

BREEDING BIOLOGY OF THE SNOW PETREL NEAR CAPE HALLETT, ANTARCTICA

By WILLIAM J. MAHER

With the possible exception of the South Polar Skua (*Catharacta skua maccormicki*), the Snow Petrel (*Pagodroma nivea*) has the most southern distribution of any bird. It has been found nesting in rocky areas on the perimeter of Antarctica and also well inland in isolated mountain ranges which project from the antarctic ice cap (Løvenskiold, 1960). North of the continent it breeds only in the South Orkney Islands and South Georgia. It is rarely found outside the ice pack either in summer or winter. Although the bird has been observed by almost every naturalist who has visited Antarctica, little is known of its biology, and the information available is widely scattered. Murphy (1936) and Falla (1937) have summarized data available. There appears to be no adequate summary of the information which has become available since their writings.

From October 30, 1960, to March 10, 1961, a period of approximately 100 days, I was at Cape Hallett in Victoria Land, Antarctica. During this period I made some observations on the Snow Petrel incidental to my main work on the South Polar Skua. These observations are the basis of this report. My objectives in this paper are threefold: (1) To present the data obtained at Cape Hallett, (2) to summarize the breeding biology of the species on the basis of my observations and the literature, and (3) to discuss what adaptations the species seems to have evolved for breeding in the antarctic.

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DESCRIPTION OF THE ENVIRONMENT

Hallett Station is located near the northeast corner of Victoria Land at latitude 72° 18' S and longitude 170° 18' E (fig. 1). The station is situated on a low peninsula, approximately 40 acres in area, which projects westward from the tip of Cape Hallett. The maximum elevation of the peninsula is about ten feet. A large colony of Adelie Penguins (*Pygoscelis adeliae*) occupies most of the site. It was possible to inspect the shores of Edisto Inlet for nesting petrels in October and November when the ice was strong enough for travel. The inlet is approximately seven miles long and three miles wide and opens to the north on Moubray Bay and the Ross Sea. The cliffs which form its eastern and western sides are 300 to 1200 feet high. Those on the eastern side are of volcanic material, whereas the cliffs on the western side are of a fine grained metamorphic rock.

CLIMATE

Climatic data for Cape Hallett are available from July, 1957, when the station was established. The climate is severely cold, the mean annual temperature being 4.3°F. Monthly averages of the daily maximum, minimum, and mean temperatures are shown in table 1. The monthly average mean temperatures never rise above freezing; they range from -17.3°F. in August, the coldest month, to 29.9°F. in January, the warmest

