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Lech STEMPNIEWICZ

Department of Animal Ecology, Institute of Biology,
Gdańsk University, Czołgistów 46, 81–378 Gdynia, Poland

FACTORS INFLUENCING THE GROWTH OF THE LITTLE AUK, *PLAUTUS ALLE* (L.), NESTLINGS ON SPITSBERGEN

ABSTRACT: The growth rate of the nestlings of the little auk is the highest among Alcidae ($K = 0.256$, $t_{10-90} = 17.2$ days). The peak weight represents 77.3%, and the fledging weight 67.3% of the weight of adult birds. The high growth rate, short nesting period and relatively small body size at fledging are the expression of an evolutional tendency of the nestlings of the little auk to precocity which is a form of adaptation of the species to reproduction in high-arctic conditions. The prefledging body-weight fall improves the locomotory capability and physiological efficiency of juvenile birds leaving a breeding colony. Egg size, related to the body size of parent birds, has a significant influence on the growth and development of the nestlings. In the period that precedes the leaving of the nest a tendency is seen towards a uniform body size of the nestlings through changes in the length of the nesting period, and the magnitude of the prefledging body-weight decrease.

KEY WORDS: Spitsbergen, the little auk, growth and development of nestlings.

Contents

1. INTRODUCTION

In recent years there have appeared very many papers on the growth and development of many bird species. The numerical results of these papers could be compared owing to the working out of objective growth indices (e.g. R i c k l e f s 1967). This made it possible to formulate general principles of the growth of birds in relation to taxonomic groups, growth mode of nestlings, etc., and to find certain evolutional tendencies (R i c k l e f s 1968a, 1973). The stage of study of the different taxonomic groups of birds in this respect varies. There is a relatively extensive literature on the Alcidae family (e.g. B e l o p o l s k i 1957, K o z l o v a 1957, T u c k 1961, M y r b e r g e t 1962, T h o r e s e n 1964, C o r k h i l l 1973, S e a l y 1973a, 1975a, 1975b, 1976, S e a l y and B è d a r d 1973, J o h n s o n and W e s t 1975 and others). The results of these studies have provided the basis for some general conclusions (e.g. C o d y 1973, S e a l y 1973b). The lack of completeness and sometimes a controversial nature of the general studies (cf. B è d a r d 1976) resulted, among other things, from the lack of detailed data on the biology of breeding of some auk species, including the little auk, *Plautus alle.* The present, as well as other (S t e m p n i e w i c z – in press) papers, are intended to complete the information.

The attention of ornithologists is focused also on the factors influencing the growth and development of nestlings, one of the object of the present study. The effect of factors such as food supplies or meteorological conditions in a breeding season has been ascertained in many studies on a considerable number of bird species (e.g. P e r r i n s 1965, L e C r o y and C o l l i n s 1972, D y r c z 1974, L e C r o y and L e C r o y 1974, V i s s e r 1974, D u n n 1975, A n d e r s s o n 1976, W h i t e, R o b e r t s o n and R i c k l e f s 1976 and others). Factors such as the egg size, for example, were only sporadically taken into account (e.g. S c h i f f e r l i 1973). The little auk is an exceptionally convenient object for studies of this type, because it occurs in large numbers while its colonies are relatively easy to access, due to which it is possible to collect sufficient material. Of importance is also the fact that the clutches consist of one egg, due to which there is no intra-clutch competition, and that as semiprecocials juvenile little auks remain in a breeding colony for an average of 27 days (S t e m p n i e w i c z – in press), being then available to studies.

2. MATERIAL AND METHODS

Field work was done during two successive Polish expeditions to Spitsbergen, in 1974 and 1975. In both years the investigations covered a patch of a little auks' colony located on the southern slope of the Arie mount (Ariekammen). The study site was near the Polish Research Station on the Bay of White Bear (Isbjörnhamna), on the northern shore of Hornsund (suth-western Spitsbergen).

The investigations were began in the middle of June and continued until the end of August, that is, until all birds left the breeding colony. A total of 72 nests (56 nests in 1974 and 16 additional nests in 1975) were found and marked. They were then tightened with stones and only the entrance hole was left. This was done to prevent the chicks from running away in the maze of rock rubble, and ensure checking the same nestlings, throughout their stay in the breeding colony. The number of adult birds captured by means of Japanese nets was 58, and 39 parent birds were caught on marked, regularly checked nests. All the birds were measured, and the parent birds were uniquely marked. The biometrical studies consisted in the measuring of eggs, nestlings and adult birds. The equipment used included spring balances (with an accuracy to the nearest 0.5 1.0 and 2.0 g), calliper rules, compasses and rulers. Egg length and breadth were measured. The volume index was calculated by using the formula for the volume of the ellipsoid, and for the calculation of the relative breadth the formula: $J = \frac{B}{L} \cdot 100$ (L – egg length, B – egg breadth) was used. Body-weight and the length of wing, bill, tarsus and tail of the nestlings were measured at one-day intervals, from the hatching time (in the case of wings and tails – from the time of appearance of primaries and tail feathers) until the departure from the colony (possibly loss or death). Additionally, stages of down disappearance and plumage growth in nestlings were recorded.

3. RESULTS

3.1. GROWTH AND DEVELOPMENT OF NESTLINGS

The growth in body-weight of the nestlings of the little auk is represented by a typically S-shaped curve with a strongly marked fall in the final phase (Figs. 1, 2). Maximum body-weight is attained between 17th and 25th day of life (on the average on 20th day) (Table I) Daily increments in body-weight grow gradually until 8th day of a chick's life, then they drop until 20th day, whereafter a body-weight fall follows (Fig. 3). As measured from 6th day on, the wing is found to grow fairly evenly throughout the developmental period of a nestling, showing a decrease in daily length increments (Table I, Figs. 1–3). The course of growth in length of the bill and tail is similar (Table I, Figs. 1, 2). Some characteristic features can be seen in the growth of the tarsus. A rapid growth in length lasts until 5th day of life, being then followed by a decrease in growth rate, whereas from 17th day until the fledging there is practically no growth in length of the tarsus (Table I, Figs. 1, 2).

The growth in size of the same elements has been expressed as a percentage of their size on 27th day of life (adopted as 100%) (Fig. 2). The angle of inclination of the particular curves shows the growth rate of an element relative to other elements. The fastest growth is recorded for the tail feathers and body-weight (until 20th day of life), followed by: the wing, bill and tarsus. This indicates that bony elements grow at the slowest rate, the growth of bony-horny elements being faster and that of horny parts and body-weight – the fastest.

If an adult little auk is taken as a model, it appears that from its hatching time until its departure a nestling has a disproportionate body size (Fig. 1). Newly hatched chicks have a relatively long bill and a very long tarsus. Later on, the proportions tend to improve, and about 23rd day of life (ignoring the tarsus length) a nestling becomes a miniature of an adult bird. In later developmental days and until the fledging, the proportions change again. At this stage a juvenile bird is relatively light and short-billed. The length of the tarsus which differs from all other elements throughout the nestling period is connected with the mode of locomotion of the nestlings at that time (S t e m p n i e w i c z – in press).

