

FALKLAND ISLANDS DEPENDENCIES SURVEY

SCIENTIFIC REPORTS

No. 18

THE BREEDING BEHAVIOUR  
AND REPRODUCTIVE CYCLE OF  
THE WEDDELL SEAL  
(*Leptonychotes weddelli* Lesson)

By

A. W. MANSFIELD, M.A.,  
*Falkland Islands Dependencies Scientific Bureau*  
and  
*Department of Zoology, Cambridge*



LONDON: PUBLISHED FOR THE COLONIAL OFFICE  
BY HER MAJESTY'S STATIONERY OFFICE: 1958

# THE BREEDING BEHAVIOUR AND REPRODUCTIVE CYCLE OF THE WEDDELL SEAL

(*Leptonychotes weddelli* Lesson)

By A. W. MANSFIELD, M.A.

Falkland Islands Dependencies Scientific Bureau  
and  
Department of Zoology, Cambridge

(Manuscript received 1st September, 1954)

## CONTENTS

	PAGE		PAGE
Section I. Introduction ... ..	2	Section IV. The Female Reproductive Cycle ... ..	20
Nomenclature ... ..	2	A. General ... ..	20
Previous Knowledge of the Species ... ..	2	1. <i>Methods</i> ... ..	20
Section II. The Weddell Seal Population of the		2. <i>Reproductive Organs</i> ... ..	20
South Orkney Islands ... ..	2	3. <i>Sexual Maturity</i> ... ..	21
A. Early Records ... ..	2	B. The Normal Ovarian Cycle ... ..	24
B. Factors Affecting Local Distribution ... ..	3	1. <i>Oestrus</i> ... ..	24
C. Ice Conditions and the Breeding Popula-		2. <i>The Corpus Luteum</i> ... ..	25
tion ... ..	5	3. <i>Sub-surface Crypts</i> ... ..	28
D. Winter Distribution ... ..	10	C. The Uterus ... ..	29
Section III. Breeding Behaviour ... ..	10	1. <i>Immature Seals</i> ... ..	29
A. The Adult Female ... ..	10	2. <i>The Uterus in Adult Seals</i> ... ..	30
1. <i>The Haul-out and the Pupping Season</i> ... ..	10	D. The Vagina ... ..	32
2. <i>Birth of the Pup</i> ... ..	11	1. <i>Histological Appearance in Immature</i>	
3. <i>Behaviour Before and After Parturition</i> ... ..	11	<i>Seals</i> ... ..	32
4. <i>Feeding Habits</i> ... ..	13	2. <i>Post-Partum Changes in Mature Females</i> ... ..	32
B. The Pup ... ..	15	Section V. The Male Reproductive Cycle ... ..	34
1. <i>Appearance</i> ... ..	15	A. Histological Changes in the Testis ... ..	36
2. <i>Sex Ratio</i> ... ..	15	B. The Epididymis ... ..	36
3. <i>Locomotion</i> ... ..	15	Section VI. Growth and Age ... ..	37
4. <i>Moult and Swimming</i> ... ..	17	A. Introduction and Methods ... ..	37
5. <i>Mortality</i> ... ..	18	B. Macroscopic and Microscopic Appearance	
6. <i>Weaning</i> ... ..	18	of the Teeth ... ..	38
C. The Adult Male ... ..	18	C. Tooth Wear ... ..	39
1. <i>Annual Disposition</i> ... ..	18	Summary ... ..	40
2. <i>Fighting Amongst Adult Males</i> ... ..	19	Acknowledgments ... ..	40
		Bibliography ... ..	41

## Section I

## INTRODUCTION

THE original observations on which this report is based were made at Signy Island in the South Orkneys, in lat. 60°43' S., long. 45°36' W., during the period February 1952–April 1953. The main object of study was the breeding behaviour of the mature cows, and most of the observations were made in the period August–September 1952. Meteorological commitments prevented a full-time study being made, and observations on the breeding population were interrupted for three weeks whilst the author recovered from an infection similar to the Baltic sealers' "Spekk-finger" (see Candolin, 1953).

Reports on all species of seals seen in the vicinity of the base were available for the years 1947–50, and much of the material contained in them has been incorporated in the present paper.

## NOMENCLATURE

Allen (1905) has given the following account of the synonymy: "This genus was made known by Gray in 1837, on the basis of specimens obtained by Captain Fitzroy on the coast of Patagonia [at the mouth of the Santa Cruz river], more fully described and figured in 1844, in the 'Zoology of the Erebus and Terror', but he unfortunately adopted for it the pre-occupied name *Leptonyx*, replaced by Gill in 1872 by *Leptonychotes*, and again in 1891 by *Poecilophoca* proposed by Flower and Lydekker, apparently in ignorance of *Leptonychotes* Gill. The species was first named by Lesson in 1826, his account being based entirely on the description (by Prof. Jameson) and drawing published by Captain Weddell the previous year in his *Voyage towards the South Pole*. Yet Lesson, believing that it had small ears which had been omitted by error in the drawing referred it to the genus *Otaria*, but afterwards in 1827 to the genus *Stenorhynchus*. Gray, in the 'Zoology of the Erebus and Terror', adopted the specific name appropriately given it by Lesson, and by which it has since been uniformly known, except in one or two instances of inadvertence." The species was sometimes referred to as Weddell's False Sea-Leopard owing to the slight resemblance it bore to the true Leopard seal (*Hydrurga leptonyx*) but the name has long since been dropped to avoid confusion between the two.

## PREVIOUS KNOWLEDGE OF THE SPECIES

Bertram (1940) gives a selected bibliography, and of the reports listed, those of Wilson (1907) and Lindsey (1937) are by far the most comprehensive. Harrison, Matthews and Roberts (1952) have made a detailed examination of the reproductive organs of many seals, including those of two Antarctic species, and their work will be referred to in the sections on the male and female reproductive cycles. The most recent account of the Weddell seal is by Sapin-Jaloustre (1952) and is compiled from observations made in Adélie Land in 1950 and 1951. It forms a useful comparison with previous accounts of this species from expeditions based on the west coast of Graham Land and the shores of the Ross Sea.

## Section II

THE WEDDELL SEAL POPULATION OF  
THE SOUTH ORKNEY ISLANDS

## A. EARLY RECORDS

THE Weddell seal has an historic association with the South Orkneys, for it was in these islands, several years after their discovery, that the type-specimen was collected by Captain James Weddell in January 1823. This specimen was for many years on exhibition in the Royal Scottish Museum in Edinburgh, and a figure of the animal, taken from the stuffed specimen, appeared in Weddell's book, *A Voyage towards the South Pole, performed in the years 1822–1824*. Unfortunately the skin had been grotesquely mounted, and was a caricature of the real animal (Plate 1a).

Only small numbers of Weddell seals were taken in 1821, during the voyages of Palmer and Powell which led to the discovery of the South Orkneys, and in Weddell's exploration of the islands in the following two years. Dumont D'Urville charted the northern coasts of Coronation Island and Laurie Island in 1838, and although a collection of birds and rocks was made at a landing on Weddell Island, there appears to be no record of any seals being sighted or taken for food. Marr (1935) records that "in 1874, a fairly large number appears to have been killed by Dallmann at the south-west corner of Coronation Island, and on either side of Lewthwaite Strait at its southern end. In 1892, some were seen by Larsen on the north coast of Laurie Island."

The members of the Scottish National Antarctic Expedition, 1902-4, were the first to winter in the South Orkneys; their vessel, the S.Y. *Scotia*, was beset in the fast ice in Scotia Bay on the south side of Laurie Island and served as winter quarters during 1903. In every month throughout this period a few Weddell seals, principally males, were seen, and numerous seal-holes were noticed in the ice. In the breeding season, large numbers of seals were present about the winter quarters, but the size and disposition of the rookeries has not been indicated in the records. Throughout the summer of 1903-4 the Weddell seal was a frequent visitor to Scotia Bay.

During January 1933, approximately 370 Weddell seals were counted on various parts of the South Orkneys. Marr (1935) states that "the majority were congregated in a large rookery, about 250 strong, on a stretch of rotten fast ice at the head of Falkland Harbour [Powell Island]. The remainder, 120 in all, were hauled out singly, or in groups of two to four, and were scattered along the coasts on rocky ledges from Wilton Bay westwards to the Inaccessibles. The total, 370, probably falls short of the actual number that were then hauled out, since some no doubt were scattered around the coast of Laurie Island which was not examined as closely as that of other parts of the group" (Table I).

LOCALITY	NUMBER
Wilton Bay	30
Fredriksen Island	4
Ellefsen Harbour	40
Falkland Harbour	250
Signy Island	20
Sandefjord Bay	20
Inaccessible Islands: High Island	6

TABLE I. Numbers of Weddell seals observed in various localities in the South Orkney Islands in January, 1933 (Marr, 1935).

During 1946 the Falkland Islands Dependencies Survey maintained a base at Cape Geddes on Laurie Island, and in March 1947 this was transferred to Berntsen Point on the east coast of Signy Island. Seal counts formed part of the regular programme of work at this base, and it has been estimated that between four and five hundred female Weddell seals haul out around the shores of Signy Island during the breeding season (i.e. from the third week in August to the second week in November). Included in this estimate are the female seals which haul out along the adjacent coast of Coronation Island, from Cape Vik in the west to Cape Hansen in the east (Fig. 1). From the second half of November throughout the summer, the Weddell seal is only occasionally seen, and counts from Signy Island have never exceeded 25 seals, though it is assumed that in this area the maximum number hauled out on any one day in the summer months would probably be nearer 50.

#### B. FACTORS AFFECTING LOCAL DISTRIBUTION

It will be seen from Table I that in 1933 most of the seals were hauled out on a stretch of fast ice at the head of Falkland Harbour. It is perhaps unusual to find ice so late in the summer, but the preference of the seals for ice rather than rocky beaches is apparent. This is borne out by observations made at Signy Island from 1947 to 1953, for when loose pack filled the bays, particularly on the south and south-west sides of the island, the number of Weddell seals increased since they tended to congregate on the floes. Several