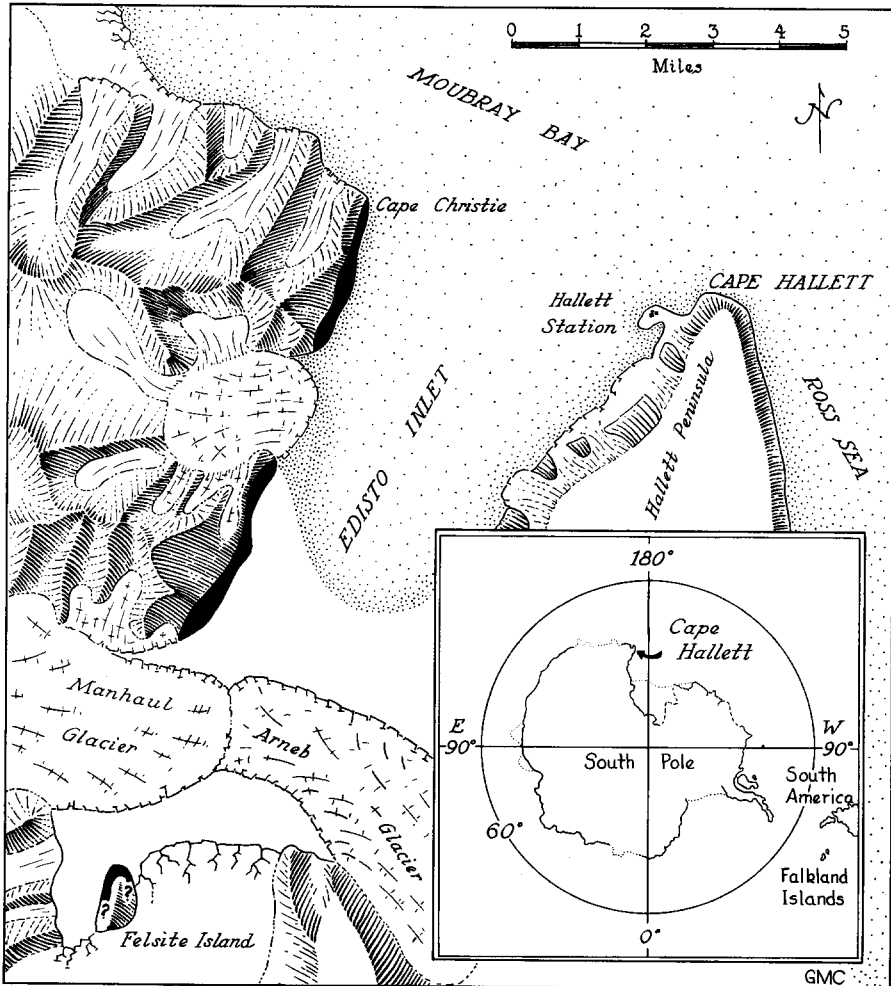


Fig. 1. Map of Cape Hallett Region, Antarctica. Solid black areas indicate breeding cliffs of Snow Petrels (*Pagodroma nivea*).

month. The average maximum temperatures, however, are above freezing in December and January and are almost 30°F. in February. Frost occurs during the entire year. All precipitation is in the form of snow or frost. The annual total precipitation (table 1) is 90.1 inches with a water equivalent of approximately 9 inches. At all times of the year the periphery of Antarctica is subject to strong winds which flow down from the continental ice mass. Thus, in the austral summer of 1960-1961, October had 66 hours in which the wind was 20 knots or more for at least three hours, November had none, December 41, January 20, February 203, and the first nine days of March 87. The occurrence and timing of these storms can have important consequences to breeding bird populations by interfering with foraging of adult birds and feeding of the young. In these storms nesting cavities are packed with snow and birds incubating in the open are often buried.

OBSERVATIONS AT CAPE HALLETT

Snow Petrels nest in rock crevices, usually in inaccessible situations, although Clarke (1906) found nests in the South Orkney Islands in a cave only 25 feet above the sea. At Cape Hallett the volcanic rocks of the eastern side of Edisto Inlet do not provide suitable nesting cavities and few petrels were seen there. A few were reported, apparently nesting, about the castellated top of the cape itself on November 13 by a station member who climbed the cliff. The main breeding areas for Snow Petrels at the cape

TABLE 1
CLIMATIC DATA FROM CAPE HALLETT, JULY, 1957, TO JANUARY, 1961

Month	Average monthly temperatures, °F.			Average precipitation
	Mean	Maximum	Minimum	Snowfall in inches
January	29.9	35.3	24.8	9.0
February	26.2	29.9	22.9	8.4
March	14.5	16.7	12.0	21.1
April	- 0.8	5.4	- 3.7	7.1
May	- 9.6	- 3.9	-15.3	14.9
June	- 9.8	- 4.0	-15.9	3.2
July	-15.7	- 7.3	-22.0	13.5
August	-17.3	- 7.5	-24.1	4.2
September	-10.3	- 3.8	-21.2	3.1
October	0.6	4.3	-10.5	3.9
November	15.9	20.5	8.9	0.2
December	28.5	33.7	23.3	1.5

were two cliffs on the west side of the bay. Each was three miles long and ranged from approximately 300 to 1200 feet in height. Petrels nested all along these cliffs; they were especially numerous near the top. The north and northwest side of Felsite Island (fig. 1) were visited on November 16 by Keith Wise, who reported the birds present and apparently breeding there also. I did not observe this colony.

Snow Petrels arrived at Cape Hallett on October 31 when one was seen flying over the station, and another was seen along the cliffs on the west side of Edisto Inlet. The rise in local numbers was gradual after this. On November 4 two flocks of 13 and 15 were seen. "A couple of dozen" were seen at the breeding cliffs on November 7. On November 9 five occupied nest cavities were found within 150 feet of the bottom of the cliffs. Three of the nests contained two birds and two of them had one bird each. Three of the nest cavities were one to two feet deep, two were more than four feet deep. There was much snow in the cavities and the petrels had obviously dug out some snow to get in. The birds did not attempt to escape although they had opportunity to do so. Defense was by the ejection of orange colored oily fluid. Fourteen specimens were taken from nest cavities by the people in the party. No eggs were found.