Table I. Growth of little auk nestlings in the breeding seasons 1974 and 1975
a – hatching day, b – data for 27th day apply only to 1974

Age of nestlings (days)		Body-weight			Wing length			Bill length			Tarsus length			Tail length		
		average (g)	σ	N	average (mm)	σ	N	average (mm)	σ	N	average (mm)	σ	N	average (mm)	σ	N
a	1	21.0	2.6	54				8.8	0.5	51	16.9	1.0	52			
	2	25.1	3.3	58				8.9	0.4	35	18.0	0.9	31			
	3	29.9	4.3	58				9.1	0.4	35	18.6	0.8	31			
	4	35.6	4.6	55				9.3	0.4	34	19.2	0.9	30			
	5	42.3	5.3	54				9.5	0.4	35	19.7	0.9	31			
	6	48.5	6.6	53	28.0		2	9.6	0.4	34	20.1	0.9	31			
	7	55.2	7.7	53	29.2		2	9.7	0.5	34	20.4	0.9	31			
	8	62.8	8.2	51	36.2	3.7	6	9.8	0.4	34	20.7	1.0	31			
	9	69.9	8.7	50	41.3	4.4	7	10.0	0.4	33	20.9	1.0	30			
	10	76.4	8.7	50	45.1	4.9	11	10.2	0.4	33	21.1	1.0	30			
	11	82.7	8.9	50	49.0	4.2	16	10.4	0.5	33	21.2	1.0	30			
	12	89.2	9.8	50	53.4	4.8	23	10.5	0.5	33	21.4	1.0	31			
	13	95.5	10.1	49	57.2	4.9	22	10.7	0.5	32	21.5	0.9	31			
	14	101.5	10.5	49	60.9	4.9	23	10.8	0.6	34	21.6	0.9	33			
	15	106.1	10.1	49	65.0	4.4	29	10.9	0.6	34	21.7	0.9	35	11.2	1.1	5
	16	110.6	9.2	48	69.6	4.0	35	11.0	0.6	33	21.8	0.8	34	13.7	1.9	12
	17	114.5	8.8	48	72.9	4.0	40	11.1	0.6	36	21.9	0.9	36	13.9	1.9	21
	18	117.9	9.6	47	76.6	3.9	44	11.2	0.6	39	21.9	0.8	38	15.7	1.9	27
	19	121.3	9.9	46	79.8	3.6	46	11.3	0.6	41	21.9	0.8	40	16.6	2.1	32
	20	123.5	9.7	45	82.8	3.5	46	11.4	0.6	40	22.0	0.8	40	18.2	2.3	38
	21	122.7	9.6	46	86.0	3.5	46	11.5	0.6	41	22.0	0.8	40	20.2	2.2	41
	22	121.5	10.4	46	88.8	3.7	47	11.6	0.6	42	22.1	0.8	42	22.2	2.2	41
	23	120.6	10.8	45	91.3	3.7	46	11.8	0.6	41	22.1	0.7	40	23.7	2.2	39
	24	118.3	11.2	44	94.1	3.6	45	11.9	0.6	41	22.1	0.7	38	25.5	2.2	40
	25	113.8	10.3	37	96.0	3.5	38	12.0	0.6	39	22.1	0.7	36	27.0	2.1	36
	26	109.8	9.4	30	97.9	3.2	31	12.1	0.6	38	21.9	0.8	36	28.6	1.9	31
b	27	105.5	11.7	9	99.7	5.1	9	11.5	0.5	5	21.5	0.5	5	29.0	3.2	9

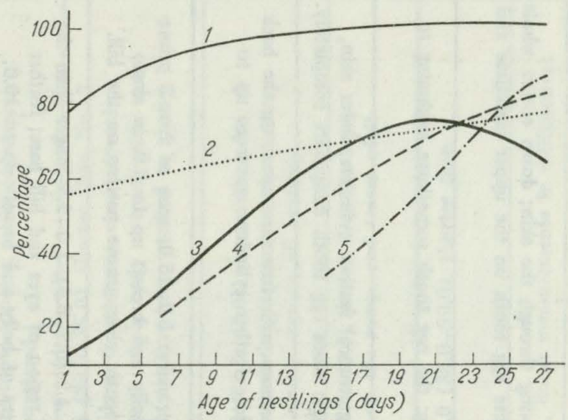

Fig. 1. Growth of little auk nestlings in two seasons, 1974 and 1975, expressed as a percentage of adult birds' body-weight (adopted as 100%)
Number of birds is given in Table I. 1 – growth in tarsus length, 2 – growth in bill length, 3 – weight increase, 4 – growth in wing length, 5 – growth in tail length

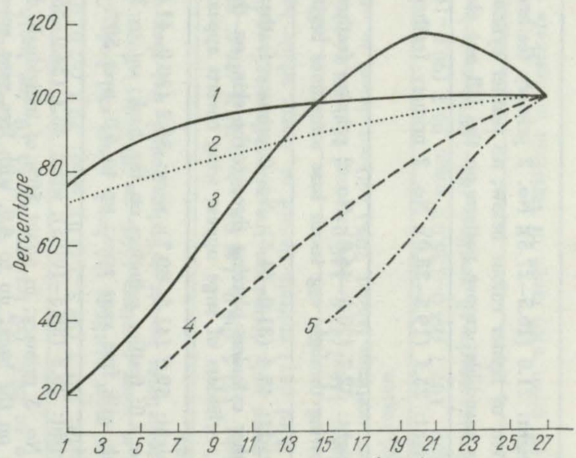

Fig. 2. Growth of little auk nestlings in two seasons, 1974 and 1975, expressed as a percentage of the average body size attained on the day of departure to sea (27th day, adopted as 100%)
Number of birds is given in Table I. Explanation as for Figure 1

With the view of future populational studies of the little auk, a guide has been prepared to be used for determining the age of nestlings (Table II).

Table II. A guide to the age of the little auk nestlings

Life day	Description*
1	Body weight: 21.0 (16.5–27.5); No. 2 primary feather cylinder: absent or showing through the skin; down covers whole body, often of lighter colour below; no feather cylinders on trunk; a clear, white egg tooth on the upper mandible and the lower mandible; groove pattern on the bill not clear.
2	Body weight: 25.1 (19.5–33.0); No. 2 primary feather cylinder: up to 3.0 long; the egg tooth sometimes beginning to turn yellow.
3–4	Body weight: 32.7 (20.0–44.8); No. 2 primary feather cylinder: up to 5.0 long; truncal feather cylinders under skin, blue, showing through; egg tooth base sometimes begins to grow thinner; in single cases egg tooth disappears completely.
5–6	Body weight: 45.4 (31.0–61.5); No. 2 primary feather cylinder: 5.0–10.0, sometimes with free vane apex; on the back blue feather cylinders piercing through the skin, on the abdomen and breast white feather cylinders are seen: up to 3.0 long; cylinders of large uppear wing coverts appearing.
7–8	Body weight: 59.0 (41.0–80.7); wing: 36.2 (30.0–41.0); the sheath of No. 2 primary: 5.0–15.0; vane of No. 2 primary: up to 4.0; feather cylinders on the back: up to 3.0; feather cylinders on belly and breast: up to 3.0, in single individuals with free vane apex: up to 4.0; over 50% of nestlings without egg tooth; clear groove pattern on the bill.
9–11	Body weight: 76.3 (50.5–100.5); wing: 45.1 (34.0–55.0); No. 2 primary vane: 4.3 (0.5–8.5), 1.0–2.5 longer than the vane of No. 3 primary; in about 50% of individuals down disappears from the region of eyes and bill base; feather cylinders on the back: up to 4.0, with free vane apex: up to 4.0; white feathers of belly and breast: up to 10.0; about 90% of nestlings without egg tooth.
12–14	Body weight: 95.4 (63.2–119.5); wing: 57.2 (43.0–71.0); No. 2 primary: 11.2 (5.0–17.0), equal to No. 3 primary (± 1.0); in most nestlings only down clumps are found on the head; no down on the distal portion of the wing (in single individuals – on the whole wing); feathers on the back: up to 10.0; white feathers found on belly, breast and flanks: up to 20.0; on the head feather cylinders or feathers are present: up to 3.0; tail feathers appear (in single individuals); nestlings covered with white powder derived from feather cylinders which desquamate.

