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The diet of penguins on King George Island, South Shetland Islands

[With 22 text-figs. and Pl. XII—XIII]

Pokarm pingwinów na Wyspie Króla Jerzego, Szetlandy Południowe

Abstract. Young Gentoo penguins *Pygoscelis papua* and Chinstrap penguins *P. antarctica* received food twice a day and Adélie penguins *P. adeliae* once. The basic food of chicks consisted of krill and that of adult birds of krill and fish. In periods when *Euphausia* was not easily available some differences appeared in food composition between sympatric species of the genus *Pygoscelis*. They resulted not only from the morhpo-ecological predispositions of the birds but also from the different feeding grounds and circadian rhythms. The feeding areas of Gentoo and Chinstrap penguins were mostly situated at a distance of 5—15 km and those of Adélie penguins up to 40 km from the colony. The average weight of the daily food ration of adults was: Gentoos — 750—850 g, Chinstraps — 450—550 g, Adélies 550—650 g and Macaronis — 650—750 g. Young Gentoos received 55—1050 g of food in various periods of growth, Adélies 48—608 g and Chinstraps 43—764 g. An indirect influence of food on the survival of chicks was exerted by the selective pressure of *Stercorarius skua lonnbergi* in relation to the chicks of lower body weights.

CONTENTS

I. INTRODUCTION

In the last thirty years distinct changes have been observed in the distribution and numbers of birds in the Antarctic regions (Conroy, 1975). Sladen (1964) suggested earlier that these changes had been caused by a decrease in the number of main krill-eaters, i. e. cetaceans. Owing to the intensive exploration of the animal kingdom in this zoogeographical region, it is essential to get exactly to know particular links of the food chain. Carrick & Ingham (1967) preliminarily recapitulated the studies on food composition in birds occurring in the Antarctic up to 1966, Ainley & Prevost (1976), Prevost (1976) and Mougin & Prevost (1980) made initial analyses of the role of birds in the biocenosis of the Southern Ocean on the basis of theoretical considerations, and Everson (1977) made an attempt to establish food interrelations of the whole biocenosis. This last study (Everson, 1977) was also carried out on the basis of theoretical calculations.

Penguins constitute the most numerous and at the same time best known group of Antarctic birds, but a survey of the literature concerning their diet (Volkman et all., 1982) has shown that the information in this respect is unsatisfactory. This state of affairs prompted the resumption of the present topic. The basic objective of this work was the determination of food composition, weight of daily rations and feeding grounds.

II. STUDY AREA AND METHOD

I carried out my study chiefly in the region of Admiralty Bay on King George Island (62°09′ S, 58°28′ W) in colonies situated in the proximity of Thomas Point, Llano Point, Demay Point, Uchatka (Fur Seal) Point and Chabrier Rock. I collected supplementary material also at Ardley I., Stranger Point, Lions Rump, Turret Point, Three Sisters Point, North Foreland and Stigant Point (Fig. 1). The distribution of some colonies and their specific composition and size are described by Croxall & Kirkwood (1979) and Jabłoński (1984, in press a). I continued my study from 5 December 1978 to 16 February 1979 and from 10 December 1979 to 14 March 1981.

Daily foraging activities of adult penguins in this area have been discussed in another paper (Jabłoński, in press b). I determined the circadian rhythm of feeding on the basis of observations of banded specimens carried out round the clock. The frequency of feeding in successive hours was recorded during

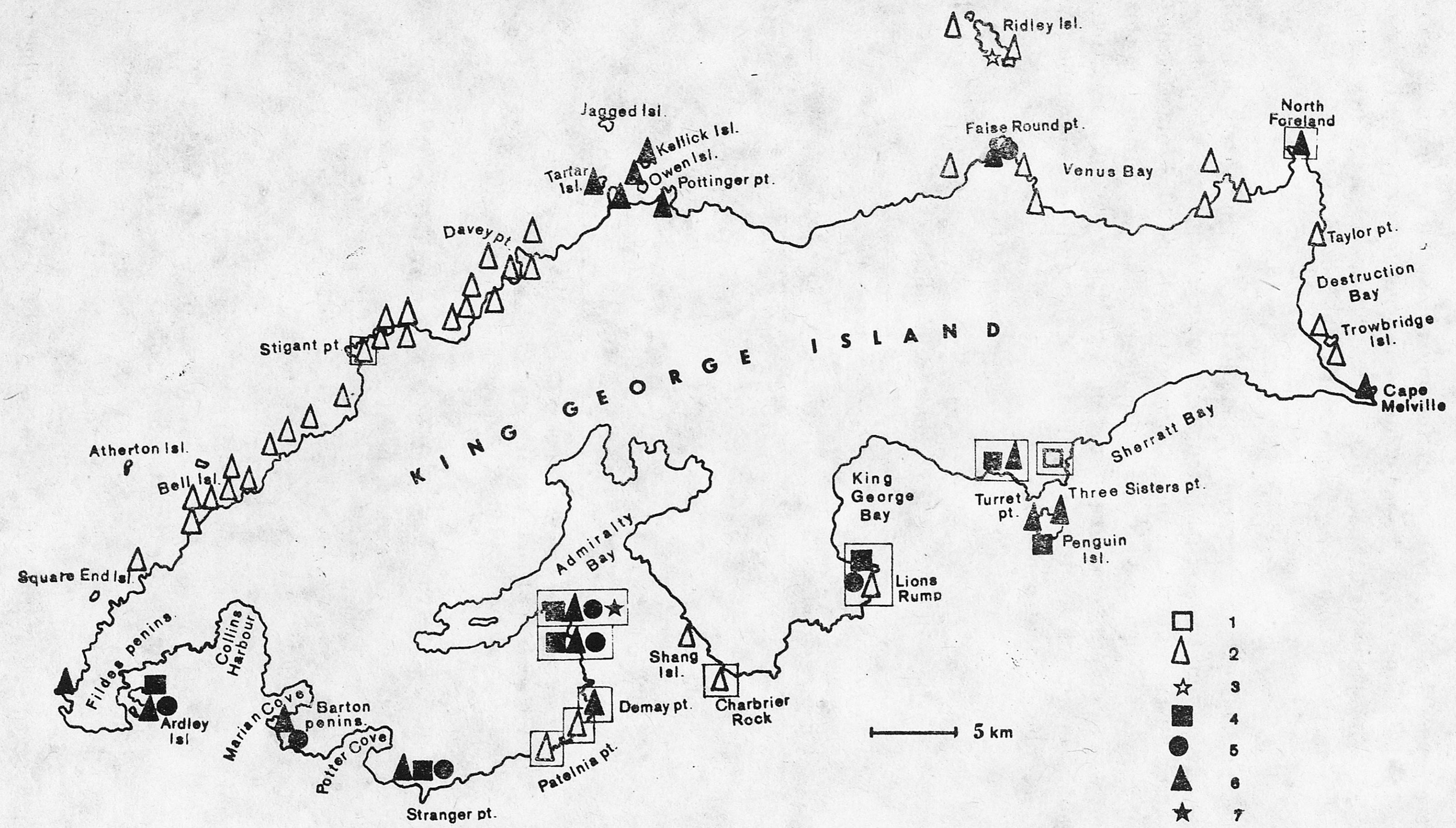


Fig. 1. The distribution of penguins colonies on King George Island Colonies that have not been reported in literature: 1 — Adélie, 2 — Chinstrap, 3 — Macaroni 4—7 — colonies described by CROXALL and KIRKWOOD (1979) and JABŁOŃSKI (1980) and checked by me in 1978—1981: 4 — Gentoo penguins, 5 — Adélie penguins, 6 — Chinstrap penguins, 7 — Macaroni penguins. Frames indicate the colonies in which food samples were taken

these observations. The total number of feedings of a chick over a 24-hour period in particular stages of stay in the colony was regarded as 100%. I distinguished the following periods in the life of chicks: 1. chicks fed in the nest territory (they stay in the nests and in their parents' territory) and 2. chicks fed outside the nest territory: a) before the beginning of the moult and b) during the moult.

I studied the food of adult penguins on birds that, having eaten their fill and having arrived from the sea, gathered together in groups at some distance from the colony. In the nursing period such groups included also some banded unsuccessful breeders which came from the same colony. The purpose of this investigation was to determine the composition of food, the weight proportions of its particular constituents and the weight of food falling to one specimen per day in various phenological periods.

Table I

Rate of action of emetic in adult Adélie penguins

Onset of vomiting in minutes after administration of emetic	Vomiting birds	
	Number	per cent
5<	26	18.0
6—10	72	50.0
11—15	29	20.1
16—20	13	9.0
21—25	3	2,1
25>	1 *	0.7

* Last check-up made after a loose of 40 min.; no vomiting reflex observed in 31 birds or 17,9% up to that time (100% = = 175 birds checked up)

I examined stomach contants using materials a) removed from the stomachs of killed birds, b) obtained from specimens by washing out their stomachs, and c) vomited by birds which had received emetic (8—10 cm^3 of 1% ammonium tartrate). Out of the 175 penguins that had been given emetic, 144 vomited (Table I). Materials obtained by these methods were used to evaluate the degree of specialization of particular birds with regard to food and to estimate the weight proportions of various food constituents. I preserved the food gathered, as did Emison (1968), first in 8% formaldehyde and, prior to its laboratory analyses, in 70% alcohol. I am aware that as a result of storage of the *Euphausiacea* in preservatives they shrank, but the length measurements obtained on them were comparable with the data given by other authors.

In the 1978/1979 season I estimated the food weight first on the basis of stomach analyses of the birds killed and next I applied the washing-out of

Table II

Representativeness of food samples gathered from Adélie penguins by the method of stomach-wash

Food, in g			Error of sample	
Washed out	Left in stomach	Total (100%)	in g	%
795	20	815	20	2.45
820	28	848	28	3.30
615	27	642	27	4.21
264	12	276	12	4.35
287	5	292	5	1.71
569	19	588	19	3.23
732	9	741	9	1.21
681	11	692	11	1.59
698	10	708	10	1.41
704	21	725	21	2.97
692	6	698	6	0.86
719	19	738	19	2.57
835	10	845	10	1.18

stomachs. The reliability of this method was checked on 13 Adélie penguins (*Pygoscelis adeliae* (Hombron et Jacquinot 1841) — Table II). It permitted a regular study of selected specimens, but was very laborious. For this reason, in following years, that is in 1979—1981, I estimated the amount of food by weighing banded specimens before they swam out to sea and immediately after their return. I verified this method on 26 Adélie penguins. The error in the food weight estimated as the difference between the body weights measured before the birds swam out to sea and after their return from the foraging areas compared with the actual weight of food determined after the killing of the bird, ranged from 0.5 to 3.7%. As the representativeness of the method by washing out the stomachs of birds was charged with an error of 0.86—4.35%, I assumed that the results obtained in 1978—1981 were comparable. I realize that the birds that fed the young may have eaten less food than did the non-breeders. Food samples taken from clutches of two chicks more than 15 days old showed that the food brought by the adult birds was designed exclusively for their young. Being in the sea, the adult birds had therefore to get food for themselves, to digest it and next to fill their stomachs with food for their chicks. However, the question of the rate of digesting in penguins is hardly known so far. It seems to change considerably in particular seasons. Observations made on 21 Adélies showed that the birds that came out of the sea to moult still had 240—32 g of food after 19—32 hrs, in which it was possible to pick out and identify *Euphausia superba* Dana 1852. On the other hand, out of the 25 Adélies with chicks about 5 days old, only 6 had still 60—150 g of krill in their stomachs after 24 hrs. Between the 10th and the 15th day of life the young received only part of the food brought by the adults from the sea. In that period the time of digesting on land averaged from 1 hr 32 min. to 2 hrs 27 min. in particular species. In the Gentoo penguin *Pygoscelis papua* (Forster 1781) and the Chinstrap penguin *P. antarctica* (Forster 1781) there were, in addition, considerable differences in digestion between birds foraging in the morning and those gathering food in the evening (Table III). It is significant that before starting egg-laying Gentoos took 4—6 hrs to feed in the morning and only 2—4 hrs in the evening (Jabłoński, in press b). So great differences in the rate of digestion and in the time adult birds take to eat their fill suggest that, while nursing their young, they may first get food for themselves and only then for their offspring. In later periods non-breeders spent as much time feeding, whereas the breeding birds stayed at sea for 6—10 hrs.

The same method as for adult birds was used to take food samples from chicks over 15 days old. As regards chicks aged less than 15 days, a different method

Table III

Time of staying at sea and time of digestion on land in adult penguins in the period of nursing 10—15-day-old chicks

Species	Number of specimens examined	Time of staying at sea	Time of digestion on land (from return to nests to appearance of excrement without chitin scales)
Pygoscelis papua	38	setting off: in the morning 6—10 hrs ↓ in the evening: 12—14 hrs* 6—8 hrs (15—18 hrs)	1 hr 36 min.— 3 hrs 25 min.; 1 hr 45 min.— 7 hrs 03 min.; x = 2 hrs 05 min. (±11 min.)
Pygoscelis adeliae	45	14—20 hrs (6—10 hrs) **	1 hr 53 min.— 3 hrs 44 min.; x = 2 hrs 37 min. (±15 min.)
Pygoscelis antarctica	101	in the morning: 3—5 hrs ↓ in the evening: 10—13 hrs *** 6—8 hrs (17—18 hrs)	48 min.— 2 hrs 11 min.; 52 min.— 6 hrs 14 min. x = 1 hr 32 min. (±18 min.)

* About 9% of the specimens leaving for foraging grounds in the morning returned to the colony after 14—12 hrs; single specimens returned even after 15—18 hrs.

** In the period when chicks formed groups (so-called creches) 8—20% of parental birds returned to the colony after 6—10 hrs. In the pre-moulting period of adults some specimens returned even after 37—41 hrs.

*** About 11% of the specimens leaving for their foraging grounds in the morning returned to the colony after 10—13 hrs; single specimens returned even after 17—18 hrs.

had to be applied, because food, given them at long intervals, was glued together into a single pellet by means of mucus. This method consisted of a) placing a ring round the neck of a chick to obtain information about the size of one food ration (i. e. one pellet) and b) carrying out a 24-hour observation to record the daily number of feedings. Next the daily food ration was calculated by multiplying the mean size of a single ration by the number of feedings per day.

The daily weight proportions of particular food constituents were computed as follows: a) the weight of food falling to one specimen over a 24-hour period was assumed to be 100%, b) on the basis of the known percentage distribution of particular constituents their weights were calculated.

Observations concerning the range of penetration and the situation of feeding grounds were made from a boat, a fishing-cutter and a helicopter on birds marked with a red stripe at the base of a flipper. They consisted of recording the swimming speed of penguins travelling to and from their feeding grounds, about 10 km off the shore, and tracing their routes leading to these areas. Owing to our limited technical possibilities this investigation covered an area reaching 45—50 km into Bransfield Strait, between the promontories Llano Point and North Foreland. The swimming speed of penguins on the way to the feeding grounds and back was estimated on the basis of 10 observations made between Chabrier Rock and the region of the H. Arctowski Station.

III. RESULTS

1. The circadian feeding activity

About 50% of the Gentoo penguins set off for the feeding grounds early in the morning, i. e. from 5 to 7 a. m., local time. Both the birds rearing their off spring and the unsuccessful breeders as well as non-breeders left for the sea at that time. They returned from the feeding grounds between 9 a. m. and 1 p. m. Then the partners changed over at the nest and the bird that had been staying in the colony in the morning left to forage. Their returns to the nests concentrated around 5 p. m. This group included also 9% of the birds that had swum out in the morning. In the nursing period the 24-hour rhythm of adult Gentoos has therefore two peaks, which is due to the fact that both parents go foraging (JABŁOŃSKI, in press b). The 24-hour feeding activity of adult birds was also reflected by the distribution of chick-feeding frequencies (Fig. 2); 91% of chicks received food twice a day (i. e. from both parents). When the chicks began to go out of their parents' territory, they were given food mainly about 11 a.m. or from 6 to 7 p.m. (Fig. 2).

The 24-hour rhythm of Chinstrap penguins was also marked by two peaks of their abundance on land (JABŁOŃSKI, in press b). The morning departures from the colony occurred from 4 to 6 a.m. and the mass returns and feeding fell between 7 and 8 a.m. (Fig. 3). The other group of parental birds left for the sea from 1 to 3 p.m. and returned with food after 5 p.m. Also this group included 11% of birds that had left the colony in the morning. The intensest evening feeding occurred between 6 and 8 p.m. (Fig. 3). The evening returns to the colony took longer than did the morning ones because the distances between the colonies and feeding grounds differed in these groups (Admiralty Bay and Bransfield Strait).

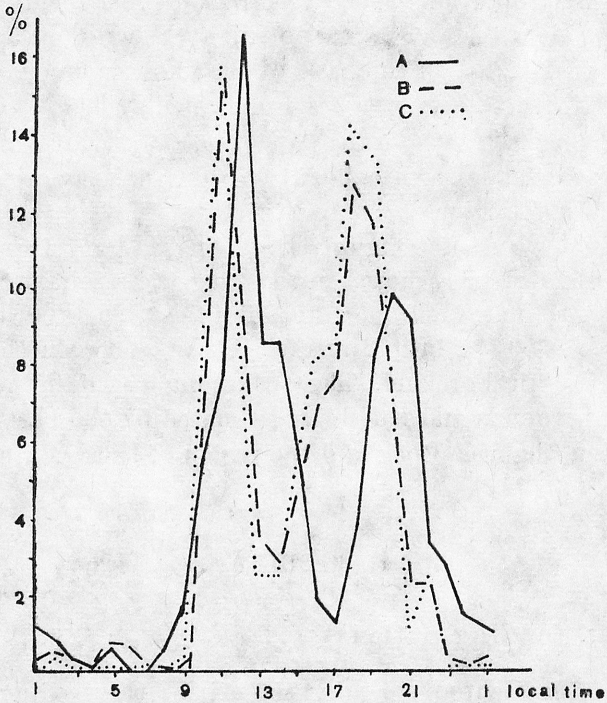


Fig. 2. Frequency of feeding of young Gentoo penguins during a 24-hour period at various stages of growth. A — chicks staying in nests (up to full development of own thermoregulation), B — chicks leaving nests (up to moult), C — at moult

The 24-hour rhythm of Adélie penguins had one peak of abundance on land (Jabłoński, in press b). During the first 14-day period of chick life the adult birds began departing after midnight. Some of them returned to the colony just after midday and then they set about feeding the young. The returns of birds from the sea were however concentrated between 8 and 9 p.m. and then they fed the young most intensely (Fig. 4). The parental birds that had been staying at the nest all day remained in the colony till midnight and did not leave it until the next day. During the period of breeding territorialism either parent was busy getting food every other day. In later developmental stages of the young the departures of adults began at 3—4 a.m. but lasted till noon. The birds returned to the colony in masses from 8 to 10 p.m. and the highest intensity of feeding was observed between 8 and 11 p.m. As the departures from the colony were extended in time, so were the feedings of chicks (Fig. 4,

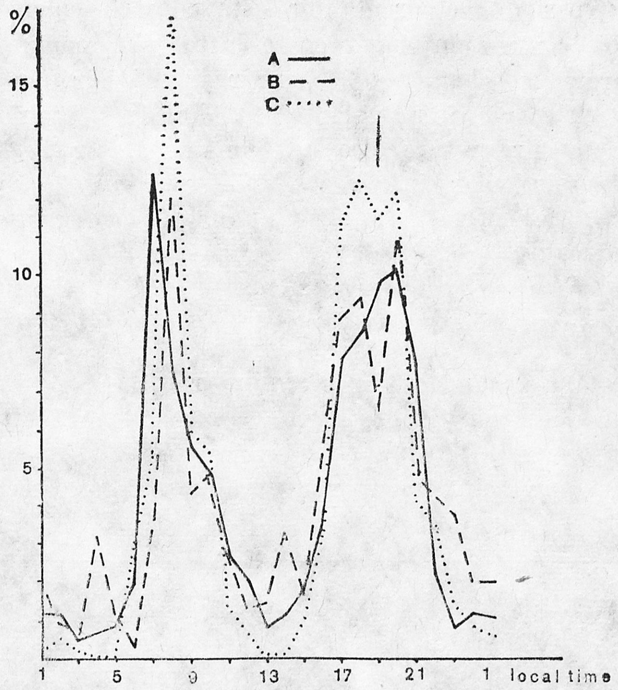


Fig. 3. Frequency of feeding of young Chinstrap penguins during a 24-hour period at various stages of growth. For explanation see Fig. 2

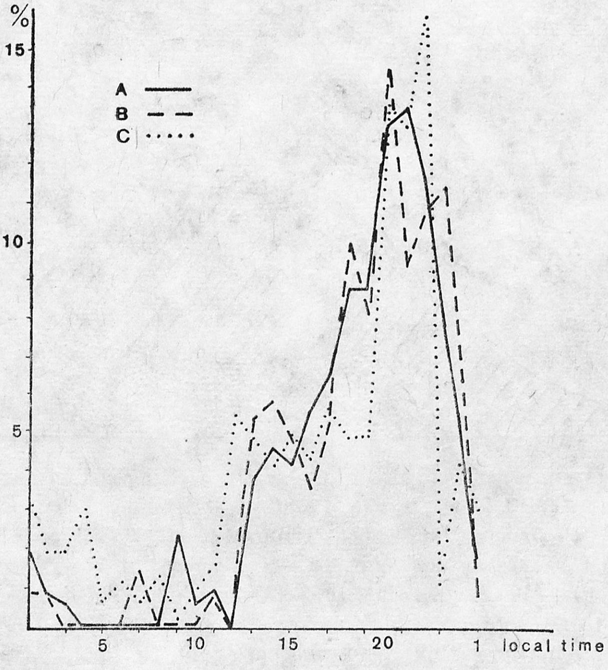


Fig. 4. Frequency of feeding of young Adélie penguins during a 24-hour period at various stages of growth. For explanation see Fig. 2

curve C). In these periods the parental birds stayed in the colony only for several hours and in this connection they were able to take food every day and to maintain the previous scheme of 24-hour rhythm characterized by arrivals of either parent with food after the lapse of 24 hrs. In the period preceding the moult of adults some birds returned to the colony only after 37—41 hrs. Although the time taken by particular birds to get food at various stages of chick rearing was considerably differentiated, the mean number of days given to foraging was fairly stable and came to 42±3 days (N = 244, P = 0.05).

