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Ecological aspects of the breeding cycle in the Wilson's storm petrel, *Oceanites oceanicus* (Kuhl), at King George Island (South Shetland Islands, Antarctica)*

ABSTRACT: The period from arrival of the Wilson's petrel to its breeding grounds to the onset of breeding covered 33 days (November 5 — December 8). The egg-laying period averaged 56 days; the frequency distribution of egg laying in different colonies was close to normal. Incubation took 44 days, on the average, and chicks stayed in nests 59 days. The weight of chicks at hatching was 7.5 g, and the maximum weight was 80 g, that is, 205% of adult weight. Growth rate of chicks depended on weather conditions, especially on the amount of snowfall, blocking the access to the neast. This caused many-day starvation of chicks and their weight could drop by 46%. The diet of chicks and adults consisted of the krill in 96%, mostly of *Euphausia superba*. High nesting losses were caused by rainfall and snowfall. Of 129 nesting attempts, 61.2% failed in the stage of eggs and 27.9% in the stage of chicks. Mortality was related to the age and weight of chicks. It has been found that the prolonged egg-laying period, rapid growth rate of chicks in their first days, and their high weight represent adaptations to the climate of Antarctica.

Key words: Antarctica, Wilson's storm petrel, ecology

1. Introduction

The breeding range of the Wilson's storm petrel covers the Subantarctic zone and the coast of Antarctica. Sometimes these birds can occur in large numbers (Beck and Brown 1972). The biology of this species was studied by many authors on the continent (Wilson 1907, Falla 1937, Mougin 1968, Pryor 1968, Lacan 1971, Kamenev 1977), Antarctic Peninsula

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* The work was done at Arctowski Station during Antarctic Expeditions IV and V organized by Polish Academy of Sciences in 1979/80 and 1980/81 as a part of the project MR-II-16.

(Roberts 1940), and also in the Subantarctic zone (Eaton 1875, Hall 1900, Loranchet 1915, Beck and Brown (1972).

Although some papers are of a monographic character (Beck and Brown 1972), many aspects of the breeding ecology of the Wilson's storm petrel requires further studies. This is the case of number dynamics during the breeding season, breeding phenology, and especially chick development, which was intensely studied only by Lacan (1971) on Adélie Coast. Also adaptive changes in the biology of the Wilson's storm petrel at different latitudes require more detail investigation. A review of the data on this subject was provided by Beck and Brown (1972).

The situation described above was a basis for planning the work on the Wilson's storm petrel population in Admiralty Bay region in 1979—1981. The aspects of breeding ecology were emphasized that can be useful in estimating the role of these birds in matter cycling in coastal ecosystems of Antarctica. Also an attempt was made to estimate population dynamics over the breeding season and to analyse the diet.

Also the phenology of the breeding cycle was analysed, with special emphasis on the duration and course of chick development in relation to climatic effects on successive phenological periods. As a result, it was possible to analyse adaptive aspects of the biology of this species along a latitudinal gradient and the corresponding climatic changes as a supplement to the already existing information.

2. Methods and study area

The study on the breeding population of the Wilson's storm petrel was carried out at King George Island in the region of Admiralty Bay. The observations were started on December 10, 1979 and ended on March 19, 1981.

The size of the study area varied according to the purpose of investigation. To estimate numbers of Wilson's storm petrels, almost the entire coast line of Admiralty Bay was surveyed. Several geomorphological types of the coast line emerging from ice cover were distinguished. These were storm ridges, postglacial moraines, rocky cliffs of various inclination, covered with stable or shifting rock debris, depending on their structure, and groups of rocks on elevated terraces, made up mostly of basalts and basalts with andesites (geomorphological description of the coast of Admiralty Bay is given by Birkenmajer (1980); also geographical names are taken from this source).

The basic method for estimating numbers over large areas was transect counts along selected sections of the coast. Relative numbers of birds obtained in this way were then recalculated so that they approximated actual numbers.

For this purpose also other methods of bird count were used, described in Section 3.1.1.

Stationary observations of the population dynamics, number estimating by different methods, and observations of breeding performance were concentrated within a radius of 2 km from Arctowski Station (62°09′51″ S, 58°27′45″ W), on the coastal section between Jardine Peak and Ecology Glacier. Ten colonies were under study, in which 135 nests were monitored in 1979/80 and 221 nests in 1980/81.

Nest inspection provided information on breeding phenology, chick development, and breeding success.

In 1979/80, nests were checked 25–31 times depending on the colony. The mean interval between successive observations was 4.5 days. In 1980/81, the number of nest observations varied form 12 to 17, depending on the colony, and the mean interval between successive observations was 4.4 days. Relatively long intervals between successive observations were caused by adverse weather — strong winds with snowstorms making impossible chick weighing or locating tagged nests. But longer intervals between observations mainly occurred at the end of the breeding season, thus in most cases breeding phenology, including egg-laying and chick hatching, was timed to the nearest two days.

3. Results and discussion

3.1. Numbers

3.1.1 Methodological aspects of estimating numbers of Wilson's storm petrels

It is difficult to estimate numbers of Wilson's storm petrels because of a specific biology of this species. Counting of nests on small plots and extending the results on the area occupied by the whole colony is extremaly labour consuming; the density of nests varies according to the type of rock debris, and this can be evaluated only when a large number of samples are taken, in addition, the location of all nests on a sampling plot is often impossible. Estimates of relative numbers by counting birds in display flight are comparable in a relatively short time period, in the first half of December, and because of a specific daily cycle of this species, they can be obtained only at night. It is possible, however, to estimate numbers in many points of the coast when using this method. Mist-netting of the total colony is limited by wheather conditions and can be used on relatively small areas.

To get a reliable estimate of numbers, several methods were used:

1) relative estimate — counting birds along transects during courtship flights;

2) intense mist-netting and then observation of ringed individuals on nests;
3) total counts of birds coming back from the sea;
4) counting nests in colonies.

Relative numbers were estimated by counting individuals in colonies (resting at their nests and flying near nests) within 100 m sections of rocky slopes or in distinct groups of rocks occupied by the colony. An attempt was made to determine the highest number of individuals observed simultaneously for a few minutes. This number was considered as a sample. This procedure was facilitated by a specific behaviour of birds during courtship flights, when individuals of the same colony fly usually close to their nests. Due to this it is easy to distinguish birds occupying the sampling area even in the case of large colonies. Flights of individual birds from one colony to another, located even only several ten meters apart, happen on rare occasions, as indicated by netting results. Thus, relative numbers represented the sum of individuals recorded during a transect census along sections of slopes, coast, or groups of rocks. Relative numbers estimated in this way cannot be considered as a measure or an index of density per unit area. The reason is that it was impossible to measure the size of the sampling area over broad expanses. Although the colonies were linearly distributed along the slopes usually running parallel to the coast line, the breadth of the rock debris inhabited by petrels markedly varied. Moreover, many colonies occurred within distinct groups of rocks, the surface area of which was even more difficult to estimate. In this situation, relative numbers could be considered first of all as an index of the total number of individuals in particular colonies. When censuses were made on relatively long sections of the coast, relative numbers calculated per 100 m sections characterized the suitability of different types of the coast line as breeding grounds.

As censuses were made on a greater part of the Admiralty Bay coast not covered with ice cap, relative numbers could be used as a basis for calculating the total population size, approximating the actual number of individuals in this region.

The birds were censused between 22.30 and 0.30 of the local time because the greatest number of individuals was present in colonies at that time. This was found when comparing the number of individuals present in the colony with the number of individuals returning to the colony from the sea over the 24 hour cycle (Fig. 1).

Birds were netted in two closely located groups of colonies for several days until the number of captured individuals dropped. The Total number of individuals captured in the two seasons was 416 adults.

The number of nests in particular colonies was determined after many inspections of the area.

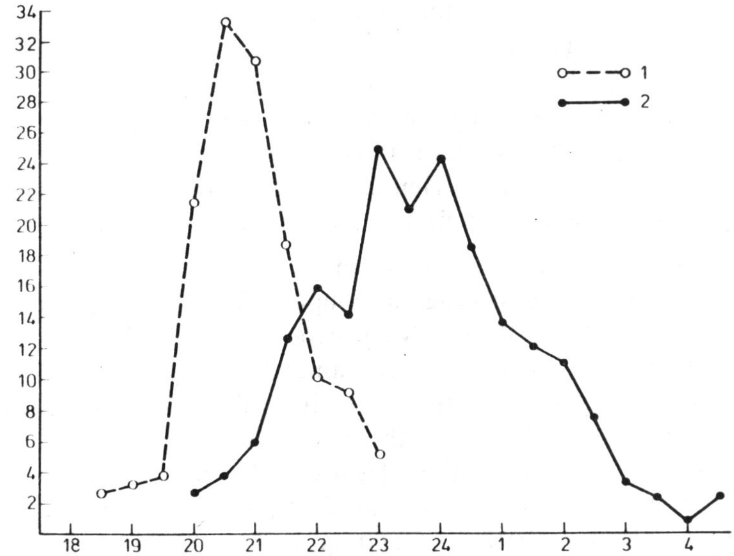

Fig. 1. Changes in numbers of Wilson's storm petrals in colonies over the daily cycle at the beginning of the breeding season, Y — Number of birds per sample, X — Local time, 1 — Number of birds returning from foraging areas to the colony (observed on the coast), 2 — Number of birds observed in the colony

Table I compares the results obtained by each of these methods in four groups of adjacent colonies. The ratio of relative numbers to the number of individuals calculated from the number of nests (on the assumption that one nest corresponds to two individuals) is very similar for all the four analysed groups of colonies. The same is true of the ratio of relative numbers to the number of individuals captured, and of the ratio of the

Table I

Estimates of the number of Wilson's storm petrels based on the number of nests located (A), transect counts (B), and mist-netting (C) in different groups of colonies

Method of number estimate	Groups of numbered colonies			
	6, 8	5, 4, 3	9, 10	1, 2
A	34	95	57	27
B	70	175	113	60
C	104	312	–	–
B: 2A	1.03	0.92	0.99	1.11
B: C	0.67	0.56	–	–
C: 2A	1.53	1.64	–	–

number of birds captured to the number of nests. This indicates that all these three methods can be used as a measure of relative numbers of the Wilson's storm petrel.

The problem of estimating absolute numbers of petrel remains open, however. As already noted, the transect count method was most effective in terms of the area covered. Hence, an attempt was made to determine to what extent this method reflected the actual numbers of petrels.

The estimates of numbers obtained from transect counts were lower than those from intense netting, although not all colony members were captured. In 1979—80, 310 birds were captured and ringed from two close groups of colonies. Assuming that the annual mortality rate of adults was 11% (after Beck and Brown 1972), 273 individuals from these two groups of colonies should survive until the season of 1980/81. In 1980/81, 106 individuals were ringed in addition. Theoretically, the total number of ringed individuals in the two groups of colonies (No. 6, 8, 5, 4, 3) should thus be 379. Upon the termination of netting in 1980/81, adult birds on nests were examined at random. The proportion of ringed individuals to the total number of birds checked was $22:48 = 0.458$, or 45.8%. Assuming that the proportion of ringed individuals on nests reflects the proportion of individuals captured in the total number of birds in the colonies, their absolute numbers can be calculated from the proportion $22:48 = 379:x$, and and $x = 827$ birds.

Thus, the ratio of the estimate obtained from the transect counts (245 birds) to the theoretical estimate of numbers is $245:827 = 0.296$. Therefore, relative numbers obtained from the transect counts should be multiplied by a coefficient equal to $827:245 = 3.38 \approx 3.4$ to get reliable absolute numbers of birds.

As the number of birds examined on their nests was relatively small, the accuracy of this result was verified using a different procedure.

On December 2 and 3, 1980, when weather conditions were good (no wind, high visibility), birds returning from foraging sites in Bransfield Strait to their colonies located along southern coast of Ezcurra Inlet were counted when they crossed the line Shag Point-Urbanek Crag. 11 × 40 binoculars were used ensuring good visibility from coast to coast at the mouth of the Inlet. The great majority of birds returned along the southern coast of the Inlet, from which observations were made. The flight occurred between 18.00 and 23.00 of the local time (Fig. 2). Counts were made for 2.5 minutes at intervals from 5 to 15 minutes, depending on the intensity of flight. Each 2.5 min. count was a sample. Mean numbers of flying birds per sample were calculated for one-hour periods, and this value was multiplied by 24, which is the number of 2.5 min. periods in an hour, to get the total number of birds flying in successive hours. The sum of estimates for particular hours represents the total number of birds returning from foraging areas to their colonies on the Ezcurra Inlet coast. As these counts were made before the onset of laying both males, and females were counted that is, the total population living in Ezcurra Inlet; during the day there were no birds in the colony at all. The results from the two counts are very similar: 1542 birds on December 2 and 1620 returning birds on December 3. Thus, a mean value of 1581 birds was used for further calculations.