In the next week several groups of birds were seen flying west toward the breeding cliffs, and some were flying east over Cape Hallett toward the Ross Sea. On November 17 a large flight of petrels passed over the station heading toward the cliffs. The birds were first observed at 6:15 p.m. Two ten minute counts were made from 6:20 to 6:30 p.m., and from 7:35 to 7:45 p.m. A total of 471 birds was seen in the former interval, a rate of 2800 birds per hour, and 259 in the latter interval, a rate of 1500 birds per hour. A few birds were flying over the station at 8:30 p.m. and none was seen in a final check at 10:30 p.m. I estimated that a minimum of four to five thousand birds passed over the

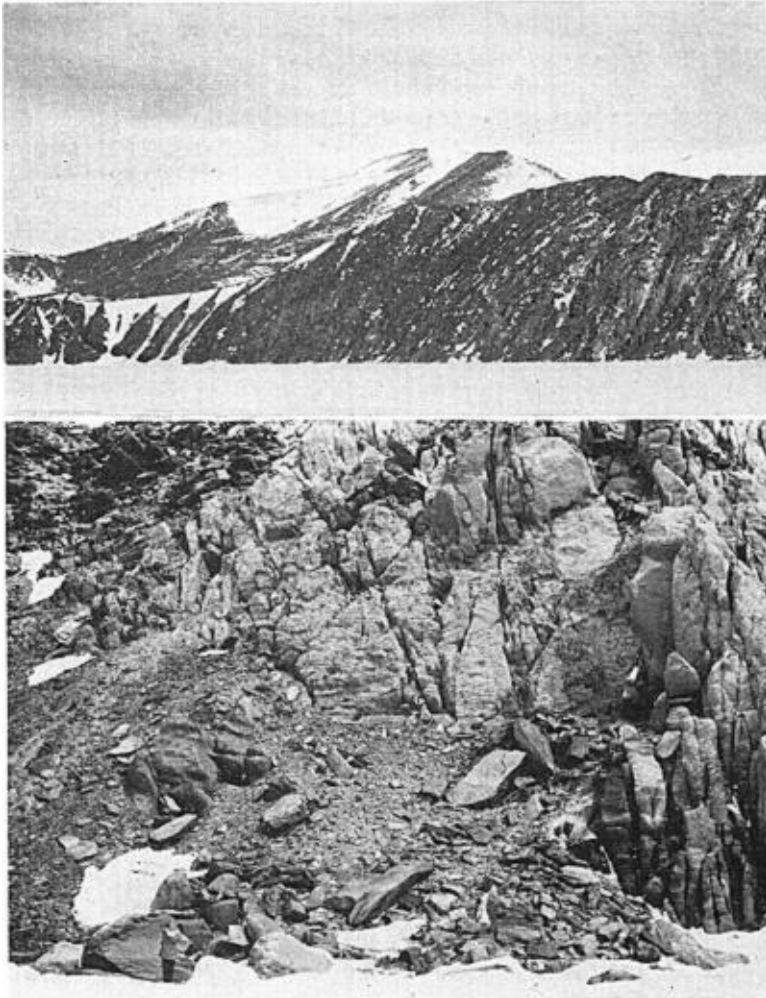


Fig. 2. Above: Southernmost of two main breeding cliffs of Snow Petrels. Maximum height of cliff is about 1200 feet. Breeding petrels were concentrated in the upper portion of the cliff.

Below: Detailed view of bottom of same cliff showing the nature of the rock which provides numerous nesting cavities for petrels.

station in this flight. The following day, November 18, a few small groups of up to 14 birds were seen flying east toward the Ross Sea.

The nest cliffs were visited on November 21. Only an occasional petrel was seen. No birds were found in 12 active nest cavities on the lower part of the cliff. Three of at least twenty active nest cavities seen at the top of the cliff were occupied. A total of two or three adults was seen flying about the upper part of the cliff. Five specimens were collected on this visit. Again no eggs were found.

Very few adults were seen flying over the station from November 21 to 29. On November 29 approximately 110 active nest cavities situated near the top of the cliff were

inspected. Two nests were occupied by single birds. Birds were noted as being scarcer than on the previous visit. One specimen was collected. No eggs were found.