2. Feeding grounds

The main feeding ground of the penguins from the Admiralty Bay region were situated in Bransfield Strait (Fig. 5). From November till mid-January the Adélie penguins inhabiting the colonies near the H. Arctowski Station and in the region of Llano Point took a route leading in the direction of Chabrier

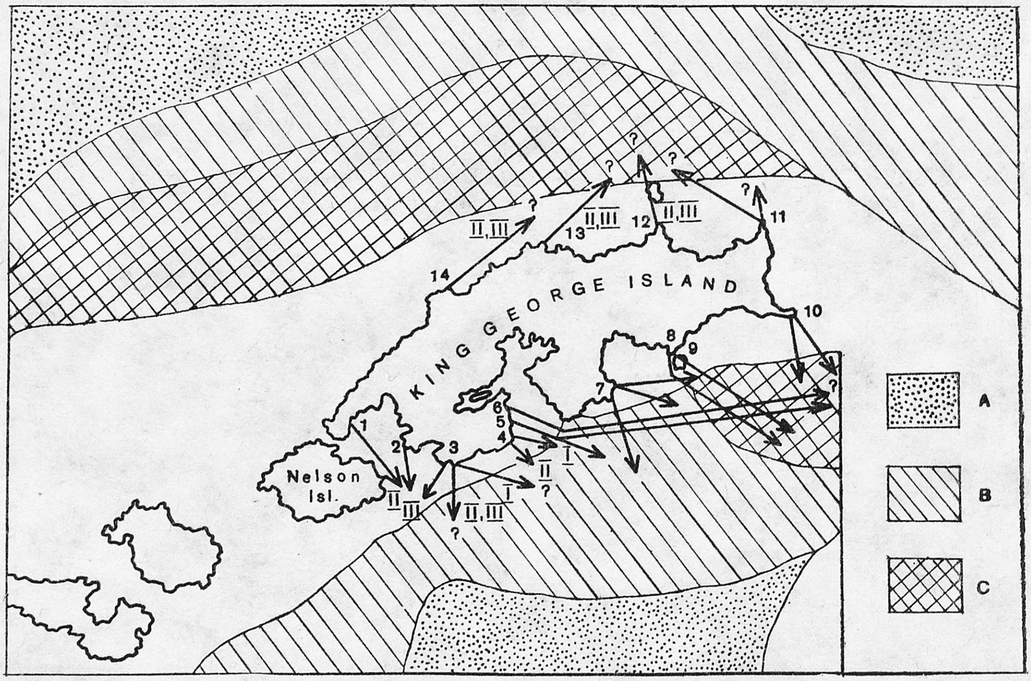
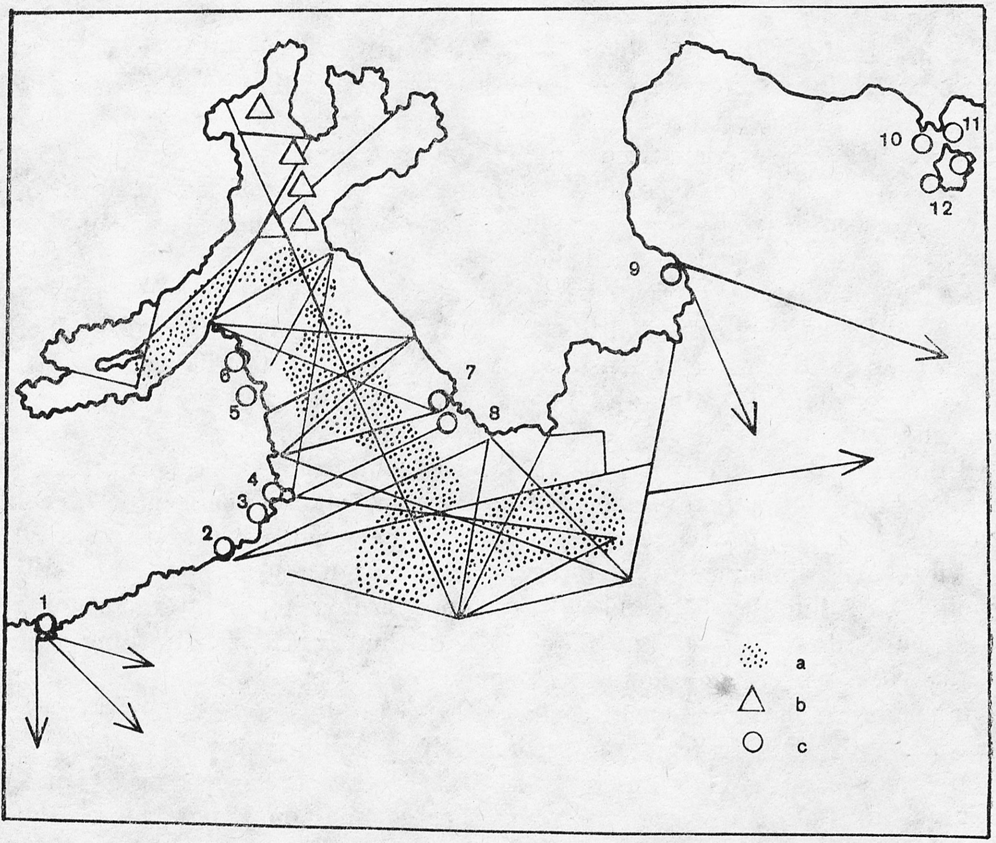


Fig. 5. Main feeding grounds of penguins in the region of King George Island. Colonies: 1 — Ardley I., 2 — Barton Point, 3 — Stranger Point, 4 — Patelnia (Telephone Point), Uchatka and Demay Points, 5 — Llano Point, 6 — Thomas Point, 7 — Lions Rump, 8 — Turret Point, 9 — Penguin I., Three Sisters Point, 10 — Cape Melville, 11 — North Foreland, 12 — False Round Point, 13 — Pottinger Point, 14 — Stigant Point. The arrows indicate the directions of the routes to the feeding grounds and the numerals, I, II and III the months. The symbol ? by an arrow indicates lack of information about the further direction of the route leading to a feeding ground. The biomass of krill estimated by KALINOWSKI (1982): A — 0.1—10 t/nM², B — 10—100 t/nM², C — 100—1000 t/nM²

Rock, to their feeding grounds. A few groups began to forage 5—7 km from this rock. Most of the groups, however, having swum past the rock at a distance of 1—5 km, turned towards Bridgeman Island. In December 1978 I came upon some groups of Adélies on this route, about 25 km off the south-eastern shore of King George Island. At that time the feeding grounds of the Gentoo and Chinstrap penguins were also situated east-south-east of Chabrier Rock. In November and December these species had besides some subsidiary feeding grounds in the Admiralty Bay region (Fig. 6). About 38% of the Gentoo and 40% of the Chinstraps as well as a small number of Adélie penguins foraged in that region.



Figl 6. Feeding grounds of penguins in the region of Admiralty Bay. a — feeding grounds penetrated regularly, b — regions of irregular foraging (solid lines — observation routes), c — colonies of penguins: 1 — Stranger Pt, 2 — Patelnia (Telephone Pt), 3 — Uchatka Pt, 4 — Demay Pt, 5 — Llano Pt, 7 — Shag I., 8 — Chabrier Rock, 9 — Lions Rump, 10 — Turret Pt, 11 — Three Sisters Pt, 12 — Penguin I. Arrows indicate the directions of routes to the foraging grounds

During my three-year investigation I observed the mass foraging of penguins in Admiralty Bay, between Dufayel Island and Chabrier Rock, only sight times in December (6 times in 1978 and twice in 1979). This was preceded by the presence of small ice-fields drifted by sea currents into the bay and the arrival of humpback whales. In such periods most probably all the Gentoos and Chinstraps and about 4500 Adélies from the colonies in the Llano Point region, in the proximity of the H. Arctowski Station and at Chabrier Rock took krill in the Bay. In December 1979 and 1980 the Chinstrap penguins from the colonies at Demay Point, Uchatka Point and Patelnia (Frying-pan) Point swam off in ESE and E directions.

From mid-January about 70% of the Gentoos inhabiting the colony on the Halfmoon Cove side foraged between Ezcurra Inlet and Napier Rock, while about 10% of those from the colony adjacent to Ecology Glacier between Napier Rock and Chabrier Rock. The remaining birds and the breeding groups from the Llano Point region got food 5—10 km south-east of Chabrier Rock. The breeding groups from Stranger Point swam to their feeding grounds in an ESE direction in January and south of this promontory in February and March. At that time the penguins from King George Bay foraged in an area 5—15 km south-east of Penguin Island. As freezing pack-ice appeared in Bransfield Strait, Gentoo penguins concentrated in the feeding grounds in the Admiralty Bay region, where they fed until the wide cracks in the ice had frozen completely. These cracks were situated halfway across the bay, between Hannequen and Shag Island, and extended towards Dufayel Island (Fig. 6). Birds gathered together to feed in these regions also in the summer season. The concentration of feeding grounds in Admiralty Bay was brought about by the prevailing sea currents.

Starting from January the Chinstrap penguins from the colony in the H. Arctowski Station region foraged in the neighbourhood of the Gentoos' feeding grounds. A detailed study carried out on 75 pairs showed however that 80% of the birds swimming off to forage in the morning penetrated the feeding grounds in Admiralty Bay and 90% of those feeding in the afternoon foraged in an area situated 5—15 km SE or ESE of Chabrier Rock. Breeding groups of this species from the colonies at Demay Point, Uchatka Point and Patelnia Point changed the direction of their routes to the feeding grounds from ESE and E to SE starting from the second half of January 1981.

In the second half of January 1981 I also localized the feeding grounds of Gentoo and Chinstrap penguins from other colonies on King George Island: 1. from Ardley Island, Barton Point and Stranger Point — in Maxwell Bay (especially where this bay joins Bransfield Strait; there the foraging penguins concentrated in the vicinity of the ice-floes drifted by sea currents); 2. from the promontories in the region of King George Bay, Penguin Island to Cape Melville — at a distance of 5—15 km S or SE and E of Penguin Island up to Cape Melville. This area was also penetrated by Adélies from the colonies situated on the shore of Admiralty Bay. I observed the penguins returning from these grounds to King George Bay at the following distances from the shore: Gentoo and Chinstrap penguins 15—20 km and Adélie penguins 20—25 km (the feeding grounds of this last species extended however farther into Bransfield Strait);

3. feeding grounds of the Chinstrap penguins from the northern shore of King George Island were situated between North Foreland and Ridley Island and farther to the north of this island. The routes of Chinstraps led in that direction even from the colonies at Stigant Point.

3. Diet of adults

Krill and fish made up the basic food of penguins from spring to winter, i.e. from November to mid-July (Table IV).

Euphausiacea. I distinguished two krill species in the food of penguins: *Euphausia superba* DANA 1852 and *Euphausia crystallorophias* HOLT et TATTERSALL 1906.

Table IV

Summary food composition of adult pygoscelid penguins at King George I. in 1978/1981

Species	Component					Total food, in g (100%)
	Euphausia	*Amphipoda*	*Euphausia* + *Amphipoda* (indeterminate mass)	*Pisces*	Others	
Pygoscelis papua	40,4%	4,3%	6,2%	48,6%	0,5%	623 708
Pygoscelis adeliae	72,7%	3,9%	11,0%	7,0%	5,4%	219 312
Pygoscelis antarctica	38,2%	3,6%	14,0%	34,9%	9,1%	176 822

Euphausia superba — the distribution of dimensions of this species from the stomachs of penguins in the second half of December 1978 was represented by a curve with two peaks (Fig. 7). The stomachs of penguins returning from their feeding grounds in Bransfield Strait contained *E. superba* averaging 45 mm in length and those from Ezcurra Inlet 46—48 mm (Gentoos — 48 mm, Adélies — 47—48 mm and Chinstraps — 46—48 mm). The specimens of *E. superba* collected from the cutter by the method described by JAŻDŻEWSKI et al. (1978), KITTEL (1980) and RAKUSA-SUSZCZEWSKI & STĘPNIK (1980) in Admiralty Bay at that time were smaller in size (Fig. 7). In February 1979 *E. superba* taken by penguins in various regions were of similar length (Fig. 8). There were no statistically significant differences in size between the specimens removed from the penguins' stomachs and those caught from the cutter at that time. In December 1979 I found differences in body length between euphausiids from particular feeding grounds of penguins. The specimens of *E. superba* from the stomachs of penguins foraging in Bransfield Strait, beyond Chabrier Rock, were more often than not 44—48 mm long and those coming from penguins in Admiralty Bay 38 and 40 mm from Gentoos and 50 and 42 from Adélies

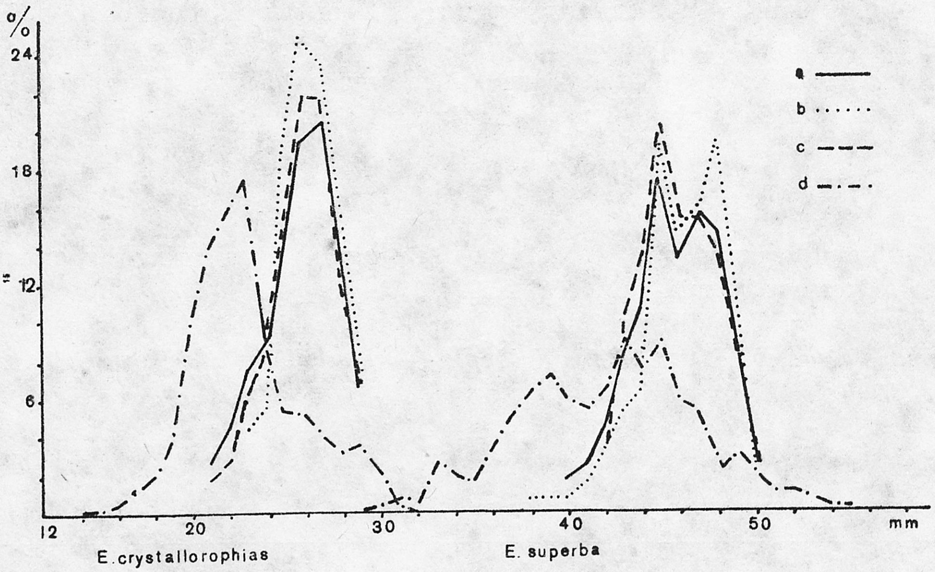


Fig. 7. The percentage distribution of length measurements of *Euphausia crystallorophias* and *Euphausia superba* caught by penguins and in a net from the cutter in the second half of December 1978. a — material from stomachs of Adélies (*E. crystallorophias* N = 102 — 100%, *E. superba* N = 157 — 100%). b — Gentoo penguins (*E. crystallorophias* N = 68 — 100%, *E. superba* N = 147 — 100%), c — Chinstrap penguins (*E. crystallorophias* N = 170 — 100%, *E. superba* N = 59 — 100%), d — material caught in a net (distribution of measurements provided by Prof. Rakusa-Suszczewski)

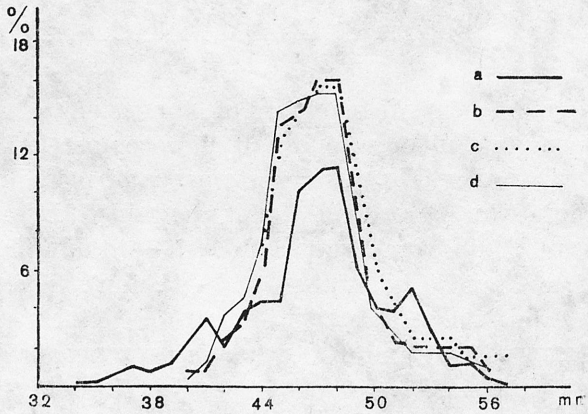


Fig. 8. The percentage distribution of length measurements of *Euphausia superba* caught by penguins and in a net from the cutter in the first half of February 1979. a — Adélies N = 155, b — Gentoos N = 163, c — Chinstraps N = 231, d — material caught in a net (data received from Prof. Rakusa-Suszczewski)

(Fig. 9). It is interesting that at that time penguins belonging to the largest species (Gentoo) took smaller specimens of *E. superba* in the bay than did Adélies (Fig. 9). In January 1980 the longest euphausiids were found in the

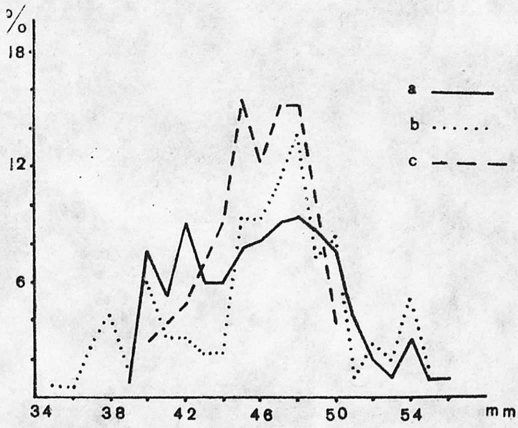


Fig. 9. The percentage distribution of length measurements of *Euphausia superba* caught by penguins in December 1979. a — Adélies N = 510, b — Gentoos N = 532, C — Chinstraps N = 198

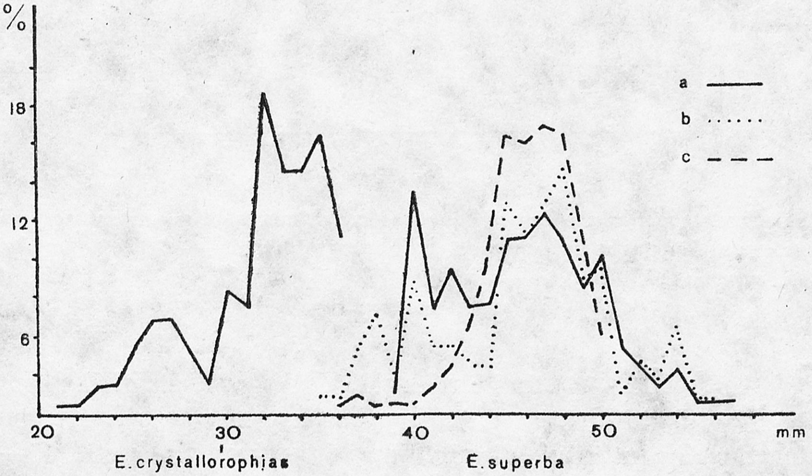


Fig. 10. The percentage distribution of length measurements of *Euphausia crystallorophias* and *Euphausia superba* caught by penguins in January 1980. a — Adélies (*E. crystallorophias* N = 640, *E. superba* N = 525), b — Gentoos (*E. superba* N = 118), c — Chinstraps (*E. superba* N = 308)

stomachs of Chinstrap penguins (Fig. 10). In that month the length of *E. superba* from the stomachs of Gentoo penguins foraging in Admiralty Bay was the same at that recorded in December 1979 (Figs. 9 and 10). The specimens of *E. superba* 40 and 42 mm long came from 7 Adélie penguins (Fig. 10) that were the last to return to the colony, suggesting that they had foraged in the farthest grounds. The remaining Adélies were than catching krill beyond Chabrier Rock and at the outlet of Admiralty Bay. The distribution of lengths in *E. superba* from the stomachs of these penguins resembled that of the krill from the stomachs of Gentoo and Chinstrap penguins (Fig. 10). The length of *E. superba* taken by

Adélie penguins in February was similar to that in January 1980 only that the curve representing the distribution of lengths of the krill from the stomachs of specimens returning latest (Figs. 10 and 11) was more distinct (length: 40 mm). Also in February 1980 the three penguin species foraging in the vicinity of Chabrier Rock and in Admiralty Bay consumed *E. superba* of similar lengths (Fig. 11). In the postbreeding season of 1980 the krill from the stomachs of Gentoo penguins outsized that obtained in the summer (Figs 7, 8, 9, 10 and 11 compared with Figs. 12—14). In March and April the shoals of *E. superba* were most probably still differentiated in respect of age structure, for the curves representing their quantitative distribution with regard to length (47—56 mm) have several peaks (Figs. 12 and 13). In May the 56 mm length characterized the most specimens of *E. superba* from the stomachs of Gentoo penguins (Fig. 14). In November and December 1980 the peaks of the length curves for the krill from the stomachs of Gentoos were at the values 45 and 48 mm and in the case of the krill from the stomachs of Adélies between 45 and 46 mm (Figs. 15 and 16). At that time both these species foraged in Bransfield Strait, but at various distances from their colonies. It is interesting that the length of the krill from the stomachs of Gentoos in December 1980 was the same as in December 1978. These were the commonest measurements of the krill from the stomachs of all Gentoo penguins in summer. In December 1980 some specimens of Adélie and Chinstrap penguins foraged in the neighbourhood of Gentoos beyond Chabrier Rock. In the 1980/81 season distinct differences were noted in length between *E. superba* taken by Gentoo penguins in this region (45 mm) (45 mm) and its specimens eaten by Adélies and Chinstraps (42 mm — Fig. 16).