In the region of Ezcurra Inlet, *O. oceanicus* occur in mixed colonies with the black-bellied petrel (*Fregetta tropica*). It is not possible to distinguish this species in the mass of flying birds, thus their numbers were estimated indirectly. On the coast of Ezcurra Inlet, three groups of mixed colonies were distinguished, in which relative numbers of Wilson's storm petrels were 113, 147, and 114 individuals, in sum 374 individuals. The proportion of individuals in these three groups of colonies were respectively 30.2‰, 39.3‰, and 30.5‰ of the total. Numbers calculated from the sums of returning birds (1581 individuals) should correspond to these proportions. They are 477, 612, and 482 birds, respectively. In turn, the proportions of nests of black-bellied petrels in these groups of colonies were 31.0, 24, and 5.2‰, respectively. It can be safely assumed that the proportion of black-bellied petrels in the birds returning to particular colonies corresponding to the proportions of their nests in these colonies. Numbers of black-bellied petrels calculated in this way are 148, 149, and 27, respectively, that is, 324 birds in sum. Hence the number of Wilson's petrels would be 1581 − 324 = 1257 individuals.

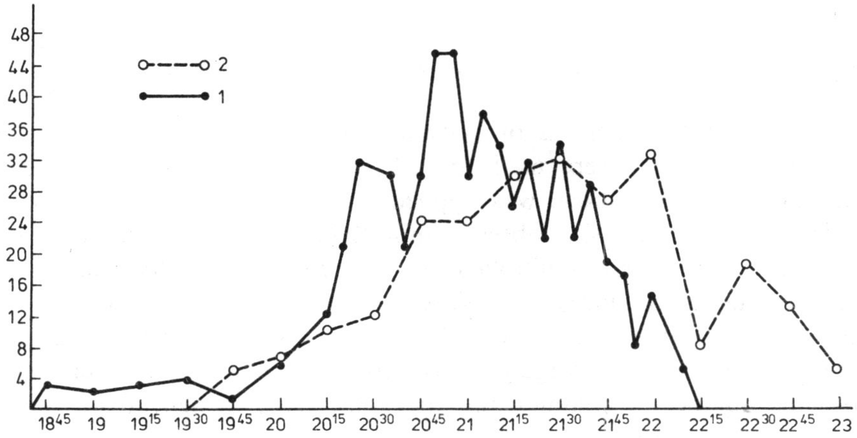

Fig. 2. Changes in the number of birds returning from foraging areas to the colony over the daily cycle, Y — Number of birds per sample, X — Local time, 1 — Observation on December 2, 2 — Observation on December 3

The ratio of relative numbers of the Wilson's petrel on the Ezcurra Inlet coast (374 birds) to their number that can be considered as close to actual numbers, that is, to the number of birds returning from foraging areas (1257 individuals) is $374:1257 = 0.298$. The coefficient by which relative numbers obtained from transect counts should be multiplied to get actual numbers is $3.361 \approx 3.4$.

This result is almost the same as that obtained from the relation between relative numbers and numbers obtained from netting and from the proportion of ringed individuals on nests. This implies that the coefficient calculated here can be used to calculate actual numbers from relative numbers of Wilson's petrels obtained from transect counts along different sections of Admiralty Bay. Numbers estimated in this way, which approximate actual numbers, are quoted later in this text as the number of pairs.

3.1.2 Numbers and distribution of Wilson's storm petrels in Admiralty Bay region

To estimate total numbers of Wilson's storm petrels in Admiralty Bay region, transect counts were made on 21 sections of the coast*), and the methodology described above was applied. Practically, the whole coast line of the bay was covered with observations. Relative numbers obtained from the transect counts were multiplied by the coefficient calcuoated above. In this way the total number of Wilson's storm petrels in Admiralty Bay region has been estimated for about 3400 pairs. Numbers of birds on particular sections of the coast largely varied from 0.85 to 167 pairs per 100 m.

Both the number of colonies and their size seem to depend on the size of suitable nesting areas.

This is indicated by a high correlation ($r = 0.99$) between the size of rocky debris slopes and colony size in places where the area covered with debris were sufficiently clear cut to measure their length along slopes (Fig. 3). Particular parts of debris slopes were not evenly occupied by birds. This was related to the thickness of the debris layer. The birds prefered parts of relatively fixed rock debris, especially of considerable thickness, along basalt-andesite slopes. In such places there may be 7 nests per 10 m^2. Wilson's storm petrels usually do not nest on lateral moraines, and they are scarce on shifting screes along steep slopes, e.g. at Dufayel Island, Ullman Spur, or between Jardine Peak and Italia Valley.

When unsuitable rocks cover long sections of the coast, petrels occupy only small fragments, and the size of such colonies is relatively low. The

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* Six sections were censused by the author; data for the 15 remaining sections were obtained by Dr. B. Jabłoński, which is gratefully acknowledged here.

Table II

Frequency distribution of colony sizes in Wilson's storm petrel (colony size is given as the number of pairs)

Number of pairs	1 – 50	51 – 100	101 – 150	151 – 200	451 – 500	1101 – 1150
Number of colonies	17	9	6	1	1	1
Percent of the population	11.1	15.9	21.4	5.0	14.1	32.5

suitability of the ground for nesting affects the frequency distribution of colony sizes (Tab. II).

It would be interesting to know whether the number of individuals in a colony depends only on the size of the area suitable for nesting, or there is a minimum, threshold colony size. The present material does not provide an univocal answer. The frequency distribution of colony sizes (Tab. II) shows that small colonies, made up of at most 50 pairs, occur most frequently but they comprise merely 11.1% of the total population. Moreover, the colonies made up of less than 25 pairs account for only 4.9% of the population. The total number of colonies analysed was 35, and it is not sufficient for more detailed conclusions when analysing the frequency distribution. The fact is that birds nesting in isolation from the colony were met on rare occasions, although when the density of a colony is low it is difficult to identify such cases.

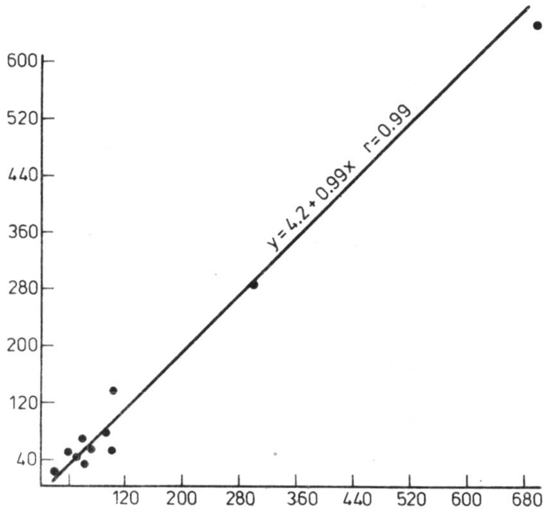

Fig. 3. Relationship between the size of a Wilson's storm petrel colonies and the extension of rocky debris occupied by these colonies. Numbers were estimated using transect counts, Y — Relative numbers, X — Extension of rocky debris in m

3.1.3 Population dynamics over the season

The first Wilson's storm petrels came back from migration to Admiralty Bay early in November (Fig. 4). But a relatively high number of birds were present not sooner than about November 20. The subsequent decrease in numbers of birds in all the three colony groups was likely to be caused by the so-called "prelaying exodus", when females leave the colony prior to laying and they forage intensely on the sea. According to Back and Brown (1972), at Signy Island, South Orkney Islands this period extends from 6 to 18 days.

In the prelaying period of 1980/81, the number of petrels stabilized between December 1 and December 16. Large differences were observed among different groups of colonies (Fig. 4), related to the date of snow melting.

It is difficult to follow changes in the population size from the onset of egg-laying to the end of the breeding season. In 1979/80, 135 nests were located and in 1980/81, 221 nests. Population size at any time moment depends on the number of adults, number of young recruited to the population, and the mortality and emigration of both young and adults. An earlier emigration of adults from breeding grounds can take place if they failed to breed, or lost eggs or chicks. Beck and Brown (1972), who monitored 33 nests, have found that after failure the birds continue to visit their nesting site for about 14 days, on the average, the range being from 3 to 32 days.

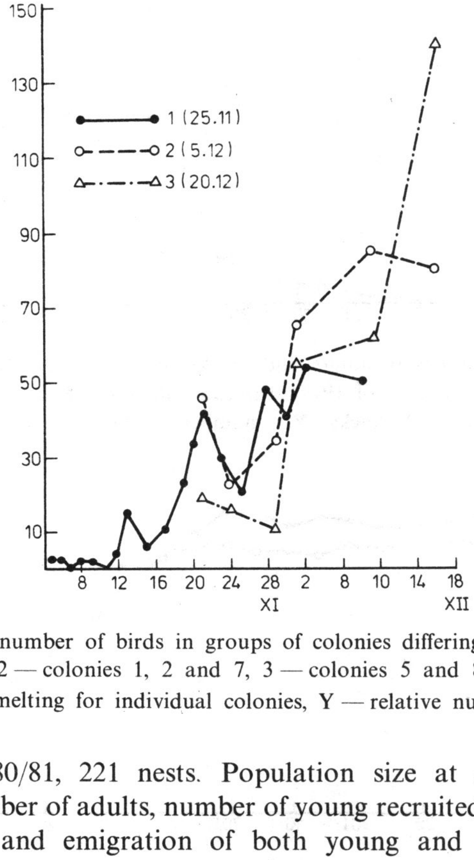

Fig. 4. Changes in the number of birds in groups of colonies differing in the dates of snow melting, 1 — colony 9, 2 — colonies 1, 2 and 7, 3 — colonies 5 and 8. In parentheses there are dates of snow melting for individual colonies, Y — relative numbers, X — month

As it was not possible to visit a relatively large number of nests at night, the mean found by Beck and Brown will be used here. Beck and Brown have also found that the nonbreeding pairs leave the breeding grounds earlier. The present data (20 cases) show that such pairs stay in the colony for 26 days, on the average, from the time of number stabilization before breeding.

On the basis of all these findings, approximate numbers of adult birds were calculated for 5-day periods (Fig. 5). Changes in the number of chicks for the same 5-day periods were calculated using the data on the number of hatched chicks, chicks already present in the population, and their elimination due to death, or emigration. Population dynamics, including changes in the number of adults and young over the two seasons (Fig. 6), is presented as a percentage of the maximum number of adults at the beginning

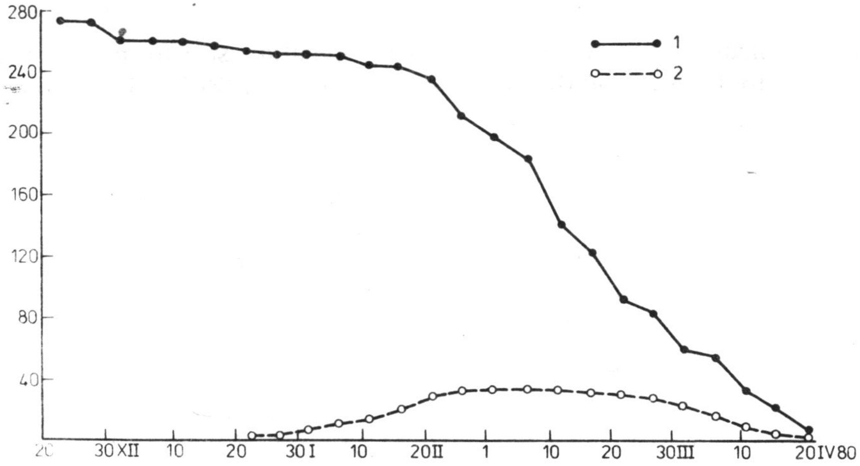

Fig. 5. Changes in numbers of adults and chicks (in nests located) from the beginning to the end of the breeding season of 1979/80 (mean values for 5-day periods), 1 — numbers of adult birds, 2 — numbers of chicks, Y — number of birds in checked nests, X — month

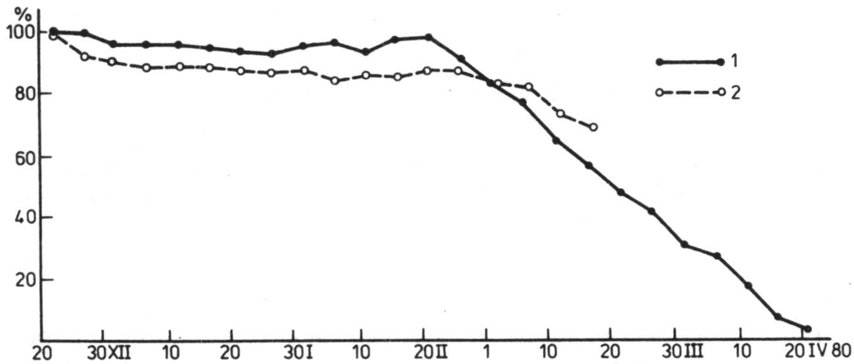

Fig. 6. Changes in numbers of Wilson's storm petrels over the breeding season. The total number of adults and chicks in 5-day periods is expressed as percentage of the maximum number of adults present on the nests checked prior to laying, 1 — breeding season of 1979/80, 2 — breeding season of 1980/81, X — percent, Y — month

of each season. Individual points on the graph represent mean numbers of both adults and young in 5-day periods.