After this visit the ice on the inlet became impassable, and no further visits to the nest cliffs could be made. From December 1 through 8 occasional flocks of up to 100 petrels were seen flying westward over Cape Hallett toward the nest cliffs, although no mass flight such as the one on November 17 was observed. Snow Petrels were rarely seen during the remainder of December, January, and February. This may have been because ice on the sea in Moubray Bay and the adjacent Ross Sea opened and the birds traveled to and from the breeding areas over the water rather than over the 1000-foot high cape.

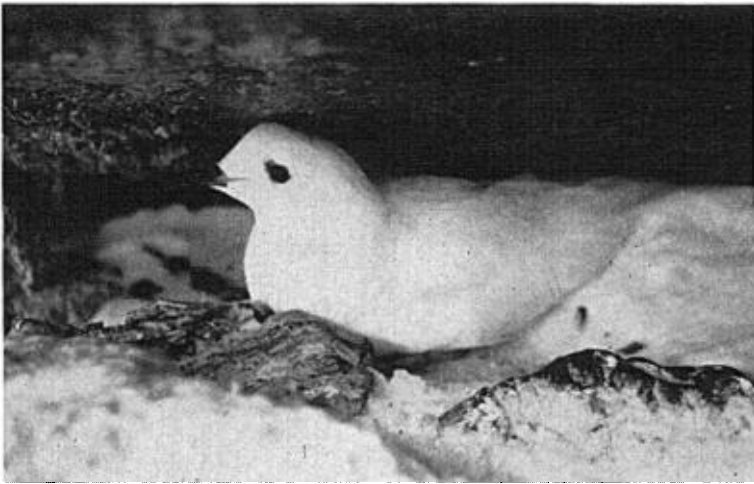


Fig. 3. Adult Snow Petrel in nest cavity in pre-egg period. Snow still present in nest.

A final visit to the petrel cliffs was made on March 6 by helicopter. On this visit only two adult petrels were seen in four hours. Many nest cavities which appeared active were inspected before a chick was found. A total of six live chicks was seen. All appeared almost ready to fly. They were fully feathered with only a few wisps of natal down still adhering to their feathers. One was seen on an exposed ledge exercising its wings. None attempted to fly when disturbed. The chicks were still being fed by the adults, as was suggested by the fact that one regurgitated pieces of fish and a fish vertebral column.

SPECIMENS COLLECTED

Data on the 25 specimens collected are given in table 2. Fourteen of 20 adults taken were male. There is no significant sexual dimorphism in weight, the adult males averaged 269.3 gm. and the females 263.1 gm. The testes of the males were fully enlarged on November 9 and showed no change in size on November 21. The follicles of the females were beginning to enlarge on November 9. The specimen taken on November 21 showed no increase in follicle size. The one taken on November 29 had one follicle slightly larger than that in any other female taken. This bird had soil on its ventral feathers suggesting that it had scraped a nest bowl.

The range of weights of the five juveniles was great. Two were of adult weight, and three were much less. The lightest one was little more than one-half the weight of the

TABLE 2

DATA ON SPECIMENS OF SNOW PETREL COLLECTED AT CAPE HALLETT

Date	Sex	Weight in gm.	Testis or follicle size in mm.		Fat**	Remarks
November 9	M	312	16.8	13.7	H	No molt
	M	307	18.4	14.0	H	Molt, few contour feathers
	*M	263	16.4	12.6	VH	
	*M	301	16.4	11.6	H	Molt, contour feathers
	M	307	16	12	H	No molt
	M	255	15.7	11.7	H	
	M	285	16.5	12.0	H	No molt
	M	274	18.2	12.3	VH	
	*M	307	17.0	13.2	VH	Molt, contour feathers
	*M	284	17.7	13.1	VH	
November 21	M	258	16.8	11.6	H	Molt extensive in dorsal, ventral, capital tracts
	*M	226	14.5	9.4	Mod.	No molt
	M	246	18.4	12.8	Mod.	No molt
	*M	244	16.7	11.7	Mod.	
November 9	F	266		3.5	VH	
	*F	302		4.0	VH	Molt, capital tract, heavy
	*F	276		4.2	VH	Molt, contour feathers
	F	260		6	H	Molt, capital tract, heavy; dorsal and ventral tracts, light
November 21	F	246		3.7	Mod.	No molt
November 29	*F	229		6.8	Mod.	Breast dirty as from scraping nest bowl
March 6	M Juv.	276			VH	
	M Juv.	212			H	
	*F Juv.	195			VH	
	F Juv.	264			VH	
	*F Juv.	178			H	

* Specimens deposited at the Dominion Museum, Wellington, New Zealand.