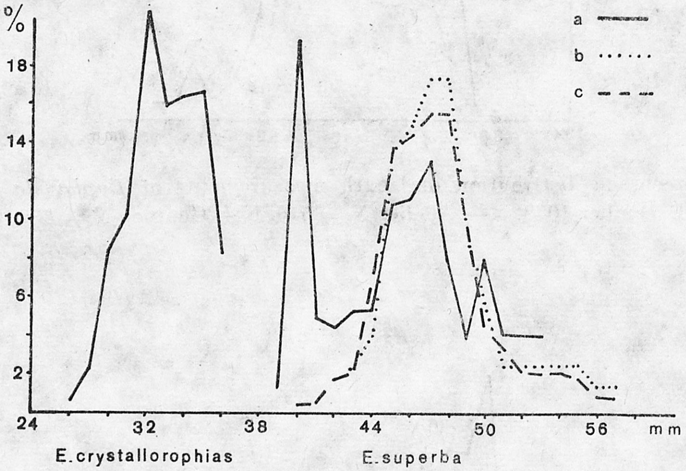


Fig. 11. The percentage distribution of length measurements of *Euphausia crystallorophias* and *Euphausia superba* caught by penguins in February 1980. a — Adélies (*E. crystallorophias* N = 218, *E. superba* N = 163), b — Gentoos (*E. superba* N = 174) c — Chinstraps (*E. superba* N = 319)

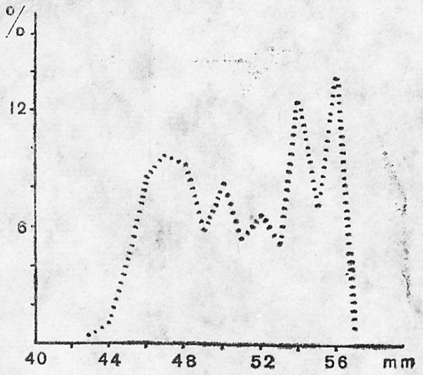


Fig. 12. The distribution of length measurements of *Euphausia superba* caught by Gentoo penguins in March 1980, N = 254

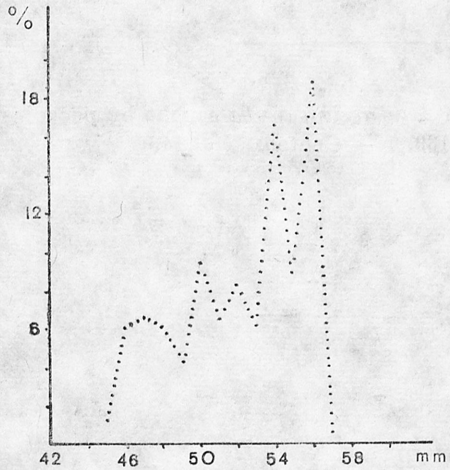


Fig. 13. The distribution of length measurements of *Euphausia superba* caught by Gentoo penguins in April 1980, N = 480

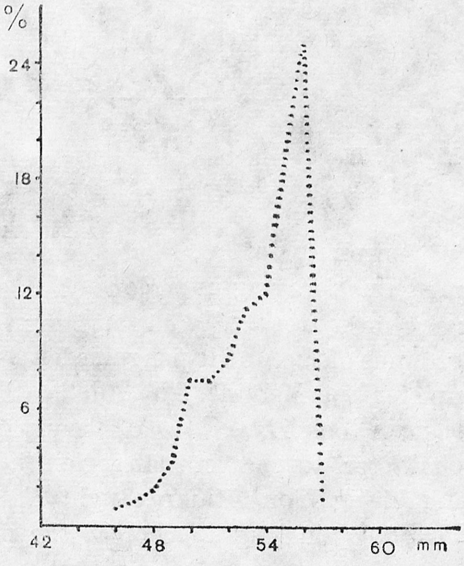


Fig. 14. The distribution of length measurements of *Euphausia superba* caught by Gentoo penguins in May 1980, N = 513

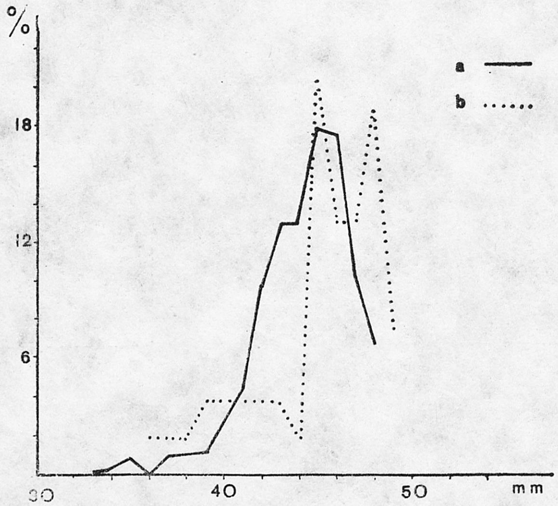


Fig. 15. The distribution of length measurements of *Euphausia superba* caught by penguins in November 1980. a — Adélies N = 133, b — Gentoos N = 146

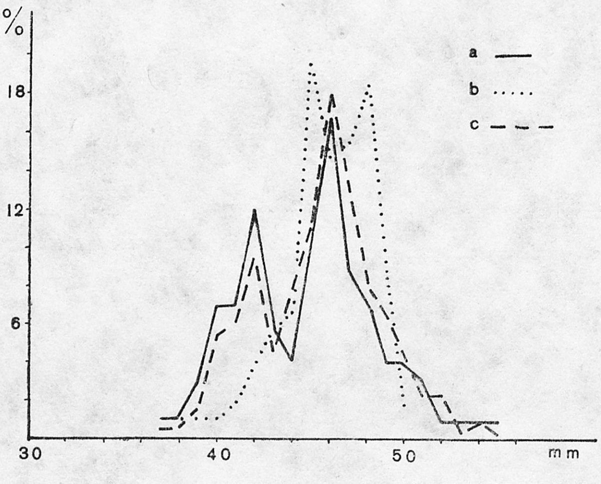


Fig. 16. The distribution of length measurements of *Euphausia superba* caught by penguins in December 1980. a — Adélies N = 100, b — Gentoos N = 103, Chinstraps N = 495

The specimens of *E. superba* found in the stomachs of the Adélie and Chinstrap penguins foraging in regions situated at greater distances from Chabrier Rock were most frequently 46 mm long (Fig. 16). In January 1981 the main feeding grounds of the Adélie penguins lay 5—15 km behind Chabrier Rock and extended up to Cape Melville. The Adélies that penetrated the feeding grounds in these regions took *E. superba* of very various lengths (38—46 mm — Fig. 17). It is characteristic that in that region (i. e. beyond Penguins I.) the Gentoo penguins inhabiting Lions Rump caught *E. superba* averaging 50.8±1.0 mm (N = 172, P = 0.05) in length, whereas the peak of the curve for the krill from Adélie

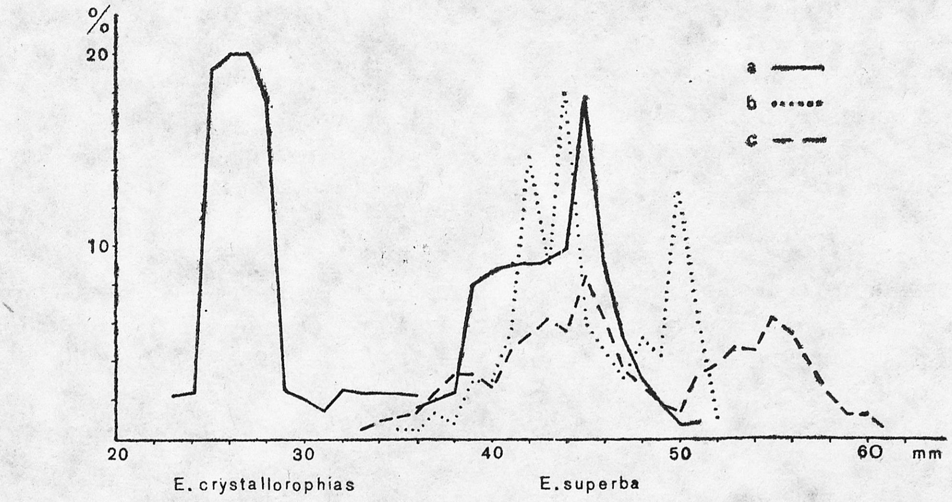


Fig. 17. The distribution of length measurements of *Euphausia crystallorophias* and *E. superba* caught by penguins in January 1981. a — Adélies (*E. crystallorophias* N = 581, *E. superba* N = 340), b — Gentoos (*E. superba* N = 316), c — Chinstraps (*E. superba* N = 928)

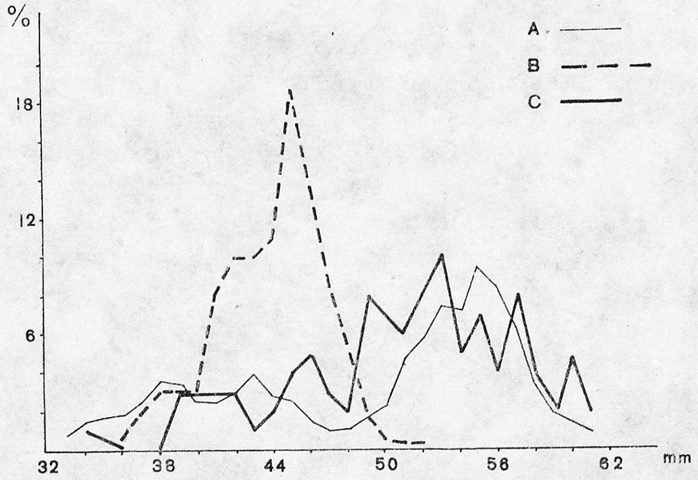


Fig. 18. The distribution of length measurements of *Euphausia superba* caught by Chinstraps and in a net from the cutter in January 1981. A — material from stomachs of Chinstraps inhabiting in the north of King George I., N = 515, $\bar{x}$ = 51.6±7.4 mm, B — material from stomachs of Chinstraps inhabiting the region of the H. Arctowski Station N = 310, $\bar{x}$ = = 45.9±2.1 mm, C — material from the cutter catches (distribution received from Dr R. Stępnik)

penguins lay at 45 mm. In January 1981 *E. superba* eaten by the Gentoo penguins foraging beyond Chabrier Rock (and so in the region penetrated also by Adélies) averaged 44,2±0.9 mm in length (N = 151, P = 0.05) and in the region of Ezcurra Inlet 42.5±1.2 mm (N = 190, P = 0.05). The there maxima illustrated by the curve of length distribution in *E. superba* from the stomachs of Gentoo penguins (Fig. 17) are therefore due to the variable length of the krill from the above-mentioned feeding grounds. In that month the greatest range of variation in the size of *E. superba* was found in the specimens from the stomachs of Chinstrap penguins ($\bar{x} = 47.3 \pm 8.9$ mm, P = 0.05, N = 928 — Fig. 17). This differentiation was caused by the fact that the data from various regions of foraging were treated together. *E. superba* taken by Chinstraps at Ezcurra Inlet were on the average 42.1±0.6 mm long (N = 103, P = 0.05), and so similar to those eaten by Gentoos, beyond Chabrier Rock — 45.9±2.1 mm (N = 310, P = 0.05) and by the specimens from the colonies at Stigant Point and North Foreland — 51.6±7.4 mm (N = 515, P = 0.05). The size of *E. superba* obtained from the stomachs of penguins of this species in the northern part of King George Island was most differentiated (Fig. 18). A comparison of the lengths of *E. superba* caught by Chinstraps in the northern and southern regions of King George Island showed that the shoals of krill around the island differed much (Fig. 18). It is also interesting that the peak of the curve representing the distribution of lengths of *E. superba* caught from the fishing cutter (locality 63, during the expedition BIOMASS-FIBEX 1981; Wolnomiejski et al., 1982) occurs at 53 mm and that for the specimens taken by Chinstraps at 55 mm.

Euphausia crystallorophias occurred in penguins' stomachs irregularly and formed a small proportion of the total of *Euphausiacea* by weight. In the second half of December 1978 its specimens formed 1.5 % of the total weight of euphausiaceans taken by Gentoos, 4.5 % of that taken by Adélies and 4.0 % by Chinstraps. In the other periods of study I found this species only in the stomachs of Adélies in the following proportions: December 1979 — 16.0 %, January 1980 — 11 %, February 1980 — 7.6 % and January 1981 — 21 %. In the second half of December 1978 large shoals of this species occurred in the region of Ezcurra Inlet. Not only penguins but also other birds gathering food from the water surface and whales fed on these aggregations of krill. The specimens of *E. crystallorophias* from the stomachs of the three penguin species under study outsized those caught from the cutter (Rakusa-Suszczewski & Stępnik, 1980 — Fig. 7). The distribution of lengths of *E. crystallorophias* from the stomachs of Adélies for January 1980 was more complex (Fig. 10); in length a small group of these crustaceans resembled the specimens from December 1978 (26—27 mm), whereas most of them were 32—35 mm long. On the basis of the feeding grounds of particular groups of Adélies I managed to establish that these penguins took *E. crystallorophias* 30—36 mm long in the region from Llano Point to Chabrier Rock and further to the east of this rock and 26—27 mm in Ezcurra Inlet (Fig. 19). The length distribution curve of *E. crystallorophias* for February 1980 resembled that for the specimens from the region between Llano Point and Chabrier Rock in January (Figs. 14 and 19). In January 1981 Adélie penguins caught smaller specimens of *E. crystallorophias* in this region than they did in the preceding year (Figs. 10 and 17).

Amphipoda. The specific composition of the *Amphipoda* found in the stomachs of penguins has been presented by JAŻDŻEWSKI (1981), who distinguished 13 species of the suborders *Gammaridea* and *Hyperidea*. The plankton species *Parathemisto gaudichaudii* (GUERIN 1825) was found in the penguins' stomachs relatively most frequently and in the largest numbers, being absent only from Gentoo penguins. According to JAŻDŻEWSKI (1981), this species usually occurs on the peripheries of krill shoals and feeds, most probably, on young euphausiaceans. Two recently described species of the genus *Eusirus*, *E. propeperdentatus* ANDRES 1979 and *E.* cf. *tridentatus* SENTINI et LEDOGER 1974 were also present in the penguins' stomachs. Common benthic forms teeming in the Antarctic littoral constituted about 15% of all the amphipods. The lengths of the amphipods from the stomachs of Gentoos were between 12 and 57 mm ($\bar{x}$ = 21.6 mm), from those of Adélies between 10 and 54 mm ($\bar{x}$ = 19.8 mm) and of Chinstraps between 17 and 55 mm ($\bar{x}$ = 25.0 mm) (VOLKMAN et all, 1982).

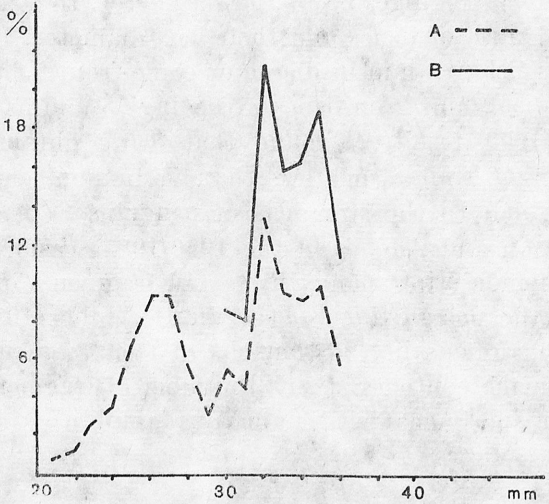


Fig. 19. The percentage distribution of length measurements of *Euphausia crystallorophias* caught by Adelies in different foraging grounds in January 1980: A — in Ezcurra Fiord, N = = 406, x = 30.1±2.9 mm, B — in Bransfield Strait, N = 234, x = 33.2±1.8 mm

Pisces. Partly digested fishes in the stomachs of penguins were 3.5—11 cm long, but 89% of them ranged from 3.5 to 6.5 cm (among these 85% from 4.5 to 6.5 cm). This material consisted chiefly of juvenile forms of the genus *Notothenia* (*Notothenia rossi marmorata* FISCHER 1905 was among the identified forms). The identified fishes exceeding 7 cm in length formed 11% of indigested specimens and belonged to the species *Pleurogramma antarcticum* BOULENGER 1902. Partly digested specimens or fragments of their bodies made above 94% of the food mass consisting of fish. Because the partly digested mass of fish forms such a high percentage. I carried out preliminary observations on the rate of their being digested by Gentoo penguins. For this purpose 6 Gentoos were kept for 24 hours deprived of food in an aviary and next offered 500 g of fish each. After four hours I found that the mass of the fish eaten decreased by 300, 260, 280 and 310 g in four of them, while in two birds the fishes decreased in length by 1.5—2.0 cm in an hour. On account of so fast digestion I found many bony fragments and eyes of fishes in the stomachs of Gentoo and Chinstrap penguins, which suggests that the total mass of fish eaten up was larger than that found in my investigation. This is chiefly true of the food of adult birds, for the young received fish digested to a lesser degree. In evaluating the correlation between the length of fishes and their lens diameter, Emison (1968) established that lenses below 2 mm in diameter come from fishes less than 75 mm long and those above 2 mm from fishes exceeding 75 mm in length. Basing myself on Emison's (1968) results, I found that 580 g obtained from penguins' stomachs (96%) came from fishes less than 75 mm in length.

Other animal food. In the stomachs of penguins (especially Chinstraps in the 1978/1979 season and Adélies in the 1980/1981 season) I found lumps of green and brown nondescript spongy mass and fragments of gastropods belonging probably to the pelagic *Pleuropoda*. In December 1980 I besides found remains of 17 cephalopods in 12 stomachs of Gentoo penguins.

Remaining stomach contents: a small number of fragments of marine algae (they occurred in specimens with numerous amphipods in their stomachs) and stones.

4. Food specificity

4.1. Food specificity in particular specimens

I chose the Gentoo penguin for studying food specificity in particular specimens of one and the same species, because, as shown in an earlier study from this region (Volkman et all, 1982), its food composition was the most varied. I carried out my study on 46 penguins, marked with numbered stripes on their flippers and, in addition, with signs made in leather dye. The marked birds included non-breeders and unsuccessful breeders, which eliminated the contents of stomachs designed for the young from the evaluation of the food specificity of the penguins under study. Inspections of 46 birds made ten times in the period from December 1978 to February 1979 revealed the existence of 3 groups characterized by different feeding habits: the first group consisted of penguins which took only euphausiaceans in summer (24 birds), the second, composed of birds that preferred fish, was the smallest and the third included penguins feeding on both crustaceans and fish (Table V). At that time krill constituted the basic food of most penguins (Tables VI—VIII). In the 1980/1981 breeding season I took 12 samples of food from 3 Gentoos banded in the summer of 1978/1979 (N 00007, N 00055 and N 00095) and then feeding exclusively on euphausiids. Eight of these samples contained only fish and 4 both fish and crustaceans. In the 1980/1981 breeding season considerably fewer penguins fed exclusively on euphausiaceans than in preceding seasons (Tables VI—VIII).

Table V

Individual food preference of the same specimens of Gentoo penguins in the seasons: 1978/1979 and 1980/1981

Breeding season	No of specimes preferring various food	Contents of particular stomachs of specimens preferring various food			
		Euphausia	*Euphausia Amphipoda*	*Pisces*	*Pisces, Euphausia, Amphipoda*
1978/1979	1. — 24	24	—	—	—
	2. 7	—	—	5	2
	3. 15	8	3	2	2
Total of samples (100%)	46 = 100%	32 = 69,6%	3 = 6,5%	7 = 15,2%	4 = 8,7%
1980/1981	→ 3*	—	—	8	4

* In the 1978/1979 season these three specimens of Gentoo penguins belonged to a group of 24 birds that fed exclusively on *Euphausia*.