In the 1980/81 season, the expedition was terminated in March, so it was not possible to keep track of population changes by the end of the breeding season. But no marked differences were found in changes in numbers over the comparable periods (Fig. 6); they result from greater egg losses at the beginning of the 1980/81 season, as compared with the earlier season.

3.1.4 Seasonal changes in numbers in relation to population structure

In addition to breeding birds, Beck and Brown (1972) distinguished a group of individuals occupying nests but not laying eggs and a group of birds making no breeding attempt at all, which do not occupy permanent nest-sites and move from one colony to another. The last group probably consisted of birds up to three years old as data for other *Procellariidae* suggest that the Wilson's storm petrel is likely to make its first breeding attempt in its third year. The birds occupying nests but not laying accounted for 4.4% in 1979/80 and 16.8% 1980/81. The figure is probably underestimated because of the lack of experience in distinguishing this category of nests. Data on this group of birds were taken into account when seasonal changes in numbers were estimated. The occurrence of the birds without permanent nest sites seems open to discussion. Beck and Brown (1972) identified this group from mist-netting, and it accounted for a large proportion of birds captured at the beginning of the breeding season. The occurrence of this group was inferred from the frequency distribution of captures of individual birds; these were birds captured only on one occasion (Beck and Brown found that they accounted for 55%) and also from the fact that the proportion of these birds declined in successive captures, suggesting, in authors' opinion, that they leave earlier the breeding grounds.

Beck and Brown (1972) used a specific method of netting. They did not change the location of nets in colonies. As the authors themselves noted, captures of birds were not random, and this fact influenced the distribution of captures.

Direct observations already indicate that nonrandom capture was due to an active avoidance of nets by birds captured on one occasion, which influences the frequency distribution of captures for individual birds; birds captured only once accounted for 92.9% of the total number captured in 1979/80 and 91.8% in 1980/81 (Tab. III). The proportions of captures on one occasion to the total number of captures were 84.9% and 84.2%, respectively. These are much higher figures than those recorded by Beck and Brown. There could have been several reasons for this: the nests used by the English authors were twice as long as those used in this study, thus they must have been less conspicuois to birds; at least some recaptured individuals were probably first captured and ringed on their nests, and finally there were differences in the technique of netting. Beck and Brown (1972) did not change the location of their nets during the three-year study period.

Table III

Frequency distribution of the number of Wilson's storm petrels captured in relation to the number of captures per bird

Season	Number of captures	Number of birds	Per cent
1979/80	1	288	92.9
	2	16	5.2
	3	5	1.6
	4	1	0.3
1980/81	1	112	91.8
	2	9	7.4
	3	1	0.9
	4	0	0.0

In the present study, two nets were used in close colonies (within a radius of 50 m) and they were moved from one place to another within these colonies. Netting was continued for about three hours from 21.00 to 24.00 of the local time.

The following patterns of the capture of Wilson's petrel were found (Tab. IV). The number of birds captured on successive days of a series of netting declined; proportion of recaptured birds in the number of individuals captured per day increased, while the proportion of recaptured birds in the cumulative number of captured birds first increased, then decreased; changes in the location of nets were followed by increases in the number of birds captured, as compared with their numbers captured on the last day of the preceding series of captures.

These findings firstly show that the birds captured on one occasion can avoid the nets — the percentage of recaptured birds in the cumulative number of captured individuals, and also the number of birds captured on successive days of a series of captures decreased; an increase in the proportion of recaptured individuals on successive days was probably due to the birds nesting closest to the nets.

Second, an increase in the number of bird captured after moving the nets implies that birds nesting relatively close are captured; hence, a decrease in the number of birds captured on successive occasion when nets are not moved results from the avoidance of nets by birds already captured and captures of birds nesting relatively close to the nets and not from a decline in the number of birds.

The fact that Wilson's storm petrels search almost exclusively the area of their colony and within the colony only the neighbourhood of their nests is also confirmed by a relatively small number of captures of the same individuals at different netting points. Of the total number of 97 captures of the birds caught at least two times, 6 birds of colony 6 were recaptured at a distance of 75 m in colony 3, 4 birds of colony 3 were recaptured at a distance of 25 m in colony 5, and 8 birds of colony 5 were recaptured in the same colony after moving the nets by 20 m. All these recaptures account for only 18.6% of the total number of recaptures.

Table IV

Characteristics of mist-netting of Wilson's storm petrels in 1979/80

Date	No. birds captured	Cumulative number of birds captured	Number of recaptured birds	Per cent of recaptured birds in the total number of birds caught	Per cent of recaptured birds in the cumulative number of birds caught
19 Dec. 79	48	48	0	0.0	0.0
23 Dec. 79	52	100	2	3.8	2.0
1 Jan. 80	3	103	2	67.0	1.9
nets moved by 75 m					
7 Jan. 80	60	163	1	1.7	0.6
8 Jan. 80	49	212	9	4.1	4.2
19 Jan. 80	32	244	2	6.3	0.8
6 Feb. 80	24	268	7	29.2	2.6
15 Feb. 80	11	279	6	54.5	2.1
nets moved by 25 m					
21 Feb. 80	31	310	0	0.0	0.0
16 Dec. 80	26	336	5	19.2	1.5
nets moved by 20 m					
4 Jan. 81	44	380	13	29.5	3.4
18 Jan. 81	20	400	5	25.0	1.3
14 Feb. 81	16	416	4	25.0	1.0

These findings suggest that even of there were nonbreeding birds in the population in 1979/80 and 1980/81, earlier leaving the breeding grounds, their number was not large. Nontheless, it cannot be theoretically excluded that after several favourable seasons, with a high breeding success, surplus birds may be abundant. But in the Antarctic climate such situations should be rate. Back and Brown (1972) have found that only 6 out of 20 seasons at Signy Island were good enough to ensure a high breeding success. Usually the percentage of nest losses is very high (see Section 3.5.1).

3.1.5 Year-to-year changes in population size

Adult Wilson's storm petrels are long-lived. Beck and Brown (1972) have found that they can survive 10.4 years, on the average. Reproductive effort is low (1 egg per season), while the mean death rate of chicks is high (see Section 3.5.1). This implies that long-term fluctuations in the population size should be rather small. At Signy Island number fluctuations over a three-year study period reached about 40% (Beck and Brown 1972). A comparison of numbers of birds in some colonies in 1979/80 and 1980/81 (Tab. V) does not reveal significant year-to-year fluctuations, and the recorded differences are probably within limits of observational error.

Table V

Comparison of the number of pairs in Wilson's storm petrel colonies in two breeding seasons

Season	Number of colony					Total
	1	2	6	8	9	
1979/80	34	85	51	51	77	298
1980/81	43	60	49	68	90	310

3.2. Breeding phenology

3.2.1. Egg laying

In 1979/80, first eggs were laid on December 8 and last eggs on January 31. In 1980/81, the respective dates were December 12 and February 8. Thus, in 1979/80 egg-laying covered 53 days and in 1980/81, 59 days. A delay of laying in 1980/81 was caused by a later snow melting, as compared with the preceding year. This is illustrated by the distribution of laying dates for groups of colonies differing in the data of snow melting (Fig. 7) (Fig. 4 in Section 3.1. illustrates the effect of snow melting on the dates of number stabilization in the same colonies). In 1979 no sufficient data were collected on the dates of laying to compare their distributions for the two years. However, figure 7 shows that the distribution of laying dates in 1980 differed for various colonies, depending on wheather conditions in Admiralty Bay. Generally, these were normal distributions skewed to the right.

On Antarctic Peninsula, the laying period of Wilson's storm petrel extended form December 12 to January 5 (Roberts 1940), but its relatively

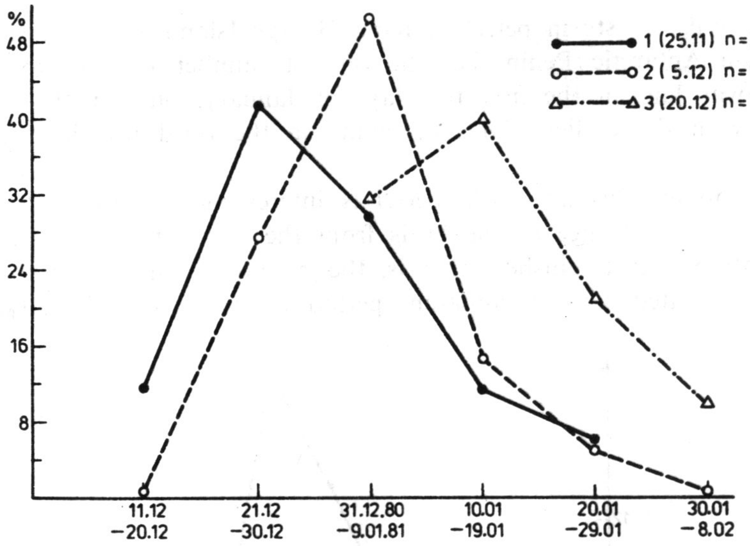

Fig. 7. Frequency distribution of laying dates in Wilson's storm petrels (percentage) in 1980/81 for groups of colonies differing in the dates of snow melting. In parentheses the dates of snow melting. 1, 2, 3 as in Fig. 4. Y — percentage of recorded laying started, X — month

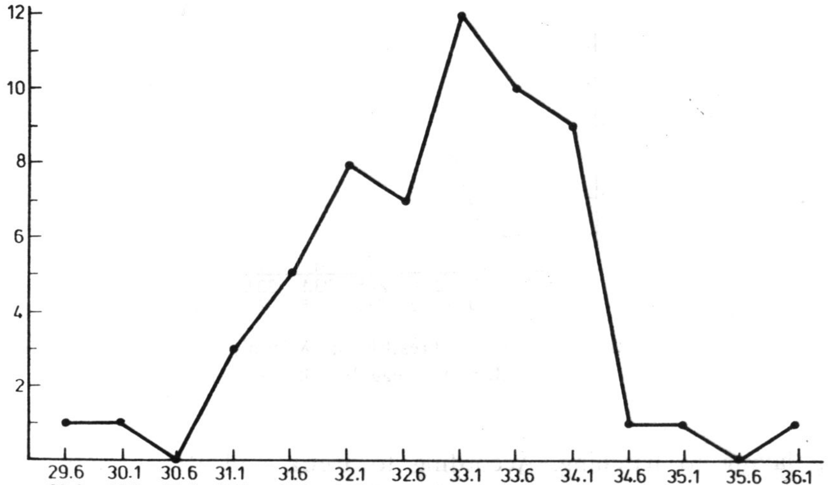

Fig. 8. Frequency distribution of egg lenghts in Wilson's storm petrel (n = 59), Y — number of eggs, X — egg length in mm

short duration is due to a small number of records. On Antarctic Continent, egg-laying begins earlier, on November 21, and is continued until January 16 (Wilson 1907, Falla 1937, Mougin 1968, Pryor 1968, Lacan 1971, Kamenev 1977). At Signy Island egg-laying period extends from December 27 to February 2 (Beck and Brown 1972). Thus the data on the laying period in Wilson's storm petrel at King George Island are most similar to those from Antarctic Peninsula. The highest number of eggs for all the colonies was laid in the first ten days of January, but for the group of colonies with the earliest dates of laying in the third ten day period of December.