15–17	Body weight: 110.6 (84.0–133.0); wing: 69.6 (57.0–81.0); No 2 primary: 19.0 (8.0–24.0), equal to No. 3 primary (± 0.5); no down on the head, or only down clumps present; distal part of wing or whole wing devoid of down; underside of body without down (except the tract along the sternum crest); feathers on the back: about 10.0; feathers on the underside as in adults; head top covered with feathers, under lower mandible and on the sides of the head feather cylinders or little feathers are found; above the eye a white eye-brow appears; white-edged scapulars: up to 20.0; tail feathers: up to 10; egg tooth absent; feathers heavily powdered.
18–20	Body weight: 121.3 (99.5–142.0); wing: 79.8 (67.0–91.0); No. 2 primary: 25.6 (20.0–35.0), shorter than No. 3 primary; in most nestlings the head, wings and body underside (except a tract along the sternum crest) devoid of down; in some nestlings (50% on 20th day) down is present only on the rump; whole body covered with feathers, sometimes feather cylinders found, but then only under lower mandible; the eye-brow marked in almost all nestlings.
21–23	Body weight: 121.5 (96.0–141.0); wing: 88.8 (76.0–98.0); No. 2 primary: 34.0 (32.0–42.0), shorter than No. 3 primary; down only found on the rump (in single individuals also along the crest of the sternum); some nestlings (30% on 23rd day) entirely devoid of down; whole body in feathers; eye-brow clearly seen in all nestlings.
24–25	Body weight: 116.0 (93.0–142.0); wing: 95.0 (84.0–106.0); No. 2 primary: 40.0 (33.0–45.0), shorter than No. 3 primary; most nestlings (about 70%) without down; in others down clumps found on the rump, and traces of it in the anal region.
26–27	Body weight: 107.7 (88.0–135.0); wing: 98.7 (90.0–109.0); No. 2 primary: 44.0 (38.0–50.0). shorter than No. 3 primary; nearly all nestlings (80–100%) entirely devoid of down.

*Average dimensions are given with range of variation in brackets (body weight in grammes, linear measurements in millimetres).

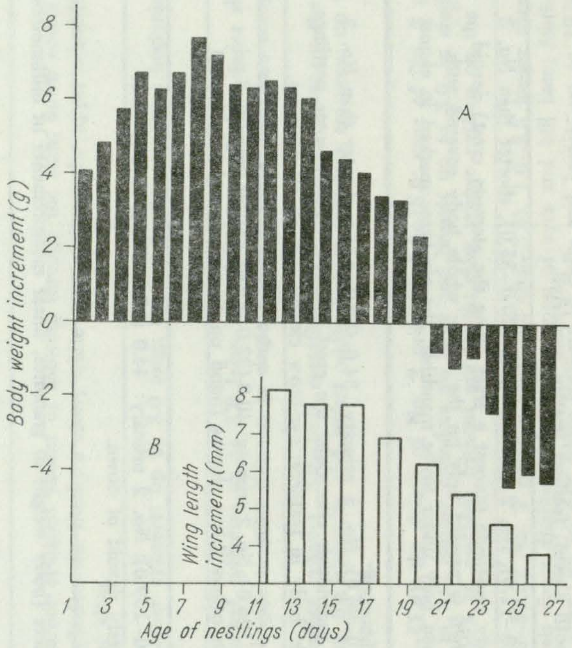

Fig. 3. Daily increase in body-weight (A) and two-days' growth in wing length (B) of little auk nestlings in two seasons, 1974 and 1975
Number of birds is given in Table I

3.2. COMPARISON OF THE GROWTH INDICES OF LITTLE AUK NESTLINGS WITH THOSE OF OTHER AUK SPECIES

For the purpose of interspecific comparisons, a number of indices have been calculated which describe the body-weight growth curve (Table III). The auk species selected for comparisons follow the same mode of development (semiprecocials), but differ by their body-weight.

In the course of its development a nestling (several days before the fledging) attains the maximum body-weight, greater than that of the nestlings leaving a breeding colony. In the least auklet the maximum body-weight is greater than the average weight of adult birds, whereas in other species it represents its fraction. The value of this fraction found for the nestlings of the little auk is the smallest (0.77). Values of similar order are attained by the nestlings of considerably larger birds of the genera *Fratecrula* and *Cerorhinca*, the adult body-weight of which amounts to 440–600 g (S e a l y 1973b). An analogous situation is found as regards the body-weight of young birds leaving a breeding colony, relative to that of adult birds. In this case, too, the value of the

Table III. Comparison of growth indices of little auk nestlings with those of other auk species[a]

Species	Asymptote A (g)	Average weight of adult birds B (g)	$\frac{A}{B}$ C	Peak weight of nestlings D (g)	$\frac{D}{B}\cdot 100$ (%)	Prefledging weight E (g)	$\frac{E}{B}\cdot 100$ (%)	Growth rate				Weight reduction		
								K^{b}	$\frac{KA}{4}$[c] ($g \cdot day^{-1}$)	$\frac{KC}{4}\cdot 100$[d] (per cent $\cdot day^{-1}$)	t_{10-90}[e] (days)	$D-E$ F (g)	$\frac{F}{B}\cdot 100$ (%)	$\frac{F}{D}\cdot 100$[f] (%)
Aethia pusilla (Pall.)	86.5	92.0	0.94	95.0	103.2	81.0	88.0	0.244	5.28	5.7	18.0	14.0	15.2	14.7
Plautus alle	126.0[g]	163.1	0.77	126.0[h]	77.3	109.8	67.3	0 256	7.90	4.9	17.2	16.2	9.9	12.9
Ptychoramphus aleuticus (Pall.)	152.0	167.0	0.91	153.0	91.6	150.0	89.0	0.150	5.70	3.4	29.3	3.0	1.8	2.0
Aethia cristatella (Pall.)	254.4	286.0	0.88	260.0	90.9	228.0	79.0	0.197	12.53	4.3	22.3	32.0	11.2	12.3

[a]Data concerning all species, except *P. alle*, have been taken from the paper by Sealy (1973b). [b]Calculated according to Ricklefs (1967), see the text. [c]Calculated according to Sealy (1973b), see the text. [d]Calculated according to Sealy (1973b), see the text. [e]Calculated according to Ricklefs (1967), see the text. [f]Except for *P. alle*, calculated on the basis of data from Sealy (1973b). [g]Asymptotic weight of little auk nestlings, calculated acc. to Ricklefs' (1967) method, appeared to be equal to peak weight. [h]The weight adopted was the average peak weight of little auk nestlings, attained regardless of the day of life.

fraction found for the little auk appears to be the smallest of all the values for the species compared, similar to that for *Fratercula* sp. and *Cerorhinca* sp. The two indices discusses above (*D* and *B*, and *E* and *B*, see Table III), indicate that in the end phases of their nest development juvenile little auks have the lowest, relatively, body-weight.