Changes in the food preference of particular specimens manifested themselves not only in the same phenological seasons of different years but also in the phenological periods following each other directly, for I found on the basis of 8 food samples that 5 Gentoo penguins (N 00038, N 00043, N 00057, N 00073, and N 00095) belonging to the group that fed exclusively on crustaceans in the summer of 1978/1979, in the winter of 1980 had their stomachs filled only with fish in 6 cases and with fish with an addition of krill in 2 cases.

4.2. Food specificity in various species

In 1980 Adélie penguins occupied their breeding territories from 28 September to 18 October and Gentoo penguins from 5—7 to 25 October. At that time the penguins did not leave land. In the period preceding the laying of eggs by Adélies (i.e. 19—27 October) I found that 18% of their population swam out to forage (Jabłoński, in press b). Subsequently, these specimens did not breed. The regular foraging rhythm of Gentoo penguins set in after 25 October (Jabłoński, in press b). Qualitative differences in food composition between these two species became visible then, as 70.4% of the Adélie penguins fed exclusively on krill, whereas fish often occurred in the Gentoo's stomachs (Tables VI and VII). In November 1980 this difference was still evident only that the Adélies that fed on euphausiids with an addition of amphipods were more numerous (Tables VI and VII). In December 1978 the numbers of specimens with only

Table VI

Stomach contents of Gentoo penguins in particular phenological periods and in different years

Phenological seasons		Breeding season	Food composition in particular stomachs				Number of stomachs examined (100%)
			Euphausia	*Euphausia* + *Amphipoda* (chiefly indeterminate mass)	*Pisces*	*Euphausia*, *Amphipoda*, *Pisces*	
Arrival in colony and building of nests (26 Oct. — 4. Nov.)		1980	47,5%	15,0%	22.5%	15,0%	40
Incubation (5 Nov. — 5 Dec.)		1980	47,3%	6,7%	22,7%	23,3%	150
Chicks feeding	chicks up to 20th-25 day of life (December)	1978/1979	81,8%	4,5%	9,1%	4,5%	22
		1979/1980	50,0%	16,7%	12,5%	20,8%	24
		1980/1981	45,1%	5.3%	23,0%	26,6%	113
	chicks from 20th-25th day of life onward (January)	1978/1979	70,0%	10,0%	10,0%	10,0%	10
		1979/1980	5,0%	3,2%	79,6%	12,2%	221
		1980/1981	12,2%	2,8%	72,4%	12,6%	254
Period preceding adult moult (Febr.- mid-April)		1979/1979	76,2%	4,8%	14,2%	4,8%	21
		1979/1980	39,3%	6,0%	22,6%	32,1%	84
		1980/1981	54,1%	10,8%	21,6%	13,5%	37
Autumn -winter nomadizing	1/2 Apr.-1/2 May	1980	23,4%	15,3%	54,4%	6,9%	419
	1/2 May-1/2 July	1980	32,8%	—	47,9%	19,3%	244

* Arrivals in the colony lasted from 7 October, but the Gentoos did not take food till the period preceding nest building.

euphausiaceans in their stomachs were similar in these species (Tables VI and VII), but only fish was found in the stomachs of some Gentoo penguins (Table VI). As regards feeding habits, Chinstrap penguins formed an intermediate group between Gentoos and Adélies at that time, i.e. most of them fed exclusively on euphausiaceans, but those taking nothing but fish with an addition of pelagic pleuropods also formed a considerable proportion (Table VIII). In the next breeding season (i.e. December 1979) the Adélie penguins showed the greatest preference for krill and the most Gentoo penguins fed on mixed food, that is, *Euphausia*, fish and *Amphipoda* (Tables VI—VIII). In December 1980 a considerable differentiation of the stomach contents was observed in all the three species accompanied by a decrease in the number of penguins that ate exclusively krill (Tables VI—VIII). The most stomachs with fish only and the fewest only with krill were found in Chinstrap penguins. At that time more Adélies fed on fish and nondescript spongy mass brown in colour than in preceding years. In January 1979 the stomachs of the most penguins contained exclusively euphausiids (Tables VI—VIII). In the next breeding season the Adélies and Chinstraps that consumed only krill formed similar quantitative proportions (Tables VII and VIII). Only 5% of Gentoos had their stomachs filled exclusively with euphausiids (Table VI). In January 1981, as in December 1979, few penguins ate only euphausiids. There was a particularly distinct decrease in the number of Gentoos taking only *Euphausia*, as compared with the data from December (Tables VII—VIII). In February 1979 most Gentoos had their stomachs filled only with *Euphausia*, just as in the other months of the breeding season of 1978/1979 (Table VI). Krill was also the basic food of Chinstrap penguins but at that time their characteristic feature was a high proportion of specimens living on fish with an addition of pleuropods (Table VIII). From February to April in the following breeding seasons (1979/1980 and 1980/1981) much fewer Gentoos took exclusively krill in favour of those eating fish or mixed food (Table VI). I have found similar food specificity in Chinstrap penguins in these seasons (Table VIII). In 1981 only 5% of its specimens took exclusively krill and 40% exclusively fish (Table VIII). It is striking that in February 1980 Chinstraps caught more fish than did Gentoos. In the autumn-winter nomadic period the differences in the contents of stomachs between Gentoo and Adélie penguins appeared most distinct. The Gentoo penguins caught chiefly fish at that time and the Adélies nearly exclusively krill (Tables VI and VII). In the short periods when the shoals of *Euphausia* were accessible (second half of June 1980) the food specificity of Gentoo penguins underwent a change, for then 75.6% of these penguins fed on *Euphausia*.

5. Weight proportions of particular food constituents in adults

Gentoo penguins. From the winter of 1980 to the autumn of 1981 the weight proportion of *Euphausia* in the food of this species ranged from 18.8 to 62.7% (Table IX). So great differences in weight proportions were caused chiefly by

Table VII

Stomach contents of adult Adélie penguins in particular phenological periods and in different years

Phenological seasons	Breeding season	Food composition in particular stomachs				Number of stomachs examined (100%)
		Euphausia	*Euphausia, Amphipoda*	*Euphausia+ Amphipoda* (chiefly indeterminate mass)	Others (*Pisces,* chiefly indeterminate mass)	
Arrival in colony and building of nests (19—27 Oct.) *	1980	70,4%	14,8%	14,8%	—	27
Incubation (28 Oct. — 28 Nov.) **	1980	36,4%	40,9%	22,7%	—	22
Chicks feeding (December — 1/2 Jan.)	1978/1979	82,9%	9,8%	4,9%	2,4%	41
	1979/1980	89,3%	7,1%	3,6%	—	28
	1980/1981	35,8%	25,9%	23,5%	14,8%	81
Period preceding adult moult (1/2 Jan.-1/2 Febr.)	1978/1979	79,3%	13,8%	3,4%	3,4%	29
	1979/1980	73,6%	17,0%	7,5%	1,9%	53
	1980/1981	23,0%	26,7%	24,4%	25,9%	135
Winter nomadizing (June — 1/2 July)	1980	91,0%	4,5%	4,5%	—	22

* Food samples taken from non-breeders, which formed around 18% of the total population. The breeding birds did not forage at that time.

** Food samples taken from specimens occurring outside the colony. They were most likely non-breeders or females. Males did not take food at that time.

Table VIII

Stomach contents of adult Chinstrap penguins in particular phenological periods and in different years

Phenological seasons	Breeding season	Food composition in particular stomachs					Number of stomachs examined (100%)
		Euphausia	*Amphipoda*+ *Euphausia* (chiefly indeterminate mass)	*Pisces*	*Euphausia Pisces, Amphipoda*	Others *(Pisces,* chiefly indeterminate mass, *Gastropoda)*	
Arrival in colony and building of nests (9—26 Nov.) *	1980	36,7%	40,0%	13,3%	10,0%	—	30
Incubation (December)	1978/1979	51,6%	9,7%	—	—	38,7%	31
	1979/1980	64,5%	25,8%	3,2%	3,2%	3,2%	31
	1980/1981	10,8%	10,8%	32,4%	32,4%	13,3%	37
Chicks feeding (January — 1/2 Febr.)	1978/1979	69,2%	7,7%	—	—	23,1 %	13
	1979/1980	64,0%	28,0%	—	8,0%	—	25
	1980/1981	10,5%	15,0%	32,9%	32,4%	9,2%	76
Period preceding adult moult (February-March)	1978/1979	65,6%	9,4%	3,1%	—	21,8%	32
	1979/1980	50,0%	33,3%	13,3%	3,4%	—	30
	1980/1981	5,0%	9,6%	40,0%	40,0%	5,4%	280

* Food samples taken from non-breeders, which formed about 22% of the total population.

Table **IX**

Weight proportions of particular food components of adult Gentoo penguins in consecutive phenological periods

Phenological period		Breeding season	Food constituent and its weight, in g					Total weight of food, in g (100%)*	Number of birds exa-mined for food amount	Mean weight of food in stomach (in g/bird/ 24 hrs) **
			Euphausia	*Amphipoda*	*Pisces*	*Euphausia* + *Amphipoda* (chiefly indeterminate mass)	Others			
Arrival in colony and building of nests (26 Oct.-4 Nov.) ***		1980	56,5% (480) ****	16,5% (140)	27,0% (230)	—	—	29 750	35	850 ± 258
Incubation (5 Nov.-5 Dec.)		1980	43,4% (354)	13,7% (112)	29,7% (242)	13,2% (108)	—	79 152	97	816 ± 240
Chicks feeding	chicks up to 20th-25th day life	1978/1979	84,6% (716)	1,1% (9)	9,8% (83)	4,5% (38)	—	18 612	22	846 ± 198
		1979/1980	63,0% (510)	3,3% (27)	29,1% (236)	4,6% (37)	—	17 010	21	810 ± 211
		1980/1981	46,0% (361)	0,2% (2)	49,6% (390)	4,2% (33)	—	81 744	104	786 ± 198
	(December)	Average	54,6% (436)	0,8% (6)	40,3% (322)	4,3% (34)				798 ± 200
		Total						117 366	147	
	chicks from 20th-25th day of life	1978/1979	85,7% (683)	1,3% (10)	8,7% (69)	4,2% (33)	0,1% (1)	7 960	10	796 ± 223
		1979/1980	11,2% (82)	4,3% (31)	65,9% (480)	14,9% (109)	3,7% (27)	78 732	108	726 ± 169
		1980/1981	11,8% (148)	4,0% (31)	76,2% (599)	1,0% (8)	—	49 518	63	786 ± 232
	(January)	Average	18,3% (138)	4,0% (30)	66,3% (499)	9,2% (69)	2,1% (16)			752 ± 192
		Total						136 210	181	

Period preceding adult moult (Febr. — mid-April)		1978/1979	79,7% (682)	0,5% (4)	15,6% (134)	2,1% (18)	2,1% (18)	17 976	21	856±138
		1979/1980	44,1% (375)	1,2% (10)	48,3% (411)	6,4% (54)	—	45 900	54	859±155
		1980/1981	62,7% (528)	2,2% (18)	32,4% (273)	2,7% (23)	—	26 944	32	842±127
		Average Total	56,7% (481)	**1,3% (11)**	**37,1% (315)**	4,5% (38)	0,4% (4)	90 820	107	849±143
Autumn-winter nomadizing	1/2 Apr. -1/2 May	1980	35,6% (310)	**3,1% (27)**	59,9% (521)	1,4% (12)	—	104 400	120	870±168
	1/2 May -1/2 July	1980	34,7% (279)	—	57,6% (464)	7,7% (62)	—	66 010	82	805±192

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* The total weight of food (i.e. 100%) is made **up** of randomized samples, 200 g of material constituting the whole of the stomach contents.

** The weight calculated on the basis of the whole of stomach contents.

*** At the time of arrival and formation of the colony (7—25 Oct.) the Gentoo penguins did not take period; the materials collected come from the period preceding the building of nests.

**** The mean weight proportion of the food constituent in the daily ration.

the small weight of *Euphausia* in the stomachs of these birds in January 1981. Apart from these differences, it could be seen that in the winter the consumption of krill was smaller than in the other seasons (Table IX). Considerable differences in weight proportions were also found in the case of amphipods (0—16.5%). The weight of amphipods in the stomachs of Gentoos changed independently of the percentage shares of krill and fish (Table IX). It may therefore be stated that amphipods constituted only a complementary food. In addition to krill the basic or complementary food of adult Gentoo penguins consisted of fish (27.0—76.2%). Its weight proportion in the diet was higher in winter than in summer (Table IX), the samples obtained in January 1981 being the only exceptions, in which fish reached 76.2% of the total mass of food. In the other breeding seasons (1978/1979 and 1979/1980) the consumption of *Euphausia* was higher (Table IX). Changes in the weight proportions of krill and fish were interrelated. It was however interesting that in January 1980 and 1981 the mass of euphausiids eaten up was small. Taking into consideration the weight proportions of *Euphausia* and *Amphipoda* in the partly digested mass of food in 1980, it may be assumed that by weight the total amount of *Euphausia* formed about 20% then. A tendency was observed for the mass of krill to decrease from autumn to spring with a simultaneous increase in the proportion of fish in the food.

Adélie penguins. In the 1980/1981 season *Euphausia* constituted 44—96% of the total mass of their food. Adélies ate the most krill in winter and when a small number of non-breeders foraged at the terminal phase of the colony. The lowest weight proportion of krill in the food of adults in that season was found before the moult (Table X). Keeping in mind the differences between the weight proportions of amphipods and euphausiids, it may be supposed that the weight share of krill in the indeterminable, partly digested mass was conspicuous. Taking into account that mass of *Euphausia*, I estimate its weight proportion at 62—98%. This however does not change the fact that in December 1980. and January 1981 the consumption of krill was lower than in other months. The weight proportion of amphipods in the 1980/1981 season ranged from 1.0 to 8.2%. An increase in the mass of these crustaceans in the food of Adélies could be seen in the periods when the share of euphausiids was smaller (Table X). The weight proportion of fish in the 1980/1981 season fluctuated between 4.4 and 15.9%. It is interesting that Adélie penguins ate fish in the periods when krill was caught in smaller amounts (Table X). In those periods a nondescript foodstuff in the form of brown spongy mass formed about 10% of the stomach contents of these penguins. In the other breeding seasons (1978/1979 and 1979/1980) krill mape up the bulk of food of the Adélies. Here, too, provided the weight proportions of *Euphausia* and *Amphipoda* in the partly digested mass of food is taken into account, it may be assumed that in December 1980 and January 1981 the weight share of *Euphausia* was 91—97%. Along with the increase of the undigested mass of krill in the stomachs of Adélie penguins, a decrease could be noted in the mass of partly digested food with

Table X

Weight proportions of particular food components of adult Adélie penguins in consecutive phenological periods and years

Phenological seasons	Breeding season	Food constituent and its weight, in g					Total weight of food in g (100%)	Number of birds examined for food amount	Mean weight of food in stomach (in g/bird/ 24 hrs)
		Euphausia	*Amphipoda*	*Pisces*	*Euphausia* + *Amphipoda* (chiefly indeterminate mass)	Others			
Arrival in colony and building of nests (19—27 Oct.) *	1980	72,0% (350)	1,4% (7)	—	26,6% (129)	—	12 150	25	486±152
Incubation (28 Oct.—28 Nov.) **	1980	69,1% (498)	8,2% (59)	—	22,7% (163)	—	10 800	15	720±82
Chick feeding (December — 1/2 Jan.)	1978/1979	92,6% (556)	0,4% (2)	1,4% (8)	5,5% (33)	0,1% (1)	14 400	24	600±116
	1979/1980	91,6% (599)	1,4% (9)	3,3% (22)	3,6% (23)	0,1% (1)	12 426	19	654±120
	1980/1981	56,2% (337)	5,2% (31)	4,4% (26)	23,1% (141)	10,7% (64)	32 346	54	599±146
	Average	72,5% (442)	3,2% (20)	3,4% (21)	14,9% (91)	5,9% (36)			610±139
	Total						59 172	97	
Period preceding adult moult 1/2 Jan.—1/2 Febr.)	1978/1979	92,3% (708)	2,4% (18)	1,9% (15)	1,4% (11)	1,9% (15)	22 246	29	767±94
	1979/1980	87,2% (621)	2,7% (19)	4,5% (32)	3,6% (26)	2,0% (14)	29 904	42	712±109
	1980/1981	44,4% (320)	5,7% (41)	15,9% (114)	24,0% (173)	10,0% (72)	73 440	102	720±142
	Average	63,1% (458)	4,4% (32)	10,7% (78)	15,1% (110)	6,7% (48)			726±125
	Total						125 590	173	
Winter nomadizing (June — 1/2 July)	1980	96,0% (557)	1,0% (6)	—	3,0% (17)	—	11 600	20	580±120

* From 28 Sep. to 18 Oct. all the birds stayed in the colony area and did not swim off to forage. Later (19—27 Oct.), non-breeders, which formed about 18% of the whole population went to forage.

** Samples taken outside the colony (they were most likely non-breeders and females). For other explanations see Table IX.

Table XI

Weight proportions of particular food components of adult Chinstrap penguins in consecutive phenological periods and years

Phenological season	Breeding season	Food constituent and its weight, in g					Total weight of food in g (100%)	Number of birds examined for food amount	Mean weight of food in stomach (in g/bird/ 24 hrs)
		Euphausia	*Amphipoda*	*Pisces*	*Euphausia* + *Amphipoda* (chiefly indeterminate mass)	Others			
Arrival in colony and building of nests (9—26 Nov.) *	1980	40,3% (160)	2,0% (8)	21,7% (86)	36,0% (142)	—	8 316	21	396±178
Incubation (December)	1978/1979	50,8% (254)	8,4% (42)	—	1,9% (10)	38,9% (195)	15 546	31	501±120
	1979/1980	68,6% (329)	1,0% (5)	3,7% (18)	24,0% (115)	2,7% (13)	15 360	32	480±152
	1980/1981	16,5% (64)	6,8% (26)	46,9% (183)	25,8% (101)	4,0% (16)	11 700	30	390±180
	Average	47,8% (219)	5,3% (24)	14,2% (65)	16,4% (75)	16,2% (74)			458±150
	Total						42 606	93	
Chicks feeding (January — 1/2 Febr.)	1978/1979	68,5% (341)	—	—	11,6% (58)	19,9% (99)	6 474	13	498±142
	1979/1980	68,1% (323)	2,8% (13)	—	29,1% (138)	—	9 480	20	474±160
	1980/1981	17,2% (81)	4,6% (22)	64,7% (304)	8,7% (40)	4,8% (23)	23 970	51	470±158
	Average	37,6% (179)	3,5% (17)	38,8% (184)	14,0% (66)	6,1% (29)			475±156
	Total						39 924	84	
Period preceding adult moult (1/2 Febr.-March)	1978/1979	65,9% (426)	6,0% (39)	1,0% (6)	4,1% (26)	23,0% (148)	20 640	32	645± 72
	1979/1980	53,9% (323)	3,1% (19)	16,1% (97)	26,9% (161)	—	18 000	30	600± 84
	1980/1981	12,3% (60)	1,6% (8)	74,6% (364)	7,3% (36)	4,2% (20)	47 336	97	488±164
	Average	33,9% (183)	3,0% (16)	44,7% (242)	10,6% (57)	7,8% (142)			540±130
	Total						85 976	159	

* From 28 Oct. to 8 Nov. all the birds stayed in the area of the colony and did not swim off to forage; later (9—26 Nov.) the non-breeders, which formed about 22% of the whole population, went to forage. For other explanations see Table IX.

remains of *Euphausia* and *Amphipoda* and that of the weight proportion of fish.

Chinstrap penguins. The weight proportions of krill in the diet of this penguin showed considerable fluctuations from November 1980 to March 1981 (Table XI). In that breeding season I found the most euphausiids in a small number of foraging specimens of Chinstraps in the final phase of their occupation of the colony (Table XI). The share of *Euphausia* was greater than it seems to have been from Table XI because of the marked predomination of krill in the partly digested mass of food. Keeping in mind the proportions of *Euphausia* and amphipods in the partly digested mass, it may be assumed that krill formed about 74% of the total of food at the time when the colony was being formed, 40% in the period of egg incubation and up to 23% in the following phenological periods. On the other hand, the weight proportion of amphipods was small throughout the season (1.6—6.8%). In the periods with diminished percentages of *Euphausia* an increase was observed in the consumption of fish (Table XI). In the remaining breeding seasons investigated (1978/1979 and 1979/1980) krill constituted the bulk of the food taken by Chinstrap penguins. To be sure, its weight proportion was 50.8—68.5%, but after the addition of the mase of euphausiids from the partly digested, indeterminate food it ranged between 77 and 94%. In those breeding seasons the consumption of fish was low and the main complementary food consisted of pelagic pleuropods (Table XI).

Macaroni penguins *Eudyptes chrysolophus*. In the stomachs of five specimens examined euphausiids formed 96.3% of the mass of food and fish 3.7%. This species also fed on cephalopods, whose remains were present in two stomachs examined.

