet in diameter although the presence of vegetation in the territory reduced the amount of aggression and enabled the nests to be closer together. It is therefore apparent that within a breeding colony a compromise must be reached, balancing social attraction on the one hand and pugnacity between neighbouring pairs on the other. This is usually achieved by having fairly large territories within a distinct breeding colony.

In 1968 the effects of the red tide on the breeding of the Arctic Terns on Inner Farne were mainly to remove the advantages of colonial nesting. The breeding of many birds was interrupted and they were probably faced with a food shortage near the Farne Islands which meant that they had to spend a considerable proportion of their time foraging for food away from the islands. The return after the main period of mortality due to the red tide was therefore not synchronised, and the total number of birds in any area at one time was less than half the usual total. Although the number of clutches laid was smaller than in a normal year, these were laid over the same area as the birds tended to show site loyalty. This had the effect of reducing the spatial density of the colony and this, together with the asynchronised return reduced the numbers and density of birds involved in breeding activities at any time. The main effect of this was that the birds were less aggressive towards predators of both eggs and young. This accounts for the very high egg loss, although some of this was due to the length of time the birds needed to spend fishing, leaving the eggs unguarded. The number of young taken by gulls was probably very high and both Herring and Lesser Black-backed Gulls were seen more frequently on the breeding areas, without being attacked.

The site of the breeding colony in many sea-birds is traditional and although apparently suitable sites exist elsewhere, the colony may be confined to a particular area and may be limited by this. Wynne-Edwards (1962) suggested that these traditions maintained the numbers at a level where they avoided direct competition for food. The spread of the Fulmar in North-Western Europe led Salomonsen (1965) to suggest that the loyalty to sites was not irreversible. Skutch (1967) considered that this restriction to traditional sites was an important adaptive limitation of the reproductive rate; this was one of the ways in which he said that some birds adjusted their reproductive rate to suit their environment. This is in contrast to Lack's ideas (1966) of maximum reproduction where birds adjust their clutch size to that brood size from which most young survive.

Skutch argued that many birds could support more young than they normally reared, and he quoted experiments on the Gannet by Nelson (1964) where a normally single-brooded bird can, if given an extra chick, successfully raise two. Some evidence for this is also given by the present study where the growth rates of chicks from broods of two were not found to be significantly lower than those from broods of one. Skutch and Wynne-Edwards argued separately that some birds were therefore deliberately adjusting their reproductive rates to maintain the population at a level where there would be no direct competition for food.

On the Farne Islands, the main food items of the Arctic Tern are the sand eels Ammodytes spp. Pearson (1968) found that Arctic Terns which were raising the maximum brood size needed to spend up to 19 hours per day in fishing to support the brood. He suggested that these birds were near the limits of their physical ability to collect food. This may explain why in 1967, when food was very abundant around the Farne Islands and the adult terns were significantly heavier than the terns in other years, they had a much higher breeding success, mainly due to an increased chick survival. In 1968 when the food supply at the beginning of the season was short, the evidence suggests that the birds had to spend long periods searching for food away from the islands and left clutches unguarded. This resulted in a very high egg predation and consequent low breeding success. It is possible therefore that in some years the breeding success of the terns may be limited by the availability of food in the immediate vicinity of the islands. Although terns are capable of flying long distances for food, if they have to do this, carrying only one fish per trip, then they will have difficulty in rearing two young, the normal maximum brood size. It is suggested that the availability of food may be the ultimate factor limiting the reproduction of the terns, by determining the amount of time spent in fishing. If food is short, the terns have to spend longer away from the colony foraging and this results in a greater loss of eggs and chicks from predation and an increased chick loss from the effects of exposure, as the adults can spend less time brooding young chicks. It is also suggested that these effects are reduced in older birds due to their greater experience in both foraging and looking after eggs and young.

SUMMARY

1. The difficulties of determining the length of life of animals were discussed. The literature on age studies and life tables was reviewed, together with recent work on the Arctic Tern.
2. The study was carried out from the end of 1965 to 1968 on Inner Farne, the innermost island of the Farne Islands, off Northumberland, and was concentrated in the sandy cove, with comparative observations from the rocky and vegetation areas.
3. The main return to the colony took place from the beginning to the middle of May and it was suggested that most birds returned directly to the ultimate nest site and carried out their display activities there.
4. Egg laying began towards the end of May and the peak was over by the first week in June; this was slightly delayed in 1968.
5. There was a significant peak of laying between 1501 and 2100 BST; the mean time interval (± S.E.) between laying eggs in a clutch of two was 46.2 ± 4.6hrs.
6. The mean length, breadth and volume (± S.E.) of eggs from all years were respectively 40.33 ± 0.12mm, 29.01 ± 0.06mm and 16.33 ± 0.09cc. The second eggs from a clutch of two were significantly

smaller than the first or the single eggs. There was some evidence of a decline in breadth and volume of eggs with season.

7. The mean clutch size (± S.E.) for 1966 was 1.66 ± .03, for 1967 1.68 ± 0.02, and for 1968 1.42 ± 0.03. In all years this showed a seasonal decline.

8. The mean incubation period (± S.E.) was 22.07 ± 0.16 days; it was suggested that both parents incubate equally.

9. The hatching success in 1966 (44.4%) was very similar to that in 1967 (47.0%); these were significantly higher than the success in 1968 (15.6%). The main cause of egg loss was predation by Starlings; this was most likely to occur in the first two days after laying and in the areas disturbed by day visitors to the island.