** Fat categories used were: VH, very heavy; H, heavy; Mod., moderate amount; L, little fat.

heaviest. This chick regurgitated several pieces of fish when handled. All the young had large amounts of subcutaneous and intestinal fat.

BREEDING CYCLE OF THE SNOW PETREL

Arrival.—Arrival dates on the continent are as early as August 10 (Eklund, 1945) on the Palmer Peninsula. On the other areas of the continent the arrival dates are generally in October. Falla (1937) reports arrival on October 6 in Enderby Land. Siple and Lindsey (1937) found that they arrived in the Bay of Whales on October 6, 1934, and October 31, 1929. Perkins (1945) reports a pair seen on September 12 in the Bay of Whales; but no other birds were seen from then until October.

Egg laying.—Egg dates in the literature range from November 25 (Clarke, Brown, and Ramsay, 1913) to January 10 (Siple and Lindsey, *op. cit.*) with 38 of 47 records occurring in December. Normal laying dates are probably early in December. Falla (*op. cit.*) reports eggs "recently laid" on December 3 and being laid between then and December 9. Perkins (*op. cit.*) found that on November 27 females had ovaries already enlarged but found no eggs. Siple and Lindsey (*op. cit.*) report eggs in very early stages of incubation on December 19.

Young.—Chicks have been seen as early as January 10 when Løvnskiold (1960) reported one newly hatched. Falla (*op. cit.*) reported one a few days old on January 11

and two others seen on January 13. Clarke, Brown, and Ramsay (*op. cit.*) found one estimated to be one-third grown on January 28. Løvenskiold (*op. cit.*) reported young in the nest on February 12 and 15 in Dronning Maud Land. Falla (*op. cit.*) found chicks almost ready to fly on February 13, and Bierman and Voous (1950) saw young flying in the field on March 19. Gain (1914) collected young birds, estimated three to four months old, on April 9, May 3, and May 6 on the Palmer Peninsula.

Departure.—Departure dates recorded in the literature range from February 8 at McMurdo Sound (Wilson, 1907) to May 15 on the Palmer Peninsula (Eklund, 1945). Siple and Lindsey (1937) give March 13, 1934, as the last sighting in the Bay of Whales, and Falla (1937) reports a large number flying east to west in Enderby Land on April 27.

MOLT

Wilson (1907) reports that molt begins in early January. Bierman and Voous (1950) first observed an adult molting primaries on January 21 and collected one molting male on January 25. Adults collected by them between March 20 and 31 had renewed all of their wing feathers, and all but one had completely replaced the rectrices. All were replacing body feathers.

Thirteen of the 20 adults taken at Cape Hallett were inspected for molt; of these, six of nine taken on November 9 were undergoing body molt. Five were replacing scattered contour feathers, of which one was also molting heavily on the head; one was molting extensively on the head only. One of four taken on November 21 was molting extensively on the head and body. Three others were not molting. Hence it appears that the body molt of this species starts, at least in some members of the population, in early November and continues through the breeding cycle. Molt of primaries appears to begin in early January, replacement continuing until the end of March. Body feather replacement continues into April.

FOOD HABITS

Many authors have stated that the principal food of this species is euphausiid shrimps, particularly the opossum shrimp *Euphausia superba* (Wilson, 1907; Murphy, 1936; Siple and Lindsey, 1937). Small fish are also known to make up a portion of their diet (Eklund, 1945; Clarke, Brown, and Ramsay, 1913; Bierman and Voous, 1950). It appears from examining several sources that fish may be as important as shrimp in the total diet in summer months. Contents of 37 stomachs summarized by Falla (1937), Bierman and Voous (1950), Clarke, Brown, and Ramsay (1913), and Eklund (1945) give the following percentages of food items. Euphausiids occurred in 54 per cent of the stomachs, crustacea in 19, cephalopods in 46, pteropods in 8, fish in 51, and refuse in 3 per cent.

These specimens were taken in the summer months when zooplankton organisms are abundant in the surface waters (Foxton, 1956). Little is known of their food habits in the winter months when zooplankton organisms, and presumably the euphausiids are much less abundant. Gain (1914) has published records of stomach contents of 19 specimens taken in the winter months, April through August, most of which (12, or 63 per cent) were feeding on seals. The stomachs of three contained euphausiids, and only two contained fish.