6. Twenty-four-hour food ration of adults

Gentoo penguins. The differences between the lowest and the highest mean daily ration (729 and 870 g, respectively) was 16.2%. The size of the daily ration changed chiefly with phenological periods (Table IX). The differences between the means from analogous phenological periods of consecutive years were however small: December — 7.1%, January — 8.4% and from February to mid-April — 1.6%. The highest values of the mean weight were noted after a break in feeding caused by a long stay on land (after the formation of the colony — 850 g and after the moult — 870 g) and before the break of feeding connected with moulting (849 g).

Adélie penguins. The differences in the level of mean values of daily rations of this species were considerably greater than in the case of Gentoo penguins (36.6%). I found the highest mean daily ration in specimens which after a long stay on land left the colony in the final period of egg incubation (720 g) and in the period preceding the moult (up to 767 g). Literature provides no data concerning the daily ration of Adélies after the moult. From the second half of March to mid-April I collected 5 stomachs of birds which had been drifting on floes. These stomachs contained only krill, 640—920 g ($\bar{x} = 772$ g) in weight.

Data from the periods of intense feeding indicate that then the Adélies ate on the average 712—772 g daily. I observed the lowest mean value of daily ration in the final period of the occupation of territories by birds in the colony (Table XII). Only 18% of the Adélies foraged at that time, namely, the ones which next did not participate in breeding (Jabłoński, in press b). They fed in Bransfield Strait, whence they returned after 10—15 hrs. In the stomachs of these birds the partly digested remains of euphausiids and amphipods formed 26.6% of the total mass of food. It might be supposed, therefore, that owing to the long distance between the feeding grounds and the colony part of the food underwent a partial digestion and this is why the estimate of the daily ration is underrated. In the three seasons of the present study the difference between the maximum and the minimum size of the ration was small (December — 8.4% and January to mid-February — 7.2%).

Table XII

Differentiation of the food composition and the size of daily ration in Chinstrap penguins according to the time of day when they were foraging (data from February 1981). Figures in brackets represent the ranges of daily rations. N — number of samples

Time of foraging	Composition and weight of daily ration, in g					
	Euphausia	*Euphausia, Amphipoda*	*Euphausia, Pisces*	*Euphausia, Amphipoda, Pisces*	*Pisces, Gastropoda*	*Pisces*
Morning foraging	—	—	—	340 (320—350) N = 12	448 (380—540) N = 15	447 (390—610) N = 22
Evening foraging	377 (280—500) N = 14	390 (380—400) N = 12	488 (420—590) N = 22	—	—	—

Chinstrap penguins. The range of mean daily rations in various phenological periods and in various years was from 390 to 645 g, the difference being 39.5% (Table XI). The most stable level of daily ration weights was found in the period of chick feeding, that is, in January. Then the differences between the successive breeding seasons were only up to 5.6%. In the other phenological seasons these differences ranged between 22.1% (egg incubation — December) and 24.3% (pre-moulting period — February). Apart from the changes in the weight proportions of particular food constituents in different phenological periods and years, there were also differences in food between Chinstraps foraging at different times of day. Fish prevailed in the food of the specimens foraging in the morning and krill in that gathered in the evening (Table XII). However, in the stomachs containing both fish and krill from evening catches fish constituted the main bulk of the food by weight (83.6%). It is characteristic that the changes in food composition were accompanied by those in the size of daily rations (Table XII).

Macaroni penguins. The weight of food from 5 stomachs collected in three years (from January to March) ranged from 660—730 g ($\bar{x} = 687$ g).

7. Weight proportions of particular food constituents in chicks

In the first days of life penguins chicks received exclusively pellets of crumbled food glued together by means of mucus; they consisted of fragments of *Euphausia* and sporadic *Amphipoda*. After the lapse of five days of life fresh krill prevailed in the pellets of food glued together. At that time both parents delivered food to chicks. Indigested amphipods appeared more often in the food of the young between the 11th and the 20th day of their life, while the weight proportion of partly digested mass of crustaceans was on the decrease and that of indigested euphausiids increased (up to 93%). It was not before the 20th day of life that small differences in food composition became visible (Tables XIII—XV). Then fish fragments began to occur in the food of Gentoo chicks (Table XIII). Fish appeared in the food of young Adélies only when they were more than 26 days old, and only in the 1980/1981 season at that, in which there was a distinct decrease in the consumption of krill (Table XIII). In the 1978/1979 season, when krill occurred in great abundance, no fish was observed in the food of Chinstrap chicks (Table XV). It is interesting that the scarcity of krill in the 1980/1981 season was not clearly reflected in the food of Chinstrap chicks, in which, after the 21st day of life, *Euphausia* formed 71.1—88.7% of the total weight of food. Adult Chinstrap brought more food from the sea in the second half of January. The most distinct changes in the weight proportions of particular food constituents in the 1980/1981 season were however found in Adélies (Table XIV), in which the period of maximum krill catches fell in the second half of December and the first decade of January.

8. Twenty-four-hour food ration of chicks

Young pygoscelid penguins were given food in the form of pellets glued together by means of mucus, weighing 1.4—2.1 g each, up to the 10th day of life (Tables XVI—XVIII). At that time feeding was done at various times of day and the number of pellets delivered ranged from 26 to 46 a day. Up to the 10th day the parents brought food in similar amounts regardless of the number of chicks in the nest. Between the 11th and the 15th day the chicks were fed a similar number of times in all the species under study, but there were already differences between the weights of single pellets and consequently also in the size of daily rations (Tables XVI—XVIII). In this age group feeding was more concentrated in time in accordance with the 24-hour rhythm of the parents. The weight of food eaten daily by chicks of this group was 3—4 times as large

Table XIII

Weight proportions of food components of young Gentoo penguins in consecutive periods of life

Age, in days	Breeding seasons	Kind of food, in %					Total weight of food in g (100%)	No of samples from stomachs*
		Euphausia	*Amphipoda*	*Pisces*	*Euphausia* + *Amphipoda* (chiefly indeterminate mass)	Others		
2—5	1978/1979	—	—	—	100%	—	50	31
	1979/1980	—	—	—	100%	—	34	20
	1980/1981	—	—	—	100%	—	275	172
	Total	—	—	—	100%	—	359	223
6—10	1978/1979	71,6%	—	—	28,4%	—	65	31
	1979/1980	69,4%	—	—	30,6%	—	68	34
	1980/1981	69,0%	—	—	31,0%	—	318	159
	Total	69,2%	—	—	30,8%	—	451	224
11—15	1978/1979	86,6%	0,6%	—	12,8%	—	151	26
	1979/1980	86,6%	1,0%	—	12,4%	—	274	49
	1980/1981	87,2%	1,9%	—	10,9%	—	650	114
	Total	86,1%	2,5%	—	11,4%	—	1 075	183
16—20	1978/1979	91,2%	0,4%	—	8,1%	—	1 980	6
	1979/1980	91,2%	1,2%	—	7,6%	—	10 800	36
	1980/1981	87,9%	2,4%	1,4%	8,3%	—	12 600	42
	Total	89,5%	1,7%	0,7%	8,0%	—	25 380	84
21—25	1978/1979	94,5%	0,4%	1,0%	3,2%	0,9%	10 296	24
	1979/1980	93,0%	2,0%	2,0%	3,0%	—	16 984	46
	1980/1981	82,4%	2,4%	10,4%	3,4%	1,4%	12 832	108
	Total	90,0%	1,7%	4,4%	3,2%	0,7%	40 112	176
26<	1978/1979	91,6%	0,5%	2,9%	3,2%	1,8%	13 080	126
	1979/1980	83,6%	2,8%	10,8%	2,8%	—	15 508	50
	1980/1981	59,6%	7,5%	17,5%	15,4%	—	16 524	162
	Total	77,1%	3,8%	11,0%	7,5%	0,5%	45 112	338

* Up to the 15 th day of life the figures placed in this column indicate the number of single portions (pellets of food glued together with mucus); from the 15 th day onward — they indicate the number of food samples from stomachs (both randomized samples and the whole amounts of stomach contents).

Table XIV

Weight proportions of food components of young Adélie penguins in consecutive periods of life

Age, in days	Breeding seasons	Kind of food, in %					Total weight of food in g (100%)	No of samples from stomachs
		Euphausia	*Amphipoda*	*Pisces*	*Euphausia* + *Amphipoda* (chiefly indeterminate mass)	Others		
2—5	1978/1979	—	—	—	100%	—	30	20
	1979/1980	—	—	—	100%	—	159	106
	1980/1981	—	—	—	100%	—	210	140
	Total	—	—	—	100%	—	399	266
6—10	1978/1979	72,0%	—	—	28,0%	—	106	56
	1979/1980	66,2%	—	—	33,8%	—	212	106
	1980/1981	67,4%	—	—	32,6%	—	252	140
	Total	67,7%	—	—	32,3%	—	570	302
11—15	1978/1979	87,5%	0,1%	—	12,4%	—	296	63
	1979/1980	88,0%	0,5%	—	11,5%	—	554	126
	1980/1981	87,7%	0,3%	—	12,0%	—	602	140
	Total	87,7%	0,4%	—	11,9%	—	1 452	329
16—20	1978/1979	92,5%	0,1%	—	7,4%	—	2 280	8
	1979/1980	93,0%	0,8%	—	6,2%	—	6 440	23
	1980/1981	90,9%	2,0%	—	7,1%	—	19 440	72
	Total	91,5%	1,6%	—	6,9%	—	28 160	103
21—25	1978/1979	95,4%	0,2%	—	4,3%	0,1%	15 004	31
	1979/1980	90,8%	2,4%	—	6,8%	—	15 776	32
	1980/1981	25,1%	5,9%	—	22,0%	47,0%*	16 240	676
	Total	69,6%	2,9%	—	11,2%	16,3%	47 020	739
26<	1978/1979	95,5%	0,2%	—	3,3%	1,0%	61 100	94
	1979/1980	89,3%	3,6%	—	7,1%	—	17 080	28
	1980/1981	57,2%	6,8%	15,4%	8,1%	12,5%	44 800	222
	Total	80,7%	3,1%	5,6%	5,6%	5,0%	122 980	344

* The food included in the column „Others" in the 1980/1981 season consisted of brown spongy mass. Other explanations as in Table XIII.

Table XV

Weight proportions of food components of young Chinstrap penguins in consecutive periods of life

Age, in days	Breeding seasons	Kind of food, in %					Total weight of food in g (100%)	No of samples from stomachs*
		Euphausia	*Amphipoda*	*Pisces*	*Euphausia* + *Amphipoda* (chiefly indeterminate mass)	Others		
2—5	1978/1979	—	—	—	100%	—	40	25
	1979/1980	—	—	—	100%	—	69	46
	1980/1981	—	—	—	100%	—	125	89
	Total	—	—	—	100%	—	234	160
6—10	1978/1979	69,8%	2,3%	—	27,9%	—	43	24
	1979/1980	68,9%	1,6%	—	29,5%	—	61	32
	1980/1981	63,0%	3,3%	—	33,7%	—	92	54
	Total	66,3%	2,5%	—	31,1%	—	196	110
11—15	1978/1979	87,2%	3,8%	—	9,0%	0,4%	78	20
	1979/1980	88,5%	3,3%	—	7,8%	0,4%	243	64
	1980/1981	83,2%	7,1%	—	9,0%	0,6%	155	42
	Total	86,6%	4,6%	—	8,4%	0,4%	475	126
16—20	1978/1979	90,2%	3,8%	—	5,1%	0,9%	5 400	24
	1979/1980	91,8%	3,4%	—	4,8%	—	19 890	90
	1980/1981	83,0%	6,5%	3,4%	5,0%	2,1%	27 690	130
	Total	87,0%	5,1%	1,8%	4,9%	1,2%	52 980	244
21—25	1978/1979	88,7%	4,6%	—	3,5%	3,2%	7 176	24
	1979/1980	81,3%	4,3%	2,0%	10,0%	2,4%	23 048	86
	1980/1981	71,1%	9,0%	7,7%	11,2%	1,0%	26 832	104
	Total	77,4%	6,6%	4,4%	9,8%	1,8%	57 056	210
26<	1978/1979	88,7%	4,6%	—	3,5%	3,2%	38 614	86
	1979/1980	82,9%	3,9%	2,0%	8,2%	3,0%	29 670	86
	1980/1981	71,3%	2,7%	16,2%	7,9%	1,9%	28 160	80
	Total	81,8%	3,8%	5,3%	6,2%	2,8%	96 444	252

* Explanations as in Table XIII.

as in the preceding period. The Gentoo and Chinstrap chicks, above 16 days old, received food twice daily and young Adélies once. At 16—20 days there was a further increase in the mass of daily rations: by 12.7% in Gentoos, 5.7% in Adélies and 47.1% in Chinstraps. It is interesting that at this age Chinstraps received the biggest daily rations, whereas their body weight was smaller than that of young Gentoos. In the next five days of life, 21st—25th, I observed quite different tendencies in the rise of the weight of food eaten up in relation to those found in chicks 16—20 days old: Gentoos — 60.4%, Adélies — 39.7% and Chinstraps — 20.2%. In chicks above 26 days old the increase in the weight of food consumed was greater in Chinstraps (28.0%) and Adélies (24.3%) than in Gentoos (18.8%).

I found the smallest differentiation of daily food rations in respect of weight in the same age groups in different years in Gentoo penguins: 16th—20th day — 5.2%, 21st—25th day — 2.1%, from 26th day onwards — 15.0%. In the same years the Adélie and Chinstrap penguins showed greater differences in daily rations (Adélies: 5.3, 18.0 and 13.1% and Chinstraps 5.3, 13.7 and 23.3%, respectively),

8.1. Differences in the 24-hour food ration of chicks relative to the density of the breeding group

In the 1980/1981 season I estimated the weight of food rations in three breeding groups differing in density within groups (Table XIX). For comparison of results I took into consideration only the findings concerning these three groups collected the same day, for the materials obtained from numbered nests showed that chicks received different daily rations in the same breeding groups on consecutive days (e.g. 28 December 1980: $\bar{x} = 404 \pm 70$ g, N = 7.; 29 December 1980: $\bar{x} = 614 \pm 150$ g, N = 44). The mean daily ration of young Adélies in the central part of a large breeding group appeared smaller than in groups consisting of 128—302 nests (Table XIX). It is characteristic that the dispersal of the data, which did not differ significantly ($P = 0.05$), from a large breeding group was considerably greater than that in less abundant groups. The maximum weights of daily rations resembled each other (Table XIX).

8.2. Differences in the 24-hour food ration of chicks relative to the number of chicks falling to a pair

Admittedly, the clutch of a pair of pygoscelid penguins consists of 1 or 2 chicks. The rations supplied once a day to single chicks, above 26 days old, were considerably larger than the mean rations calculated from the data for twin chicks (Table XX). These differences fluctuated between 23.8 and 28.5% for Gentoo penguins, between 29.8 and 38.1% for Adélies and between 13.8 and 32.8% for Chinstraps. The single rations of twin chicks differed most in weight in Adélie penguins (21.8—40.3%). It is worth reminding that this species showed the greatest preference for krill. In the years when krill was deficient fish constituted a great weight proportion of Gentoo and Chinstrap penguins'

Table XVI

Weight and composition of food of young Gentoo penguins falling to one specimen per 24 hrs in particular periods of life

Age, in days	Breeding seasons	No of samples *	No of feedings per 24 hrs	**Weight of food, in g**		Kind and weight of food in daily ration, in g **				
				per one feeding ***	per 24 hrs	*Euphausia*	*Amphipoda*	*Pisces*	*Euphausia*+ *Amphipoda* (chiefly indeterminate mass)	Others
2—5	1978/1979	31 (15)	30—36	1,6	54±5	—	—	—	54	—
	1979/1980	20 (11)	29—37	1,7	56±5	—	—	—	56	—
	1980/1981	172 (24)	28—39	1,6	54±5	—	—	—	54	—
	Average				55±5	—	—	—	55	—
6—10	1978/1979	31 (12)	30—42	2,1	79±10	57	—	—	22	—
	1979/1980	34 (11)	32—44	2,0	79±10	55	—	—	24	—
	1980/1981	159 (21)	33—41	2,0	80±12	55	—	—	25	—
	Average				79±11	55	—	—	24	—
11—15	1978/1979	26 (8)	42—58	5,8	296±40	256	2	—	38	—
	1979/1980	49 (9)	40—62	5,6	295±52	255	3	—	37	—
	1980/1981	114 (17)	44—59	5,7	295±42	257	6	—	32	—
	Average				295±43	256	4	—	35	—
16—20	1978/1979	6	2	165	330±76	301	1	—	28	—
	1979/1980	36	2	174	348±58	317	4	—	26	—
	1980/1981	42	2	168	336±56	295	8	5	28	—
	Average				338±62	304	4	2	27	—

21—25	1978/1979 1979/1980 1980/1981	24 52 121	2 2 2	429 430 421	858±108 860±110 842±110	811 800 694	3 17 20	9 17 87	27 26 29	8 — 12
	Average				853±110	768	13	38	27	7
26<	1979/1979 1979/1980 1980/1981	96 72 116	2 2 2	580 502 493	1160±104 1004±300 986±286	1063 839 588	6 28 74	34 108 172	37 28 152	20 — —
	Average				1050±228	830	36	105	72	7

* Number of samples from specimens less than 15 days old is the number of pellets received; in brackets — number of birds examined.

** Calculated on the basis of the percentage distribution from Table XIII.

*** Before the 15th day of life denotes the weight of one pellet.

Table XVII

Weight and composition of food of young Adélie penguins falling to one specimen per 24 hrs in particular periods of life

Age, in days	Breeding seasons	No of samples *	No of feedings per 24 hrs	Weight of food, in g		Kind and weight of food in daily ration, in g **				
				per one feeding	per 24 hrs	*Euphausia*	*Amphipoda*	*Pisces*	*Euphausia*+ *Amphipoda* (chiefly indeterminate mass)	Others
2—5	1978/1979	20 (16)	28—34	1,5	50±3	—	—	—	50	—
	1979/1980	106 (11)	28—33	1,5	47±5	—	—	—	47	—
	1980/1981	140 (29)	27—34	1,5	48±5	—	—	—	48	—
	Average				48±5	—	—	—	48	—
6—10	1978/1979	56 (20)	32—46	1,9	75±10	54	—	—	21	—
	1979/1980	106 (24)	7—44	2,0	72±16	48	—	—	24	—
	1980/1981	140 (24)	33—52	1,8	78±14	53	—	—	25	—
	Average				75±14	52	—	—	23	—
11—15	1978/1979	63 (22)	44—63	4,7	285±32	249	1	—	35	—
	1979/1980	126 (36)	48—65	4,4	259±40	228	1	—	30	—
	1980/1981	140 (20)	41—63	4,3	241±60	211	1	—	29	—
	Average				262±47	230	1	—	31	—
16—20	1978/1979	8	1	285	285±64	264	1	—	20	—
	1979/1980	23	1	280	280±60	261	2	—	17	—
	1980/1981	72	1	270	270±86	245	5	—	19	—
	Average				278±78	256	3	—	20	—

21—25	1978/1979	31	1	484	484 ± 56	461	1	—	21	1
	1979/1980	32	1	493	493 ± 42	448	12	—	33	—
	1980/1981	242	1	404	404 ± 160	101	24	—	89	190
	Average				460 ± 137	337	12	—	47	64
26<	1978/1979	94	1	650	649 ± 56	621	1	—	21	6
	1979/1980	28	1	610	610 ± 82	545	22	—	43	—
	1980/1981	192	1	565	565 ± 144	323	38	87	46	71
	Average				608 ± 112	496	20	29	37	26

* ** *** Explanations as in Table XVI.

Table XVIII

Weight and composition of food of young Chinstrap penguins falling to one specimen per 24 hrs in particular periods of life

Age, in days	Breeding seasons	No of samples *	No of feedings per 24 hrs	Weight of food, in g		Kind and weight of food in daily ration, in g **				
				per one feeding ***	per 24 hrs	*Euphausia*	*Amphipoda*	*Pisces*	*Euphausia*+*Amphipoda* (chiefly indeterminate mass)	Others
2—5	1978/1979	25 (12)	28—34	1,6	48±4	—	—	—	48	—
	1979/1980	46 (10)	27—32	1,5	45±6	—	—	—	45	—
	1980/1981	89 (25)	26—33	1,4	46±6	—	—	—	46	—
	Average				46±6	—	—	—	46	—
6—10	1978/1979	24 (10)	33—51	1,8	83±19	58	2	—	23	—
	1979/1980	32 (12)	35—49	1,9	79±12	54	2	—	23	—
	1980/1981	54 (20)	32—50	1,7	77±10	49	2	—	26	—
	Average				80±14	54	2	—	24	—
11—15	1978/1979	20 (17)	42—62	3,9	230±42	200	9	—	21	—
	1979/1980	64 (12)	45—62	3,8	238±40	211	8	—	18	1
	1980/1981	42 (17)	44—63	3,7	228±46	190	16	—	20	2
	Average				232±42	200	11	—	20	1
16—20	1978/1979	24	2	225	450±56	406	17	—	23	4
	1979/1980	90	2	221	442±54	406	15	—	21	—
	1980/1981	130	2	213	426±78	354	28	14	21	9
	Average				439±67	389	20	5	22	4

21—25	1978/1979	24	2	299	598±58	530	28	—	21	19
	1979/1980	86	2	268	536±98	435	23	11	54	13
	1980/1981	104	2	258	516±134	367	46	40	58	5
	Average				550±96	444	33	17	44	12
26<	1978/1979	86	2	449	898±73	797	41	—	31	29
	1979/1980	86	2	345	690±116	572	27	14	56	21
	1980/1981	80	2	352	704±110	502	19	114	56	13
	Average				764±99	624	29	42	48	21

* ** *** Explanations as in Table XVI.