10. There was a high correlation between the weight of the egg and the weight of the chick on hatching (r = + 0.83). Second chicks had a calculated hatching weight 0.5g less than first chicks and, in the same nest, hatched on average over a day later.

11. The growth curve of chicks showed a steady rate of increase from the third to the fourteenth day; at this age the chicks had attained adult weight.

12. The average number of feeds brought to a chick per hour was 0.67 and the mean length of fish 2.4in (6.1cm); the average weight of fish given per day was calculated from field observations to be 26.6g. Chicks were reared in the laboratory

and it was found that they needed 26.2g of fish per day to maintain a daily growth rate of 6.8g.

13. The main direct causes of chick mortality were probably exposure and starvation. Percentage chick mortality ± S.E. in 1967 (20.9 ± 2.6) was significantly lower than in any other year (1965 40.3 ± 3.1, 1966 44.3 ± 2.5, and 1968 37.9 ± 4.8); this may have been due to an abundance of food in 1967. In all years the chick mortality increased to a high level towards the end of the season and was highest in the vegetation. In 1966 and 1967, second chicks had a significantly higher mortality (75% and 54%) than first chicks (25% and 12%). The majority, 66%, of the chick mortality took place within three days of hatching.

14. Fledging took place at about three weeks; the mean weight of flying juveniles (± S.E.) was 95.05 ± 2.66g in 1966.

15. Total breeding success was 23.3% in 1966, 37.2% in 1967, and 9.7% in 1968. More re-laying occurred in 1968. The total numbers of chicks ringed for the three years were respectively 1189, 1243, and 112. Dimorphism of chicks was discussed.

16. The reasons for the high mortality of the second chicks and the seasonal decline in reproductive success were discussed.

17. There was a significantly higher proportion of 'Pikei' birds among the two year old birds (69%) and the birds over nine years (18%) than among any other age group.

18. Older birds tended to be heavier; there was an increase in wing and tail length with age. Males were slightly larger than females.

19. Cage trapping was found to be the most effective way of catching adults; these were subsequently colour ringed and released. It was possible to read ring numbers on some birds without catching them, using a telescope of magnification x15 to x60.

20. The mean age of breeding males for all years (± S.E.) was 8.1 ± 1.1 and for females 7.9 ± 1.1 years. The mean annual mortality rate of adults was calculated to be 13.3 ± 4.6% from the survival of colour ringed adults.

21. A life table for the Arctic Terns of three years old and over was presented. There was no evidence of a change in adult mortality with age; some birds survived to over 15 years, two individuals to 27 amd 29 years respectively. The mean mortality rate (± S.E.) from 3 to 21 years was calculated from the life table as 15.1 ± 3.0% and the average expectation of life 4.48 ± 0.36 years.

22. There was a high positive correlation ($r = +0.92$) between the ages of a pair; where the age of only one member of a pair was known, this was therefore assumed to be the mean age of the pair.

23. Older birds returned to the colony first; there was a clear correlation ($r = -0.93$) between age and the date of return, the time of egg laying was synchronised for birds of all ages. Older birds were more likely to nest at a higher density.

24. Clutch and egg size were found to be highest in the middle age group, 6, 7 and 8 years, and smallest in the three year old birds, i.e. birds breeding for the first time.

25. Hatching success tended to increase with age, particularly with clutches of two eggs. Birds over nine years old were more likely to re-lay (59%) than younger birds (21% in 6-8 years, 44% in 4-5 years, and 20% in 3 years).

26. The mean daily growth rate (± S.E.) of chicks from parents over nine years old (7.5 ± 0.4g) was greater than from any other age group.

27. There was some evidence of an increase in fledging and total breeding success with age in 1966 and 1967; birds over eight years produced 0.54 and three year old birds produced 0.26 young per adult female.

28. The reasons for the general increase in reproductive success with age were discussed; this was probably due to the greater experience of the older birds although the best physiological age for breeding was middle age, 6-8 years.

29. A bloom of dinoflagellates, red tide, occurred near the Farne Islands in late May 1968. This caused the death of many sea-birds, particularly Shags; 71 Arctic Tern corpses were found, representing 1% of the birds at risk.

30. Clutches were left unguarded during and after the red tide; this led to an increase in Starling predation, accounting for 93.9% of the total egg loss.

31. Evidence of a food shortage from the middle of May to early June was presented.

32. An increase in gull predation was observed, but this was difficult to quantify. Chick mortality was estimated at 38% but from ringing totals of chicks it was suggested that the total production on Inner Farne in 1968 was 70 to 100 chicks. This may have been directly due to the food shortage, or an indirect result of this; the terns losing the advantage of colonial breeding as they had to spend more time foraging, resulting in an increase in egg and chick predation.

33. The reasons for deferred maturity and the lack of success of inexperienced birds were discussed. It was suggested that the more successful, older birds may gain more benefit from colonial breeding, particularly from protection against predators and social stimulation, as they nest in denser areas than the younger birds. The reproduction of the Arctic Tern may be limited by the amount of time they have to spend fishing; the effects of this may be reduced in older birds due to their greater experience.

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