As measures of the growth rate the following indices were calculated: K, $\frac{KA}{4}$, $\frac{KC \cdot 100}{4}$, t_{10-90} (see Table III). K – calculated according to Ricklefs' (1967) method – is a constant describing the total growth rate, being useful in interspecific comparisons. The value of this constant, calculated for the little auk, is highest not only among the species compared, but also within the whole Alcidae family (several species have not yet been studied). This indicates the fastest total growth rate of the little auk nestlings. The two other indices are a combination of the growth constant (K), the asymptotic weight (A) and average body-weight of adult birds (B) (Cody 1973, Sealy 1973b). The former describes the average daily gain in nestling weight in grammes, the latter in per cent of body weight of adult birds. The value of $\frac{KA}{4}$ is essentially directly proportionate to the ultimate body size of a bird. An exception is *Ptychoramphus aleuticus*, a species with an incommensurably low growth rate (Table III). The value of $\frac{KC \,.\, 100}{4}$ is a measure of growth dependent on the A : B ratio, that is to say, the asymptotic weight to the body-weight of adult birds. The nestlings of the smallest-bodied species *Aethia pusilla* daily attain the highest percentage of the body-weight of adult birds. This results from a high total growth rate (K = 0.244) and a slight difference between the asymptotic weight and the body-weight of adult birds (C = 0.94). In spite of the highest growth constant (K = 0.256), found for the little auk, the value of the $\frac{KC \cdot 100}{4}$ index recorded for this species is slightly lower due mainly to a low asymptotic weight (C = 0.77). The last growth rate index (t_{10-90}) is the time (in days) needed by a nestling to attain from ten to ninety per cent of the asymptotic weight. This coefficient can be used in interspecific comparisons (Ricklefs 1967, Sealy 1973b). The lowest value of this coefficient is found for the little auk (17.2 days), which means that during this period the little auk nestlings gain in weight from 10 to 90% of the maximum weight (the asymptote). For all other auk species this period is longer.

Very typical, of almost all auk species, is a loss in body-weight preceding the fledging (Table III). The loss in weight, expressed in per cent of the body-weight of adult birds (*F* and *B*), is found to be highest in the least auklet, the least marked in the cassin's auklet, whereas in the crested auklet and the little auk it attains intermediate values. However, when this loss in weight is presented as a percentage of the maximum weight (*F* and *D*), similar values are obtained for all the three species (except *Ptychoramphus aleuticus*). In this way the loss in body-weight is related to the growth curve fo the nestlings, and becomes independent of the body size of a species. Though the little auk nestlings attain the lowest, relatively, maximum body-weight ($D : B$ = 77.3%), the prefledging loss in body-weight attains the same level as in the nestlings of species the maximum body-weight of which is similar to the body-weight of adult birds ($D : B$ = 90–103%) (Table III). An average daily decrease in body-weight in the little auk nestlings is 3.44 g.

3.3. FACTORS AFFECTING THE GROWTH OF NESTLINGS

3.3.1. Egg size

The one-egg clutches of the little auk considerably facilitate the observation of the individual development of the nestlings. The nestlings to be observed hatched from eggs divided into volume classes. Curves of growth in body-weight, wing length and in tarsus length of little auk nestlings are presented in Figure 4. Differences in body-weight and wing length of nestlings hatched from small and large eggs are shown in Figure 5. Untill 9th life day daily increments in weight were higher in groups of nestlings hatched

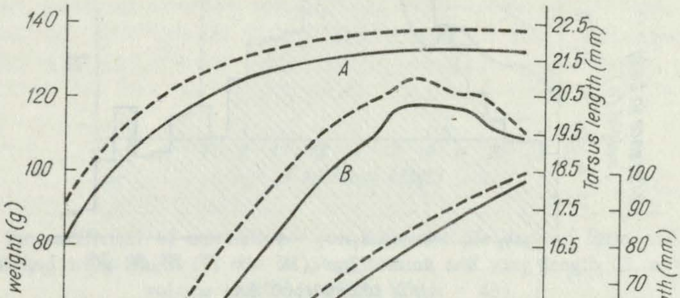

Fig. 4. Growth of tarsus length (A), body-weight (B) and of wing length (C) in little auk nestlings hatched from eggs of larger size (dashed line, in the case of A volume was over 30.0 cm^3, in the case of B and C it was over 31.0 cm^3) and of smaller size (continuous line, in the case of A egg volume was bellow 30.0 cm^3, in the case of B and C – below 28.0 cm^3)

Number of individuals in groups and on different developmental days varied between 15 and 29

from larger eggs. Because of this, the diffference in weight increased gradually. On 10th to 14th day daily weight increments in both nestling groups became equalized, and the difference did not change at this time. From 14th life day until the leaving of the colony by the nestlings the weight differences gradually disappeared owing to higher daily weight increments by the nestlings derived from smaller eggs.

The average body-weight for the whole developmental period (total daily weight gains for the nesting period divided by the number of days) of the groups of nestlings hatched from eggs differing in volume was found to vary. Nestlings hatched from the smallest eggs (V = 25.0 –27.9 cm^3) attained an average total weight of 80.4 g, those hatched from medium-sized eggs (V = 28.0–30.9 cm^3) attained an average weight of 85.9 g, and those from the largest volume eggs (V = 31.0–33.9 cm^3) attained the highest average total weight 89.7 g.

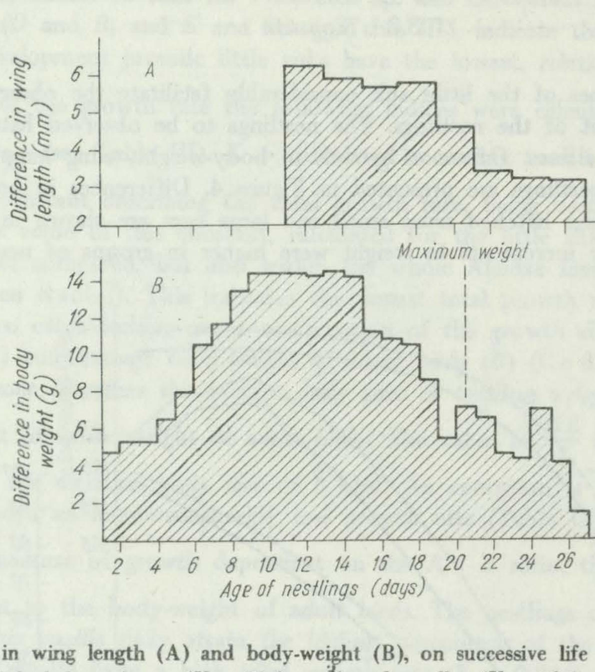

Fig. 5. Differences in wing length (A) and body-weight (B), on successive life days of little auk nestlings, hatched from larger (V = 31.0 cm^3) and smaller (V = 28.0 cm^3) eggs
Number of individuals as in Figure 4

Wing length differences, fairly considerable on 11–12th day (over 6 mm), later on decreased gradually (Fig. 5 A). The differences in tarsus length remained at the same level throughout the nestling stage.

A significant positive correlation has been found between egg volume and the average total body-weight of the nestlings ($r = 0.50 \pm 0.13$, $P < 0.001$), and between egg volume and the peak body- weight of the nestlings ($r = 0.40 \pm 0.15$, $P < 0.02$). Correlation coefficients have also been calculated for each day of nesting development of the nestlings, between egg volume and body-weight, egg volume and wing lenght, and between body-weight and wing length of the nestlings (Fig. 6). The highest values have been obtained for the correlation between the length of wing and the weight of the body. Initially (12–13th day), the value of the correlation coefficient exceeded 0.80, whereas in later phases it tended to decrease down to an insignificant level. On 18th day of a nestling's life (immediately before the attainment of the peak body-weight) a clear, rapid change in the value of the coefficient was seen. In the initial phase (12th day) the correlation between the volume of the egg and the length of the wing attained the value $r > 0.60$. During the next days this relationship gradually decreased (an insignificant rapid change was seen on the day of the attainment of the maximum body-weight), and from the 22nd day of the nestlings' life on it grew to attain the value $r = 0.67$ on the day preceding the leaving of the nest. Statistically significant differences ($P < 0.05$) have only been found between the values of the correlation coefficients for the days: 12 and 22, and 22 and 26. The degree of correlation between the body-weight of the chicks and the volume of their eggs showed a general tendency to decrease during the nesting stage. The variations in the value of *r*, seen in the initial stage of the nestling's life, are probably connected with the establishing of homoiothermy.