Incubation in Wilson's strom petrel is interesting because of sometimes long periods of absence of the birds from the nest. Hence, a real period of incubation is distinguished, that is, the period of time when the egg is actually incubated, and an apparent period of incubation, extending from egg laying to hatching. According to Beck and Brown (1972), the real incubation period lasts 38—42 days, and the total incubation period 38—55 days, with a mean of 44.5 days (data for 22 nests). In the region of Admiralty Bay, the mean period from laying to hatching did not differ much from that found by Beck and Brown at Signy Island; the mean values for 32 nests was 44±4.1 days, and it ranged from 38 to 54 days. The real incubation period was not analysed.

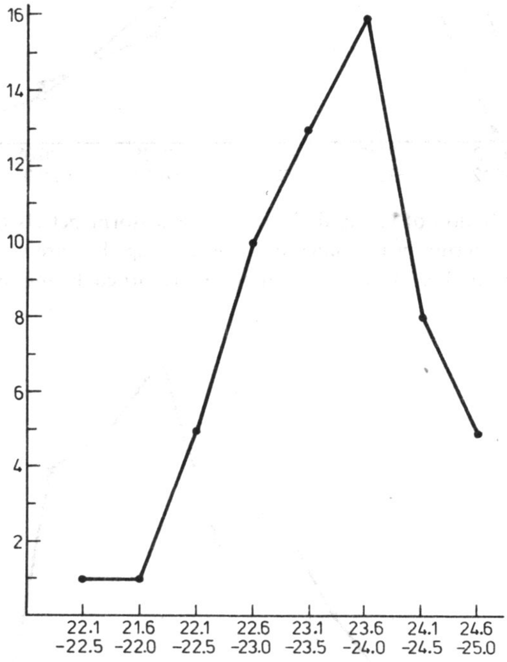

Fig. 9. Frequency distribution of egg breadth in Wilson's storm petrel (n = 59), Y — egg number, X — egg breadth in mm

Wilson's storm petrel lays only one egg, and no replacement laying was recorded after failure. Mean egg size slightly differed from those recorded by Beck and Brown (1972). These differences resulted from a higher number of measurements (n = 52), hence mean values of the length nd breadth of eggs are lower, and the range of variation larger than for British data, based on 15 measurements. Frequency distributions of length and width measurements are slightly skewed, with most frequent values in classes of 33.1—33.5 mm (Fig. 8) and 22.6—24.0 mm (Fig. 9), respectively.

3.2.2. Hatching period

In 1979/80 the hatching period, as determined for 50 chicks with known hatching dates, extended from January 21 to March 16 (56 days). In 1980/81, the dates of hatching were known for 81 chicks, and the hatching period lasted from January 20 to March 16 (56 days).

Although the duration of the hatching period was similar in the two season (Fig. 10), hatching in 1980/81 was in fact delayed as compared with the preceding year. In 1979/80, 70% of the chicks hatched by February 15, while 60.7% in the following season, and the frequency distributions of hatching dates for the two seasons are shifted in time (Fig. 10). The delayed hatching in 1980/81 was due to a prolonged presence of snow cover in some colonies, and it is consistent with the frequency distributions of egg laying in particular colonies, which can be seen when comparing figures 7 and 11. Some discrepancies between laying and hatching distributions are due to losses in eggs.

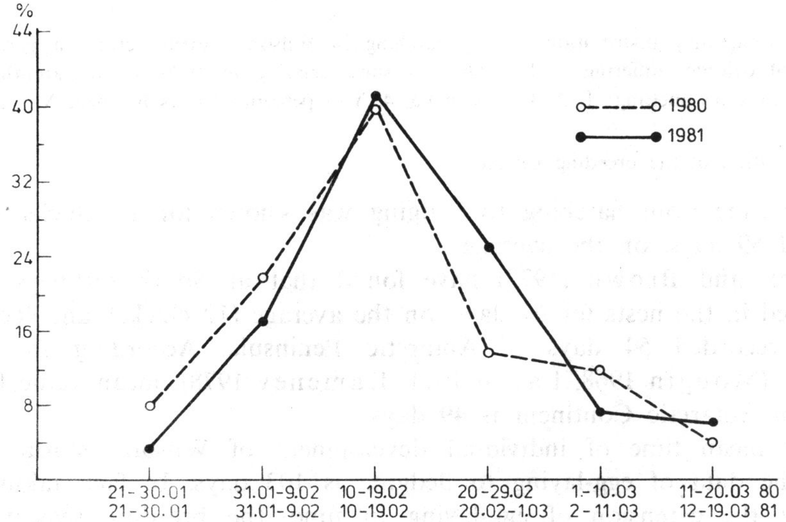

Fig. 10. Frequency distribution of egg hatching in Wilson's storm petrel (in percent) in 1979/80 (n = 50) and 1980/81 (n = 81), Y — percent of chicks hatched, X — month

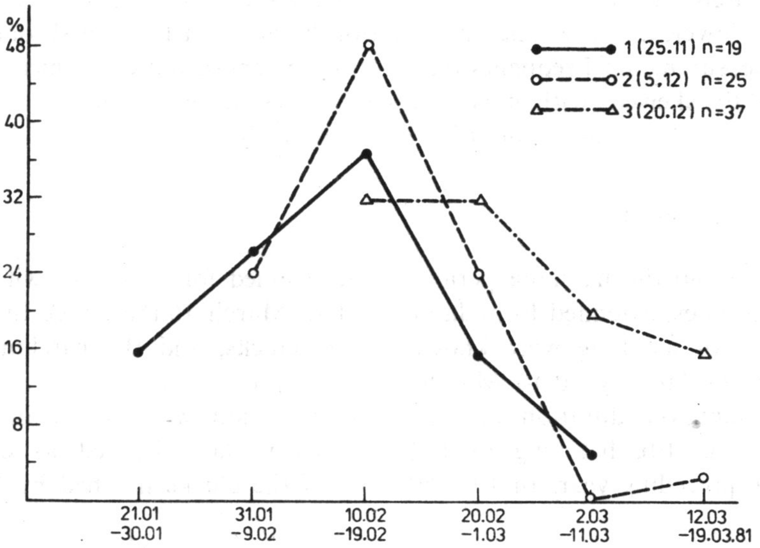

Fig. 11. Frequency distribution of egg hatching in Wilson's storm petrel (in percent) for groups of colonies differing in the dates of snow melting in 1980/81. In parentheses the dates of snow melting; 1, 2, 3 — as in fig. 4, Y — percent of eggs hatched, X — month

3.2.3. Duration of the breeding period

The time from hatching to fledging was known for 14 chicks, and it covered 59 days, on the average.

Beck and Brown (1972) have found that at South Orkneys chicks remained in the nests for 60 days, on the average (12 chicks), and Roberts (1940) recorded 54 days at Antarctic Peninsula, According to several authors (Mougin 1968, Lacan 1971, Kamenev 1978), mean value for the coast of Antarctic Continent is 49 days.

The mean time of individual development of Wilson's storm petrels from the data of egg-laying to fledging is 103 days. In fact, taking into account the extension of egg-laying in time, the breeding season (from the data of the first egg to the date of fledging of last chicks) at King George Island was continued for 133 days, that is, from the first ten-day period of December to the third ten-day period of April. The probability of survival of latest eggs and chicks is very low at South Shetland Islands because of adverse weather. Otherwise last chicks would be likely to fledge about May 10.

3.3. Chick growth

3.3.1. General characteristics

Growth rate of Wilson's storm petrels was analysed for 1979/80. A total of 56 chicks were weighed to the nearest 1 g, using a Pesola balance periodically checked in laboratory. In 1979/80, 241 weight measurements were taken. Most chicks were aged to the nearest day, the others to the nearest ±2 days. No significant differences were found in weight between chicks aged more precisely and less precisely, thus they were pooled. These data were supplemented with 88 weight measurements taken in 1980/81.

During their 55—65-day stay in the nest, chicks averaging 7.5 g at hatching can reach 80 g, that is, their weight may be higher than the mean weight of adults (39.0 g, n = 276) by 105%. Mean maximum weight of chicks, however, is much lower; in 1979/80 it was 60.8 g. Mean body weight on the day of fledging or three to four days earlier averaged 49.7 g, ranging from 35 to 66 g (n = 12).

Growth curves of individual chicks were similar by the age of 20 days but later large differences appeared, resulting in a wide scatter of weights on successive days (Fig. 12).

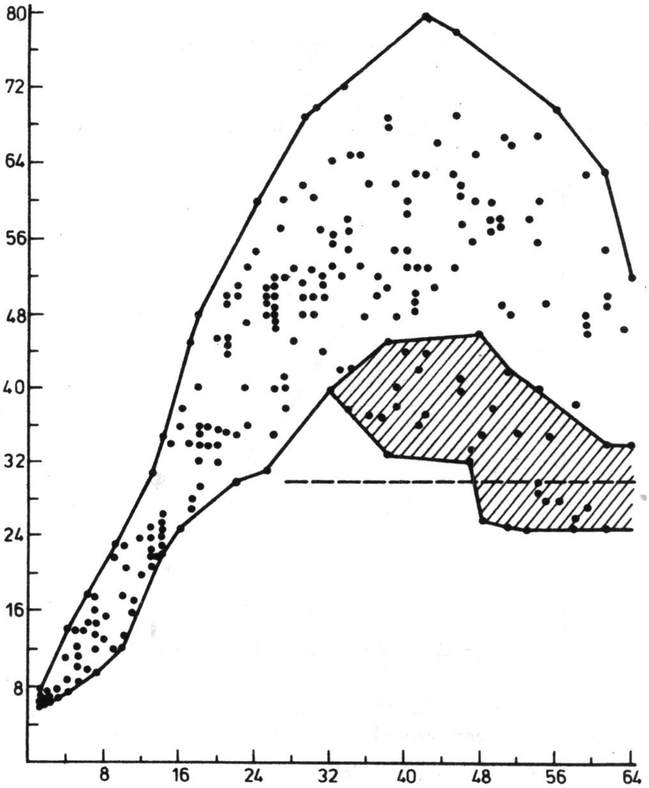

Fig. 12. Upper and lower limits (continuous lines) of variability in body weight for Wilson's storm petrel chicks on successive days of life in 1979/80. Points denote individual measurements (n = 241) of body weight. Points in the hatched area denote body weights of chicks blocked in their nests by snow. A decrease in weight below 30 g (dashed line) is followed by the death of a chick, Y — body weight in g, X — age in days

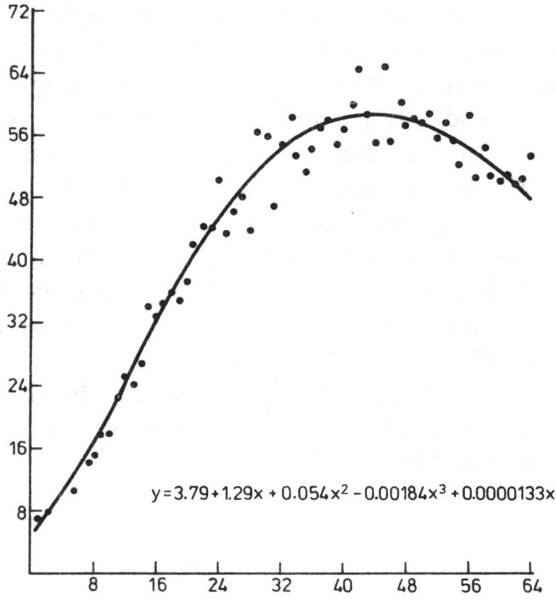

Fig. 13. Growth curve of Wilson's storm petrel chicks calculated from mean body weights on successive days of life, Y — body weight in g, X — age in days

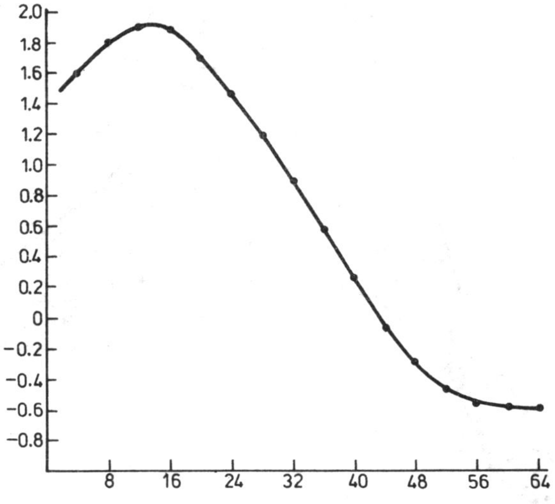

Fig. 14. Increase in the body weight of Wilson's storm petrel chicks on successive days of life, calculated from the mean growth curve, Y — increases in body weight in g/day, X — age in days

To characterize mean growth rate of chicks, measurements from the two seasons were pooled (329 weights of 127 chicks), and the weight of chicks isolated by snow for a few days were excluded. Mean growth curve (Fig. 13) has been calculated using mean body weights of chicks on successive days of life. These data can be well approximated by a polynomial of the 4th degree (R = 0.98), but the form of the curve should be considered with caution. Both the maximum weight of chicks and the age at which this maximum is reached are likely to depend on weather, and can be different in various seasons.