Table XIX

Relationship between the weight of daily ration of young Adélie penguins and breeding-group density

Number of nests	1552	302	128
Density of nests inside the breeding group (nests/m^2)	2,60	2,00	1,23
Mean weight of daily food ration, in g	496±152	615±72	609±84
Number of food samples	94	35	31

food. That is most likely why the weight differences between the rations of twin siblings were smaller (Gentoo: 15.5—19.5%, Chinstrap: 9.9—19.5%). The differentiation of food rations in consequence found its reflection in differences between the body weights of single chicks and those of twin chicks, notably the twin chick that had hatched later (Table XX). In Gentoo penguins these differences were 6.6—12.9%, in Adélies 13.5—18.1% and in Chinstraps 6.7—19.2%. Twins differed in weight by 6.2—7.9% (Gentoo), 7.0—9.5% (Adélie) and 3.2—17.0% (Chinstrap).

Table XXI

Body weight of young Adélie penguins killed by *Stercorarius skua lonnbergi* (N — number of birds examined)

Classes of body weight of victims, in kg	Per cent of victims in particular classes	
	Season 1978/1979 N = 36	Season 1980/1981 N = 60
2,8—3,0	44,4	45,0
3,1—3,3	41,7	38,3
3,4—3,6	13,9	16,7
Total	100%	100%

The differentiation of food rations in respect of weight had an indirect effect through body weight upon the survival of chicks in these breeding groups which were under pressure from *Stercorarius skua lonnbergi* (Mathews, 1912), for Brown Skuas killed chiefly chicks from twin pairs, above 26 days old, with a lower body weight (Table XXI).

Table XX

Relationship between the weight of a portion, the body weight of chicks in the final phase of growth (final phase of moult) and the number of chicks in a clutch

Species	Breeding season	Weight of food ration, in g				Body weight, in g			
		1 chick per pair	2 chicks per pair			1 chick per pair	2 chicks per pair		
			chick 1	chick 2	Average		chick 1	chick 2	Average
Pygoscelis papua	1978/1979	625 ± 53 (N = 28)	* 529 ± 49 (N = 18)	447 ± 85 (N = 18)	488 ± 60 (N = 36)	5104 ± 196	5083 ± 59	4767 ± 57	4903 ± 57
	1979/1980	580 ± 120 (N = 30)	549 ± 121 (N = 15)	442 ± 185 (N = 15)	495 ± 153 (N = 30)	5054 ± 192	4791 ± 242	4413 ± 237	4602 ± 240
	1980/1981	560 ± 192 (N = 30)	489 ± 120 (N = 32)	420 ± 184 (N = 32)	459 ± 148 (N = 64)	4919 ± 232	4698 ± 308	4346 ± 365	4522 ± 346
Pygoscelis kdeliae	1978/1979	713 ± 107 (N = 40)	486 ± 84 (N = 21)	380 ± 60 (N = 21)	441 ± 83 (N = 42)	4000 ± 200	3561 ± 140	3276 ± 125	3418 ± 200
	1979/1980	744 ± 82 (N = 14)	606 ± 50 (N = 7)	362 ± 55 (N = 7)	484 ± 53 (N = 14)	3850 ± 120	3576 ± 119	3324 ± 100	3450 ± 118
	1980/1981	684 ± 96 (N = 93)	601 ± 25 (N = 24)	359 ± 51 (N = 24)	480 ± 49 (N = 48)	3930 ± 132	3757 ± 104	3400 ± 120	3579 ± 112
Pygoscelis kntarctica	1978/1979	480 ± 50 (N = 22)	444 ± 41 (N = 22)	400 ± 57 (N = 22)	422 ± 48 (N = 44)	3920 ± 80	3780 ± 59	3657 ± 51	3678 ± 509
	1979/1980	385 ± 44 (N = 31)	308 ± 52 (N = 17)	248 ± 82 (N = 17)	278 ± 60 (N = 34)	3936 ± 121	3692 ± 98	3457 ± 192	3574 ± 124
	1980/1981	421 ± 48 (N = 20)	313 ± 50 (N = 20)	254 ± 62 (N = 20)	283 ± 55 (N = 40)	3746 ± 168	3646 ± 258	3025 ± 321	3335 ± 258

IV. DISCUSSION

As regards Gentoo and Chinstrap penguins, during the period of chick feeding either parent went out to sea once daily and so the young, more than 15 days of age, received food twice a day (i.e., from either parent). On the other hand, the Adélie chicks were fed only once daily, since the food-supplying parents changed over every 24 hrs until the chicks entered crèches. Then both parents began foraging every day, but the chicks still received food once daily, because the parents took turns in supplying food. It should be supposed that the differences in frequency of chick feeding resulted from the hereditarily fixed feeding habits of the species derived from different geographical regions. Adélie penguins have been numbered among the continental forms, Gentoo and Chinstrap penguins among the subcontinental ones (KOROTKEVICH, 1960; WATSON et all., 1971). The colonies of Adélies on the continent are sometimes 10—15 km (MURPHY, 1936) and even 22—97 km (TAYLOR, 1962; PRYOR, 1968) away from the sea free from ice. The climatic conditions prevailing on the continent made the birds develop adaptations permitting them to take food at long intervals. There, some species of flying birds, which sometimes nest a long distance from the sea, also receive food once a day (KONOVALOV and SULIATIN, 1964; SØMME, 1977).

The different foraging rhythms of the three species of the genus *Pygoscelis* caused also differences in the habits of chick guarding. When one of the Gentoo or Chinstrap parents was busy foraging, the other stayed at the nest to guard the young. This system of guarding was also practised by Adélie penguins until the chicks had developed thermoregulation, i.e. until they began to join in créches after the 20th day of life. To be sure, during the following growth stage of chicks both their parents stayed out of the colony at the same time for many hours, but then great differences appeared in the foraging rhythm of particular pairs. Since they arrived with food for their chicks at various times, there were always some adult Adélies in the colony and they guarded the chicks in créches.

The problem of the extent of penetration of foraging penguins is still controversial, because I did not use telemetrical equipment in my investigation. Basing myself on observation I managed only to determine the routes leading to the feeding grounds and roughly to localize these grounds, situated in the close vicinity of King George Island. If the direction of the routes leading to feeding grounds, the swimming speed of the penguins and the time they spent at sea are known, the foraging area can be established according to WILLIAMS and SIEGFRIED (1980). However, the data concerning swimming speeds are very various: from 2.1 to 58 km/hr (WILLIAMS and SIEGFRIED, 1980), for we must be aware of the fact that the mean daily speed of the penguin over a distance of 900 km is different from that attained over the route from the colony to the feeding ground or at the time of foraging. In addition, the calculations carried out by the above-cited authors lack information about the time of effective foraging, which is influenced not only by various concentrations of krill and fish shoals but also by the depth of these shoals. The results of my studies on this problem are not quite representative, as the number of samples was small. Basing myself on 10 observations concerning swimming speed, I found that Adélies swam to and from their feeding grounds at a rate of 10—15 and 6—10 km/hr, respectively (the mean speed at which they travelled in both directions was 9.9 ± 2.4 km/hr). On the other hand, the speed of Gentoo penguins, when they foraged over 2—3 km sections of a submerged krill shoal, ranged from 2 to 4 km/hr (6 observations). On the basis of these observations I determined the time of foraging of penguins on euphausiacean shoals in Ezcurra Inlet. I carried out these observations on 10 Gentoos, 24 Adélies and 198 Chinstraps, marked with yellow dye and red stripes on their flippers before they departed from the colony. The mean time they took to forage in that area was 1.5 hrs for Gentoo penguins, 2 hrs for Adélies and 1 hr for Chinstraps. An analysis of the stomach contents of the birds observed showed that only the Adélies fed exclusively on krill during that forage, whereas the other two species, in spite of the abundance of these crustaceans, ate fish as well. These observations showed besides that the mean travelling speed of the three species was about 10 km/hr. I estimated the distances between the colonies and the other feeding grounds of penguins on the basis of their routes and preliminary information about how long they stayed at sea, the time of effective foraging being allowed for. For simplification I assumed that the circumstances of foraging in the other grounds were similar to those at Ezcurra Inlet. These computations indicate that the feeding grounds of the most krill-eating species (Adélie) were situated farthest from Admiralty Bay (Table XXII). The longest distance between the colony and a feeding ground was 42 km for Gentoo penguins, 165 km for Adelies and 25 km for Chinstraps. WILLIAMS and SIEGFRIED (1980) found that the penguins of the genus *Eudyptes* inhabiting the subantarctic

Table XXII

Mean distances of the penguins' feeding grounds from their colonies in the region of the H. ARCTOWSKI Station calculated on the basis of the time of the birds stay at sea

Species	Distance between the colony and the foraging ground, in km	
	December	January
Pygoscelis papua	5—15 (20—30)	5—10
Pygoscelis adeliae	45—85	40—55
Pygoscelis antarctica	5—15 (10—20)*	5—15

* Figures in brackets refer to small numbers of specimens; it may well be that long time of their stay at sea was due to the presence of sea leopards.

islands covered a distance up to 190 km, the mean radius of foraging penetration being 95 km. It may be inferred from the data given by CROXALL and FURSE (1980) and CROXALL and PRINCE (1980) that the radius of foraging penetration of penguins of the genera *Pygoscelis* and *Eudyptes* in the region of South Georgia and Elephant Island (South Shetlands) was about 50 km. In the area of the present study the penetration radius was similar, for the centre of foraging of the Adélie penguins from the region of Admiralty Bay was situated south-east of Cape Melville. It should however be realized that the results given above are charged with a grievous error, because so far we lack data needed to compute the multiple correlation between the varied estimate of krill concentrations, the shoal depth and the time taken to forage. It seems also that my calculations cannot be generalized indiscriminately for other regions, for the distance of foraging trips depends on the situation of the colony in relation both to the krill concentrations encountered most frequently and to the sea currents that carry these krill concentrations. Moreover, it seems that the regular sea area exploited by penguins should not be computed on the basis of the range of foraging penetration (WILLIAMS and SIEGFRIED, 1980), because krill occurs in concentrations. It would rather be more expedient to evaluate the biocenotic significance of these birds on the basis of the degree to which krill was consumed. Changes in the direction of the routes leading to the feeding grounds in various months prompted us to be supposition that dense concentrations of krill come to Bransfield Strait from the east in the summer. This opinion is supported by CHŁAPOWSKI and GRELOWSKI'S (1978) paper. Literature provides many data on the causes of the formation of krill concentrations and its vertical migrations (e.g. KALINOWSKI, 1978; KALINOWSKI and WITEK, 1980; RAKUSA-SUSZCZEWSKI and OPALIŃSKI, 1978), whereas as regards its long-distance drifts and the terms of translocation during these drifts, lack of data makes itself felt. These data are indispensable to the estimation of the abundance of krill, whereas the so far obtained estimates of the biomass of these crustaceans do not allow for the dynamics of biomass in the same regions.

An analysis of the food composition and the weight proportions of its constituents in the years 1978—1981 may also support the proposition about the shifting of krill, for in the same phenological periods but in different years I found various weight proportions of krill and other constituents in the food of pygoscelid penguins (Tables IX—XV). It was noteworthy that in periods of low krill consumption most crustaceans from the penguins' stomachs showed traces of advanced digestion, which permits the conclusion as to a long stay of the birds at sea and, consequently, a considerable distance of the feeding grounds. The drifting of krill concentrations occurred also during one phenological period as evidenced by an analysis of the Gentoo penguin's food in the winter (fish was the basic food in the first half of June, krill in the second and fish again in the first half of July).

Changes in length observed in krill from the penguins' stomachs in different phenological periods showed that krill grows from spring to winter (Figs. 7—19).

These results confirm the earlier data (JACKOWSKA, 1980; KITTEL, 1980; RAKUSA-SUSZCZEWSKI and STĘPNIK, 1980) gathered on the basis of materials derived from the catches taken from the cutter. The data concerning the body length and the age and sex structures of the krill population in the region of Admiralty Bay presented in my studies and those given by other authors (JACKOWSKA, 1980; KITTEL, 1980; RAKUSA-SUSZCZEWSKI, STĘPNIK, 1980; VOLKMAN et all., 1982) revealed that in the same months of different years the shoals of krill were different. Information coming from this study area therefore confirms the conclusion of WITEK et all. (1980) that the period of the main growth and reproduction of krill in the Antarctic region undergoes changes in particular years.

In the 1977/1978 season the three species of the genus *Pygoscelis* examined ate less krill (data presented by VOLKMAN et all., 1982) than in the following breeding season (author's own data). In a season of lower krill consumption there were distinct differences in the length of euphausiids taken by particular penguin species (VOLKMAN et all., 1982), which induced those authors to state that between the pygoscelid species there exists a subtly operating mechanism of alimentary isolation, connected with the differences in their head morphology (ZUSI, 1975). In a season of great food abundance (1978/1979) I found no such dependence. It may therefore be supposed that the abundance of basic food governs the appearance and disappearance of isolating mechanisms. In my opinion, this problem is however more complicated, as the sympatric species extremely rarely forage together at the same time and this happens only in periods abounding in krill. Sure enough, it is possible that the hereditarily governed morphological differentiation enables these penguins to take specimens of various lengths without competitive pressure from other species. However, a comparison of Figs. 20—22 shows that the range of length measurements of *E. superba* and *E. crystallorophias* was — within the limits of statistically not significant variation — very large both in the same region in successive years and in various regions of the Antarctic. The dimensions of krill eaten up by the three pygoscelid species superimposed on each other within a range of statistically not significant changes (Figs. 20—22). A particularly great dispersion of the length values was observed for the material from the stomachs of Chinstraps (Fig. 21). The information about the length of the krill from penguins' stomachs has hitherto been analysed without taking into account the distribution of their feeding grounds. EMISON'S (1968) paper, in which he describes the differentiation of dimensions in *E. crystallorophias* from the stomachs of Adélie penguins according to their feeding grounds, is an exception in this respect. My materials from the 1980/1981 season also showed great variation in the length of krill in different regions of King George Island and, at the same time, a great resemblance of these dimensions in the krill from the stomachs of the three penguin species feeding in the same region. In the light of these data it seems that the subtle food differentiation found sometimes in the stomachs of particular penguin species is not due to the action of isolating mechanisms connected with

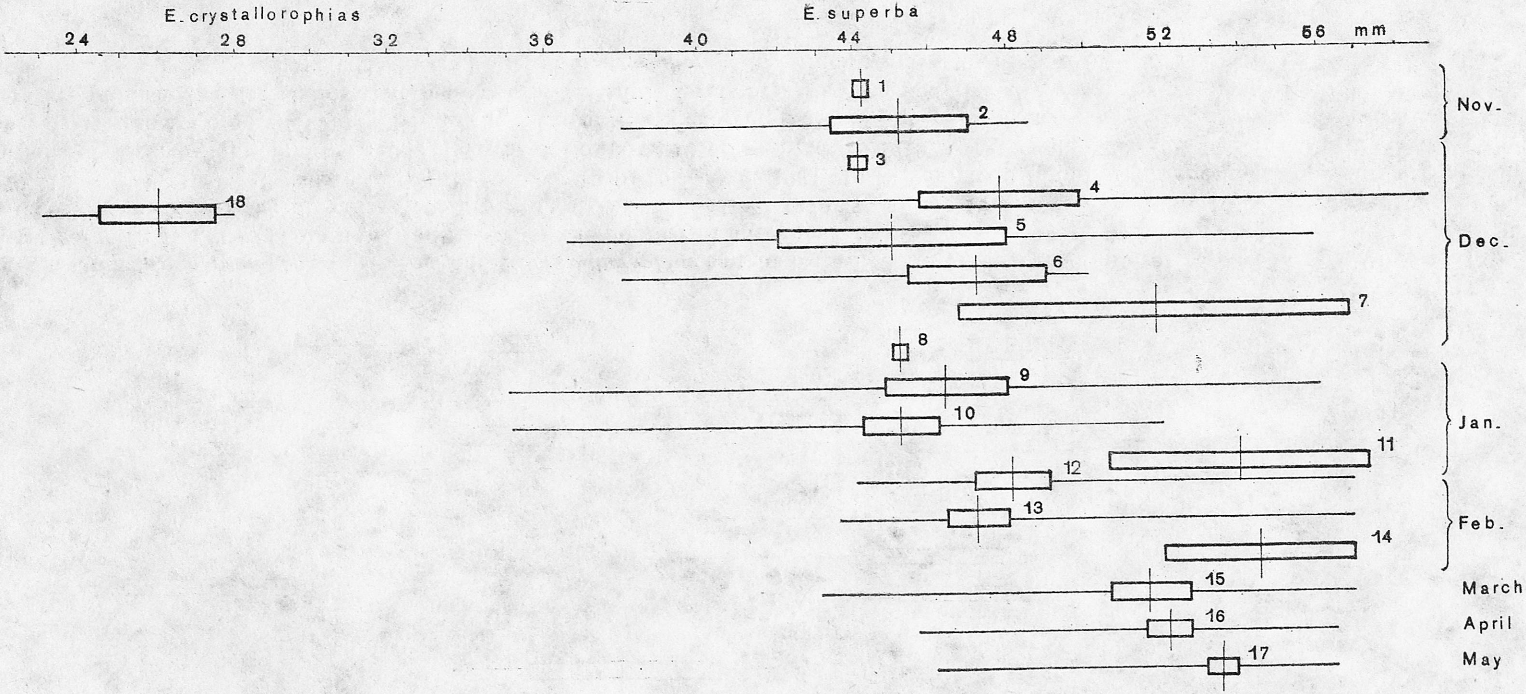

Fig. 20. Length measurements of *Euphausia superba* and *E. crystallorophias* caught by Gentoos in various geographical regions and in particular months. King George I.: 1,3,8 — (Volkman et all, 1982 — the number of specimens measured is given jointly for the whole summer of 1977/78, N = 2014); own materials: 2 — Nov. 1980, 4 — Dec. 1978, 5 — Dec. 1979, 6 — Dec. 1980, 9 — Jan. 1980, 12 — Feb. 1979, 13 — Feb. 1980, 15 — March 1980, 16 — Apr. 1980, 17 — May 1980, 18 — Dec. 1978 (number of specimens measured given in captions of Figs. 7—18); South Georgia (Croxall & Prince, 1980): 7 — Dec. 1976 (N = 47), 11 — Jan. 1977 (N = 310), 14 — Feb. 1977 (N = 186)

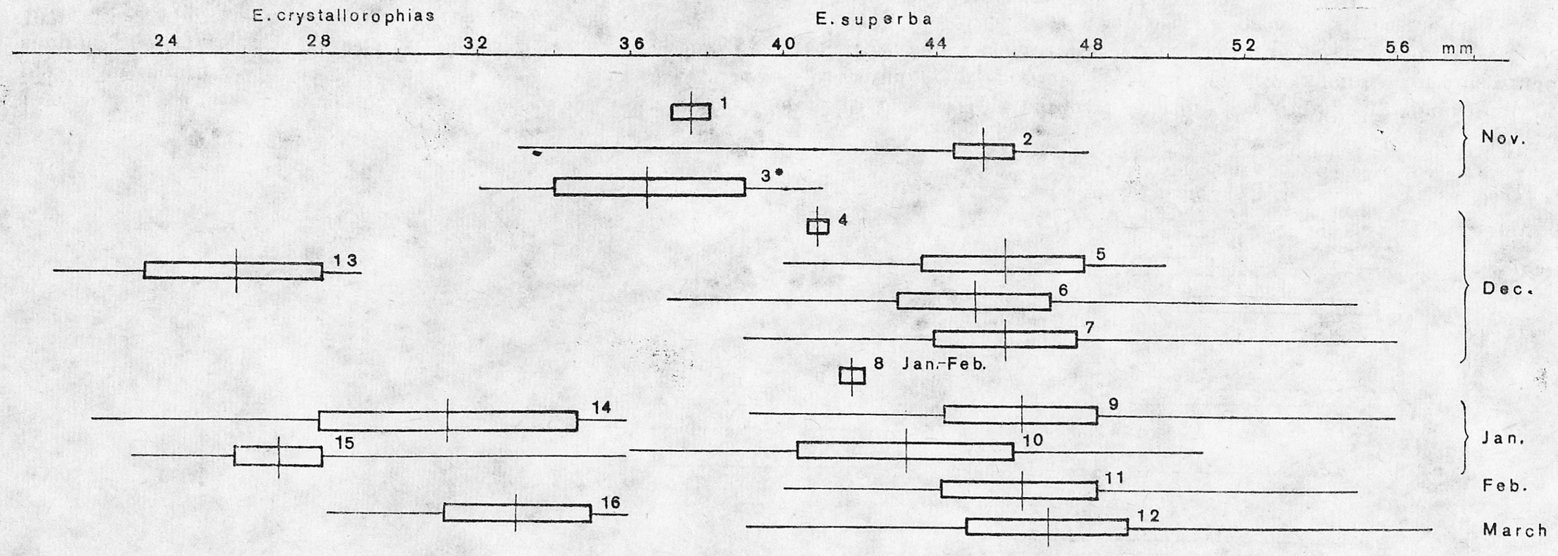

Fig. 21. Dimensions of *Euphausia superba* and ***E. crystallorophias*** caught by Adélies in various geographical regions in particular months. King George I.: 1, 4, 8 — (Volkman et all, 1982, — the number of specimens measured is given jointly for the whole summer of 1977/1978, N = 2046); own materials: 2 — Nov. 1980, 5 — Dec. 1978, 6 — Dec. 1979, 7 — Dec. 1980, 9 — Jan. 1980, 10 — Jan. 1981, 11 — Feb. 1979, 12 — Feb. 1980, 13 — Dec. 1978, 14 — Jan. 1980, 15 — Jan. 1981, 16 — Feb. 1980 (number of specimens measured given in captions of Figs. 7—18); Signy I.: 3 — (White & Conroy, 1975, summer 1972/1973, N = 65). * The dimensions of krill given in the paper by White & Conroy (1975) lie within the range of length characteristic of juvenile specimens of *E. superba*. On the other hand, the literature published so far claims that penguins prefer adult forms of krill. The material described by White & Conroy (1975) may have contained also adult ***E. crystallorophias***, which reaches a length of 32—36 mm