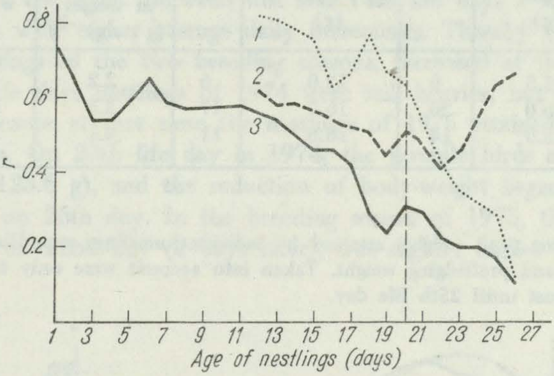

Fig. 6. Value of the coefficient of correlation *r* (on successive life days of little auk nestlings) between body-weight and wing length (1, $n = 21$), egg volume and wing length (2, $n = 21$), and egg volume and body-weight (3, $n = 45$)

The vertical dashed line denotes the average day on which the peak weight was attained

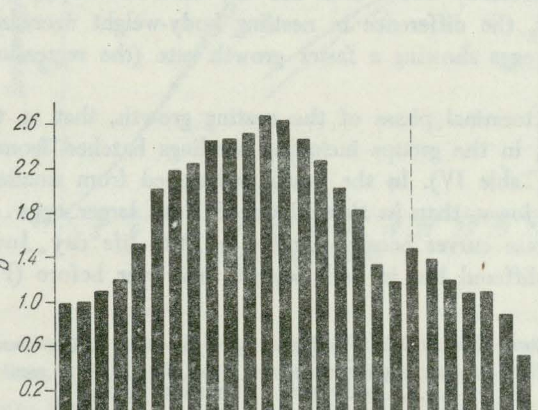

Fig. 7. Value of the coefficient of regression $b(b = r \cdot \frac{y}{x}$, x – egg volume, y – egg weight) on successive life days of little auk nestlings ($n = 45$)

The vertical dashed line denotes the average day on which the peak weight was attained

In Figure 7 the relationship between the size of the egg (V) and the increase in nestling body-weight has been presented in a different way. Shown in it are values of the regression coefficient *b* for the characteristics named above, for the particular days of development. The greater the value of the *b* coefficient, the steeper the course of the

Table IV. Prefledging body-weight reduction in little auk nestlings from eggs varying in size, in the breeding seasons of 1974 and 1975

Egg volume classes (cm^3)	Peak weight[a] (g)	N	Reduction in weight[b] (g)	N	Daily reduction in weight ($g \cdot day^{-1}$)	Relative to peak weight (%)	Relative to adult birds' weight (%)
25.0–28.0	121.5	6	12.0	6	2.2	9.9	7.4
28.0–31.0	126.0	20	16.7	17	3.3	13.2	10.2
31.0–34.0	128.0	14	18.8	11	4.1	14.7	11.5

[a]Calculated by averaging peak weights attained by individual nestlings regardless of life day. [b]Differences of peak weight and prefledging weight. Taken into account were only those nestlings which were under control at least until 25th life day.

regression line, which in this case indicates an increased difference in body-weight between the nestlings which hatched from smaller eggs and those that hatched from larger eggs During the first 12 days nestlings which had hatched from smaller. eggs grew more slowly, and as a result, the difference in nestling body-weight increased (the value of the regression coefficient increased). From 12th life day until the departure of the juvenile birds from the colony, the difference in nestling body-weight decreased gradually, chicks hatched from smaller eggs showing a faster growth rate (the regression coefficient decreased).

The course of the terminal phase of the nesting growth, that is, the prefledging decrease in body-weight, in the groups including nestlings hatched from various-sized eggs, was found to differ (Table IV). In the nestlings hatched from smaller eggs the rate of weight reduction was lower than in those hatched from larger eggs . As a result, the individual weight-increase curves became similar on 26th life day. Juvenile birds leaving the breeding colony differed less in body-weight than ever before (Fig. 4).

3.3.2. Body size of parent birds

Biometric measurements of parent bird pairs have been compared with the dimensions of the actual eggs and growth parameters of the nestlings hatched from these eggs. For the comparisons average measurements for both birds of each breeding pair were used, because, among other things, of the impossibility to sex the birds (lack of sexual dimorphism).

A significant positive correlation has been found between the average wing length of the parent birds and the volume of the eggs laid by the females belonging to different pairs ($r = 0.45 \pm 0.22$, $P < 0.05$). The maximum nestling body-weight was found to be positively correlated with the average body-weight of the parents ($r = 0.67 \pm 0.23$, $P < 0.02$).

3.3.3. Breeding season

In 1974 and 1975, the egg dimensions did not differ in a statistically significant way. The growth of the nestlings in the two years was similar, but there were certain, fairly characteristic differences (Fig. 8). Up to 6th life day the weight growth rate was in both years almost the same. Between 6th and 14th life days a faster nestling was recorded for 1974, with higher average daily increments. Thereby the weight differences, dividing the nestlings of the two breeding seasons, increased at that time. Between 14th and 20th life days nestlings of 1974 were still heavier, but the difference decreased gradually, because at that time the nestlings of 1975 attained higher average daily weight increments. On 20th life day in 1974, the juvenile birds attained the peak weight (on the average 123.6 g), and the reduction of body-weight began down to the level of 107.5 g reached on 26th day. In the breeding season of 1975, the maximum body-weight, attained on 22nd day (2 days later), was slightly higher (on the average 125.0 g).

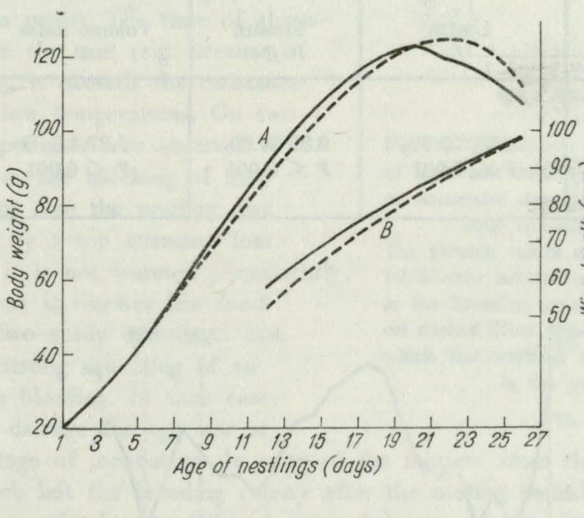

Fig. 8. Growth of body-weight (A) and wing length (B) of little auk nestlings in the breeding season of 1974 (continuous lines, n = 21–35), and in the breeding season of 1975 (dashed lines, n = 19–23)

In 1975, the rate of body-weight decrease was slower. On 26th day the chicks weighed on an average 111.8 g. Wing length on successive days on the chicks' life was on the average also higher in 1974. The differences increased until 14th day whereafter they began to disappear gradually (Fig. 8).

3.3.4. Growth of nestlings originating from the same nest

Eggs laid in the same nests in the two breeding seasons showed a considerable similarity, of dimensions and shape (Table V). Certain common features could also be seen in the growth of the nestlings from the same nests. A significant correlation has been found between the average total weights of the nestlings in the two years ($r = 0.64 \pm 0.25$, $P < 0.05$, $n = 22$), and between their maximum weights ($r = 0.53 \pm 0.26$, $P < 0.05$, $n = 24$). The correlation of the body-weights of these two groups of nestlings on individual days of their nestling development has been presented in Figure 9. The correlation coefficient (r) decreased for the first 3 life days, which may have been connected with the establishing of homoiothermy. Subsequently, its value grew to attain the maximum level on 11th day, then it decreased again, gradually, until 17th day. In the last phase of the nesting development it showed clear variations connected with the attainment of the peak weights on different days of the nestlings' life in the two seasons.