Growth rate of chicks in relation to age, as calculated from the mean growth curve, is shown in figure 14.

Mean maximum growth rate was observed between ages of 12 and 16 days. Positive growth was continued by day 43, that is, until mean maximum weight was reached (Fig. 13). From days 43 to fledging, the body weight of chicks decreased, growth rate was negative.

In fact, the maximum body weights of different chicks were observed between ages of 26 and 64 days. Using the data on growth of 23 chicks surviving at least 50 days, the frequency distribution of maximum body weights was analysed, and also their mean values in relation to age (Tab. VI).

Table VI

Mean maximum body weights of Wilson's storm petrel chicks (in g) and their frequency distribution in different age classes for chicks surviving at least 50 days

Age class in days	Mean maximum weight	Number of cases	Per cent
26–30	57.2	4	16
31–35	56.6	7	28
36–40	65.0	5	20
41–45	70.7	3	12
46–50	63.5	2	8
51–55	66.0	1	4
56–60	63.0	2	8
61–65	52.0	1	4

For two chicks, the maximum body weight was noted twice in the time considered, hence the number of cases analysed was 25.

Although maximum body weights can be largely spaced along the age axis, this being noted by Lacan (1971) at Terre Adélie they often occur in relatively young age classes. This may suggests that the strategy of chicks growth in Wilson's storm petrel consists in a realtively fast storing of fat. This is supported by the fact that neither the values of the maximum weight nor the age of its attainment influence the number of days the chick remains in the nest, this being also noted by Lacan (1971).

Mean maximum body weights were highest in the age class of 45 days. According to Lacan (1971), maximum weights are reached between days 35 and 40, while Beck and Brown (1972) have found that at Signy Island, maximum weights occurred at an age of about 55 days.

The highest weight recorded for the chicks examined here was 80 g. But high maximum weights were relatively rare (Tab. VII). Most maximum weights recorded by Lacan (1971) were between 75 and 85 g, thus at a much higher level, the mean value on the growth curve being about 70 g. The mean value at Signy Island was 62. 5 g (Beck and Brown 1972). This value is close to the mean maximum of the growth curve for chicks at King George Island, which was 58 g. These differences do not seem to be related to latitudinal climatic changes, but rather reflected the actual weather conditions during the study period.

3.3.2. The effect of weather on chick growth

Large differences in growth rate of Wilson's storm petrel chicks in the population under study were firstly due to weather conditions. As hatching is largely extended in time, chicks of the same age grow under different weather conditions. An especially critical situation obviously hindering growth is due to snowfalls blocking the entrance to the nest, in combination with low temperatures, when chicks starve even for several days. Starved chicks loose much weight. This is shown in figure 12, where weights

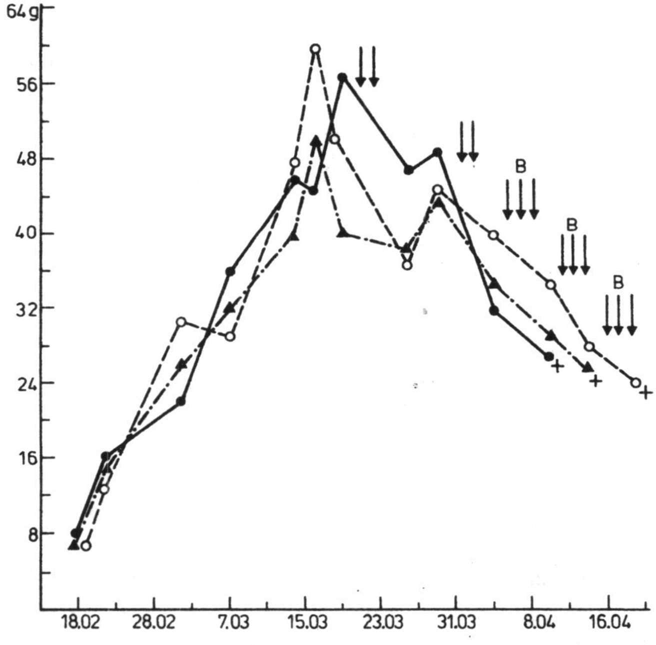

Fig. 15. Growth curves of chicks subject to adverse weather at the same time and age. Arrows periods of adverse weather. B denotes blocking of the nest entrance by snow, crosses denote death of a chick, Y — body weight in g, X — month

of the chicks isolated by snow (closed circles in the hatched area) are much lower than those of the chicks at the same age but not clocked by snow.

Generally, growth curves of the chicks hatched at the same time were well synchronized (Fig. 15), this being not the case for chicks of the same age but hatched at a different time, thus exposed to differential weather conditions (Fig. 16).

Significant declines in body weights of the chicks starved as a result of nest blocking by snowfall were also noted by Roberts (1940), Lacan (1971), and Kamenev (1977) on the Antarctic coast, and by Beck and Brown (1972) at Signy Island. According to Lacan, during 4—5-day snowstorms the daily loss in weight is about 2 g, and in extreme cases 3.5 g, which can ultimately reduce the weight by 40 to 63%.

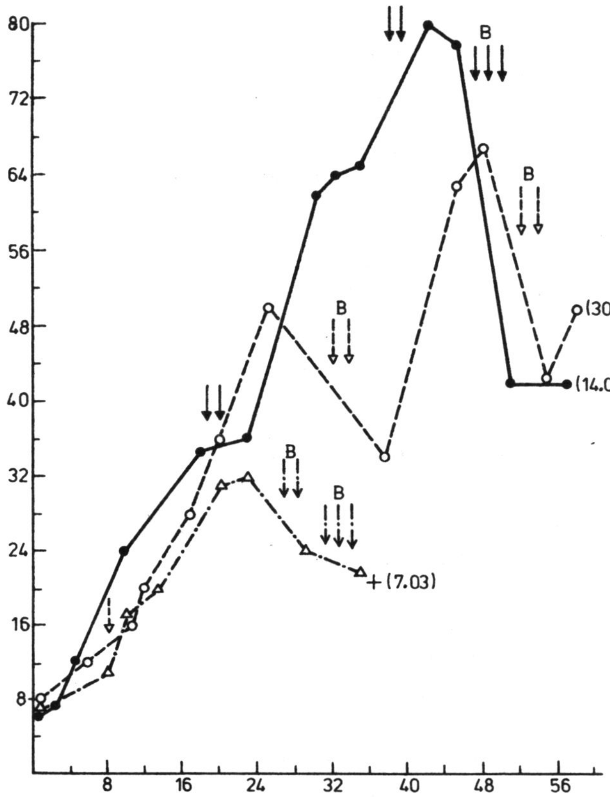

Fig. 16. Growth curves of chicks subject to adverse weather at different ages. In perentheses the dates of hatching; other symbols as in fig. 15, Y — body weight in g, X — age in days

In the breeding season of 1979/80, at King George Island there were several snowfalls combined with strong wimds, and they blocked many nests. It was not possible to determine precisely the duration of starvation, but most probably some chicks starved at least 4 to 5 days. As a result, their body weights declined from 14.3 to 46.2% of the weight prior to starving. On the average (n = 18), the daily weight loss in starved chicks was 2.0 g, ranging from 0.8 to 6 g.

Losses in weight seem to depend on the weight prior to nest blocking: losses in weight in g/24 hours were proportional to the weight prior to starving (Fig. 17). Only the cases are considered here in which chicks starved 4—5-days at ambient temperatures between -6°C and -10°C. The correlation coefficient $r = 0.94$ is significant at $P < 0.001$. This relationship can be due to hypothermy during prolonged starvation. Torpidity periods were observed in many starved chicks, probably combined with low body temperature and low basic metabolic rate. Torpidity periods in starved chicks were also observed by by Beck and Brown for *Fregetta tropica* (1971) and Wilson's storm petrel (1972); this phenomenon was also described for other *Hydrobatidae* (Davis 1957), Allan 1962).

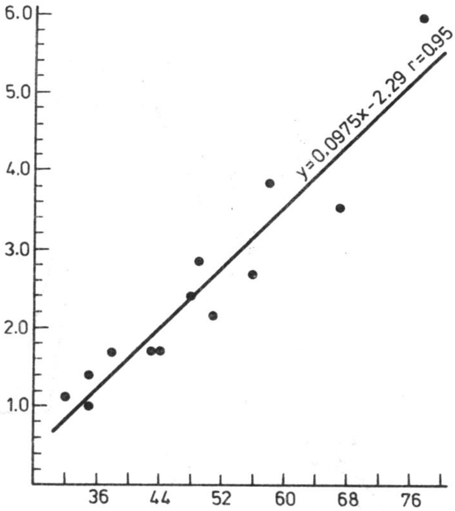

Fig. 17. Decrease in body weight of starved chicks in relation to their body weights before starvation, Y — decrease in weight in g/day, X — body weight prior to starvation in g

If snowstorms do not take more than a few days and the snow is not too compact because of wind action, the parents can often rescue their chicks burried in snow. Generally, such chicks gain weight rapidly, 2.6 g/day on the average, while the mean maximum growth rate of nonstarved chicks at an age of more than 20 days is only 1.6 g/day.

But if the body weight of chicks more than 20 days old drops below 30 g, the chicks die even if they are excavated and alive for a few days more. Perhaps this is related to ambient temperature, which usually drops from a few to more than ten degrees below zero (in °C) during heavy snowfalls.

Violent drops in the weight of chicks were also observed after heavy rainfalls preceded by thaw. In mid-March after a two-day rainfall of 7.5 mm/day, nine chicks that got wet (unsuitable location of nests, which were flooded with rain waters and the water from melting snow) were loosing weight rapidly for three days, at a rate of 3.2 g/day, on the average.

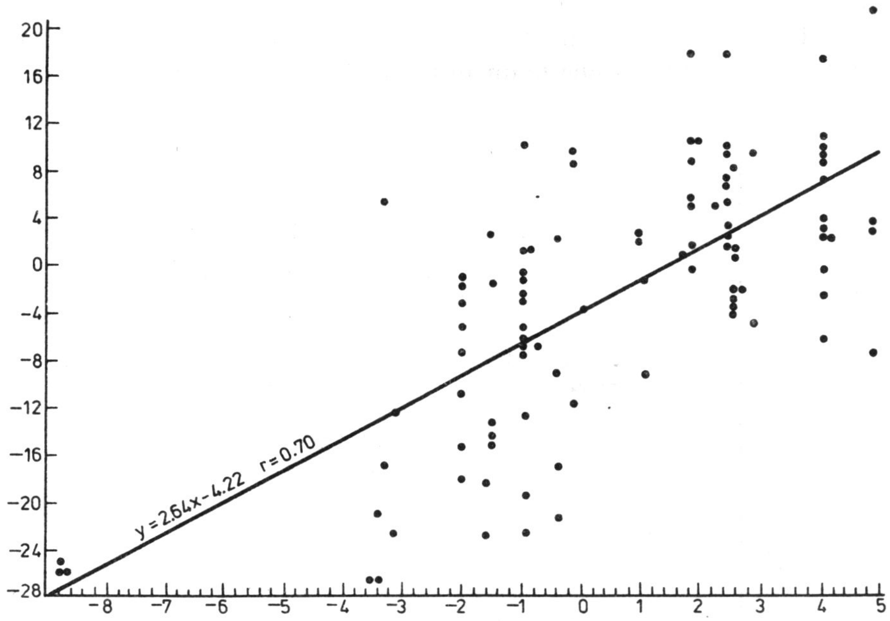

Fig. 18. Deviations in the body weight of chicks from the mean value at a given age in relation to the mean daily temperature of four days preceding each observation, Y — deviation of body weight from mean in g, X — mean daily temperature in °C

Both body weight on successive days and increases in weight are likely to depend not only on the factors discussed above but also on air temperature, or, more precisely, on the rate of cooling.