Of the 25 specimens collected in this study only five had food items in the stomach. Four of these were adults taken on November 9, and one was a chick taken on March 6. Three contained fragments of large crustacea presumed to be *Euphausia*, and two (including the chick already mentioned) contained the remains of fish.

DISCUSSION

The observations on the petrels in the pre-egg period at Cape Hallett are difficult to interpret. The birds were present and relatively numerous on the lower parts of the cliffs examined on November 9. They were also seen flying about the upper part of the cliff at the same time and were presumed to be numerous there also. On the second visit on November 21, the birds were not present on the lower cliff area and were present though very scarce higher up. A week later, November 29, they were rare and only one bird was taken although many nest cavities which appeared active were seen. The lower section of the cliff was not inspected on the third visit. The large passage of petrels westward over Hallett Station on November 17 occurred between the first and second visit. It is possible that this flight marked the return of the bulk of the population to the nest area. Their scarcity on November 21 and virtual absence on November 29 suggests that they may desert the nesting area for a period before egg laying as does the Short-tailed Shearwater, *Puffinus tenuirostris* (Marshall and Serventy, 1956). The flocks seen flying toward the nest area over Hallett Station in early December could then have been the adults returning to the nest to lay eggs.

Information now available indicates that the breeding cycle of the Snow Petrel takes approximately 150 days, or four and one-half to five months. Reported egg dates span 46 days, from November 25 to January 10, and chicks have been found in the nest from January 10 to March 6, a total of 55 days. The earliest sight record of fledged young is March 19, so that the chick period may be as long as 70 days or even more. Thus, on a population basis, the breeding cycle of the species lasts for about 100 to 120 days from egg laying until the young are fledged, and an additional 20 to 30 days between the average date of arrival on the nesting grounds and egg production.

In comparison, the Short-tailed Shearwater, a larger bird (450 to 700 grams), nesting in Bass Strait off southeastern Australia was found to take an average of 148 days from egg laying to fledging (Marshall and Serventy, 1956). The incubation period of this species averaged 54 days, and the chick period 94 days, with a range from 88 to 108 days. The Wilson Petrel (*Oceanites oceanicus*), a much smaller bird (35 to 40 grams) breeding on the Palmer Peninsula, took about 95 days from egg laying to fledging (Roberts, 1940). Another hydrobatid of similar size, the British Storm Petrel (*Hydrobates pelagicus*) breeding in Great Britain averaged about 100 days from egg laying to fledging (Lockley, 1932).

It does not appear as if the Snow Petrel has shortened either its incubation period or the rate of development of the chicks in adapting to the antarctic. Its incubation period appears to be similar to that of the Wilson Petrel which also breeds in Antarctica and may be slightly shorter than that of the much larger Short-tailed Shearwater which breeds in the temperate latitudes of Bass Strait. The chick period of the Snow Petrel, estimated here at more than 70 days, is longer than that of the Wilson Petrel which was determined to be 52 days for one chick (Roberts, 1940), but not as long as that of the Short-tailed Shearwater which averages 94 days in the nest (Marshall and Serventy, 1956).

There is much circumstantial evidence that birds time their breeding cycles so that the young are raised during the portion of the breeding season when food is most abundant (Lack, 1950; 1954). In view of the interest in the causation and significance of the timing of breeding events, I would like to consider the seasonal abundance of the food supply of petrels and the timing of the breeding cycle with respect to food supply. The data on the food habits of the Snow Petrel already discussed indicate that, in the summer months at least, its food consists mainly of euphausiid shrimps and fish in approximately equal amounts.

There is no measurement of the changing levels of abundance of these food species, but Foxton (1956) has published data on the abundance of zooplankton in subantarctic and antarctic waters which seem applicable here. His data, 2185 samples from 366 stations, indicate that within the antarctic zone there is a gradient in the quantity of zooplankton from low to high latitudes reaching a maximum between 50° and 55°, and that there is little circumpolar variation in the zooplankton standing crop. Further, examination of his data on the mean latitudinal variation in quantity of zooplankton in the upper 100 meters of water (table 5, p. 215) indicates that the order of magnitude of the change in volume of zooplankton between the summer and winter months is about the same between 50° and 60° as it is between 60° and 70°. Thus it appears that the mean concentrations for all the antarctic samples should allow a discussion of relative seasonal abundance of the zooplankton in the higher latitudes. In using these data I am assuming that the abundance of the petrel's food is directly related to the amount of zooplankton available, either because of relationship in a common food chain or because of mutual dependence on phytoplankton.