Table V. Relationship between the size and shape of little auk eggs laid in the same nests in the breeding season of 1974 and in the breeding season of 1975

	Length L	Breadth B	Volume index V	Relative breadth J
Correlation coefficient (r) ± standard error	0.89 ± 0.09 $P < 0.001$	0.88 ± 0.09 $P < 0.001$	0.87 ± 0.09 $P < 0.001$	0.89 ± 0.09 $P < 0.001$

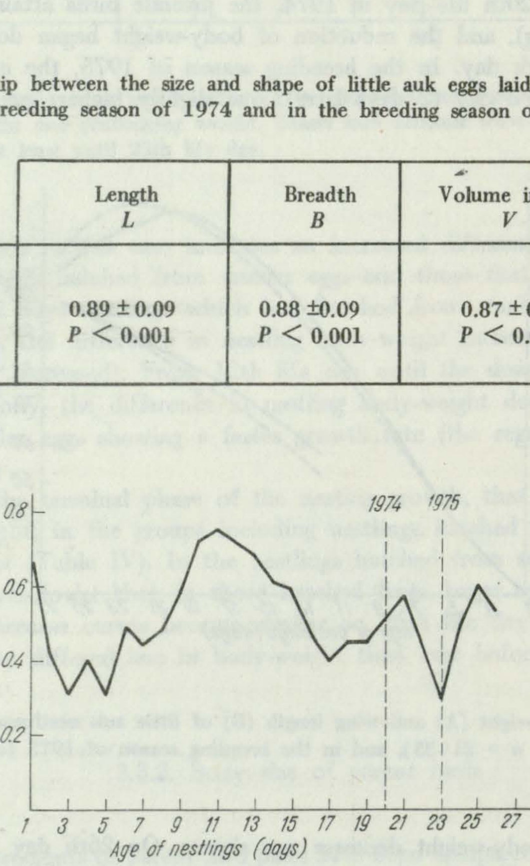

Fig. 9. Value of the coefficient of correlation r (on successive life days) between body-weight of little auk nestlings from the same nests in the breeding seasons of 1974 and 1975 ($n = 11$) The vertical dashed lines denote the average day on which the nestlings attained the peak weight in the given season

Nestlings which hatched in the same nests were on an average smaller in 1975 than in 1974. Figure 10 shows the differences in body-weight observed during the nesting development. The differences increased until 15th life day whereafter they gradually disappeared until 22nd day when the nestlings of the 1975 breeding season had for several days higher average body weights. Immediately before their departure from the colony, young auks of the two breeding seasons did not virtually differ in body-weight.

In 1974, the nestlings attained their peak body-weight (128.4 g) on 20th developmental day, whereas in 1975, the maximum weight was attained 3 days later, and amounted to 123.7 g.

3.3.5. Chance factors

During the field studies the author was able to observe several accidents directly affecting the development of embryos and chicks. If one of the birds of a breeding pair gets lost during incubation, the embryo will die, even if the other bird continues incubating (Stempniewicz – in press). The time of absence of the bird from the nest (e.g. because of feeding) is too long, it exceeds the resistance of the embryo to low temperatures. On two occasions the disappearance was observed of one parent bird after the hatching of the nestling. Also in this case the nestling dies. Its death is caused by a too excessive loss of energy, because it is not warmed permanently, and at the same time it receives less food.

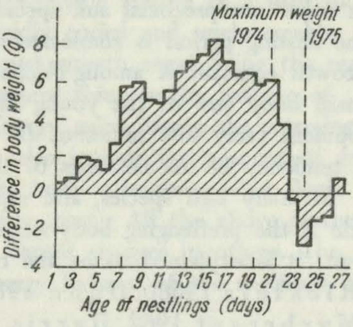

Fig. 10. Differences in average body-weight of little auk nestlings from the same nests, on successive days in the two breeding seasons considered (n = 11)

The average values of weight attained in 1975 were subtracted from those attained in the breeding season of 1974. The vertical dashed lines denote the average day on which the nestlings attained the peak weight in the given season

In each of the two study seasons, a case was recorded of a strong squeezing of an egg, connected with bleeding. In each case at the time of the damage the egg was at a fairly advanced stage of incubation. In spite of the injuries, from these eggs normal chicks hatched which left the breeding colony after the nesting period. Their growth and development were clearly retarded and proceeded more slowly. On 5th life day the body-weight of these nestlings represented only 35% of the average body-weight of normally growing nestlings. At the later stages this disproportion gradually decreased, and on 10th day the nestlings attained about 45% of the average weight, and on 15th day as much as about 60%. The two nestlings hatched from the damaged eggs attained their maximum body-weight on 21st and 22nd days, and the value of the weight was similar to the minimum weight attained by nestlings developing normally. Very characteristically, in these two nestlings there was no weight decrease, or only a slight one in the later growth phase. Because of this, the body-weight of each of the two nestlings was at the time of their departure from the colony similar to the average weight of other nestlings. One of the nestlings disappeared from the nest on 25th life day, the other one only on 33rd day. The stages of down disapearance, plumage development and the growth in length of the wing were clearly retarded and corresponded to those of the nestlings about 6 days younger.

4. DISCUSSION

4.1. SPECIFICITY OF THE GROWTH OF LITTLE AUK NESTLINGS

One of the most important adaptations of the little auk to living in the high-arctic zone (a short polar summer, snow staying for a long time on the slopes where the breeding colonies are found) is the shortening of the breeding season. Both the time of egg incubation and the nesting period of the nestlings of the little auk are shorter than in other semiprecocial auk species (S t e m p n i e w i c z – in press). The shortening of the nesting period is connected with the high growth rate (the highest value of the growth constant K among Alcidae, and the lowest value of t_{10-90}) and the relatively small body size of the young little auks in the terminal phases of their nesting development (very low values of $D : B$ and $E : B$, see Table III). This is an expression of a tendency in the nestlings of the little auk towards precocity.

In many bird species, and especially in Procellariformes and Alcidae, very characteristic is the prefledging body-weight recession. The causes of this phenomenon are different. It is explained to be the result of maturation and a loss of water by the tissues (R i c k l e f s 1968b, D u n n 1975), of a limitation or cessation of feeding by parents (M y r b e r g e t 1962, H a r r i s 1966), or of an increased mobility of the juvenile birds in this period (S e a l y 1973b). All these causes probably act simultaneously, though in an individual species one of the causes may play a decisive role (e.g. the prefledging starvation in the manx shearwater, *Puffinus puffinus* Brünn.; H a r r i s 1966).

In juvenile little auks an important factor is the increased motoric activity (wing exercising) in the period preceding the fledging. This is followed by an increased demand for food which is supplied by the parents with increasing difficulty. Though the daily food ration supplied to the nestlings increases with the passing of the nesting period (N o r d e r h a u g 1970), in the young little auks there probably occurs a food deficit in the last days of their stay in the breeding colony. In the stomachs of 17 juvenile birds which were sectioned (on 26th life day) (L. Stempniewicz – unpublished data) no trace of food was found, but only slight amounts of dry mosses, lichens and egg shell fragments. The presence in the alimentary tract of these substances, non-edible to the little auk, may be interpreted as a sign of unquenched hunger (it would be difficult to accept an explanation that they function as a "quern" grinding the plankton). An increasing food deficit is maybe one of the stimuli causing the departure of the young birds from a breeding colony.