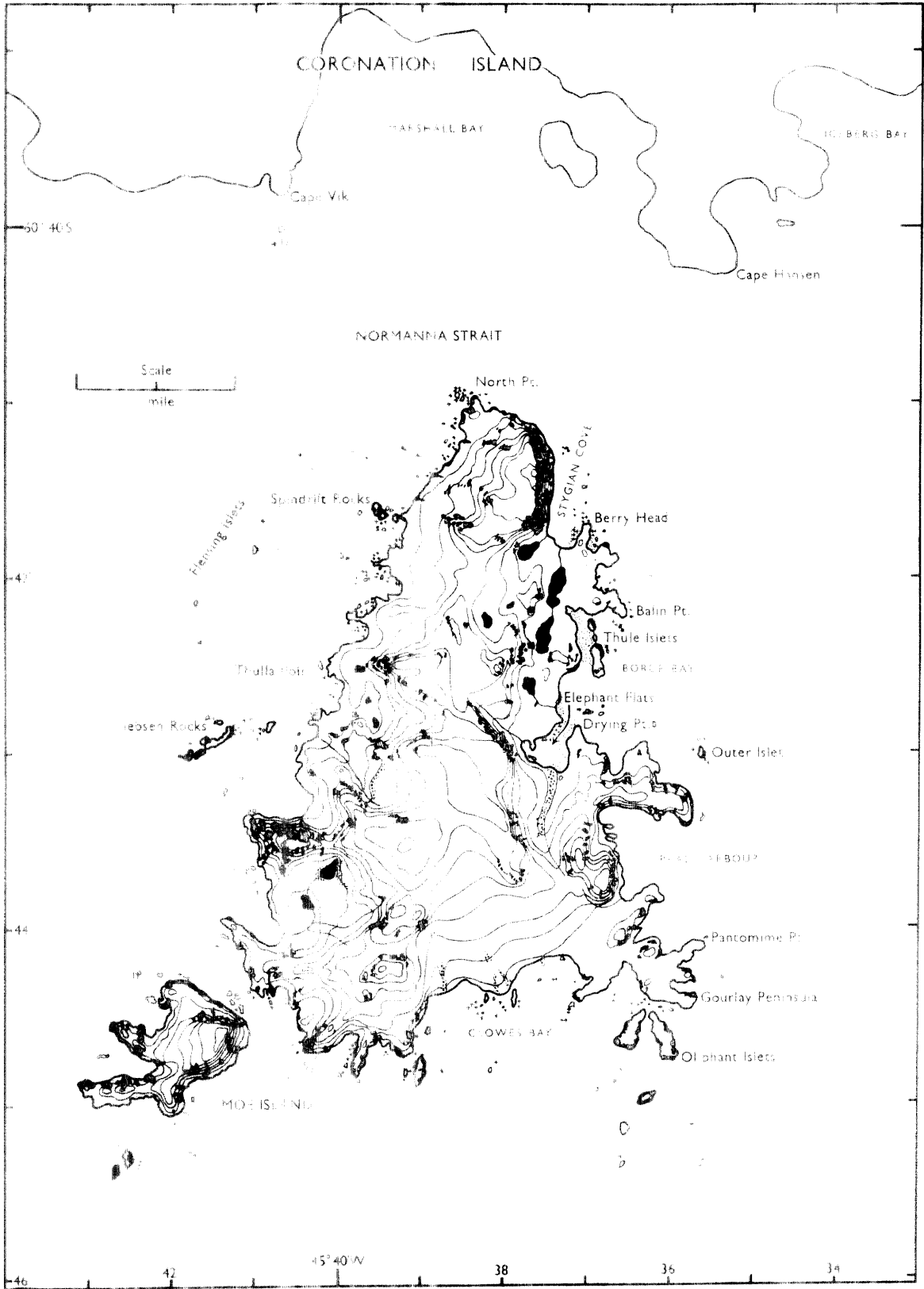


FIGURE 1. Signy Island, South Orkneys.

shingle beaches occur around the coast of Signy Island, and these appeared to be next in order of preference; this is supported by reports from the *Scotia* Expedition. for Brown, Mossman and Pirie (1906, p. 227) record seeing "often a hundred Weddell seals lying on a small raised beach on the west side of Scotia Bay, asleep on the pebbles".

At Gourlay Peninsula, on the north side of Pantomime Point, the dip of the metamorphic schists is such that fairly smooth slabs slope gently into the sea, and a few Weddell seals were always found at this spot during the summer months. Boulder beaches seemed to be the least favoured, but a flat-topped rock, easily surmountable at high tide, was occasionally used as a resting place.

C. ICE CONDITIONS AND THE BREEDING POPULATION

At the end of the autumn, the mean limit of the pack ice extends well north of the South Orkneys (Mackintosh and Herdman, 1940). Though an easterly current is experienced about the group, the general set in the open sea is north-eastwards, and southerly winds bring up the pack ice and icebergs from the Weddell Sea. Since the greater proportion of winds from the southern quarter have westerly components,

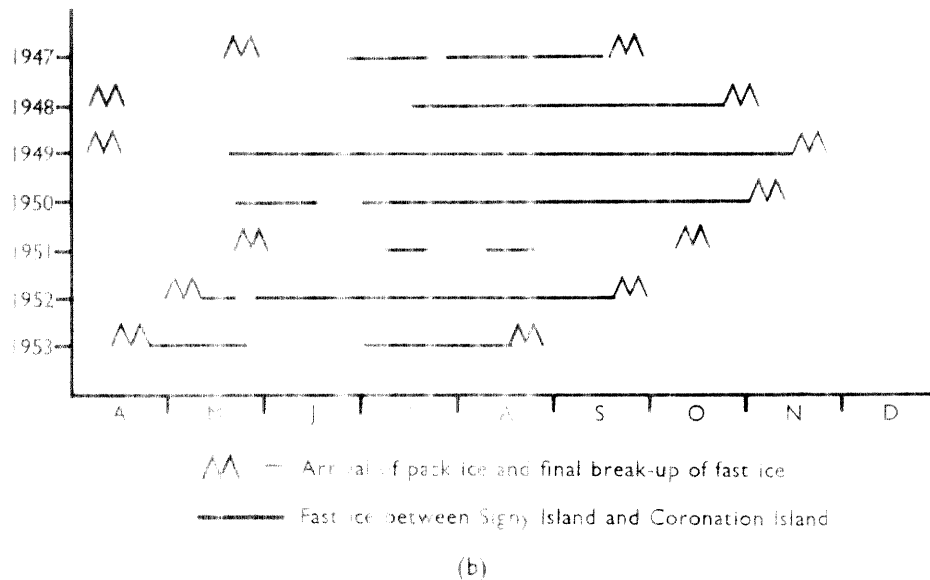
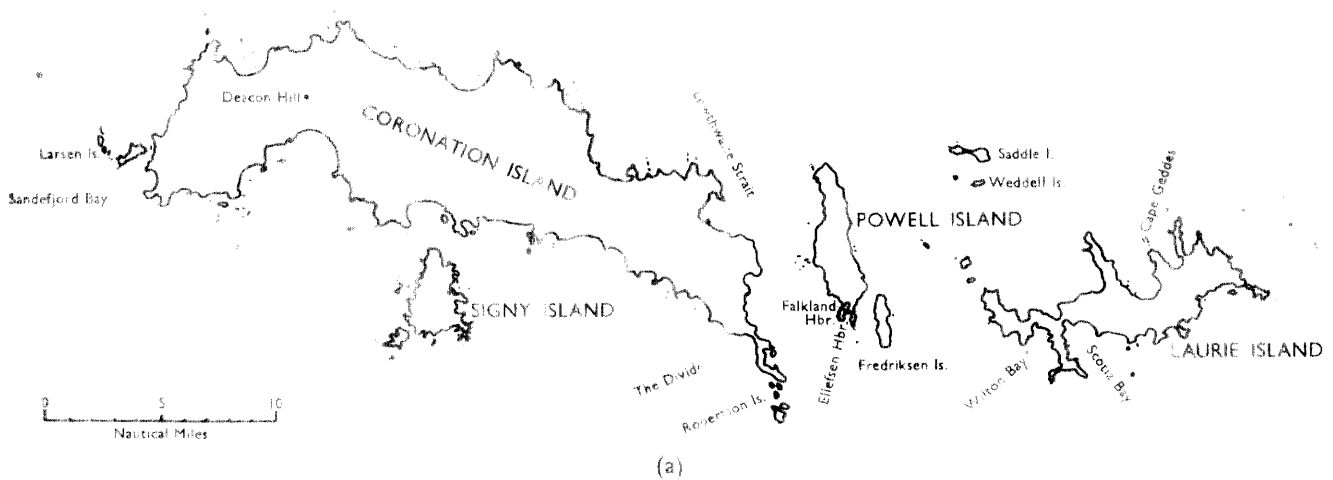


FIGURE 2.

(a) The South Orkney Islands: the Inaccessible Islands lie 21 nautical miles north-west of Sandefjord Bay and are not shown  
 (b) Ice conditions at Signy Island, 1947-53.

the pack ice tends to jam along the west and south coasts of Signy Island, whilst Paal Harbour and Borge Bay to the east of the island remain clear. When the temperature falls rapidly, the pack ice consolidates in the bays to the west and south, and new ice forms to the east of the island, and often in Marshall Bay and Normanna Strait to the north. Before consolidation occurs, however, increasing pressure invariably heaps up the pack ice around the off-lying islets and rocky headlands, and provides the seals with readier access to the surface. Furthermore, the submarine contours of the west, south and south-east coasts are steeper than in Borge Bay, and the areas of confused ice blocks are more easily approached from deeper water. This confused state of the pack ice occurs more particularly along the north-west coast where rocks and small islets extend up to half a mile from the shore (Fig. 1); the associated pressure-cracks in the ice effectively define the limit of the hauling-out area for the breeding cows. A large eddy from the main easterly current running through Normanna Strait sweeps down from Cape Vik as far as the Spindrifft Rocks, and the fast ice in this area soon becomes undermined.

Sea ice conditions vary widely from year to year (Fig. 2 b), and a sudden break-up of the fast ice in spring may affect much of the breeding population about the island. After the disruption of a seal rookery by such a break-up, the cows and more advanced pups collect again on the protected and easily accessible areas of fast ice, and swell the numbers in the small rookeries which may be already established there. It is only through a breeding season when the ice remains fast that a clear picture of an undisturbed population can be obtained.

In 1947 an early break-up of the ice on the south and south-east coasts of Signy Island led to the formation of a rookery in Elephant Flats (Fig. 3). The entrance to the Flats is protected by a bar formed by a terminal moraine, and the fast ice remains here usually between one and two months after the general

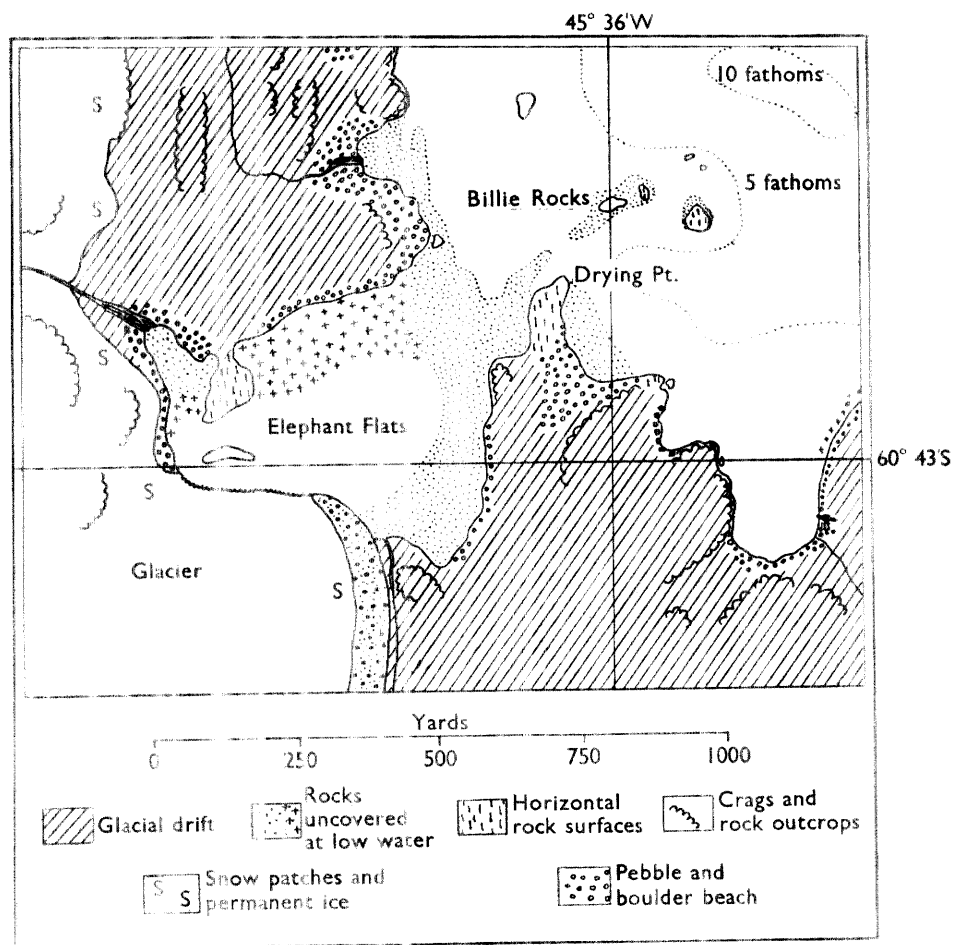


FIGURE 3. Map of Elephant Flats on the east coast of Signy Island.

break-up of ice around the island. Though the adult seals in this rookery were not sexed, the great majority must have been females, for counts made in other breeding seasons have shown an average of only 8 or 9 per cent males hauled out at the rookery sites. The close correlation between the pup and adult population curves after the first ten days and until the end of the third week in October, indicates that most of the pups were able to accompany their mothers into the water (Fig. 4). Few pups were born in this rookery and in Borge Bay. The small proportion of pups to cows suggests that, in other areas, also, many mothers lost their young during the break-up of the ice.