A correlation method was used to analyse growth of chicks in relation to the rate of cooling, as measured by Bodman's formula (Simonov 1971), and to mean daily temperature. Only chicks more than 20 days old were used, for which individual growth curves markedly varied. To eliminate the possible effects of chicks age, the deviations of weight from mean values for respective ages on the growth curve (Fig. 13) were used, and not direct measurements of weight. A similar procedure was used to analyse the effect of weather on the rate of weight increases; deviations of real increases from mean increases calculated from the mean growth curve were calculated. As a result, the data for chicks at different ages could be pooled, providing a sufficient material for these analyses. Measurements of weights and increases in weights for chicks blocked in their nests by snow or taken in the period of heavy rainfall were excluded from this analysis. Both weights and increases in weight were correlated with mean values of Bodman's coefficient and mean daily temperatures of four days preceding the date of measurement, that is, of the period corresponding to the mean time interval between successive observations.

First, the relation of weight to simultaneous effects of temperature and wind speed was examined using Bodman's formula $S = (1 - 0.04\ t)(1 + 0.272\ V)$,

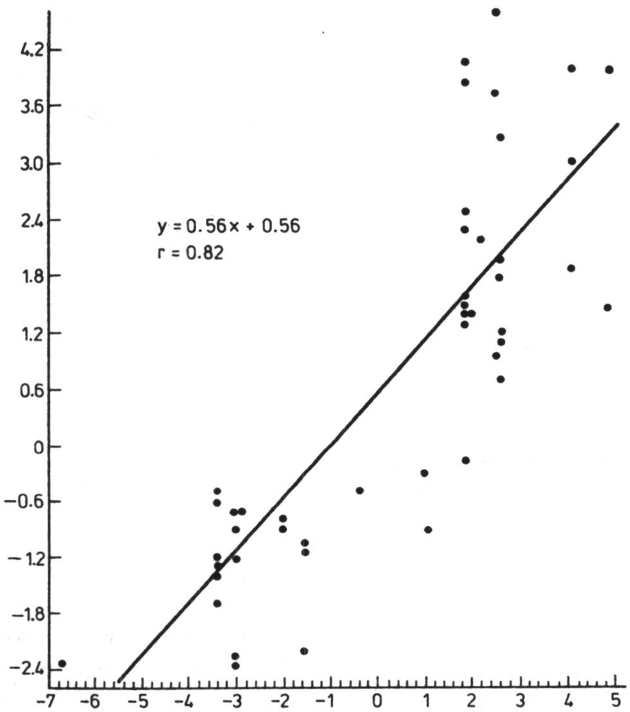

Fig. 19. Deviations of increases in body weight of chicks from the mean increase at each age in relation to the mean daily temperature of four days preceding each observation, Y — deviation of weight increase in g, X — mean daily temperature in 0°C

where t is the mean daily air temperaature in °C, V is the mean wind speed in m/s, and S is a coefficient of climatic severity in conventional units.

Although the correlation coefficient between relative weights chicks and Bodman's coefficients was significant ($0.01 > P > 0.001$, for $n = 94$), its value was very low ($r = -0.27$).

The correlation between the relative weight of chicks and mean daily temperature was rather high: $r = 0.70$ ($P < 0.001$, $n = 94$). Although the data were largely scattered (Fig. 18), this indicates that temperature markedly affected growth. A low correlation between body weight and cooling rate measured by Bodman's coefficient shows that the speed of wind was of low importance. This was due to the fact that the nests were located under boulders or in rock crevices, thus relatively well sheltered. This is confirmed by the measurements of cooling in Wilson's storm petrel nests and in an open area at Haswell Island (Siple and Passel 1945, in Kamenev 1977): in the latter case cooling was up to 2.11 times higher than in the nests.

As the effect of wind was insignificant, only the effect of mean daily temperature on weight increases was analysed. As above, deviations of weight increases from the mean increases, that is, relative increases were correlated with mean daily temperature of four days preceding each measurement. The correlation coefficient was high: $r = 0.82$ ($P < 0.001$, $n = 46$), indicating that the relationship between increases in weight of chicks and mean daily air temperatures was significant. Fig. 19.

The higher correlation between air temperature and increases in weight, as compared with that between air temperature and weight (the respective correlation coefficients were 0.80 and 0.70, and they differed statistically at $0.2 > P > 0.1$), can be explained by the fact that increases in body weight can be high even after a marked loss in weight. In such cases, the response to improved weather conditions in the form of weight increases is considerable, while the weight still remains below average. But even if increases in weight are correlated with air temperatures, the scatter of data about the regression line is wide (Fig. 19), indicating that growth of chicks also depends on other factors, of which feeding rate may be the most important.

As the data presented above imply such factors as rainfall, snowfall combined with heavy wind, and also air temperature can largely modify individual growth curves of Wilson's storm petrels.

The mean growth curves of this species are characterized by a large scatter of data used to calculate the mean. It should be remembered that mean growth curves depend on weather conditions in a given season, and can thus generalized only to a limited extent.

3.4. Diet of Wilson's storm petrels during the breeding period

To analyse the diet of Wilson's storm petrel, mainly the regurgitation defensive of netted adults was used in the period from December 19, 1979, to February 21, 1980. In this way, 82 food samples were collected, containing 125 specimens of three taxonomic groups*).

The food samples were dominated by krill. It occurred in 96.4% of the samples, and accounted for 93.6% of the 125 specimens recorded. The

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* I wish to thank Hanna Filipowska for identifying krill to species and measuring mean body weights of the krill in samples.

other specimens represented *Amphipoda*, except for one larval fish. Krill was represented by *Euphausia superba* in 94.9% and by *Euphausia crystallorophias* in 5.1%.

The data on the diet of Wilson's storm petrel during the breeding season are generally consistent with those obtained by other authors from the coast of Antarctic Continent and Antarctic Peninsula. Falla (1937) has found that at Kerguelen Island, the diet of Wilson's storm petrel is dominated by *Amphipoda* (*Euthemisto* sp.), while on the Antarctic coast, krill (*Euphausiidae*) and *Cephalopoda* are the most important components. Roberts (1940) suggests that krill, mostly *Euphausia superba*, is the most frequent components of the diet in all regions of Antarctica. Kamenev (1977), who analyses 7 stomachs of this species at Haswell Island, has found *cephalopods* in 6 stomaches, *Crustacea* (*E. superba*) in 5 stomachs, and remains of penguins in one stomach. Beck and Brown (1972), who collected 20 samples of food regurgitated by captured birds, recorded mostly adult and larval *E. superba*.

Table VII

Frequency distribution of maximum body weights in Wilson's storm petrel chicks in weight classes

Maximum weight classes (in g)	Number of birds	Per cent
41 – 50	3	12
51 – 56	6	24
57 – 62	6	24
63 – 68	5	20
69 – 74	4	16
75 – 80	1	4

At King George Islands, food samples were taken from adult birds, but indirectly they provide information on the food brought to chicks. 61 samples were collected in the period preceding hatching, between December 19, 1979 and January 19, 1980. The remaining 21 samples were collected between February 6 and February 21, 1980, thus when most chicks were already hatched. As the birds were caught late in the evening and chicks are fed mainly at dusk, it can be assumed that much of the food collected in the latter period of sampling was to be fed to chicks.

Table VIII compares the diet before and after hatching. Differences were insignificant: before hatching a small proportion of *Amphipoda* was in the diet, while after hatching only krill. However, krill was the basic omponent in both these periods, with *E. superba* as the dominant species.

These findings were confirmed by the analysis of food samples taken

Table VIII

Diet composition of adult Wilson's storm petrels prior to hatching — 1 (61 samples) and in the period of feeding the chicks — 2 (21 samples) in 1979/80

Taxonic group	Number of individuals in samples		Per cent individuals		Number of samples with a given prey		Per cent samples with a given prey	
	1	2	1	2	1	2	1	2
Euphausia superba	70	23	72.9	79.3	45	19	73.8	90.5
Euphausia crystallorophias	3	2	3.1	6.9	3	2	4.9	9.5
Euphausia sp.	15	4	15.6	13.8	12	2	19.7	9.5
Amphipoda	7	–	7.3	–	3	–	4.9	–
Pisces	1	–	1.0	–	1	–	1.6	–

directly from chicks during weighing them, as older chicks often vomited in response to handling. In this way, 21 food samples were taken from February 10, 1980 and to Aprill 14, 1980. They consisted exclusively of krill (not identified to species).

It is difficult to estimate food consumption in chicks since they are fed mostly at night, starting at dusk. During the day feeding occurs only on rare occasions. The distribution of returning of the adults to the colony suggests that chicks are not likely to be fed more than twice in the daily cycle. A mean length of the krill in the food was 42.8 mm, which corresponds to about 595 mg fresh weight. In the food samples regurgitated by chicks there were from 2 to 7 specimens, 4 on the average. Assuming that the maximum number is closer to the real (it is little probable that chicks vomited the whole content of the alimentary tract), this was 4.2 g of food. If chicks were fed by each adult one, they would receive about 8.3 g of food per day. Croxall and Prince (1982) assumed that the mean frequency of feeding was 1.5 per day, and the mean weight of a food ratio was 8 g. This yielded 12 g of food per chicks per day. Both these estimates of food consumption are rather similar, taking into account lack of sufficient data on this subject.

3.5. Mortality

3.5.1. Mortality of eggs and chicks and its causes

In the breeding seasons of 1979/80 and 1980/81, nesting losses were high in the Wilson's storm petrel population. Of 129 nests monitored in 1979/80, 89.1% were lost, including 79 nests (61.2%) with eggs and 36 nests (27.9%) with chicks. Only 14 chicks survived until fledging, that is, 10.9% of all the nests.

In 1980/81, observations were continued only by March 19. By that time, 112 out of 165 nests were lost, that is, 67.9%, including 84 nests with eggs (50.9%) and 30 nests with chicks (18.2%). In the same period of 1979/80, that is, by March 19, losses were slightly higher, up to 75.9%, including 61.2% of nests with eggs and 14.7% of nests with chicks.

This comparison implies that the breeding success was very low in both seasons, although in 1980/81, 43 chicks were in the nests (26.1%, of the nests observed) upon termination of the study.

High nesting losses seem to be frequent in Wilson's storm petrels. Lacan (1971) estimated that nest losses at Petrel Island accounted for 69.2%, and Beck and Brown (1972) reported 80.5% nest losses during 3 seasons at Signy Island.

The main direct or indirect cause of such a high mortality is heavy rainfall and especially snowfall combined with strong wind. In the latter case eggs can be covered with snow and frozen, or chicks can be blocked in their nests after a few-day snowfall. From this point of view, Beck and Brown (1972) analysed data provided by the meteorological station on Signy Island for a period of 22 years. They have found that at least six seasons were extremely unsuitable for the Wilson's storm petrel population.

At King George Island, of the total number of 79 eggs lost in 1979/80, 65.8% were covered with snow and frozen, 19% were washed out of the nests during heavy rainfalls, and only 5.1% were predated by sheathbills (*Chionis alba*, 3 eggs) and skuas (*Catharacta maccormicki*, 1 egg). 10.1% of eggs were lost for unknown reasons; some of them were probably washed out by melting snow. Thus mostly unsuitable weather accounted for egg losses.

Of 50 chicks hatched in 1979/80, 36 died. Like in the case of eggs, the main reason was weather conditions. 33% of the chicks who died got wet during heavy rains and then cooled; the remaining 67% died as a result of blocking the entrance to the nest by snow. In the latter case not only the amount of snow is important but also the force of the wind. Usually, snow cover of about 20 cm present for a few days at a wind speed of 6 m/s accounts for clocking many nests.

In 1980/81, nesting failures were also due to rainfall and snow storms, but the data were not analysed in detail because the observations were not continued by the end of the breeding season.

3.5.2. Chick mortality in relation to their age and weight

The mortality of Wilson's strom petrel chicks depends on age. In 1979/80, 38.9% of the total number of chicks hatched died by the age of 10 days, and 50% died by the age of 20 days (Tab. IX). From day 30 a slight increase was observed in the perecentage of chicks dying in successive age classes. It was due to long spells of adverse weather conditions at the end of the breeding season, when the nests were blocked by snow

Table IX

Frequency distribution of Wilson's storm petrel chicks who died in 1979/80 in different age classes (n = 36)

Age class in days	1—10	11—20	21—30	31—40	41—50	51—60	> 61
Number of chicks dead	14	4	0	4	5	6	3
Per cent chicks dead	38.9	11.1	0.0	11.1	13.9	16.7	8.3

and almost all chicks died independent of age. The relationship between mortality and age is more clear-cut when the period of extreme weather is excluded and only the data by March 19 are considered (Tab. X).