Regardless of the causes, the prefledging decrease in body-weight entails a number of consequences which are very important to the life of the juvenile birds. Due to the decrease in body-weight there occurs a decrease in the load of the wings and feet and an increase in the relative weight of the heart and other inner organs. As a result, the physiological efficiency of the whole body is improved. About 23rd life day the little auk nestlings attain the best proportions, relative to the adult birds, of body size (except the tarsus; Fig. 1). It is on that day that the leaving of the colony begins (S t e m p n i e w i c z – in press). In the later developmental days the body proportions of the young birds change, but the changes lead towards an improvement of the locomotory capabilities. The body-weight is reduced, the wing and the tail grow considerably in size, the bill increases slightly, while the length of the tarsus remains unchanged (Fig. 1). All these morphological changes are of fundamental importance to the juvenile little auks that leave a breeding colony. It is to be the first flight in their life the role of which is to a large extent decisive in their survival until reproductive age (Stempniewicz – in press).

4.2. FACTORS AFFECTING THE GROWTH OF NESTLINGS

The growth and development of nestlings are a characteristic feature of a bird species (Ricklefs 1973). This does not mean that it is rigidly coded and unchangeable. It is subject to the influence of very many factors, the real growth curve being the resultant of the action of all these factors. The most important thing is the balance of energy expenditure and gains in the nestling period. Energy gains means the warming and feeding of the nestlings by the parents. The gains also include the amount of energy brought out of the egg. Energy expenditure includes body subsistence cost (basic metabolism, motoric activity, growth and thermoregulation cost). All the above factors are closely interrelated, and a change in one of them causes changes in others. The amount of information on the factors affecting the energy balance of the nestlings during their growth varies.

The rate of feeding, the effect of which on the growth of the nestlings is very clear, is connected first of all with the amount of food available to the parents in the given period (Perrins 1965, Lack 1967, Le Croy and Collins 1972, Visser 1974, Andersson 1976 and others). The distance between a breeding colony and the feeding areas, current weather conditions and the presence of predators which harass the birds cyrrying food also affect the frequency of the feeding of the nestings, and thereby the rate of their growth (Cody 1973, Sealy 1973b, Birkhead 1976 and others). The weather conditions prevailing in a particular season very often have an important effect on the availability of the food supplies, and indirectly on the growth of the nestlings, as well as directly on the rate of heat energy expenditure by the nestlings (Dyrcz 1974, Le Croy and Le Croy 1974, Visser 1974, Dunn 1975, White, Robertson and Ricklefs 1976 and others).

Parent birds usually supply less food than the nestlings are able to eat and efficiently utilize. This is indicated by the supplementary-feeding experiments on young rhinoceros auklets, *Cerorhinca monocerata* (Pall.) (Cody 1973), in which a clear acceleration of the growth rate of the nestlings could be seen. On the other hand, in years in which food supplies are not a limiting factor, many bird species are able to rear a larger number of offspring. This applies also to species with a fixed number of eggs in a clutch, as has been proved by results of Corkhill's (1973) experiments on the puffin, *Fratercula arctica* (L.), and Lloyd's (1977) experiments on the razorbill, *Alca torda* (L.). In double broods, of both the puffin and the razorbill, some nestlings were fed by the adult birds until the fledging time. However, their growth rate was clearly lower than normal.

Various-sized eggs (within the same species) contain a varying amount of energetic material. Lachlan (1968, after Schifferli 1973) has demonstrated that the eggs of the blue tit, *Parus caeruleus* L., contain more proteins and carbohydrates. Thus the size of an egg affects the growth of the chick that has hatched from it. This relationship has been confirmed by sporadic studies (Skoglund, Seeger and Ringrose 1952, Schifferli 1973, Myrberget 1977). The effect has also been demonstrated of the egg size on the mortality of the nestlings of the herring gull, *Larus argentatus* Pont., in the first week of their life (Parsons 1970), and of the nestlings of the great tit, *Parus major* (L.) in late broods (Schifferli 1973). The results of the present study have also confirmed a significant effect of the egg size on the growth and development of the nestlings of the little auk.

According to Schifferli (1973), there may be two theoretical causes of a faster, at least at the beginning, growth of nestlings hatched from bigger eggs. These nestlings may have either a bigger body size (not only weight) already on hatching, or larger supplies of yolk. Romanoff (1967, after Schifferli 1973) did not find any significant correlation between the weight of newly hatched chickens and the weight of the yolk reserve. Parsons (1970) found a high positive correlation between the volume of the eggs and the content of fats in the bodies of newly hatched nestlings of the herring gull. Newly hatched nestlings of the little auk, derived from larger-volume eggs, were found to have a larger body-weight and a bigger body size, as expressed by the length of the tarsus (Figs. 4–6). On the basis of these data it may be presumed that already in the period preceding the hatching the reserve yolk is utilized in a varying degree for building the embryo's body. Maybe, in larger eggs more yolk is destined for this purpose, and consequently the newly hatched chick is of a bigger body size. This interpretation explains the seemingly contradictory results obtained by Romanoff (1967, after Schifferli 1973) and Parsons (1970).

The laying of eggs varying in size by females of the same species may be connected with the amount of food available in the period preceding the egg laying (Perrins 1965, Lack 1967, Andersson 1976). After the courtship and copulation period many sea bird species laying relatively large eggs (mainly Procellariiformes, and among Alcidae the ancient murrelet, *Synthliboramphus antiquus* (Gm.)) leave for their feeding areas, where they spend the so-called honeymoon after which they return to the breeding colony and the females lay eggs (Ashmole 1971, Sealy 1975c). In many bird species the effect has been found of the date of egg laying in a season on the size of the eggs, which may be related to the seasonally varied food basis (Coulson 1963, Bayes, Dawson and Potts 1964, Barth 1967/68, Coulson, Potts and Horobin 1969, Perrins 1970, Pikula 1971, Väisänen et al. 1972, Murton, Westwood and Isaacson 1974). The body size of the females, often connected with the latitude, age of the birds and with the food situation in the environment, also affects the size of the eggs laid (Coulson 1963, Jenkins, Watson and Miller 1963, Myrberget 1977). In the present study a correlation has been demonstrated between the average wing length of the parent birds and the egg volume of the little auks. The clutch size, too, is reflected in the egg dimensions, although in this case the results obtained by different authors studying different bird species often vary (Kendeigh, Kramer and Hammerstrom 1956, Jenkins, Watson and Miller 1963, Bezzel and Schwarzenbach 1968, Winkel 1970, Pikula 1971, Myrberget 1977).

The effect of the genetic factor, manifested by the laying of similar eggs by the same female in successive breeding seasons, has been found for several bird species (Ratcliffe 1962, Coulson 1963, Myrberget 1977). Little auks show an attachment to nesting crevices, as they use the same crevices from year to year (Norderhaug 1968). Following this statement, the dimensions and shapes were compared of eggs laid in two seasons in the same nests. A very high similarity has been found, confirming the results of the above authors (Table V). Nestlings hatched from similar eggs grow and develop in a similar way, at least in the initial period (Fig. 9).

Egg size is related to the age, and thereby to the breeding experience of the female. The egg volume generally tends to grow with the age of the female, at least for the first several years of the female's life (Romanoff and Romanoff 1949, Richdale 1955, Preston 1958, Coulson 1963, Sternberg and Winkel 1970, Myrberget 1977). All the above-named factors act simultaneously, and it is difficult to consider them separately.

Apart from the rate of feeding by parents, meteorological conditions and egg size, the growth and development of the nestlings are also affected by chance factors (e.g. crashing of an egg). The course of the growth curve is the outcome of the resultant action of the genetic factors, peculiar to the species, and the ecological factors, described above, independent of the bird species. The intensity of action of the particular factors varies, being different at each of the stages of the nest development of the nestlings. The egg size exerts the strongest influence in the initial growth phase of the little auk nestlings, and tends to decrease with the age of the nestlings (Figs. 6, 7). Similar results have been obtained by Schifferli (1973) for the nestlings of the great tit, and by Skoglund, Seeger and Ringrose (1952) for the chickens. Other ecological factors, such as weather conditions or the feeding rate which depends on the availability of food in a given season, activity of the parents, intrabrood competition, etc., may affect the nestlings' growth curve for a longer time, but their effect as a rule clearly weakens towards the end of the nestling period, prior to the fledging. It seems that at that time the genetic factors take the lead, muffle the effect of ecological factors, and at the final stage of the nestlings' growth a tendency is observed towards a uniform body size, characteristic of the species.