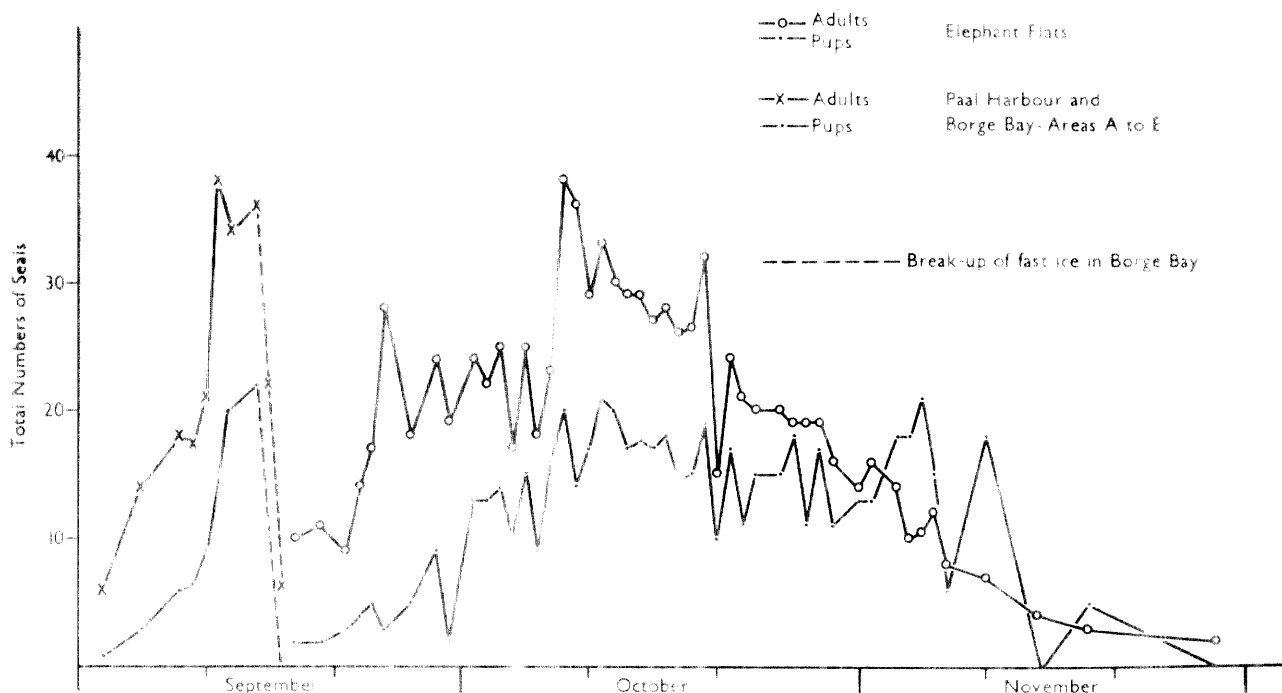


FIGURE 4. Numbers of adult seals and pups in Borge Bay and Elephant Flats in 1947.

The numbers of seals in Areas I and J (Fig. 6 b) on 7th October, 1947, did not differ appreciably from those seen in 1948 and 1949. The count in 1947 was as follows: Area I, 110 adults and 70 pups; Area J, 41 adults and 19 pups.

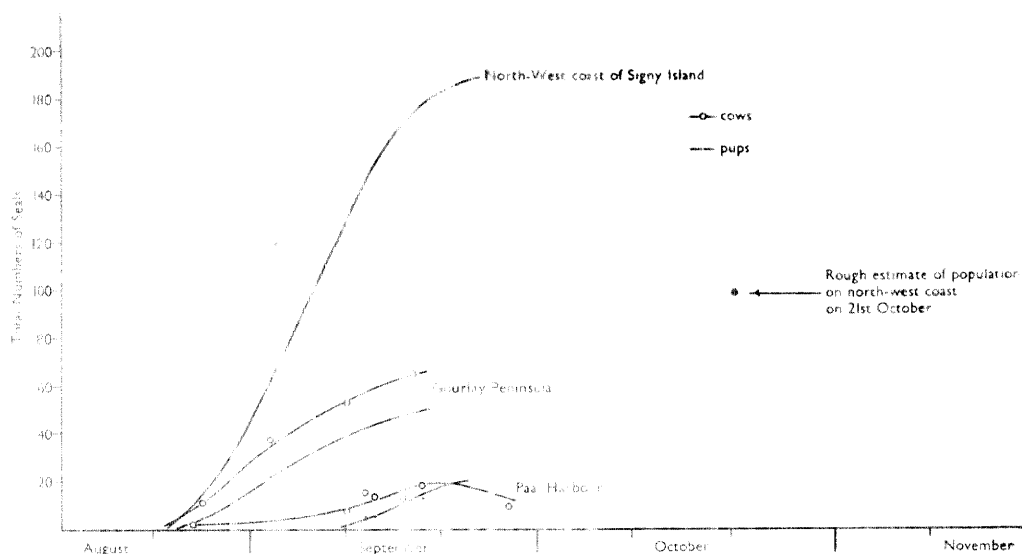


FIGURE 5. Numbers of adult cows and pups in three breeding localities about Signy Island in 1948.



In 1948 and 1949, the break-up of the fast ice was late, and the distribution of the rookeries was unaffected during the breeding season. Though few observations were made, the numerical increase of the main rookeries has been estimated (Fig. 5). The three areas studied were the north-west coast, from North Point to Thulla Point (Fig. 6), Gourlay Peninsula (Areas N and O), and Paal Harbour. In addition, isolated counts were made in Areas J, K, L and M, and revealed a population similar in number to that along the north-west coast. At this time, the coastal ice strip between the Flensing Islets and the north-west coast was mostly composed of consolidated pack ice. The greater part of Gourlay Peninsula was surrounded by level fast ice, but confused pack ice surrounded the Oliphant islets. Until the first week in September, a wide lead extended northwards from Gourlay Peninsula, and the cows were able to haul out easily. On the other hand, in Paal Harbour there was only smooth fast ice, and the population of cows and pups was correspondingly smaller. Few seals were seen in Borge Bay, which was also covered with smooth fast ice.

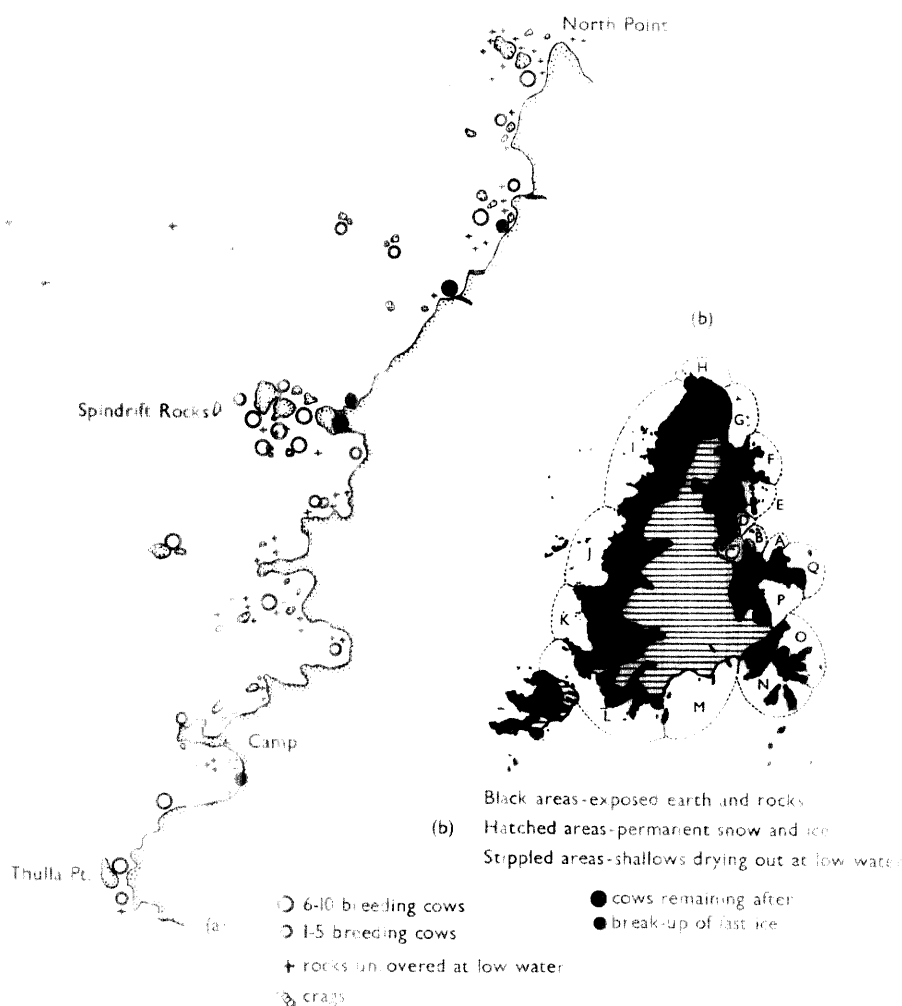


FIGURE 6. (a), Large-scale map of north-west coast of Signy Island showing Spindrift rookery and disposition of breeding cows on the fast ice in 1952; (b), Small-scale map of Signy Island showing seal census areas.

Detailed data concerning the breeding populations are not available for 1950 and 1951 as regular counts were not made in these years.