Table X

Frequency distribution of Wilson's storm petrel chicks who died in both 1979/80 and 1980/81 by March 9 in different age classes

Age class in days	Number of chicks dead		Total	Per cent of the total number of chicks dead
	1979/80	1980/81		
1–10	14	19	33	67.3
11–20	4	5	9	18.4
21–30	0	5	5	10.2
31–40	1	1	2	4.1
	19	30	49	100.0

The effect of short spells of adverse weather on chick mortality in relation to age is shown in Table XI. The weather deteriorated between March 13 and March 18, 1981: temperature fell below freezing, it was snowing and a strong wind was blowing. On the preceding day, 62 chicks were in the nests checked, of which 19 died by March 19. Although the number of cases was low, an age-related trend can be seen, showing that the mortality of younger chicks was higher than that of older chicks (Tab. XI).

This relationship between chick mortality and age resulted from age-related changes in the weight of chicks, or, more precisely, from changes in fat reserves increasing in proportion to weight. Individual growth curves are very similar by the age of 20 days (Section 3.3.1). In this period, death was usually caused by getting wet of the down, especially by the age of 10 days. Also a relatively short-term blocking of the nest with snow accounted for chick death in this period. The scatter of body weights of chicks more than 16—20 days old (Section 3.3.1, Fig. 12) suggests the proportion of fat in the body may markedly increase at this age.

This is confirmed by the fact that if the weight of chicks more than 25 days old falls below 30 g, which may happen when they are blocked in their nests, they usually die, even when excavated. The weights of 14 chicks on the day of their death ranged between 24 and 29 g, being 25.4 g on the average.

The tendency to reach maximum weight in a short time, this being related to storing fat reserves, is certainly an adaptation to severe weather causing often many-day starvation when the nests are blocked by snow.

Nontheless, it is difficult to show a direct relationship between the weight of chicks and their survival. The reason is that the data available so far are scarce and also that the nest location modified the effect of weather on survival. Some nests are particularly sensitive to blocking by drifting snow, which accounts for death of chicks independent of their age and actual weight. It was possible, however, to show that the mean weight on the day of fledging ($\bar{x} = 65$ g, $n = 13$) was higher by 8.1 g than the mean maximum weight of more than 25-day-old chicks that died ($\bar{x} = 56.9$, $n = 12$), though the difference is not statistically significant.

The importance of weight is better pronounced when the weight of dead chicks is compared with the weight of chicks fledged immediately prior extreme weather deterioration, as it was the case at the end of the breeding season of 1979/80 (mean daily temperature between March 30 and April 19 was −4.1°C, ground temperature was −7.4°C, the depth of snow cover reached 29.5 cm, the proportion of days with snowfall was 65%, and the mean wind speed was 7.2 m/s). The mean body weight of the chicks that survived was 59.3 g, as compared with 46.6 g for the chicks that died. Although the number of cases is low ($n_1 = 9$, $n_2 = 9$) the difference (12.8 g) is statistically significant ($0.01 > P > 0.002$). Like in the earlier case, only chicks more than 25 days old are considered here.

Table XI

The effect of adverse weather during March 13-March 18, 1981 on the mortality of Wilson's storm petrel chicks in relation to their ages

Age class in days	Number of chicks on March 12	Number of chicks dead in March 13-March 18	Per cent chicks dead
1−10	12	7	58.3
11−20	17	6	35.3
21—30	17	5	29.4
31−40	16	1	6.3

3.5.3. Changes in chick mortality over the breeding season

In 1980/81, when the number of dated clutches were relatively high, a trend in nesting losses was observed, related to the date of laying (Tab. XII). Three periods have been distinguished. Although the highest number of eggs was laid in the second period, the lowest proportion of egg failures was in the first period, and than it increased for the next two periods. A similar trend was observed in total losses, though differences between particular periods are less acute because of lower differences in the mortality of chicks, which are less susceptible to adverse weather than eggs.

This may suggest that the early Antarctic summer is the best time for laying, and the melting of snow cover is a factor limiting earlier breeding (Section 3.2.1, Fig. 7).

On the other hand, it should be noted that although the modal value of laying distribution is clearly shifted to the beginning of the breeding season, the frequency distributions of laying in each of the colony groups in figure 7 approximate normal distributions. The distribution of hatching dates (Section 3.2.2, Fig. 10) suggests that the distribution of laying dates in the preceding season was similar.

Table XII

Nesting losses in Wilson's storm petrel in relation to the data of egg laying in 1980/81

Period of egg-laying	11 Dec. – –30 Dec. 80	31 Dec. 80– –19 Jan. 81	20 Jan. – –8 Feb. 81
Number of eggs lost	40	102	23
Per cent eggs lost	37.5	60.0	69.7
Number of chicks hatched	25	49	7
Chicks dead in per cent of chicks hatched	32.0	36.7	57.1
Total nesting losses in per cent	57.5	69.7	87.0

Hence, it seems that early summer is at most more frequently suitable for future egg survival than later periods. An analysis of the probability of unsuitable weather conditions in particular periods of the breeding season over many years could help in answering this question.

3.5.4. Adult mortality

Beck and Brown (1972), using data on ringed and recaptured birds over several years, have found that the death rate of adult Wilson's storm petrels is about 9% (8—11%). For the population living at King George Island only an indirect estimate of adult mortality is possible. A fact was used that these birds generally occupy the same nests from one year to another (Roberts 1940, Beck and Brown 1972). Of 129 nests occupied in 1979/80, 100 was reoccupied in the following season. Of 29 nests not reoccupied, 14 were destroyed (flooded, burried), thus, in fact, only 15 nests were not reused. If it can be assumed that these nests were not reused because of the death of adult birds, their annual mortality would be 15: 129 · 100% = 11.6%. Although this is a very rough estimate, it is close to that calculated by Beck and Brown (1972).

During the breeding season, adult mortality is probably very low. No one of not destroyed nests was abandoned; in no case adult birds were blocked on the nests by snow — they always left the nests during snowfalls.

3.6. Adaptations of Wilson's storm petrel populations to climatic conditions of Antarctica

Wilson's storm petrel populations are adapted to the life in Antarctica not only in the way typical of this species but also in the way characteristic of the whole family Hydrobatidae and of many other representatives of Procellariiformes, inhabiting high and low latitudes.

First of all, a characteristic type of chick development should be considered here. In all *Hydrobatidae*, chick development from hatching to fledging is largely extended ni time. For example, the mean time of nesting development in *Hydrobates pelagicus* (51°42′ N) is 63 days (Davis 1957). In *Oceanodroma castro* (7°57′ S) it covers 63 days (Allen 1962), and in Wilson's storm petrel from 60 days at South Orkneys (60°43′ S) (Beck and Brown 1972), up to 49 days on the Antarctic coast (66°40′ S) (mean from data of several authors, see Tab. XIII). All representatives of the family are sea birds collecting food from water surface; they can carry food to chicks from large distances hence the frequency of feeding is low, which, in turn, determines the considerable duration of nesting development. The shortening of this period in Wilson's storm petrel populations with increasing latitude (Tab. XIII) is probably related to an increase in food abundance.

Chicks of all the family members reach much higher body weights during their development than adults. The maximum weight of *H. pelagicus* chicks is higher than adult weight by 80% (Davis 1957), in *O. castro* it is higher by 70% (Allan 1962), in Wilson's storm petrel by as much as 105%. This is due to storing large fat reserves. Chicks of this family develop thermoregulation relatively early, within several days. This type of growth curve also determines a considerable extension of the nesting period in *Hydrobatidae* and also their reproductive strategy: one relatively large egg over the breeding season.

Considering specific features of chick development for the whole family *Hydrobatidae*, it may be concluded that primarily it represents an adaptation to temporal food shortage. But in the case of such species as Wilson's storm petrel or *Fregetta tropica* it certainly allows the survival of not only several-day starvation periods, as shown earlier, but also of low temperatures, reaching −14°C.

As already noted by Lacan (1971), Wilson's storm petrel chicks grow faster during their first days and develop homoiothermy earlier than other *Hydrobatidae*, living in lower latitudes; *O. castro* and *H. pelagicus* chicks are brooded at least by the age of 7 days, while Wilson's storm petrel chicks ussually by the age of 2—3 days.

A specific adaptation enhancing survival in extremely adverse weather is tropidity period in Wilson's storm petrels blocked in the nests by snow, when the metabolic rate is probably very low. This ability also occurs in

Table XIII

Phenology of the breeding period of Wilson's storm petrel in Antarctica and Subantarctica

Breeding groups Phases of breeding cycle	Kerguelen Is. 49°20′ S	South Orkney Is. (Signy I.) 60°43′ S	South Shetland Is. (King George I.) 62°09′ S	Antarctic Peninsula (Argentine I.) 65°15′ S	Antarctic Continent 66°40′ S 66°31′ S
Arrival date	21 Nov.	8 Nov.	5 Nov.	6 Nov.	4 Nov.
Number of days from arrival to the first egg	50	49	33	36	17
Date of the 1st egg	10 Jan.	27 Dec.	8 Dec. 79 12 Dec. 80	12 Dec.	21 Nov.
Duration of egg-laying period in days	29	38	53 (1979) 59 (1980)	25	57
Mean incubation period in days	–	44.5	44	43	41.5
Mean duration of nestling period in days	–	60	59	54	49
Date of departure of last birds from colonies	–	15 May	19 April	–	7 April
Duration of the breeding season from first egg to departure	about 132	140	133	–	138
Total duration of the breeding season — from arrival to departure	about 182	188	165	–	154
References:	Eaton (1875) Hall (1900) Loranchet (1915)	Beck and Brown (1972)	Author's data	Roberts (1940)	Wilson (1907) Falla (1937) Mougin 1968 Pryor (1968) Lacan (1971) Kamenev (1977)

other *Hydrobatidae* (Davis 1957, Allan 1962, Beck and Brown 1971) and, like growth curves, it represents a primary adaptation to temporal starvation

Adaptations of Wilson's storm petrels to the Antarctic climate can be observed in the phenology of the breeding period. This becomes obvious when comparing phenological aspects of particular reproductive phases for a sequence of populations ranging from northernmost to those living farthest to the south, on the Antarctic coast.

Particular phases of the reproductive cycle along the gradient of increasing latitude are compared in Table XIII. Similar comparisons were made by other authors (Lacan 1971, Beck and Brown 1972, Kamenev 1977). This table includes a large range of data reported by other authors and also present data from King George Island.

Except for Kerguelen Island, no significant difference exists in the dates of returning of particular Wilson's storm petrel populations to their breeding grounds, and, as many authors suggested, these dates coincide with snow melting. But the number of days from the arrival of first individuals to the date of the first egg clearly decreases with increasing latitude from 50 days at Kerguelen Island to 17 days on the Antarctic Coast (Tab. XIII). It, is so because egg laying starts earlier with increasing latitude.

At first sight it is surprising that the duration of egg-laying increases in the same direction from 29 days at Kerguelen Island to 57 days on the Antarctic Coast. Data from Antarctic Peninsula do not fit to this pattern. This probably results from a small sample size, consisting of only 18 records, hence the range of laying dates may be shortened. The sample size from Kerguelen Island is also small; hence the differences in egg-laying duration between northern and southern population of the Wilson's storm petrel are probably smaller than those in Tab. XIII. However, the tendency to prolongation of the egg-laying period with increasing latitude seems to be really existing.

In some situations, for example, at King George Island in 1980/81, laying period could be extended because of a delay in laying caused by delayed snow melting in some colonies. But independent of this, in each of these colonies a characteristic, close to normal distribution of egg-laying in time was observed (Section 3.2.1, Fig. 7), being of basic importance to the duration of laying period. Thus, the prolonged laying period in Wilson's storm petrel populations living farther to the south does not result from a delay in breeding in some colonies but it is an effect of the specific dictribution of laying in these populations.

Beck and Brown (1972), who first noticed this phenomenon, suggested that this might be an adaptation to randomly distributed in time unfavourable weather conditions, mostly snowstorms, accounting for high egg mortality. They may occur at the beginning, in the middle, or at the end of the breeding season, depending on the year. Under such climatic conditions, the prolonged laying period can ensure better survival. The onset laying depends on the date of snow melting and the end of laying occurs when the chance for chick survival is extremely low because of obligatory adverse weather.