Little auk nestlings hatched in different seasons from eggs differing in size, or damaged, attained a similar body size at the time of their departure from their breeding colony. Nestlings hatched from smaller or damaged eggs attained a body size similar to an average body size, owing to a relatively smaller prefledging weight reduction and an elongation of the nesting period (Table IV).

In many papers dealing with the growth of nestlings of different bird species data can be found confirming the tendency towards an equalized body size among young birds in the period preceding the fledging. Schreiber (1976) has not found any statistically significant differences in the body size of juvenile brown pelicans, *Pelecanus occidentalis* (L.), leaving the nests. The pelicans he studied were from broods of different sizes, hatched in different sequence.

In the nestlings of the common tern, *Sterna hirundo* L. (especially those hatched from the third egg), a reverse relationship was found between the hatching weight and the fledging age of the juvenile birds (Le Croy and Le Croy 1974). This means that nestlings which are initially smaller and grow more slowly leave their nests at a later time, because they develop a longer time, and for this reason they differ less by their body size from other individuals. Statistically significant differences in body-weight and wing length of the nestlings of the common tern, in the two seasons compared, could be seen on 1–7th days (weight) and on 4–14th days (wing). With the passing of the nestling period these differences disappear (Le Croy and Le Croy 1974).

V i s s e r (1974) has found a gradual disappearance of body size differences and a lowering of the variation coefficient in the nestlings of the coot, *Fulica atra* L., hatched in different seasons, in early and late broods of the same season, and in broods varying in size. The author's explanation that this phenomenon was the result of a higher mortality of those nestlings the growth of which proceeded in worse conditions, due to which the range of variation in body size in older age classes was smaller, does not seem to be satisfactory. Moreover, in a season which was very favourable for the coots, the author found a higher nestling growth rate and acceleration of the fledging.

For nestlings of experimental twin broods of the puffin and razorbill a slower, relative to the average, growth rate was found, and a marked elongation of the nesting period (C o r k h i l l 1973, L l o y d 1977).

In the nestlings of the great tit, hatched from large and small eggs, body-weight differences which were considerable at the early stages, were found to have disappeared before fledging (S c h i f f e r l i 1973). A shortening of the chick stage was found in the late broods of the great tit (G i b b 1950).In Wytham Wood these broods are charecterized by larger, on an average, egg dimensions (P e r r i n s 1970).

According to R i c k l e f s (1973), nestling growth proceeds within rather narrow limits determined by the adult body size of the particular species, and the mode of development. S c h r e i b e r (1976) is of the opinion that when the growth falls below the lower limit, the nestling dies. It must be added here that the width of these limits depends on the nestlings' age, and in the period preceding the fledging it shows a tendency to decrease. At the fledging time the body size of juvenile birds appears to be rather clearly species-determined and more stable than the length of the nesting period. Little auk nestlings, the development of which is poor (hatched from smaller eggs, or poorly fed), attain a fledging body size similar to the average, owing to an elongation of the chick stage and to a markedly lower prefledging body-weight reduction (or even a lack of this reduction). Because of this, they are in a worse situation at the time of leaving the colony when the pressure of predators is strongest (S t e m p n i e w i c z – in press), since their physiological capacity in lower (e.g. lower relative heart weight) and so are the indices of their motoric system (smaller relative area of the wings and a higher load to them). Apart from this, eggs which are on an average smaller are laid in the breeding colony at the earliest and the latest, thus the nestlings hatched from them miss the peak departure from the breeding colony (S t e m p n i e w i c z – in press). Consequently, these nestlings are less likely to reach the sea and start an independent life there; and thereby to survive until the reproductive age.

It may be presumed that this selective mechanism applies not only to the little auks, but is of a more general importance.

5. SUMMARY

The growth of the nestlings of the little auk proceeds in a typical way, according to the precocial mode of development (Figs. 1, 2). The peak body-weight, usually attained on 20th life day, represents 77.3% of the body-weight of adult birds (Table I, Fig. 1). Presented in Table II are different developmental stages.

When compared with other semiprecocial auk species, the nestlings of the little auk show the fastest growth rate (K = 0.256), a shortened nesting period (t_{10-90} = 17.2 days), and a very low body-weight at fledging ($\frac{E}{B} \cdot 100 = 67.3\%$) (Table III). This is the expresssion of an evolutional ten-

dency of the species towards precocity which is a form of adaptation to reproduction in the high-arctic zone. The marked prefledging reduction in body-weight (Tables I, III) improves the locomotory and physiological capacity of the juvenile birds leaving a breeding colony.

The growth and development of the nestlings are significantly influenced by the size of the eggs connected with the body size of the parent birds (Figs. 4–7, Table IV), the breeding season (Fig. 8) and chance factors. All these factors have the strongest effect at the initial stage of development of the nestlings. This effect markedly decreases in the period preceding the leaving of the breeding colony by the juvenile birds. At that time the differences in the nestling body size tend to disappear, and the body of the nestlings tends to attain a size peculiar to the species (Figs. 4–8, 10). This is effected via changes in the length of the nesting period and in the course of the growth as indicated by the growth curves for individual nestlings (there is a change in the magnitude of the prefledging body-weight reduction).

6. POLISH SUMMARY

Wzrost piskląt traczyka lodowego przebiega typowo, zgodnie z półzagniazdownikowym modelem rozwoju (rys. 1, 2). Ciężar maksymalny, osiągany przeciętnie w 20 dniu życia stanowi 77,3% ciężaru ciała ptaków dorosłych (tab. I, rys. 1). Stadia rozwojowe piskląt traczyka lodowego przedstawia tab. II.

W porównaniu z innymi półzagniazdownikowymi gatunkami alek pisklęta traczyka lodowego charakteryzują się najwyższym tempem wzrostu ($K = 0{,}256$), skróceniem okresu gniazdowego (t_{10-90} = 17,2 dnia) i bardzo niskim ciężarem ciała przy wylocie $\left(\frac{E}{B} \cdot 100 = 67{,}3\%\right)$ (tab. III). Jest to wyraz ewolucyjnej tendencji gatunku do zagniazdowości, będącej formą adaptacji do reprodukcji w strefie wysokoarktycznej.

Wyraźny, przedwylotowy spadek ciężaru ciała (tab. I, III) wpływa na wzrost możliwości lokomotorycznych i wydolności fizjologicznej młodych ptaków opuszczających kolonię lęgową.

Istotny wpływ na wzrost i rozwój piskląt ma wielkość jaj związana z rozmiarami ciała ptaków rodzicielskich (rys. 4–7, tab. IV), sezon lęgowy (rys. 8) i czynniki przypadkowe. Wszystkie te czynniki oddziałują najsilniej w początkowym okresie rozwoju piskląt. Przed opuszczeniem kolonii lęgowej ich znaczenie wyraźnie słabnie. W okresie tym obserwuje się tendencję do zaniku różnic w rozmiarach ciała piskląt i do osiągania rozmiarów specyficznych dla gatunku (rys. 4–8, 10). Odbywa się to kosztem zmian w długości okresu gniazdowego i w przebiegu krzywej wzrostu poszczególnych piskląt (zmienia się wielkość przedwylotowego spadku ciężaru ciała).

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