In 1952, the rookeries were greatly disturbed by an early break-up of the fast ice. On the reports of previous observers, the north-west coast had been selected for detailed observation (Fig. 6 a), and daily counts were made of the population (Fig. 7 a). On 4th September, open water was visible beyond the Flensing Islets, and the ice edge was moving slowly to the west. On 7th September, under an increasing

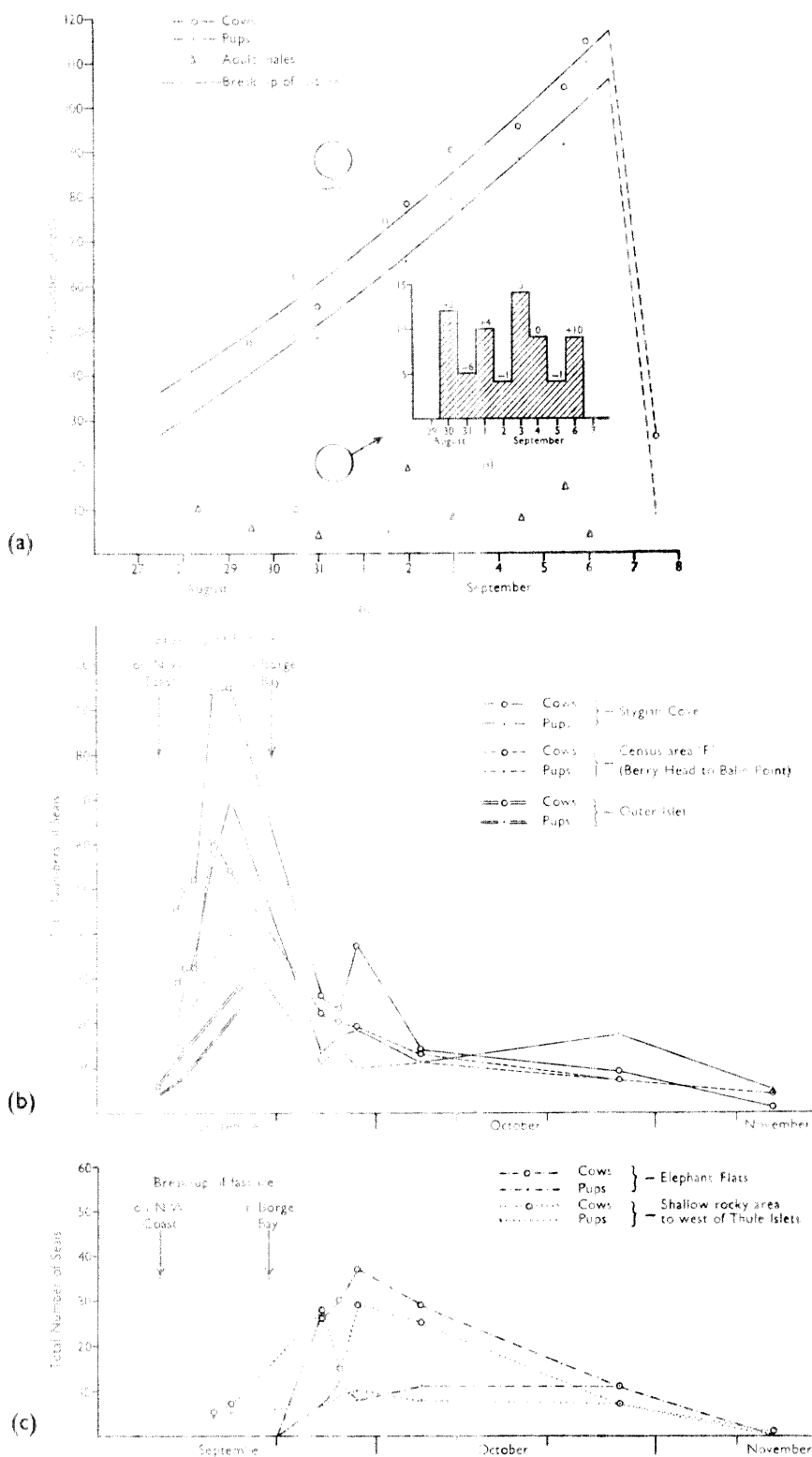


FIGURE 7. (a), i, Weddell seal population of north-west coast of Signy Island from North Point to Thulla Point, 1952; ii (inset), Number of births recorded per day. The numerals above the daily columns of the histogram indicate the difference between the observed number of pups and the expected number (as obtained from the previous day's total and the number of pups newly born); (b), Numbers of adult cows and pups in three localities along the east coast of Signy Island after break-up of the fast ice along the north-west coast; (c), Numbers of adult cows and pups on two areas of protected fast ice on the east coast of Signy Island, 1952.

swell from the west, and a strong north-westerly breeze, the consolidated pack and fast ice on the west and south coasts began to break up, and by the evening only loose floes remained in the bays. Of the 120 adults and 104 pups hauled out on the fast ice along the north-west coast, only 29 adults and 9 pups remained on the following day (Fig. 6 a); these were on the landward side of the tide cracks when the break-up occurred. Though the pup mortality was probably as high as 50 per cent, a large number of mothers with young were able to swim back to the fast ice remaining on the east coast of Signy Island (Plate II b), for counts made in Borge Bay after the break-up on the west coast show a significant rise in numbers. It is interesting to note that the maximum growth of the population in Stygian Cove and Area F did not occur until 15th September, that is eight days after the disruption of the west coast rookeries (Fig. 7 b). In all probability, the cows and pups remained on the floes until they became untenable, and then sought the land-fast areas of ice again.

The occupation of areas of fast ice in Borge Bay, most particularly in Stygian Cove, was interrupted by a further break-up on 19th September. The only areas of ice which remained after this were those covering Elephant Flats and the shallow rocky area to the west of the Thule Islets, and they became quickly colonised (Fig. 7 c). The final break-up of the ice took place quite slowly, and a few grounded floes remained in these protected areas until as late as the second week in November.

#### D. WINTER DISTRIBUTION

In the late autumn when the sea ice has formed, the adult seals are not seen, but most authors believe that they remain under the ice in the vicinity of the rookeries and maintain breathing holes in the pressure areas and tide cracks, and the zones of weak ice. At Signy Island during the winter months of 1952, a watch was kept for seal-holes, but few were seen, and it was assumed that the majority of seals had left the locality.

The few ice observations made on winter and spring journeys indicate that ice conditions off the northern coasts of Laurie Island and Coronation Island are very variable, and it is doubtful whether fast ice is able to persist there for more than several weeks at a time (Marr, 1935; Choyce, 1946; Skilling, 1949; Cheal, 1951; Johnson, 1952). These unstable ice conditions to the north of the South Orkneys are in marked contrast to conditions on the south of the group, particularly along the coast of Coronation Island. There, the areas of fast ice, including those surrounding Signy Island, are sheltered from the effects of north-westerly winds and swell, which are perhaps the most damaging to ice fields about the South Orkneys. It is possible that a local movement of Weddell seals to the north coasts occurs in autumn and winter, and this is supported by the fact that few seals were seen hauled out along the edges of leads in the fast ice and pack, even on fine and relatively calm days.

### Section III

## BREEDING BEHAVIOUR

### A. THE ADULT FEMALE

#### 1. *The Haul-out and the Pupping Season*

THE earliest pregnant females were seen hauled out along tide cracks at the end of the first week in August, especially in the areas of rotten ice at Cape Vik and Cape Hansen; numbers never exceeded twelve until the end of the third week in August, when the main spring haul-out of breeding cows began. New-born pups have been found as early as 24th August (1947 and 1948), and it is probable that the first birth takes place one or two days earlier. By the end of the month, the pupping season is advanced, and the numbers of pregnant cows hauling out steadily increases. It is apparent from the close similarity between the population curves for both the cows and pups (Fig. 7 a i) that nearly every female hauling out at this time is pregnant. Though daily observations on a particular rookery could not be made throughout the pupping season of 1952, owing to the early break-up of the ice, isolated counts made in 1947, 1948 and 1949 show that the end of the season is reached about the 22nd September; this gives 7th September as the middle of the pup-

ping season. In Southern Graham Land, in latitudes 65° to 68° S., Bertram observed that the middle of the pupping season occurred in the third week in September. On the other side of the continent, in the Bay of Whales in lat. 78° S., long. 164° W., the pupping season is just one month later than this, with the median date on 23rd October (Lindsey, 1937). This apparent correlation of breeding season with latitude does not apply to the Weddell seal population of South Georgia in lat. 54° S. In September 1914, the resident magistrate, J. I. Wilson, visited Larsen Harbour in Drygalski Fjord at the south-eastern end of the island. He was able to report (Wilson, 1914) a small rookery of about 30 Weddell seals, including young pups nearly two weeks old, which must have been born on or before 13th September. Matthews (1929) mentions 20 or 30 "Fisk Sael" which were found in Larsen Harbour, and records the taking of an old female in pup in Elsehul on 25th September, 1929. It seems probable that the pupping date differs little from that found at the South Orkneys, and this supposition is substantiated by the fact that female M87, which was taken by Laws in Larsen Harbour on 7th September, 1951, contained a full-term foetus measuring 53 inches from nose to tail in the right uterine cornu.

## 2. Birth of the Pup

Observations on the number of pups born in the Spindrift rookery on the north-west coast of Signy Island show that the average time between haul-out of the gravid cows and birth of the pups is approximately 27 hours (Fig. 7 a i). The birth of a pup was not observed by the author, and the following account is taken from the field notes of another member of the Survey (Owen, 1953). "My attention was first attracted by convulsions of the cow's body. Then she lifted her hind end and dropped it down immediately afterwards (1550 G.M.T.). These rhythmic convulsions continued for about a minute. Some light brown fluid trickled from the vagina and stained the snow in the immediate vicinity. At 1555 I noticed a tautening and then relaxing of the body, accompanied by contractions of the vulva. At 1558, the pup's nose appeared but was then withdrawn. During the next minute, the head was forced out to varying degrees, and then withdrawn, until at 1559, it remained exposed; the pup's eyes were closed and its tongue hung limply from its mouth. At this moment the mother paused, but she soon continued her struggle, and at 1601 the whole of the pup's head down to the neck was revealed, and its nose touched the snow. After this, the cow paused and relaxed for almost a minute. Then she lifted her hind flippers clear of the ice, and stretched them apart, remaining thus for nearly three minutes, straining continuously until the birth was accomplished. When the pup's flippers were free, it slithered rapidly on to the ice (1605). Immediately, it started to wriggle and its eyes opened. At the end of a minute, the mother swung her hind-quarters deftly over the pup, rolling over in the same movement; it was then seen that the umbilical cord had been severed. After a moment's pause, the mother moved some ten feet away from the pup. Within five minutes the pup had slithered to her side and was evidently groping with its muzzle for the nipples. The pup uttered its first sound in answer to its mother's lowing call at 1645, 40 minutes after birth. At 1715, the pup had still not suckled and the mother still retained the placenta."

On one occasion, a cow which had recently given birth to a pup was seen with part of the umbilical cord still attached to the placenta, which had not been expelled. Whilst the cow was being marked with paint (see Section IV, A 1) it made several convulsive movements, and during one particularly sharp swing of its hind flippers, the placenta was flung out a distance of several yards. Davies (1949) notes that in the grey seal (*Halichoerus grypus*), "delivery takes place very rapidly, and the umbilical cord appears to be severed by the cow suddenly whipping her hindquarters around. Sometimes considerable thrashing about is necessary, and on one occasion a dead calf was noted which had been bleeding from the head and mouth, and which was still attached to the placenta by an intact cord."

## 3. Behaviour Before and After Parturition

In the first few days of the pupping season, the gravid cows which have recently hauled out move away and enter the water when disturbed, but this desire to avoid an observer quickly diminishes as the number of cows hauled out increases. Time did not permit individual marking of all the cows under observation, and they were distinguished only according to the day on which they had pupped. Consequently, no information could be obtained of the individual wanderings of cows and pups in breeding areas. It seems certain, however, that the pregnant cows do not wander far from the place where they have hauled out on

to the ice. This is probably due to their increased gregariousness at this time, and to their tendency to concentrate about suitable tide cracks, and zones of rotten ice and tumbled ice-blocks, where there is easy access to the water.