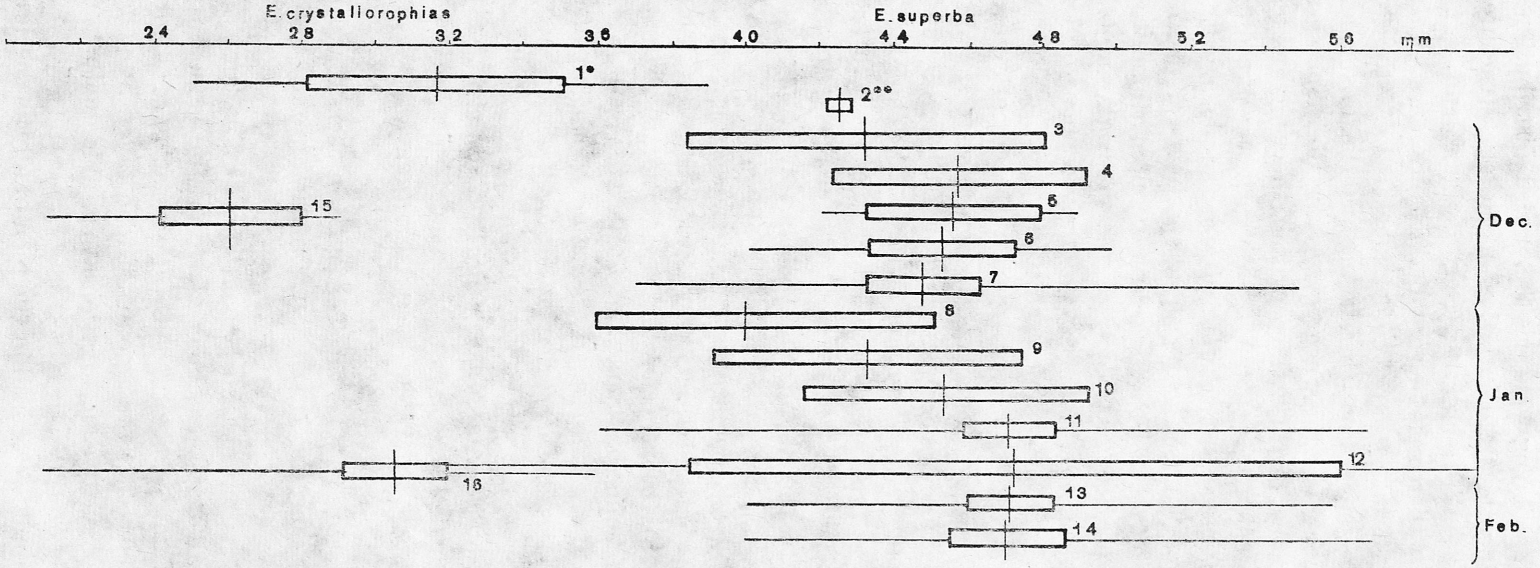

Fig. 22. Dimensions of *Euphausia superba* and *E. crystallorophias* caught by Chinstrap in various geographical regions in particular months. Signy I. 1 — (White & Conroy, 1975 — summer 1972/73, N = 53); King George I. 2 — (Volkman et all., 1982, number of specimens measured given jointly for the whole summer of 1976/1977, N = 1190); own materials: 5 — Dec. 1978, 6 — Dec. 1979, 7 — Dec. 1980, 11 — Jan. 1980, 12 — Jan. 1981, 13 — Feb. 1979, 14 — Feb. 1980 (number of specimens measured given in captions of Figs. 7—18); O'Brien I. (Croxall & Furse, 1980) 3 — Dec. 1976 (N = 40); Clarence I. (Croxall & Furse, 1980) 4 — Dec. 1976 (N = 100), 9 — Jan. 1977 (N = 90); Gibb I. (Croxall & Furse, 1980) 10 — Jan. 1977 (N = 146 *E. superba*); King George I. — own materials: 15 Dec. 1978, 16 Jan. 1981 *(E. crystallorophias)*. * For explanation concerning White and Conroy's (1975) materials the caption of Fig. 21. ** The mean lengths of *Euphausia* in November and January were identical

some differences in their morphology but to the varied distribution of their feeding grounds. In studying the differentiation of the age structure of krill in the area extending from South Georgia to King George Island, Jażdżewski et all. (1978) ascertained that there may be very distinct differences in the length of *E. superba* occurring in various groups in the same area. At the same time the above-mentioned authors pointed out that young krill (i.e. of smaller length) abounds in shelf waters, while the adults aggregate over the slope of the shelf and in the open sea. In connection with the fact that the penguins fed nearly exclusively on adult euphausiids (Figs. 20—22), which in the breeding season were caught in shelf waters, the existence of a distinct preference with respect to the age of krill may be regarded as a fact, for adult specimens of krill, especially females with eggs, are characterized by a higher lipid content than are juvenile stages. This preference was particularly clearly seen at the beginning of summer (Fig. 7), when in the region of Admiralty Bay young specimens of *Euphausia* prevailed in number. At the end of summer, when the period of maturation of krill also comes to an end, the results of measurement of its length on specimens caught in a net and those from the stomachs of penguins were similar (Fig. 8). In connection with penguins' preference for feeding on adult krill, which, according to Jażdżewski et al. (1978), forms groups as far off the shore as the steep shelf slope and in the open sea, the problem arises whether adult forms of these crustaceans occur in coastal waters and in fiords, where penguins, especially Gentoos, foraging nearest to the shore, had their main feeding grounds. It may well be that in summer sea currents drift adult euphausiids from the open sea to shelf regions. Such a displacement of water masses is particularly distinct in the region of the South Shetland Is. (Clowes, 1934; Deacon, 1964; Chłapowski and Grelowski, 1978). It has been found, in addition, that the periodical exchange of water is a phenomenon typical of fiords (Pruszak, 1980).

The mean body length of the amphipods from the stomachs of the Adélie penguins living in the colonies in the region of Admiralty Bay was 19.8 mm and in that of Cape Crozier 16.3 mm (Volkman et all., 1982; Emison, 1968). In respect of length 58% of the amphipods from the stomachs of penguins from the Cape Crozier region ranged between 14 and 25 mm. Also the most specimens of *E. superba* caught by Adélie penguins belonged to the same size group.

In the Admiralty Bay region 96% of the fish found in the stomachs of penguins were less than 75 mm long and in the Cape Crozier region this proportion was 98% (Emison, 1968).

On the basis of the data so far obtained about euphausiids, amphipods and fish consumed by penguins, it may be assumed that these birds most frequently take prey measuring 14—75 mm in length. The differentiation of this dimension is considerable and so it seems that the amount of food taken by penguins depended chiefly on the degree of its concentration at suitable depths and not on subtle differences in length of the prey.

In the years of great abundance of krill in the food of all the species the tendency to feed on fish manifested itself only in some specimens. On the other hand, in the years when in the regions of the colonies there were few concentrations of krill or it was difficult of access, it became evident that food specialization is connected with the foraging abilities of a given species. The individual food specificity also underwent changes in dependence on the phenological rhythm of birds. It may be supposed that irrespective of their not very common individual specialization in complementary-food preference, penguins took food which was the easiest of access in a given period. This relationship is illustrated by rapid changes in the stomach contents of Gentoo penguins in the winter of 1980 (in the first half of June and that of July most specimens fed only on fish and in the second half of June only on krill). The presence of krill shoals in the second half of June was evidenced by its remains in the excrement of other birds: *Macronectes giganteus* (GMELIN 1789), *Larus dominicanus* LICHTENSTEIN 1823 and *Chionis alba* (GMELIN 1789). Neither did all the pygoscelid species take small amounts of krill at the same time, which was probably connected with different situations of their feeding grounds. Examples: in January 1980 only 5% of Gentoos against 64% of Chinstraps ate exclusively *Euphausia*; in January 1981 12.2% of Gentoos had only euphausiids in their stomachs, in February 50.1%, whereas these proportions in Chinstraps are 10.5% in January and 5.0% in February.

So far studies on food composition have been carried out mostly on scanty material collected in different phenological periods. At the time of sampling no division was usually made into breeding specimens, which brought food exclusively for their young, and non-breeders, which caught prey only for themselves. This state of affairs makes the evaluation of food preference in adults of particular species difficult. The most controversial opinions in this respect concern Gentoos basic food (Table XXIII), for krill has been found to make the basis of food of this species in 7 studies and fish in four. Besides, in 2 cases fish was present as a complementary food constituent (i.e. forming more than 20% of the total). However, the views are more uniform as regards food habits in the remaining species (Table XXIII). Krill has been mentioned as the basic food of Adélie penguins in eleven papers and fish in one (in one case fish was also given as a complementary food constituent). In seven studies on Chinstrap penguins krill has been stated to be the main food and only in one fish is classified as a complementary food. Four papers on the diet of Macaroni penguins mention krill as the basic food. It may therefore be assumed that in periods of abundance and accessibility of krill it constitutes the main food of penguins in various regions of the Antarctic. In such periods the differentiation of the diet of Gentoo, Adélie and Chinstrap penguins is slight and the lengths of krill caught similar. Differences in the weight proportions of particular food constituents were not visible until krill became difficult of access or very scarce. In such periods the number of samples containing a mass of euphausiids and amphipods heavily digested increased, indicating a long foraging or distant situations of the feeding grounds. This relationship was particularly distinctly marked in the species

Table XXIII

Composition of penguins' food in various regions of the Antarctic. +++ chief or exclusive sort of food (above 40%); ++ complementary food (20—40%); + additional or sporadic food (up to 20%); — not present

Species	Kind of food			Study area	Authors
	Euphausia	*Pisces*	Others		
Pygoscelis papua	+++	—	—	South Georgia Isl.	Murphy (1936)
	+++	++	—		Croxall, Prince (1980)
	+++	++	—	Kergulen Isl.	Murphy (1936)
	++	+++	+ *(Cephalopoda)*	Heard Isl.	Ealey (1954) after Volkman et all. (1982)
	—	+++	+ *(Gastropoda)*		Downes et all. (1959)
	++	+++	—	South Orkneys Isl. (Signy Isl.)	Conroy, Twelves (1972)
	—	+++	—		White, Conroy (1975)
	+++	+	+ *(Amphipoda)*	South Shetland Isl. (King George Isl.)	Volkman et all. (1982)
	+++	++*	+ ***(Amphipoda, Cephalopoda)***		**This study**
	+++	—	—	Graham Land	**Bagshawe (1938)**
	+++	++	+ ***(Amphipoda)***	West Antarctica	Murphy (1936)
Pygoscelis adeliae	+++	—	—	South Orkneys Isl. (Signy Isl.)	Sladen (1958); White, Conroy (1975)
	+++	+	+ *(Amphipoda)*	South Shetland Isl. King George Isl.)	Volkman et all. (1982)
	+++	+	+ *(Amphipoda)*		This study
	++	+++	—	Palmer Land	Eklund (1945)
	+++	—	—	West Antarctica	Dobrowolski (1925)
	+++	—	—	Ross Sea	Falla (1937) after Volkman et all. (1982)

Table XXIII cont.

Species	Kind of food			Study area	Authors
	Euphausia	*Pisces*	Others		
Pygoscelis adeliae	+++	++	+ *(Amphipoda)*		Emison (1968)
	+++	—	—	Wilkes Land	Lewick (1914)
	+++	—	—	Wilkes Station	Penny (1968)
	+++	+	+ *(Cephalopoda)*	Antarctica and West Antarctica	Murphy (1936)
	+++	—	—	Haswell Isl.	Syroyechkovskiy (1958, 1966)
Pygoscelis antarctica	+++	—	—	South Orkneys Isl. (Signy Isl.)	Sladen (1958); White, Conroy (1975)
	+++	+	—	South Shetland Isl. (O'Brien, Clarence Isl.)	Croxall, Furse (1980)
	+++	+	+ *(Amphipoda)*		Volkman et all. (1982)
	+++	++	+ *(Amphipoda, Gastropoda)*	King George Isl.	This study
	+++	—	—	Graham Land	Bagshawe (1938)
	+++	+	—	West Antarctica	Murphy (1936)
Eudyptes chrysolophus	+++	+	—	South Georgia	Croxal, Prince (1980)
	+++	+	—	South Shetland Isl. (Clarence, Gibbs Isl.)	Croxall, Furse (1980)
	+++	—	—	King George Isl.	This study
	+++	—	+ *(Cephalopoda)*	West Antarctica	Murphy (1936)

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* In various years and seasons the weight proportions of *Euphausia* and *Pisces* changed, but fish constituted chief food only when krill was lacking. For this reason fish has been included in complementary food.

that shows the greatest preference for krill, i.e. in the Adélie penguin. The foregoing data permit the statement that krill is its basic food; it was being sought even in periods of its deficiency. Then it became necessary to take vicarious food, which different species realized to a varying extent. The problem of the operation of the species-isolating mechanism, discussed for a long time, emerges at the evaluation of such phenomena. According to BEKLEMISHEV (1931), commonly active competition leads to the manifestation of various forms of isolation. On this assumption the food isolation of penguins may be interpreted as follows: in the presence of deficiency of common food *(Euphausia)* and under the competitive pressure of other species, at the time of foraging penguins employ their fixed morpho-ecological characters, which have been discussed by ZUSI (1975) and DZIERZYNSKI and KORZUN (1977, 1981). According to LACK (1933, 1940, 1944), MACARTHUR (1958), MACARTHUR, R. H. and MACARTHUR, J. W. (1961), permanent isolation between sympatric species occurs owing to the existence of subtle morphological differences. It may therefore be supposed that at the time when *Euphausia* is deficient in the region of feeding grounds penguins take various food because their different morphologies enable the easiest acquisition of food peculiar to the given species. It should be added that in the periods when krill was deficient the three pygoscelid species still maintained different 24-hour rhythms and their feeding grounds overlapped only sporadically. In this connection it may be assumed that the food isolation observed had been conditioned by the birds innate morpho-ecological characteristics and not by the then existing competition.

The estimation of food abundance in particular years is also a controversial problem. To be sure, such estimation was carried out using an echo-sounder in 1981 (KALINOWSKI, 1982), but not in the centres of the feeding grounds of penguins. The biomass of krill north of the island was determined on the basis of data from four stationary points (Nos 54, 62, 63 and 64 — WOLNOMIEJSKI et all., 1982), which were situated outside the range of penetration of the Chinstrap penguin. The estimate of the euphausiid biomass to the south of King George Island was formed on the basis of data from seven stationnary points (Nos 77—80 and 86—88 — WOLNOMIEJSKI et all., 1982), of which four were situated outside the range of foraging penetration of the Gentoo and Chinstrap penguins. During that investigation (BIOMASS — FIBEX, February — 15 March) the Adélie penguins left the colonies nearly completely. In KALINOWSKI'S (1982) opinion, north of the shore of King I. the mean density of krill was 100—1000 t/nM^2 and south of it 10—1000 t/nM^2. It should be added here that in January the krill biomass in Adélies' feeding grounds was considerably higher (100—1000 t/nM^2). In estimating krill supplies for penguins, one should however keep in mind that echo-sounding detected only definite concentrations of these crustaceans, omitting those at depths to 8 m. Neither is it known whether krill groups having a density that eludes recording by echo-sounder are utilized by penguins after all. It should also be remembered that a concentration of krill below 100 m is not easy of access for penguins (KOOYMAN, 1975). On the other hand, investigation on the vertical distribution of krill (e.g. HOLZLÖHNER, 1981) showed that most concentrations of *Euphausiacea* are situated at a depth between 180 and 350 m. In this connection I had to employ a relative estimate of krill supplies. As the reference point for the abundance of krill I assumed the 1978/1979 season, for in that breeding season the weight proportion of *Euphausia* was the highest in the diet of all the species and whales appeared in Admiralty Bay as well as flocks of flying birds which caught euphausiids from the water surface. The catches of krill with a net from the fishing-cutter were also abundant in the 1978/1979 season. Such an evaluation, although very inexact, seemed more reliable, because it had been based on the observations providing evidence of the presence of krill concentrations within the range of the penguins' penetration. I am aware that the suggesting of deficiency of the basic food constituent in various seasons may be controversial, for ANDREWARTHA (1964) put forward the statement that the environmental supplies are excessive. According to STONEHOUSE (1964) and MOUGIN and PREVOST (1980), the density of plankton in the Arctic waters in summer is sufficiently great to meet the food requirements of all animals. There are however no data about these resources in the plankton-penguin relation. It can be seen from STONEHOUSE'S (1964) data that a distinct decrease in the density of zooplankton occurs in January and its level reached then resembles that in the second half of October or at the end of April and the beginning of May. In the season when krill constituted a smaller weight proportion of the penguins' diet a distinct decrease in its mass in the stomachs of adult Gentoos occurred just in January. These two pieces of information support the supposition that there may be periods when penguins' possibilities to catch *Euphausia* are restricted. It is interesting that the maximum *Euphausia* requirement of Adélie penguins (and so the most krill-eating species) fell at the end of December and the beginning of January, that is before that decrease in the density of zooplankton. The spring concentrations of krill are in all probability correlated in time with the spring emergencies of diatoms in the regions of pack-ice. In 1980 the close ice-fields persisted long in the regions of the Weddell Sea and it seems very probable that krill concentrations situated at their edges reached Bransfield Strait later than usual.

The daily food rations of adult penguins did not undergo great changes in were marked differences in the weight proportions of particular food constituents. Considerably greater differences were seen between the mean weights of rations from different phenological periods. These differences were due to penguins' specific adaptations for surviving long periods without taking food thanks to their deposits of fat reserves.

Although there are many works concerning penguins' diet (Table XXIII), there is only scanty information about the mass of daily rations (Table XXIV). The weight of the daily food ration of the Gentoo penguin calculated by me resembles the data presented by CROXALL and PRINCE (1980) and given in Table XXIV. EVERSON (1977) gave a similar value of the daily ration weight for this species. The weight mentioned by MURPHY (1936) and VOLKMAN et all. (1982)

Table XXIV

The weight of food from penguins' stomachs in various regions of the Antarctic (number of samples (N) is given in brackets)

Species	Weight of food, in g	Time of study	Study area	Authors
Pygoscelis papua	500	Summer	South Georgia	Murphy (1936)
	767±127 (N = 3)	December		Croxal, Prince (1980)
	877±228 (N = 10)	January		
	807±198 (N = 10)	January		
	861±155 (N = 10)	February		
	911±321 (N = 10)	February		
	$\bar{x}$ = 857±223 (N = 43)	Dec.-Febr.		
	432 (N = 46)	Nov.-Febr.	South Shetland: King George	Volkman et all. (1982)
	816±240 (N = 130)	November		This study
	798±200 (N = 199)	December		
	752±192 (N = 485)	January		
	853±142 (N = 101)	February		
	$\bar{x}$ = 805±210 (N = 915)	Nov.-Febr.		
Pygoscelis adeliae	250	Summer	West Antarctica	Dobrowolski (1925)
	400	Summer		Murphy (1936)
	350 (N = 48)	Nov.-Febr.	South Shetland: King George	Volkman et all. (1982)
	720±82 (N = 22)	November		This study
	612±131 (N = 281)	December		
	684±125 (N = 107)	January		
	720±121 (N = 82)	February		
	$\bar{x}$ = 687±131 (N = 492)	Nov.-Febr.		
	1000	Jan.-March.	Haswell Isl.	Syroyechkovskiy (1966)
	600 (N = 37)	Dec.-Febr.	Ross Sea	Emison (1968)
Pygoscelis antarctica			South Shetland:	Croxall, Furse (1980)
	185±72 (N = 3)	December	O'Brien Isl.	
	344±98 (N = 10)	December	Clarence Isl.	
	283±120 (N = 10)	January		
	436±152 (N = 5)	January		
	527±178 (N = 16)	Jan.-Febr.	Gibbs Isl.	
	$\bar{x}$ = 387±180 (N = 46)	Dec.-Febr.	Elephant Isl. Group	
	363 (N = 29)	Nov.-Febr.	King George Isl.	Volkman et all. (1982)
	396±178 (N = 30)	November		This study
	457±150 (N = 100)	December		
	480±152 (N = 270)	January		
	531±141 (N = 192)	February		
	$\bar{x}$ = 512±159 (N = 592)	Nov.-Febr.		