Foxton (1956) found that in antarctic waters there is little seasonal variation in the total standing crop of zooplankton in the entire water column sampled (0 to 1000 meters), but that during the summer months the volume of the zooplankton in the upper 50 meters, as plotted in figure 4, increases from mid-October through mid-December; there is a plateau or a slight decline between mid-December and mid-January, and a second more rapid increase after mid-January. The food supply reaches a peak in mid-

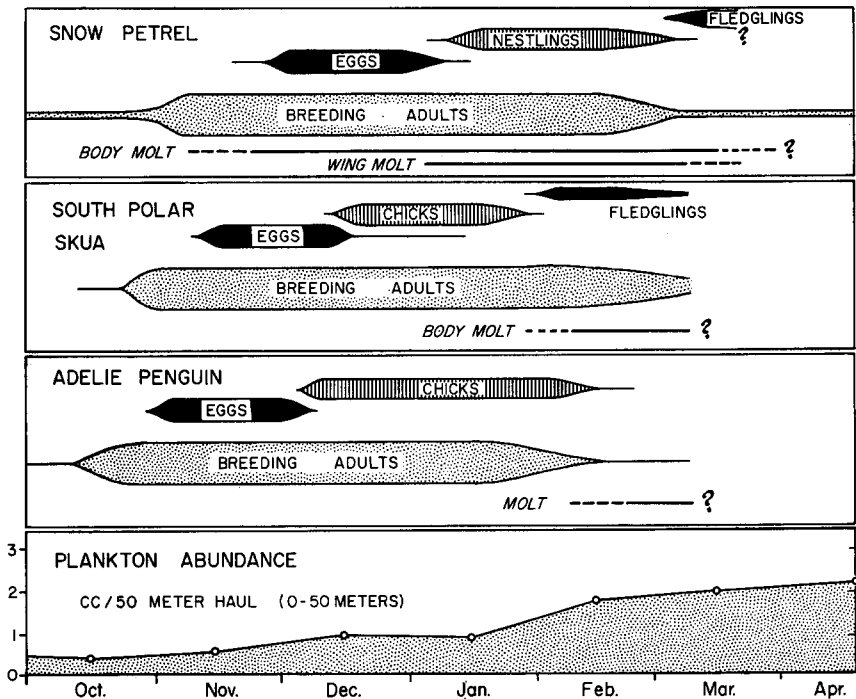


Fig. 4. Comparison of breeding cycle and molt of the Snow Petrel with that of the South Polar Skua (*Catharacta skua*) and the Adelie Penguin (*Pygoscelis adelie*). Seasonal variation in volume of zooplankton is shown at bottom of figure (from Foxton, 1956).

April when all the bird species have left the breeding grounds. The interesting point is that the volume of zooplankton apparently levels off during December and January the two warmest months of the season for terrestrial animals, and begins to increase again in February when the average daily maximum temperature falls below freezing.

The breeding cycle of the Snow Petrel is plotted in figure 4 with those of the South Polar Skua and the Adelie Penguin. The latter two are based on my notes taken at Cape Hallett. The breeding cycle of the Snow Petrel is timed later than that of either the skua or the penguin. Its eggs are produced later than either of the latter, and with its comparatively longer incubation period the chicks do not hatch until early January when those of the latter two species are already well grown. The Snow Petrel thus seems to show no tendency to advance its breeding cycle so as to bring its young out in the warmest period as do the other two species. The food peak is so late in the season that any adjustment to it must be a compromise between food abundance and the onset of subfreezing temperatures. I presume that the present timing is maximally adaptive since it appears that it would be possible for the petrel to alter its cycle and bring the young out earlier in the summer as has been done by the Emperor Penguin, *Aptenodytes forsteri* (Stonehouse, 1953; 1960). The breeding cycle could be advanced by simply shortening the pre-egg period as has been done by the Parasitic Jaeger (*Stercorarius parasiticus*) in northern Alaska (Maher, MS). My observations at Cape Hallett indicate that the species can dig its way into snow-filled burrows several weeks before the eggs are laid, thus it is not limited by the necessity of waiting for the burrows to thaw open.