The large size of the full-term foetus, and the development of the mammary glands is probably an important factor in limiting the wanderings of pregnant cows, though some still manage to move on the ice in the normal manner if sufficiently disturbed. In the southern elephant seal (*Mirounga leonina*), at least, such movement causes little or no harm to the full-term foetus. One gravid female Weddell seal observed was so distended that she appeared able to move along only on one side, yet her movements were quite as rhythmic as normal. Post-partum cows have also been seen to progress in this manner, but the reason is not apparent. Similar observations have been made on the grey seal by Davies (1949), for he remarks that "at Ramsey [Pembrokeshire], all seals aged 12 months and more were commonly observed to progress over land by moving on their sides."

In phocids which breed in colonies, the cows tend to become increasingly aggressive after the birth of their pups. This was frequently observed amongst the Weddell cows within only a few hours of the birth, and Davies (1949) has noted a similar change of temperament in the grey seal: "one cow was seen to give birth while lying in the middle of the congregation of non-breeders. The placenta appeared two minutes after the calf, and the cow immediately set about the surrounding bulls with much snarling and yapping."

Cows with newly born pups will often behave aggressively towards an intruder when up to twenty-five to thirty yards away, but they will seldom move more than five or ten yards away from the pups, before returning to them once again. Not all cows with newly born pups are so aggressive, however, and on several occasions the mothers deserted their pups and took to the water after showing little or no reaction. Laws (1948) has suggested that the relative fierceness of certain cows may often be attributed to lack of ability to escape rather than to a strong protective instinct towards the pup. Though individual temperaments may vary, a progressive decline in maternal fierceness is evident as the pup develops.

In the more concentrated areas of the rookeries, the breeding cows appear to exhibit territorial behaviour, and other cows which approach within two or three yards are usually attacked. This response is rarely violent, and the cows usually remain on their sides and snap their jaws rapidly at one another. The pup also will often attempt to bite intruders, though this action is often aimless, and may even be directed towards its own mother. Such direct responses to human intruders and other seals are not unusual, but other behaviour patterns are shown which seem to bear no direct relation to the situations involved. A cow which has been suddenly alarmed by an observer sometimes shows a very characteristic pattern of behaviour. The mouth is opened widely with the chin pressed back to the chest, and the surface of the ice is scored heavily by the upper and sometimes the lower canines during a rapid swinging of the head from side to side; alternatively the cow may make downward jabbing bites at the ice. Pregnant cows nearing parturition have also been seen to display this behaviour pattern when sufficiently disturbed. This was first noted by Laws (1949), who suggested it might be a displacement activity, while Tinbergen (1951) attributes similar actions to the "conflict of two strongly activated antagonistic drives". In the mother, these drives are probably the instincts of self-preservation by escape into the water, and the protection of the pup. This displacement activity is evidently instinctive, for pups may show the same behaviour pattern; one two-day-old pup was seen to exhibit this activity, and another pup began "snow-boring" after its mother had been shot preparatory to dissection.

Although displacement activity may result from disturbance by a human intruder, it has been observed that, under normal conditions, complex situations may arise which result in similar activities being displayed. The following description of such a situation is taken from field notes (Laws, private communication): "a two-week-old pup in its first moult coat was seen using its teeth to assist itself out of an enlarged breathing hole. The mother was trying to make a step by rasping away the ice at the edge, and she occasionally supported the pup on her back. Then she got behind the pup and apparently tried to push it up. All this was accompanied by much noise from both animals, and occasional trembling from the pup. Then the mother came out of the hole, and began nosing and rasping in the snow, looking round several times as if seeking a larger hole by which the pup could escape. She repeated this behaviour several times."

A third type of behaviour which is often exhibited by cows with pups, is apparently related to the displacement activity described, and may be termed "undirected aggression". Undue disturbance may result in a fierce response from the mother, and more often than not her own pup is the object of the attack. Apparently several dead pups observed had been killed in this way and another pup was paralysed behind

the umbilicus, and had evidently been savaged by its mother. Other cows have been seen to seize their pups and shake them violently to and fro and on one occasion this resulted in one of the pup's eyes being punctured by the mother's teeth. Laws (1949) notes that one mother was observed to be scraping the side of her pup until the fur flew, in a manner which closely resembled the snow-boring reaction. Although human interference is probably responsible for many of these behaviour patterns, it is known that occasionally such reactions may take place under normal undisturbed conditions.

It is certain that the majority of mothers are able to distinguish their own pups, at least from the first few days after birth. Nevertheless, cows will frequently snap at their own pups after they have been forcibly taken away and then returned, and the pups have been seen to retaliate sufficiently hard to draw blood from the mother's snout. Laws (1948) tested the ability of the cows to recognise their own pups by dragging three pups away from two cows which were lying near a hole in the ice. One cow was observed to sniff the three pups in turn until apparently satisfied that she had found her own, and the mother and pup then moved off together. The second cow, however, took the extra pup, leaving her own behind. When her own pup was taken to her she moved off, followed by both pups, and appeared unable to distinguish between the two. It is unlikely that the pups were twins, for a lactating cow lay on the ice about two hundred yards off, and was probably the mother of the third pup. On several other occasions it was observed that the cows always snapped at the pups which were not their own, and then moved away from them.

Certain other observations indicate that a strong maternal link usually exists between cow and pup. Cow H1014 was marked on 30th August, and close to her lay a dead pup which had evidently been squashed shortly after birth. Throughout the next nine days the cow lay near the pup, occasionally nosing its body. She defended it vigorously for two or three days, and then her aggressiveness declined, although she continued to lie near the pup's body. Another cow lay near her pup for only a few days before she left the rookery. Lindsey (1937) remarks "that when a young one dies on the ice, the bereaved female mopes about the carcass for several days". He also quotes the instance of "a youngster [which] fell into a crack and disappeared, its mother remained despondently with her head over the spot long after heavy ice had formed there".

Occasionally cows were seen which were quite indifferent to their pups. One cow, which was under observation for four days, was invariably lying well away from her pup, and whenever it was carried to her, she moved away about 20 yards. Presumably this pup was not being fed, but it is possible that it could have survived the break-up of the fast ice. Similar cases of neglect may explain the presence of the few starvelings which are seen in the summer months.

#### 4. Feeding Habits

Until the pup is weaned it is doubtful if the cows feed at all, for the stomach of each of the 12 post-partum cows examined was empty of food and contained only small amounts of yellowish-green fluid and a variable number of nematode worms. Cows which take to the water during the lactation period, at least during the first two or three weeks (Fig. 4), are invariably accompanied by their pups, and feeding may well be of secondary importance to protection of the pup. Observations on the harp seal (*Phoca groenlandica*) in the White Sea by Sivertsen (1941) indicate that this is the usual course of events in that species as well, though the fasting period lasts for 9 to 12 days only. Cows of polygynous species such as the southern elephant seal are known to fast during the lactation period, for they are confined to the breeding harems by the dominant males at this time.

At birth the weight of the pup averages 64 pounds, and at the end of six weeks, when nutritional independence is reached, it has increased to 250 pounds (Lindsey, 1937). This average increase of 186 pounds in weight of the pup is correlated with an estimated decrease of 300 pounds in the weight of the cow; of this 300 pounds, approximately 140 pounds represents a loss in weight of the skin and blubber alone (see Lindsey, 1937, p. 137). This efficient transfer from cow to pup parallels that found in other species (Laws, 1953c; Amoroso and Matthews, 1950). The great drain on the resources of the lactating cow is reflected in her emaciated appearance towards the end of the weaning period; the neck becomes very thin, and the iliac processes of the pelvis become prominent. This reduction in girth slightly alters the mode of progression, for observation of moving seals and their tracks reveals that during this period the anterior edge of the fore flippers may be used to a small extent. At other times of the year, the ventral cushion of blubber is so thick that the fore limbs are not used, and pelvic thrust only is possible.

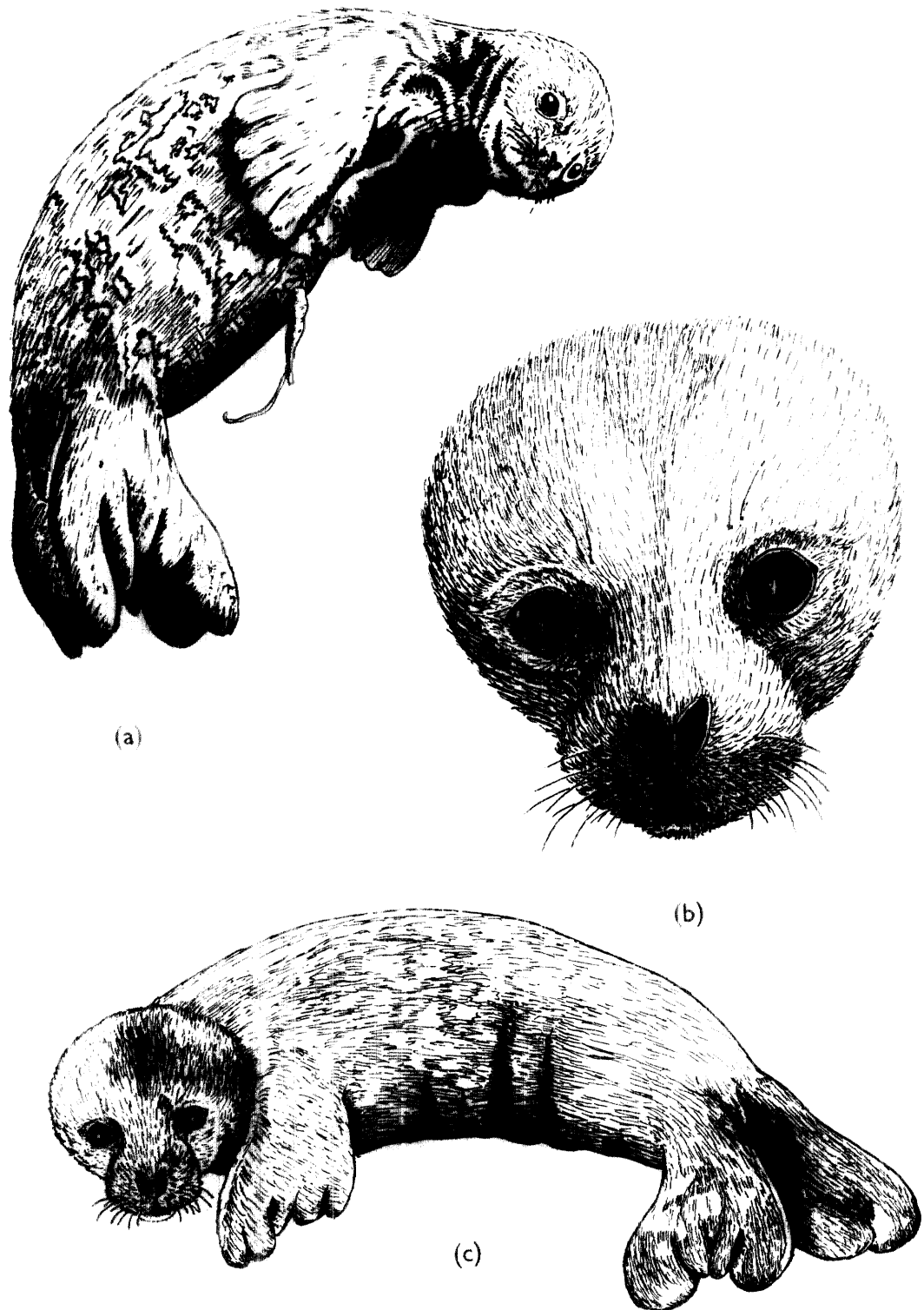


FIGURE 8. New-born Weddell pups.