Table XXIV cont.

Species	Weight of food, in g	Time of study	Study area	Authors
Eudyptes chrysolophus	697±88 (N = 10) 740±208 (N = 10) 665±95 (N = 10) 657±131 (N = 10) $\bar{x}$ = 692±227 (N = 40)	January January February February Jan.-Febr.	South Georgia	Croxall, Prince (1980)
			South Shetland:	Croxall, Furse (1980)
	300±101 (N = 9)	January	Clarence Isl.	
	452±87 (N = 4)	January	Gibbs Isl.	
	$\bar{x}$ = 347±119 (N = 13)	January	Elephant Isl. Group	
	687 (660—730), N = 5	Jan.-March.	King George Isl.	This study

is strikingly small in comparison with the data above. The material gathered by these authors may have come from parental birds and have been designed for their young. The estimate of the Adélie's food ration is also differentiated. Dobrowolski (1925) writes that the specimens of this species consume not less than 250 g of krill daily and Murphy (1936) mentions 400 g. Volkman et all. (1982) also reported small amounts of food (Table XXIII), but in relation to the present results these data show differences which are statistically not significant. Emison (1968) also presented results much resembling my data (Table XXIV). In the region of the Ross Sea the well-filled stomachs contained 500—1000 g. According to Emison (1968), 62.2% of the stomachs gathered contained 400—1000 g of food. Syroyechkovskiy (1958, 1966) found the largest fillings of stomachs and estimated the mass of food from Adélie's stomach at about 1000 g (Table XXIV). He assumed that it was food designed for chicks (Syroyechkovsky, 1958) and next that such an amount is eaten by an adult or adolescent specimen (Syroyechkovskiy, 1966). The estimate of the amount of food from Chinstraps' stomachs is also differentiated (Table XXIV). The dispersion of Croxall and Furse's (1980) data shows that they took samples from the stomachs of specimens that had eaten their fill and from those of birds that had fed some dozen hours earlier. The former samples contained an amount of food similar by weight to that found by me in this study (Table XXIV). The amount of food observed in stomachs by Volkman et all. (1982) was smaller than that in the present study but their results compared with mine do not show differences that are statistically significant. The tentative data (because of the small number of samples) concerning the amount of food from the stomachs of Macaroni penguins from King George Island and South Georgia are very similar (Table XXIV), whereas a small number of stomachs from Clarence Island (Croxall and Furse, 1980) were derived from specimens that had taken food more than ten hours before sampling.

The following daily ration ranges may be assumed preliminarily on the basis of the data obtained so far for adult specimens of particular species: Gentoo — 750—850 g, Adélie — 550—650 g, Chinstrap — 450—550 g and Macaroni — 650—750 g.

Differences in daily ration between Adélie and Chinstrap penguins also constituted a controversial problem, for the adult Chinstraps consumed less food than did the Adélies, although their body weights were similar. The Adélies ate more krill at that, the calorific value of which is higher than that of fish. To be sure, it may be supposed that the differentiation found was brought about by a higher proportion of fish, which undergoes faster digestion, in the Chinstrap's diet. Thus reasoning we might also suggest that eyes and other fragments of fish were not picked out of the large mass of food and for this reason its proportion in the food presented in the study is lower than the actual one. This reasoning is however contradicted by the data obtained from the period of young nursing in the 1979/1980 season. Then 68.1% of the Chinstrap's food consisted of *Euphausia*, 29.1% of indeterminate mass of *Euphausia* and *Amphipoda* and 2.8% of *Amphipoda* (no fish was found). And so also when fish was lacking, the Chinstrap penguins consumed less food by weight than did the Adélies. There is still another possibility, namely, that the Adélies ate up more food, because their feeding grounds were situated farther and they spent more energy for travel. As regards chicks, I found higher daily rations in Chinstraps as early as the 16th day of life, although the chicks of both species fed nearly exclusively on *Euphausia*. These differences were still observed between the 21st and 25th day of life or in the period when the chicks were leaving the nest. An increase in the weight of the daily ration was then only 20.2% for Chinstrap, 39.7% for Adélie and 60.4% for Gentoo penguins. These differences were due to the varied agility of chicks. The Chinstrap penguins usually nested on rocks and, most likely, because of that their chicks spent more time motionless in the close neighbourhood of the nest. The daily rations of young Chinstrap penguins, higher than those of Adélies, are therefore still more puzzling.

The differences in weight between the daily rations of chicks in consecutive seasons were greater than in the case of adults. It should be assumed that krill was indispensable food-stuff for chicks and this is why at the time of its shortage the daily rations were reduced. It is characteristic that the smallest differences in weight between food rations occurred in the Gentoo penguins, which showed a greater preference for vicarious food.

The changes observed in the mean values of the food weights on consecutive days in the same chicks were in all probability brought about by different conditions of the catching of krill. These data indicate krill's great mobility.

The mean daily ration of young Adélies from large colonies was lower than that from small breeding groups, which nested less densely (Table XIX). The mechanism of this phenomenon should be sought in Adélie penguins habits. At various stages of young nursing a marked number of specimens that had lost their clutches and non-breeders stayed in the colonies (Sapin-Jaloustre, 1955, 1960; Taylor, 1962; Penny, 1968). Many of these birds built nests again and defended their territories. They displayed a "bellicose" attitude and were the so-called "hooligan cocks" of Lewick (1914), Sladen (1955) and Sapin-Jaloustre (1955). In the period when materials which indicate an interrelation between the density of nests and the weights of daily rations were being gathered, a large number of breeding pairs still stayed in their nests and defended the territories. The parental birds that were returning with food for the chicks to their nests or to the chicks in the creches crossed the defended territories, inside which flights were started. During such individual fights, the Adélies often spat the food out. The dispersion of the mean daily rations of chicks changed according to the frequency of these fights and, in consequence, to the frequency of the spitting-out of the food. The fights were more frequent in large breeding groups because of a longer distance from the edge to the centre of the group and a greater density of nests. It should be added here that the density of nests inside the breeding groups examined by me was very great (1.23—2.60 nests/m^2) against the data from the Antarctic continent: 0.49—0.92 nests/m^2 (Penny, 1968) and 0.57—1.47 nests/m^2 (Oelke, 1975). No frequent occurrences of large breeding groups have been observed on the continent (Jabłoński, 1984).

In the land period of chick life food may be an agent that influences the breeding success indirectly in connection with the selective action of the birds of prey (Table XXI). In literature there are many records of predation of penguins by skuas in various Antarctic regions (Stonehouse, 1956; Elklund, 1961; Young, 1963a, b, 1970; Burton, 1968; Spellerberg, 1971, 1975; Wood, 1971; Müller-Schwarze D. and Müller-Schwarze C., 1973; Trillmich, 1978; Trivelpiece et all, 1980). The undernutrition of chicks in the period of growth results in the greatest attenuation of the development of the pectoral muscles (Beshir, 1970), which in the case of penguins seems to decrease their competence for flying from sea predators: sea leopard, sea lion and orca. The relationship between the survival rate of young penguins and the size of food rations may present itself in a different manner from that in other birds occurring in various regions of the temperate zone. The mortality rate of young birds in warmer regions is directly influenced by the limiting effect of food resources in the period of their nestling stage. Lack (1970) analysed that problem in many species. In literature there are also detailed reports on this subject: birds of prey — Mebs (1964), *Corvidae* — Loockie (1955), Rustamov and Mustafaev (1958), Owen (1959), Tenovuo (1963), Riabov (1970), Konstantinov (1971). The selective activity of birds of prey played a considerably smaller role in the temperate zone, after the chicks had left the nests. It might be supposed that food is easier of access under polar conditions and because of that only an indirect effect of this factor on the survival of chicks was observable. In the presence of numerous adaptations of penguins allowing them to live under severe weather conditions, the main factor limiting their survival is predation.

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STRESZCZENIE

Badania prowadziłem na Wyspie Króla Jerzego (Południowe Szetlandy) od 5 XII 1978 roku do 16 II 1979 roku oraz od 10 XII 1979 roku do 14 III 1981 roku. W celu ustalenia dobowego rytmu żerowania oraz tras i areałów żerowiskowych zaobrączkowałem 3 tys. pingwinów. Skład pokarmu oraz jego masę zebrałem z osobników zabitych, poddanych działaniu emetyku (winian amonu) oraz płukaniu żołądków. Próby dotyczące masy pokarmu uzupełnione zostały materiałami z ważenia ptaków. Ptaki dorosłe ważyłem przed ich wyjściem do morza i po powrocie z łowiska. Ocena masy pokarmu młodych wykonana tą metodą dotyczyła osobników, które wychodziły już z gniazd; ważenie odbywało się przed karmieniem i po jego zakończeniu. Materiały uzyskane od młodych do 15 dnia życia zebrałem z prób, które pochodziły z przewiązek okołoszyjnych. W tym okresie życia pokarm podawany był przez osobniki rodzicielskie w oddzielnych pakietach w dużych odstępach czasu. Dobową rację pokarmową dla tych młodych obliczyłem z przemnożenia średniej masy jednego pakietu oraz średniej liczby karmień w ciągu doby.

W okresie poprzedzającym wykluwanie się młodych oraz w okresie polęgowym pingwiny odżywiały się nieregularnie (Jabłoński in press b). W okresie karmienia młodych dorosłe *P. papua* i *P. antarctica* żerowały 1 raz dziennie, a młode otrzymywały pokarm od obu osobników rodzicielskich. Dorosłe *P. adeliae* odżywiały się co drugi dzień do czasu wyjścia młodych poza gniazdo, a w następnych etapach rozwoju młodych codziennie. Młode adele otrzymywały pożywienie 1 raz w ciągu doby. Wymienione gatunki reprezentowały odmienny rytm dobowej aktywności żerowiskowej (ryc. 2, 3, 4). Areały łowcze *P. papua* i *P. antarctica* zlokalizowane były najczęściej w odległości 5—15 km od kolonii, a *P. adeliae* powyżej 40 km. Należy sądzić, że zróżnicowanie rytmu dobowego oraz oddalenie łowisk od kolonii uwarunkowane było odmiennym pochodzeniem gatunków. Gatunki o pochodzeniu subantarktycznym (tj. *P. papua* i *P. antarctica*) mogą w areale swojego zasięgu żerować bliżej kolonii ze względu na małe zalodzenie morza. Kolonie ptaków o pochodzeniu kontynentalnym (jak *P. adeliae*) oddziela natomiast na początku lata rozległy pas lodu od otwartej

wody (10—20 km, wyjątkowo 97 km). W takich warunkach zmiana osobników rodzicielskich w ciągu kilkunastu godzin jest niemożliwa. Główne areały łowcze pingwinów zasiedlających Zatokę Admiralicji znajdowały się w Cieśninie Bransfielda. Lokalizacja tych areałów ulegała zmianie w zależności od nanoszenia kryla przez prądy morskie w kierunku zachodnim. Długość kryla wzrastała od wiosny do zimy (ryc. 7—18), ale na początku lata pingwiny łowiły wybiórczo dorosłe formy kryla, ponieważ zawierały one więcej lipidów. W okresach, kiedy kryla było mało lub był on trudno dostępny, dało się zauważyć przypadki zróżnicowania jego długości w pokarmie poszczególnych gatunków. Nie należy jednak sądzić, aby spowodowane to było działaniem subtelnych mechanizmów izolujących, które ujawniały się wskutek konkurencji międzygatunkowej. Ponadto próby pokarmowe pobrane w czasie tych samych dni w różnych areałów łowczych wykazały, że w tych samych areałach pingwiny różnych gatunków zjadały kryla o zbliżonej długości. Stwierdzone zróżnicowanie wymiarów kryla z żołądków pingwinów spowodowane było eksploatacją różnych skupień skorupiaków w odmiennych areałach łowczych.

W okresach obfitości i dostępności kryla stanowił on podstawowy pokarm wszystkich gatunków. W takich okresach zróżnicowanie między trzema sympatrycznymi gatunkami z rodzaju *Pygoscelis* było niewielkie, a długość kryla zbliżona. W okresie niedoboru kryla w zasięgu penetracji pingwinów ujawniły się dopiero predyspozycje do zdobywania pokarmu zastępczego (głównie ryb), dzięki istnieniu odmiennych zwyczajów żerowiskowych oraz odmiennej morfologii. Dobowe racje pokarmowe dorosłych nie ulegały większym wahaniom w następujących po sobie latach, pomimo znacznego zróżnicowania wagowego poszczególnych składników pożywienia (tab. IX, X, XI). Znacznie większe różnice uwidoczniły się natomiast w poszczególnych okresach fenologicznych. Szczególnie wyraźne różnice w masie dobowej racji pokarmu istniały w okresach poprzedzających pierzenie, po zmianie piór oraz po okresie długiego przebywania na lądzie w czasie zajmowania kolonii. Na podstawie własnych materiałów oraz danych z piśmiennictwa (tab. XXIV) można przyjąć, że przeciętna masa racji dobowej z różnych okresów fenologicznych mieści się w przedziale 750—850 g dla *P. papua*, 550—650 g dla *P. adeliae*, 450—550 g dla *P. antarctica* oraz 650—750 g dla *E. chrysolophus*. Różnice w dobowych racjach pokarmu młodych powyżej 15 dnia życia w następujących po sobie latach były wyższe niż u dorosłych. Można przypuszczać, że kryl był niezbędnym pokarmem dla młodych w okresie wzrostu i dlatego w okresach jego niedoboru osobniki rodzicielskie nie łowiły w większej ilości pokarmu zastępczego. Ze względu na ograniczony czas łowienia, porcje pokarmu w okresach niedoboru kryla były mniejsze. Oprócz zmian masy racji dobowej w następujących po sobie sezonach lęgowych, uwidoczniły się też różnice w masie tych racji w poszczególnych dniach. Można przypuszczać, że spowodowały to odmienne warunki łowienia kryla. Średnia racja pokarmu młodych adeli z dużych grup lęgowych była niższa niż z grup małych, w których pingwiny gnieździły się w mniejszym zagęszczeniu (tab. XIX). Zjawisko to uwarunkowane było wojowniczością adeli, a zwłaszcza osobników nielęgowych lub tych, które utraciły lęgi. Te wojowniczo nastawione osobniki zostały określone przez Lewicka (1914), Sladena (1955) i Sapin--Jaloustre (1955) mianem "Hooligan cocks". W miarę wzrostu zagęszczenia gniazd i dystansu dzielącego krawędź kolonii od jej wnętrza wzrastała liczba walk, w czasie których najedzone osobniki wypluwały część pokarmu przeznaczonego dla młodych. Według opinii Beshira (1970), niedożywienie powoduje zmiany w rozwoju mięśni piersiowych. Należy sądzić, że niedożywione osobniki w okresie pelagicznego okresu życia będą bardziej narażone na ataki ze strony drapieżników. Pośredni wpływ pokarmu na przeżywanie młodych ujawnił się wyraźnie jeszcze w okresie przebywania młodych na lądzie. Skua chwytały bowiem selektywnie dorastające młode o mniejszej masie ciała (tab. XXI). Przytoczone materiały upoważniają do stwierdzenia, że w warunkach polarnych istnieje inny mechanizm działania pokarmu jako czynnika ograniczającego liczebność młodych niż w strefie klimatu umiarkowanego. Na skutek większej dostępności pokarmu w rejonach polarnych uwidacznia się tam tylko jego pośrednie oddziaływanie przez selektywną rolę drapieżników. W klimacie umiarkowanym presja drapieżników jest mniejsza, ale mniejsza jest też dostępność zasobów pokarmowych. W takich sytuacjach pokarm wpływa bezpośrednio na przeżywalność młodych (Lack, 1947; Loockie, 1955; Rustamov, Mustafaev, 1958; Owen, 1959; Rustamov, 1959; Tenovuo, 1963; Mebs, 1964; Riabov, 1970).

Redaktor pracy: prof. dr Z. Bocheński

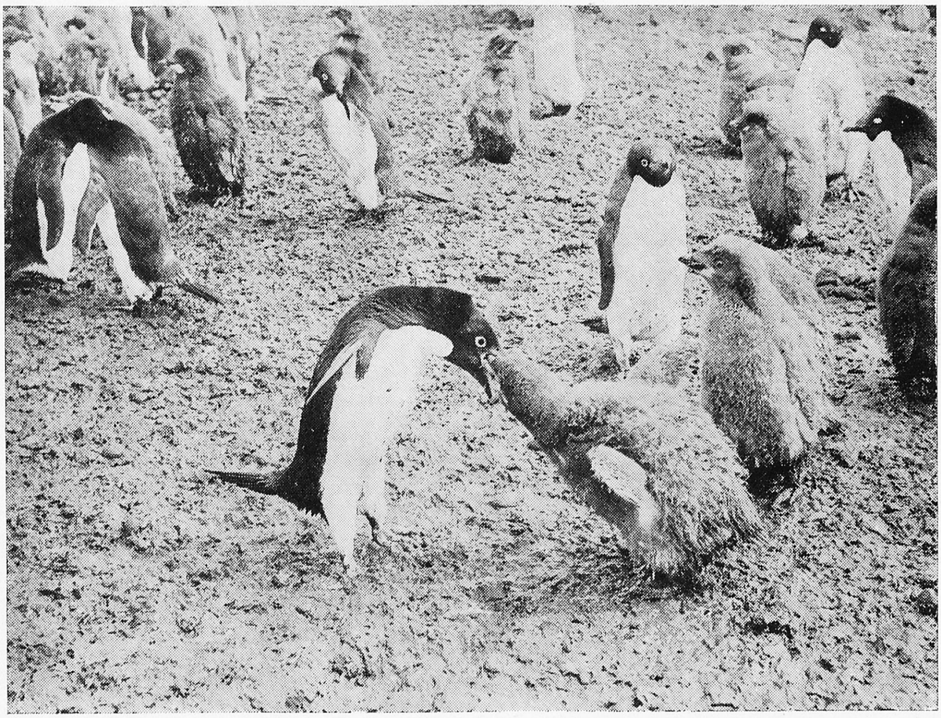
Plate XII

Feeding of the young *Pygoscelis adeliae*

Phot. 1. Young taking first morsels of food from the edge of the beak of its parent

Phot. 2. Young taking last morsel of food by putting its head into the gullet of its parent

Phot. B. Jabłoński



Phot. 1

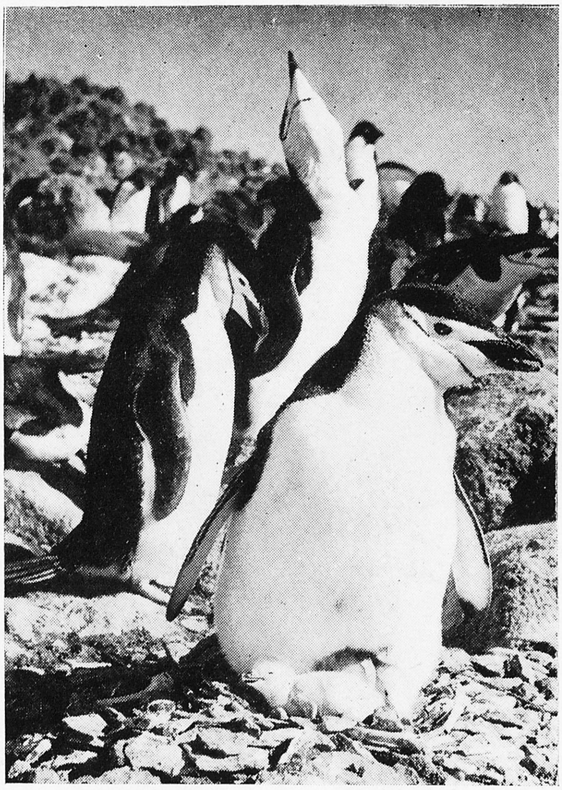
Phot. 2

B. Jabłoński

Plate XIII

Phot. 3. A couple of young of *Pygoscelis antarctica* at an age of 10 days at a poot of a parent
Phot. 4. *Pygoscelis papua* — feeding of young 10—15 days old

Phot. B. Jabłoński



Phot. 3

Phot. 4

B. Jabłoński