It appears that the Snow Petrel is faced with two problems in timing its breeding cycle. The breeding cycle must occur within the period in which the climate permits breeding, and secondly it must make the best use of the food supply as it normally occurs in that period. The peak of food abundance is not available in the possible nesting period but occurs just after it.

There are three points in which the present timing may be adaptive. The first point concerns late egg production. The Snow Petrel, in common with other procellariiforms, produces one relatively large egg each breeding season. That of the Short-tailed Shearwater, for example, weighs 85 gm. or 16 per cent of the female's body weight (Marshall and Serventy, 1956). The production of this huge egg must be a considerable metabolic drain on the bird. Marshall and Serventy (1956) have shown that this species regularly deserts its breeding grounds for two to three weeks just prior to egg laying, and that the male incubates the newly laid egg while the female returns to sea, presumably to feed. These facts suggest behavioral adaptations to the effort involved in producing a large egg, that is a period of feeding just prior to and just after egg laying. The delay in egg laying by the Snow Petrel may in fact be necessary for the birds to produce the egg, as their egg laying coincides with the first upswing in the food supply in late November and early December. It is interesting in this connection that in the Emperor Penguin and the Adelie Penguin, the females also return to sea immediately after egg laying while the male does the bulk of the incubating. These two species have an advantage over the Snow Petrel, however, since they "fly" in a more buoyant medium than the petrel does, they can bring to the breeding ground sufficient reserves, in the form of stored fat, to sustain them in the courtship period and in the production of the egg.

The second point is suggested by the observation of Roberts (1940) that the young Wilson Petrel is brooded for only a day or two and then is left alone in the burrow and is fed at night. Also, Farner and Serventy (1959) have shown that the young

Short-tailed Shearwater can maintain adult or near-adult body temperatures when it is one day old. The Snow Petrel does not use nest cavities as protected as those of the Wilson Petrel; many cavities are open to the wind from several directions, although all that I saw were well protected overhead. It does not build a nest as does the Wilson Petrel. The young Snow Petrel has a luxuriant coat of down; and possibly it is also essentially homeothermic a day or two after hatching and can be left alone in the nest. The present timing of hatching is such that in late January when the chicks are partly grown, the second seasonal increase of food supply begins. The chance that sudden cold and stormy weather will kill the chicks is minimized by the early attainment of homeothermy and the species is able to take advantage of an increasing food supply.

Finally, one result of the present timing is that the recently fledged juveniles encounter a maximum food supply in their early period of independence. This may in fact result in enhanced survival in this period, which in other environments is usually one of high mortality for young birds. What is therefore relatively more significant to the petrel population in the long run is not the number of young fledged but the number which survive to become breeding adults.

Body molt begins in the Snow Petrel populations in November. The report by Bierman and Voous (1950) indicates that the molt of the flight feathers occurs during the period in which adults are normally feeding nestlings. The Snow Petrel, then, unlike the skua and Adelie Penguin, performs its annual molt simultaneously with breeding. Complete molt must last approximately five months for the population.

SUMMARY

Observations of the Snow Petrel made in the vicinity of Cape Hallett, Antarctica, in the austral summer of 1960-1961 are presented. It was found that the birds returned to their breeding grounds on October 31. Subsequent observations are interpreted as suggesting that after a gradual increase in numbers and presumably a period of courtship and renovation of nesting cavities, the species deserts the cliffs for a period of feeding at sea prior to egg laying. A visit to the cliffs occupied by petrels on March 6 showed that the petrel chicks were still in the nests and still being fed.

The nesting cycle of the Snow Petrel takes approximately 150 days from arrival until the young fledge. The cycle is found to be late compared with two other species which nest at Cape Hallett, the South Polar Skua and the Adelie Penguin. The lateness is presumed to be adaptive and three features of the timing are discussed with this point of view.

It is suggested that the lateness of egg laying is the result of the metabolic effort of producing the relatively large egg characteristic of the Procellariiformes. The species delays egg production to take advantage of the initial rise in food supply in spring. The survival of nestlings growing in late January, February, and March, as the weather is turning colder, is enhanced by an increasing food supply in that period. Finally, the peak of food supply comes in late autumn as the young are fledging and may assure a relatively high survival in the critical post-fledging period. The timing is thus seen as a series of adaptive compromises related to the short season available for breeding and to the cycle of change in the food supply.

Molt occurs during the breeding cycle.

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