## B. THE PUP

1. *Appearance*

The newly born pup may be recognised by the red or flesh-coloured umbilical cord, the thin loose skin with little subcutaneous fat, and the large size of the cranium compared with the remainder of the head (Fig. 8 b). The natal coat has been described by Wilson (1907) as "of a rusty greyish colour, presenting but the faintest indications of any marking". In the large number of pups examined at Signy Island (Laws, 1949), it was found that the pup coat colours could be divided roughly into three types, distinguished as "dark", "light" and "normal". Intermediate markings occurred, especially between the dark and normal variations, but the pups with the light coats were quite distinct. These markings may be summarised as follows:

**Dark.** Dark olive drab or chocolate brown dorsally, with many fleckings of the same colour on the flanks; belly lighter than back.

**Normal.** Grey green or olive drab dorsally, with a darker stripe along the spine from crown to tail, sandy green ventrally with lateral flecks of the same colour; tips of hind flippers black.

**Light.** Fawny brown dorsally with sand-coloured belly and brown fleckings on the flanks.

The greenish hues which are due to the staining of the fur with amniotic fluid, as in the young of other phocids (e.g. the "whitecoats" of the harp seal), tend to fade quickly. Before the natal coat is shed, the colour patterns tend to merge and the rusty greyish coat colour noted by Wilson becomes prevalent, but it is still possible to distinguish dark and light phases. Although colour differences have not been observed in the first hair coat which follows the natal fur, these pup coat colours may be reflected in later hair coats, for most observers have noted that many adults have strikingly light or dark coats when freshly moulted.

The analysis of pup coat colours has been set out in Table II a.

	DARK			NORMAL			LIGHT		
	1949	1952		1949	1952		1949	1952	
Male	6	10	(16)	19	33	(52)	7	9	(16)
Female	7	10	(17)	38	18	(56)	12	4	(16)
	13	20	(33)	57	51	(108)	19	13	(32)

TABLE II a. Analysis of pup coat colours of the Weddell seal. The bracketed figures are the combined totals for 1949 and 1952.

	1949	1952	TOTAL
Male	25	52	127
Female	21	22	103
	146	84	230

TABLE II b. Sex counts of Weddell seal pups before weaning.

2. *Sex Ratio*

In 1949 and 1952 counts of pups were made during the weaning period; the results are set out in Table II b and agree with the rule general amongst other phocids examined that slightly more males than females are born.

3. *Locomotion*

In his description of the birth of a Weddell seal pup, Owen (1953) noted that immediately after being born the pup began to wriggle about, and its eyes opened; it was also able to move towards the mother



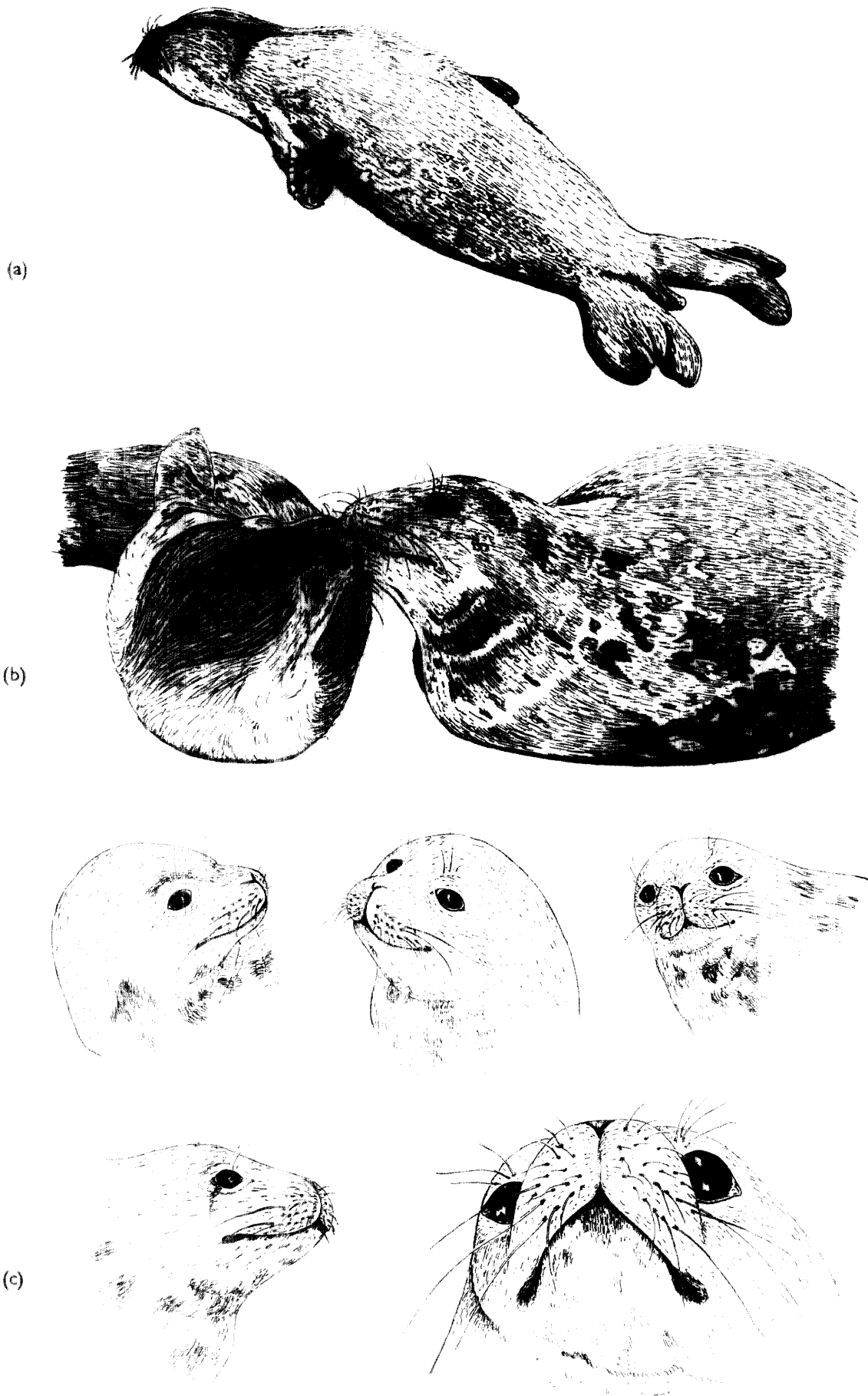


FIGURE 9. (a), Young pup, showing use of hind flippers in progression during first few days after birth; (b), Mother and pup; (c), Adult female Weddell seals.

even though she had moved ten feet away (see p. 11). The same behaviour was observed when a full-term foetus was extracted from the uterus of a freshly killed female seal (H1020) which had recently hauled out and was due to pup within a day (p. 11). On this occasion, however, the pup lay still with its eyes closed for three minutes before it began to move about. In newly born pups there is a marked tendency for both fore and hind limbs to be used in progression, though the movements of the limbs are not always co-ordinated; Fig. 9 a illustrates the manner in which the plantar surfaces of the hind flippers are spread on the ice when only small movements are made. If the pup is much disturbed at this age, the fore limbs may be used alternately, whilst the hind flippers are swung from side to side in a manner strikingly similar to the sinuous movements seen in the terrestrial locomotion of the crabeater seal (*Lobodon carcinophagus*). This stage is quickly replaced by one of bilateral co-ordination, and the fore limbs, which are of a disproportionately large size, are used to drag the remainder of the body along. Within two or three days the pup begins to arch the back and draw up the hind end of the body, but there is no pelvic thrust as yet; at this stage, the pup invariably has to make at least three forward movements of the fore flippers before the body has been straightened sufficiently for the next movement of the pelvis to be made. The carpal-phalangeal joint of the first digit bears most of the weight, for the rest of the limb flops about loosely. It is not until two or three weeks have elapsed, and the pup has increased considerably in girth, that the mode of locomotion characteristic of the adult is adopted; then the arching of the back and drawing up of the hind-quarters is followed by a pronounced thrust from the pelvis, which extends the body, and allows the cycle of movement to begin again. At this stage, too, the young seal does not always lie on its belly, but often rests on its side in the manner of the adult. Similar behaviour has been recorded in young pups of the grey seal by Davies (1949).

#### 4. Moulting and Swimming

Lindsey (1937) states that "the moult from the natal wool of 22 individuals of known age began at from 9 days (in 5 cases) to 21 days of age, averaging 13.8 days. The average duration of the moult is 30.2 days, so that at 44 days the average pup has replaced its woolly fur with a velvety black and white coat of short hair identical with that of a freshly moulted adult." In considering swimming of the pups, he states further that they "do not postpone entering the water until after completing the moult, but are to be found swimming at frequent intervals throughout this period. In fact two pups took to the water at 8 and 9 days of age, before the moult had begun. One was observed swimming at 10 days, another at 14, one at 16, and seven more before 20 days."

Similar observations were made by the present author in 1952, and there can be little doubt that even when disturbance of the rookeries is at a minimum, a few of the pups will take to the water at an early age. In the Spindrift rookery on the north-west coast of Signy Island, a cow and a seven-day-old pup were seen in a hole in the ice. The pup stayed in the water for three minutes whilst being observed, and it was assumed to have been in the water for ten minutes before that as the area of ice surrounding the hole had been deserted for at least that time; then the pup came out of the hole with the cow, and rolled in the snow. Several days later, a nine-day-old pup was seen in the water with its mother, and at an adjacent hole a pup lay with its head hanging over the edge, looking into the water. The mother appeared to be coaxing the pup to swim, for she frequently poked her head through the slush in the hole, and uttered hoarse little barks before submerging again. None of these three pups had begun to moult its natal fur. Later in the season, after the break-up of the fast ice, a thirteen-day-old pup was seen swimming offshore with its mother, and another pup, also in half moult, was seen off an adjacent beach.

It was observed that on three occasions (31st August, 2nd and 5th September) the pup population of the Spindrift rookery was less than expected, and it was assumed that the missing pups were in the water with their mothers. This assumption is supported by the daily counts which were made on the population of Elephant Flats in 1947 (Robin 1947). Fig. 6 shows that, although the population fluctuated markedly, there was a good correlation between the pup and adult curves until the end of the third week in October.

On 30th August, and 1st and 6th September, 1952, the total number of pups was greater than expected (Fig. 7 a b), and this was most probably due to an influx of older unmarked pups from other rookeries. The larger influx on 6th September was a good indication of undue disturbances in other rookeries, and this was confirmed on the following day when the fast ice on the west coast of Signy Island began to break up (see p. 10).