The adaptive character of this pattern to Subantarctic and Antarctic climate raises no doubt, but the evolutionary mechanisms of this adaptation within populations reamins unclear. It is only possible to state that individual pairs show at least a tendency for laying eggs either earlier or later in successive years, when observing dates of hatching in the same nests, occupied in two successive years (32 nests). The adults occupying these nests were not marked but Roberts (1940) and Beck and Brown (1972) have shown that a large proportion of nests is occupied by the same birds year after year. For example, according to Roberts, 20 nests out of 22 were occupied by the same pair in the following year, and in the two remaining nests only one partner was new. Thus, it can be assumed that the 32 nests analysed here were generally occupied by the same pairs in the two years.

A high correlation coefficient was found ($r = 0.76$, $P < 0.001$) between the dates of hatching for the same nests in 1979/80 and 1980/81 (Fig. 20). Consequently, the dates of laying showed a similar relationship. A relatively high coefficient $a = 11.9$ reflected the delay of laying in 1981 due to delayed snow melting in some colonies. As it has been shown after analysing the attachment of individual nests to the colonies, the general character of the relationship days not depend on environmental conditions.

Hence, it may be suggested that the Wilson's storm petrel population is characterized by a certain structure with respect to the dates of laying, perhaps genetically determined. But the explanation of this interesting problem requires further studies.

The time of incubation tends to decrease in the gradient of latitudes (Tab. XIII), though the differences are not likely to be statistically significant. The shortening of incubation is possible due to the shortening the breaks in incubation, characteristic of this species; the real time of incubation is probably relatively constant. This tendency does not seem to be of adaptive value, and it rather reflects the improved food conditions with increasing latitude. This would be conformed by a clear tendency to a shorter stay of chicks in the nest in southern populations of Wilson's storm petrels.

The dates of depature from breeding grounds are earlier towards the south. However, the period from the first egg to leaving the colony is similar for all populations. The total duration of the breeding season, from arrival to departure from the breeding grounds, decreases with increasing latitude, being shorter by one month for the population on Antarctic Continent (Tab. XIII).

As shown in Section 3.5, egg and chick mortality is very high in Wilson's storm petrel populations, fecundity is low, while the life span of adults very long. The survival strategy of the species is directed towards the survival of adults. One of the symptoms of the behaviour consistant with this strategy is leaving the nests with eggs or chicks by adults during snowstorms threatening with blocking the entrance to the nest. During the two breeding seasons no adult bird died as a result of nest blocking by snow, though the number of nests checked was high. The same was recorded by Lacan (1971) and Beck and Brown (1972). Kamenev (977) recorded some cases of dead adults found in the nests from the preceding season but these might have been chicks who died immediately prior to fledging, thus in full plumage.

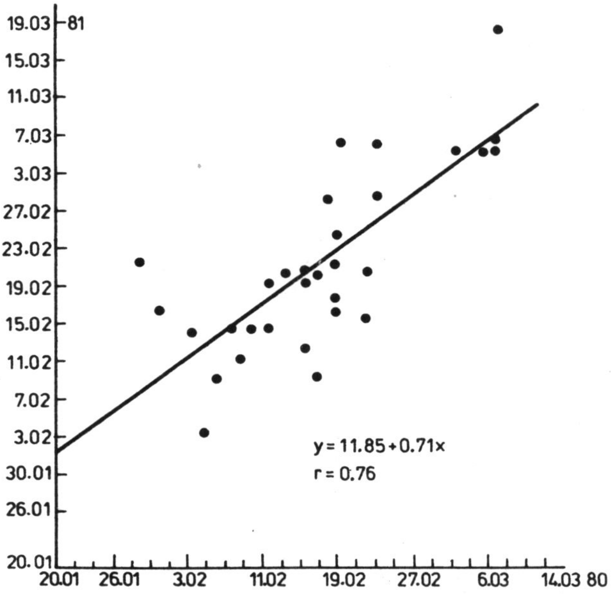

Fig. 20. Relationship between the dates of egg hatching in individual nests in 1980/81 and the dates of egg hatching in the same nests in the preceding season (1979/80), Y — date of hatching in 1980/81, X — date of hatching in 1979/80

To sum, up, it can be stated that Wilson's storm petrels have many morpho-physiological and biological features characteristic also of other Hydrobatidae, enhancing the survival of this species under severe climate of Antarctica and Subantarctica; however, specific, direct adaptations to these climatic conditions are mostly behavioural, and, in particular, they concern breeding phenology of individual populations.

I wish to thank Dr. Bolesław Jabłoński for making available his data on Wilson's storm petrel numbers in Admiralty Bay; Hanna Jackowska-Filipowska for identifying krill to species and estimating mean weights of the krill in food samples; Dr. Jacek Rożyński for invaluable help in material collecting.

4. Резюме

Исследования популяции качурки Вилсона на о-ве Кинг Джордж (Южные Шетландские о-ва) велись в 1979—81 г. в районе Залива Адмиральты. Используя метод оценки численности по трансекту прослежены изменения численности популяции качурок от прилёта до начала яйцекладки (Рис. 4). Последующие изменения численности основаны на балансе взрослых особей присутствующих в колонии, вылупляющихся птенцов и их гибели с течением времени (Рис. 5 и 6).

Используя разные методы оценки численности (учёт по трансекту, отлавливание и контроль окольцованных особей, поголовный учёт птиц возвращающихся с моря в колонию) численность популяции качурки Вилсона в районе Залива Адмиральты установлено примерно на 3400 пар.

Яйцекладка была значительно растянута во времени, в среднем она длилась 56 дней (18.12—30.01.79/80, 12.12—8.02.80/81). Распределение частот яйцекладок во времени в отдельных колониях приближалось к нормальному, с некоторой положительной смещенностью. Начало яйцекладок было обусловлено таянъем снежного покрова (Рис. 7). Инкубация длилась в среднем 44 дня, в пределе 38—54 дней. Период вылупления птенцов растягивался в среднем на 53 дня (Рис. 10). Птенцы оставались в гнезде в среднем 59 дней.

В моменте вылупления птенцы весили около 7 г. Максимальный вес птенцов достигал 80 г, превосходя вес взрослой птицы на 105% (Рис. 12). Средний максимальный вес птенцов находился однако на более ниском уровне (Рис. 13). В большенстве птенцов растягивался в среднем на 53 дня (Рис. 10). Птенцы оставались в гнезде случаев птенцы достигали максимальный вес между 31—35 днём жизни, однако наивысший максимальный вес отмечен в возрасте 41—45 дней (Таб. VI). Перед вылетом из гнезда птенцы весили от 35 до 66 г.

До 20 дня жизни кривые роста всех птенцов сходны, но в последующих днях сильно колеблются (Рис. 12), что обусловлено атмосферическими условиями в которых развиваются отдельные птенцы (Рис. 15 и 16). Особенно сильно воздействует на рост птенцов засыпание гнезд снегом, что вызывает голодание птенцов даже несколько дней и в последствии падение их веса от 14% до 46%. Обнаружено, что вес птенцов в данном классе возраста, а также величина прироста их веса зависят от окружающей температуры (Рис. 18 и 19).

Используя факт, что отлавливаемые особи сбрасывают пищу, собрано 103 образца пищи взрослых птиц и птенцов. В пище доминировал криль, выступающий в 96.4% образцов (Таб. VIII).

В оба сезона в исследуемой популяции качурки Вилсона обнаружено большие потери кладок. Из 129 кладок контролированных в сезоне 1979/80 погибло 89,1%. Гибель кладок зависела прежде всего от атмосферических условий: из 79 утраченных яиц 65.8% погибло вследсвие снегопадов, 19% было вымытых из гнезд талой и дождевой водой, а только 5.1% истребили поморники. Среди 36 павших птенцов 33% погибло вследствие промокания пуха а остальные 67% вследствие засыпания гнезд снегопадами. Смертность птенцов принадлежащих к младшим классам возраста была выше, чем у старших птенцов, что связано с их весом (Таб. X и XI).

Установлено, что относительно большой вес птенцов качурки Вилсона и быстрый темп их роста в течении первых 16 дней жизни по сравнению с представителями того же семейства обитающими в ниских широтах, представляет собой приспособление к жизни в Антрактике. Адаптации к климатическим условиям Антарктики обнаружены также и в области фенологии размножения (Таб. XIII).

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5. Streszczenie

Badania nad populacją nawałnika Wilsona (*Oceanites oceanicus*) na wyspie King George (Szetlandy Południowe) prowadzono w latach 1979—81 w rejonie Zatoki Admiralicji. Stosując metodę taksacji liniowej prześledzono dynamikę liczebności populacji od przylotu do rozpoczęcia lęgów (Fig. 4). Dalszy przebieg zmian liczebności zrekonstruowano kontrolując gniazda, na podstawie bilansu obecnych w kolonii osobników dorosłych, wykluwających się piskląt i ich ubywania wskutek śmiertelności (Fig. 5 i 6).

Wykorzystując różne metody (taksacja liniowa, odłowy i kontrola znakowanych osobników, totalne liczenie osobników wracających z żerowisk do kolonii) oszacowano liczebność populacji w rejonie Zatoki na około 3400 par.

Zniesienia były znacznie rozciągnięte w czasie i na wyspie King George obejmowały średnio 56 dni (8.12—31.01, 12.12—8.02). Rozkłady zniesień w poszczególnych koloniach były zbliżone do normalnego, dodatnio skośne; początek zniesień uwarunkowany był terminami zaniku pokrywy śnieżnej (Fig. 7). Przeciętny czas inkubacji wynosił 44 dni w zakresie 38—54 dni. Wykluwanie się obejmowało średnio 53 dni (21.01—16.03 i 26.01—16.03) (Fig. 10). Pisklęta przebywały w gnieździe średnio 59 dni.

Pisklęta ważące w momencie wyklucia około 7.5 g osiągnąć mogą ciężar 80 g (105% powyżej ciężaru osobnika dorosłego) (Fig. 12). Przeciętny maksymalny ciężar przypadający na 43 dzień życia jest jednak niższy (Fig. 13). Najczęściej pisklęta osiągają maksimum ciężaru w wieku 31—35 dni, choć przeciętny maksymalny ciężar w tej klasie wieku jest niższy niż w wieku 41—45 dni. (Tab. VI). Tuż przed wylotem pisklęta ważyły od 35 do 66 g.

Do 2- dnia życia krzywe wzrostu piskląt kształtują się podobnie, natomiast w następnych dniach podlegają znacznej zmienności (Fig. 12), zależnie od warunków pogodowych na jakie trafiają poszczególne pisklęta (Fig. 15 i 16). Szczególnie ostry wpływ na wzrost piskląt ma blokowanie gniazd przez opady śniegu, co powoduje nawet kilkudniowe głodowanie piskląt i w efekcie spadki ich ciężaru od 14% do 46%. Wykazano, że ciężar piskląt w danej klasie wieku, jak też wartość przyrostów ciężaru ciała zależne są od temperatury zewnętrznej (Fig. 18 i 19).

Wykorzystując obronny odruch wymiotny u łowionych osobników dorosłych i piskląt zebrano 103 próby pokarmu. W pokarmie osobników dorosłych dominował kryl, występujący w 96.4% prób (Tab. VIII). Wśród okazów oznaczonych do gatunku 94.9% stanowiły *Euphausia superba*. W 21 próbach pokarmu piskląt występował wyłącznie kryl.

W obu sezonach w badanej populacji nawałnika Wilsona stwierdzono wysokie straty w lęgach. Na 129 lęgów kontrolowanych w sezonie 1979/80 zginęło 89.1%. Straty powodowane były głównie przez warunki atmosferyczne: na 79 zniszczonych jaj 65.8% zginęło wskutek zasypania przez śnieg, 19% zostało wypłukanych z gniazd przez deszcze a tylko 5.1% zniszczyły skuy i pochwodzioby. Na 36 padłych piskląt 33% zginęło naskutek zamoknięcia puchu a pozostałe 67% wskutek zablokowania gniazd przez śnieżyce. Stwierdzono, że śmiertelność młodszych piskląt jest znacznie wyższa niż starszych (Tab. X i XI), co jest związane z ich ciężarem.

Stwierdzono, że znaczne ciężary ciała piskląt nawałnika Wilsona i szybkie tempo ich wzrostu w pierwszych 16 dniach życia, w porównaniu z przedstawicielami tejże rodziny z niskich szerokości, stanowią adaptację do życia w Antarktyce. Adaptacje do warunków klimatu antarktycznego występują też w zakresie fenologii rozrodu (Tab. XIII). Szczególne znaczenie ma tu rozciągnięcie okresu zniesień u południowych populacji nawałnika Wilsona.