### 5. Mortality

In many years the spring break-up of the fast ice must be a major cause of mortality amongst the pups, though it would be difficult to obtain a precise figure for the death-rate from this cause. The increase in population of Stygian Cove after the break-up of the west coast rookeries in 1952 is shown in Fig. 7 b and this reached the maximum figure of 95 cows and 70 pups on 15th September; it is assumed that in a year when the ice remains fast until late in the season, few seals haul out and pup here. On the same day, the total population remaining on the areas of fast ice on the east coast from Paal Harbour to North Point was 187 cows and 141 pups. The estimated population of breeding cows for Signy Island lies between 400 and 500 (see p. 3), and it is likely that the majority of pups surviving the break-up of the ice on the west coast in 1952 returned with their mothers to the fast ice remaining to the east of the island. It may be assumed that these 141 pups represent the remnant of the population of between 400 and 500 that were present before the break-up of the ice, giving a mortality rate of between 65 and 72 per cent. Many of the pups would not necessarily have returned to the fast ice or shore again, as they were probably able to swim well. Others may have been carried away on floes sufficiently large to resist quick fragmentation, and the pups may have had time enough in which to grow to a moderate size before having to take to the water. For these reasons, a figure of between 30 and 50 per cent for pup mortality resulting from the break-up of the ice would be more likely to be correct.

Other factors affecting mortality have been mentioned, including the undirected aggression of some mothers, and the indifference shown by others. Several cows have died shortly after giving birth to their pups, but this indirect cause of pup mortality is probably rare. Stillborn pups were observed only on two occasions in 1952. These and other dead pups were invariably attacked by skuas (*Catharacta skua*), gulls (*Larus dominicanus*) and giant petrels (*Macronectes giganteus*), and mutilated corpses have previously led to the idea that these birds were responsible for the death of the pups. Providing the mother is alive this seems most unlikely, but starvelings could easily fall victim to these predators.

When the ice remains fast during the pupping season, the mortality is likely to remain low, and Lindsey (1937) gives a figure of 18 per cent for the pup mortality in one rookery in the Bay of Whales where the ice remained fast throughout the year. There, however, mean daily temperatures were usually 30° to 40° F. lower than those experienced in the South Orkneys during the corresponding period of the life cycle, and it is to be expected that some of the more precocious pups would become frozen into the seal-holes after venturing into the water. Since it is doubtful if this would ever happen in the South Orkneys, the mortality of the pups in this group is probably even less than 18 per cent during a season when the ice remains fast.

### 6. Weaning

From observations made in undisturbed rookeries in the Bay of Whales, Lindsey (1937) was able to make a detailed study of the lactation period and weaning. "The mean age of 13 young when last observed suckling was 45.2 days. Five of these were seen nursing at from 50 to 55 days of age. The age of permanent separation of 18 young from their mothers averaged 50.3 days which probably is also more nearly the correct average age for weaning." Reference to Fig. 4 shows that the correlation existing between the population curves of the adults and the pups is no longer apparent after the third week in October. Up till then, the pups remain with their mothers, and fluctuations in numbers of pups are paralleled by similar fluctuations in the numbers of adults; but after 20th October the number of adults decreases fairly regularly, whilst the pups show great daily fluctuations in numbers. This lack of correlation between the population curves of the pups and adults indicates that by then the pups have reached nutritional independence.

## C. THE ADULT MALE

### 1. Annual Disposition

Comparison of Lindsey's data for the Bay of Whales, with counts made in the South Orkneys, shows that the lying-out habits of the males vary with locality. Concerning conditions during the breeding season, Lindsey remarks that the "few males seen in October and November were wounded and very old", and he also notes "the rarity of bulls in the Bay whilst cows and pups are together. The bulls frequented the vicinity of open water 8 miles north of the rookeries. An area 40 yards square contained 29 bulls and 18 non-pregnant and largely yearling females." It was not until after the first week in December that bulls became

common in the rookery area. This lack of males in the breeding area has also been observed by Brown (1913) at Laurie Island in the South Orkneys: "males were not seen at the rookeries or on the floe[s] until September 21st, i.e. three weeks after pupping commenced . . . they remained rare for some time. By the end of October . . . the males begin to return . . . in a fat and sleek condition."

Daily counts over a period of nine days in the Spindrift rookery at Signy Island in 1952 showed that a small number of males was present on every occasion; there was no significant increase in the number of males during this period whereas the population of females steadily increased (Fig. 7 a). Numbers varied from 4 to 19, giving an average of 8.8 males per count, and representing 10.9 per cent of the adult population for this period. After the break-up of the fast ice on the west coast, counts were continued for the areas of fast ice on the east coast of Signy Island for a further week; the males represented 6 per cent of the total number of adults hauled out here. In 1948, which was undisturbed by an early break-up of the ice (Fig. 2 b), a representative sample of the population along the north-west coast consisted of 10 per cent males, 80 per cent females with pups, and 10 per cent females without pups (Laws, 1948). The males which were hauled out in the rookeries in the breeding season of 1952 were not fasting, for each of the four seals taken as specimens had fish remains in the stomach. Population records are incomplete, but during the summer and early autumn there appears to be little difference in the hauling-out habits of the two sexes.

In July and early August the numbers of seals hauling out begin to increase, and most counts reveal that the majority are males. Bertram (1940) states that of the 21 seals killed in the winter months of 1935 and 1936 off the west coast of Graham Land, 17 were males and 4 were females. Brown (1913) quotes no figures, but says that "in July and August in the vicinity of Laurie Island only males were seen". From observations made at Laurie Island in 1946 there seems to be no significant difference in hauling-out habits during the winter months, though few of the seals which were seen were sexed (Fig. 10). Further observations made during the years 1948 to 1952 at Signy Island show that males tend to lie out at the end of July, and in early August the gravid females appear on the ice on calm sunny days.

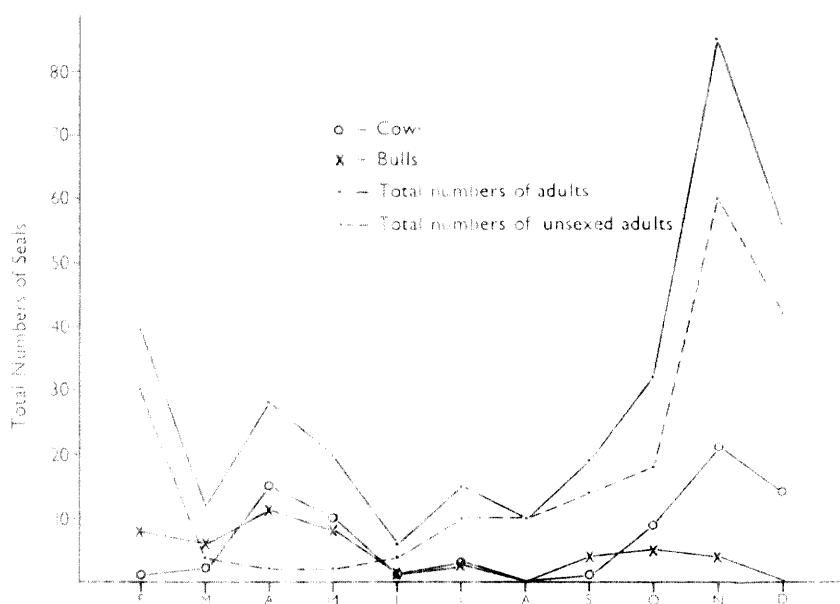


FIGURE 10 Numbers of Weddell seals seen at Cape Geddes, Laurie Island, 1946.

## 2. Fighting Amongst Adult Males

The earliest fights between males were observed at the end of the first week in August in the area of rotten ice about Cape Vik, and in the same week a bull with wounds in its abdomen was seen near the eastern end of Coronation Island (Laws, 1948). This remarkably early fighting must be uncommon, as freshly wounded bulls were not seen hauled out in any numbers until the last week of September.

Robin (1947) gives details of a fight between two males in the cove below the base hut on 27th September,

and the following is a summary of his observations: The fight lasted for twenty minutes, and for the first five minutes was close inshore near the old whaling factory. The seals appeared to bite at one another's head and flippers, and one seal was bleeding moderately. After thrashing about for perhaps half a minute, and rolling over and over in an attempt to bite each other, they surfaced close together and rested for a quarter to three-quarters of a minute until one had sufficiently recovered to renew the attack. After this had been repeated several times the fight moved to deeper water, and rests became longer. Finally, the bleeding seal climbed on to a small floe but the other male continued the attack by biting into its hind flippers. The bleeding seal wrenched its flippers free, and whilst the pursuer climbed out to continue the attack, it slid off the other side of the floe and fled out to sea, surfacing about 400 yards out. Then the fight ended as the pursuer either was satisfied with victory, or had lost the trail.

Concerning the Weddell seals in the Ross Sea area, Lindsey (1937) remarks that "fights are not strictly confined to the mating season, for freshly wounded bulls were seen as early as the 15th October." This, however, is at least a week after the beginning of the pupping season, whereas the fighting observed between males at Signy Island occurred at least a fortnight before the commencement of the pupping season.

The correlation of the rut with testicular activity is discussed in the section on the male reproductive organs.

#### Section IV

### THE FEMALE REPRODUCTIVE CYCLE

#### A. GENERAL

##### 1. Methods

THE collecting methods described in detail by Laws (1953c), were used with few modifications. It should be noted that all nose-tail measurements were taken along the curve of the back, but to conform with other authors, these have been corrected in Fig. 14 to give the direct nose-tail length.

During the daily counts made along the north-west coast of Signy Island in 1952 (Figs. 6 and 7 a), and later in Borge Bay, the cows with newly born pups were marked with a distinctive splash of cellulose paint, the same mark being used for all the cows known to have pupped since the previous day. By using different colours of paint, and varying the positions of the marks, it became an easy matter to identify the date of pupping of each cow. The marks lasted well, provided that the paint was rubbed into the fur, and few had to be remade. For convenience and personal safety, the brush was fitted with a bamboo handle four to five feet in length.

Material was fixed in Bouin's fluid (picro-formal-acetic) until arrival in this country almost a year later, and in spite of such prolonged fixation, results proved to be adequate. Several staining methods were tried, but Delafield's Haematoxylin counterstained with alcoholic eosin gave the only consistent results with the female material.

##### 2. Reproductive Organs

The gross anatomy of the reproductive organs of both male and female young and adult seals has been described by Harrison *et al.* (1952), and the author has only one observation to add to their account. It was noticed whilst dissecting the parturient and post-partum females that the clitoris appeared to be unusually large, and when examined more closely, an *os clitoris* was invariably found. Two of these female homologues of the *os penis* are shown in Fig. 11 b. For comparison the *os clitoris* of a second year immature female crabeater seal (*Lobodon carcinophagus*), taken on 12th September, 1952, is included (Fig. 11 b); in this specimen the bone was invested in a thick cartilaginous envelope, but this has not been figured in the drawing as it had become distorted with drying and subsequent boiling.

The *os clitoris* is known to occur sporadically in the southern elephant seal (Laws, 1953a) and Scheffer (1949) has reported specimens from the northern pinniped species *Callorhinus ursinus* and *Phoca vitulina*. In the Weddell seal, at least, the *os clitoris* is of normal occurrence and is found occasionally even in the youngest pups.

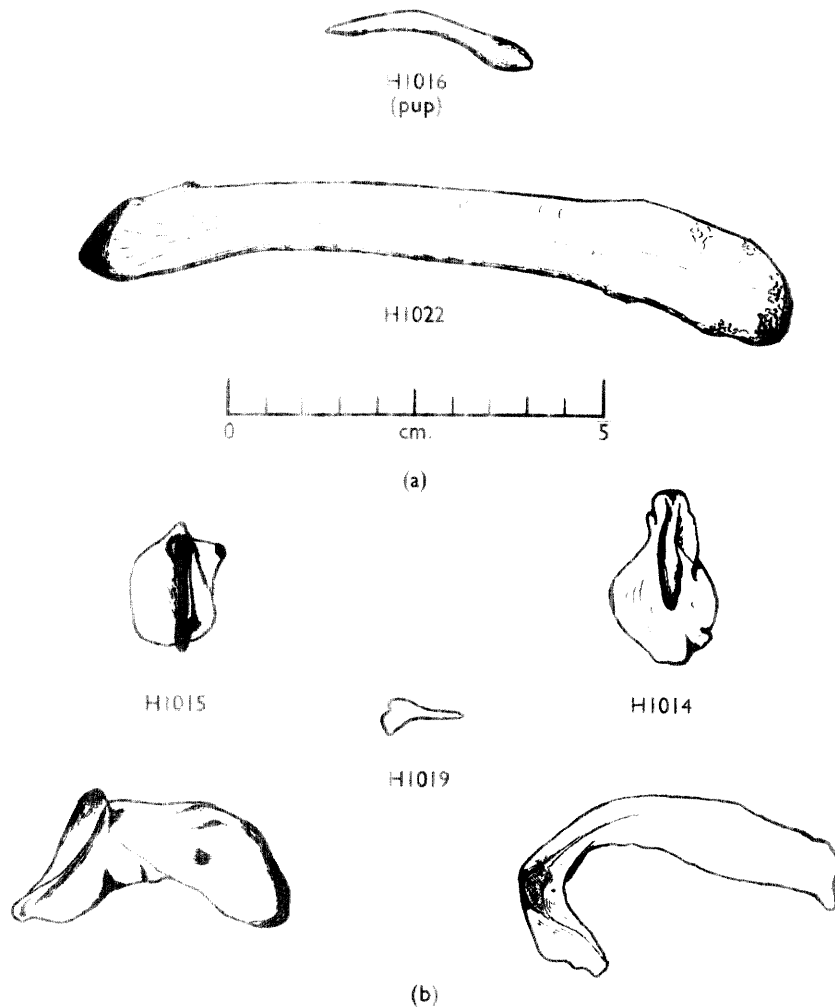


FIGURE 11. (a), *Os penis*, left lateral view; (b), *Os clitoris*, right lateral and anterior views.

### 3. Sexual Maturity

The nose-tail length of each of the four adolescent specimens (Table IV) has been compared with the curve for probable rate of growth shown by Bertram (1940, Fig. 10). From the curve, it appears that H123 and H1006 are yearlings, whilst H1007 is in its second year. Macroscopic examination of the ovaries shows that only in H1007, taken on 6th August, are maturing follicles present (see Table III). H1001, taken on 3rd June, is slightly above the average length for a twenty-month-old female, if the growth curve is assumed to be correct. It has only a few follicles of more than 1 mm. in diameter in the ovaries, and, both macroscopically and microscopically, the ovaries differ little from those found in the two yearling seals (Fig. 13). However, the structure of the teeth suggests that this seal is in its second year (see p. 38) and it may be assumed that follicular development, as well as other changes in the reproductive organs, occur relatively rapidly before the time of the first impregnation.

It is of further interest to note that the right ovary of H1007 contained a large ripe follicle of mean diameter 8 mm., and this was much larger than the average diameter of maturing follicles present in the early post-partum cows examined (Figs. 12a and 13). This may indicate that virgin cows in their second year ovulate several weeks earlier in the season than the cows which have pupped, and so become the first to be impregnated by the males.

In general, the blastocyst implants in the uterine cornu on the same side as the ovary from which the ovum was shed. However, in H1020, the only gravid cow taken in the present series, the *corpus luteum*

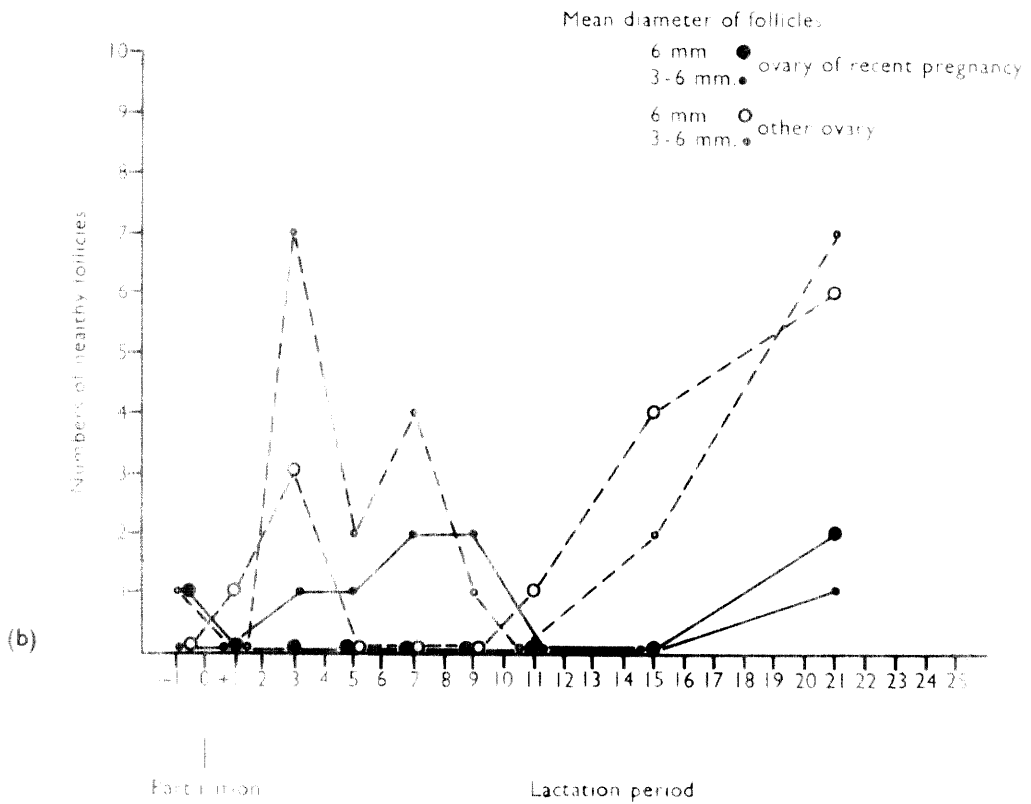
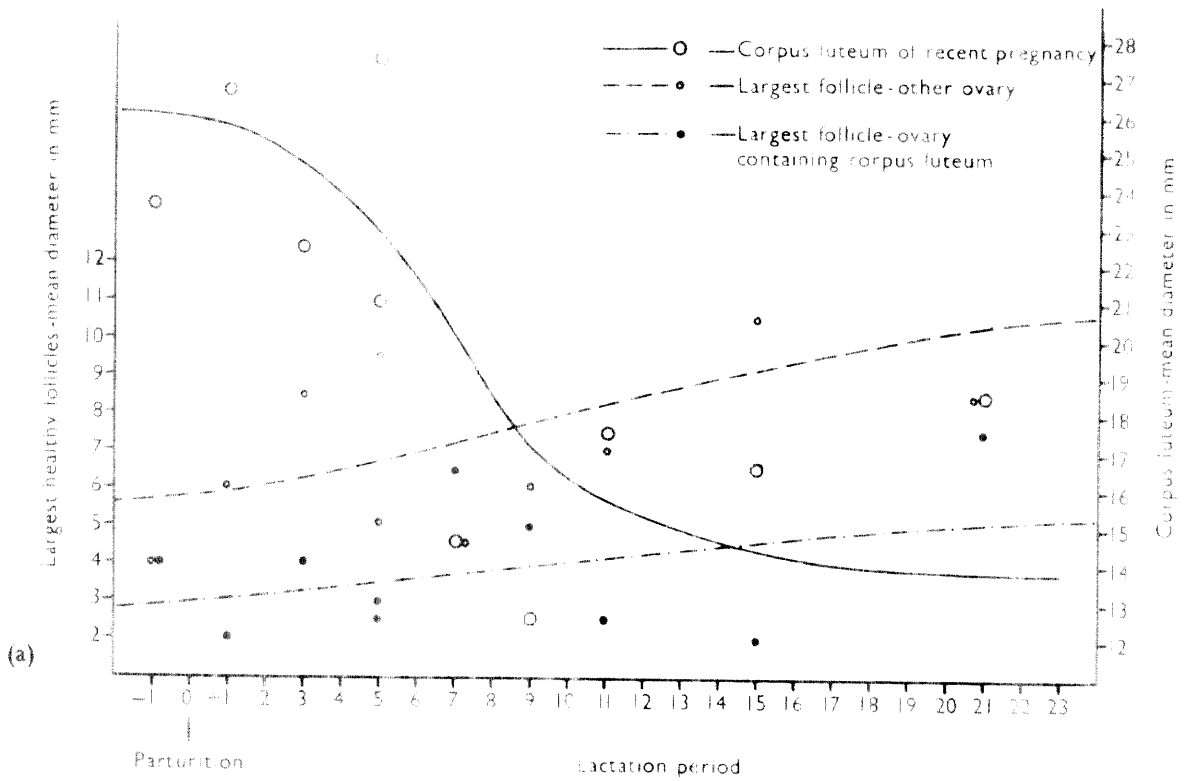


FIGURE 12. (a), Post-partum regression of the *corpus luteum* and development of follicles; (b), Post-partum ovaries; numbers of healthy follicles.

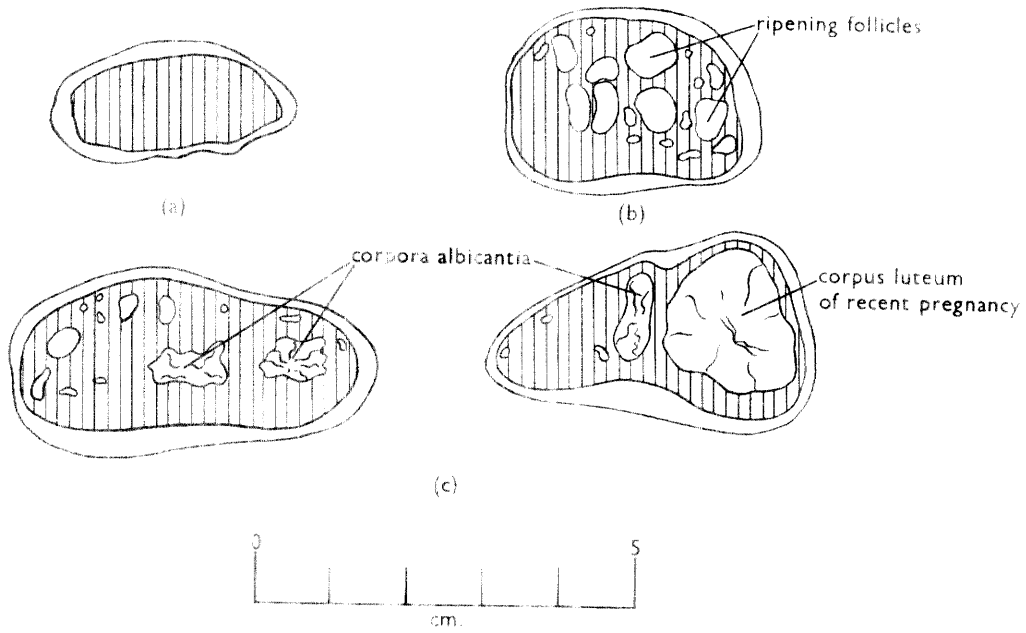


FIGURE 13. Macroscopic sections of the ovaries of (a) yearling, (b) two-year-old nearing maturity and (c) adult after parturition.

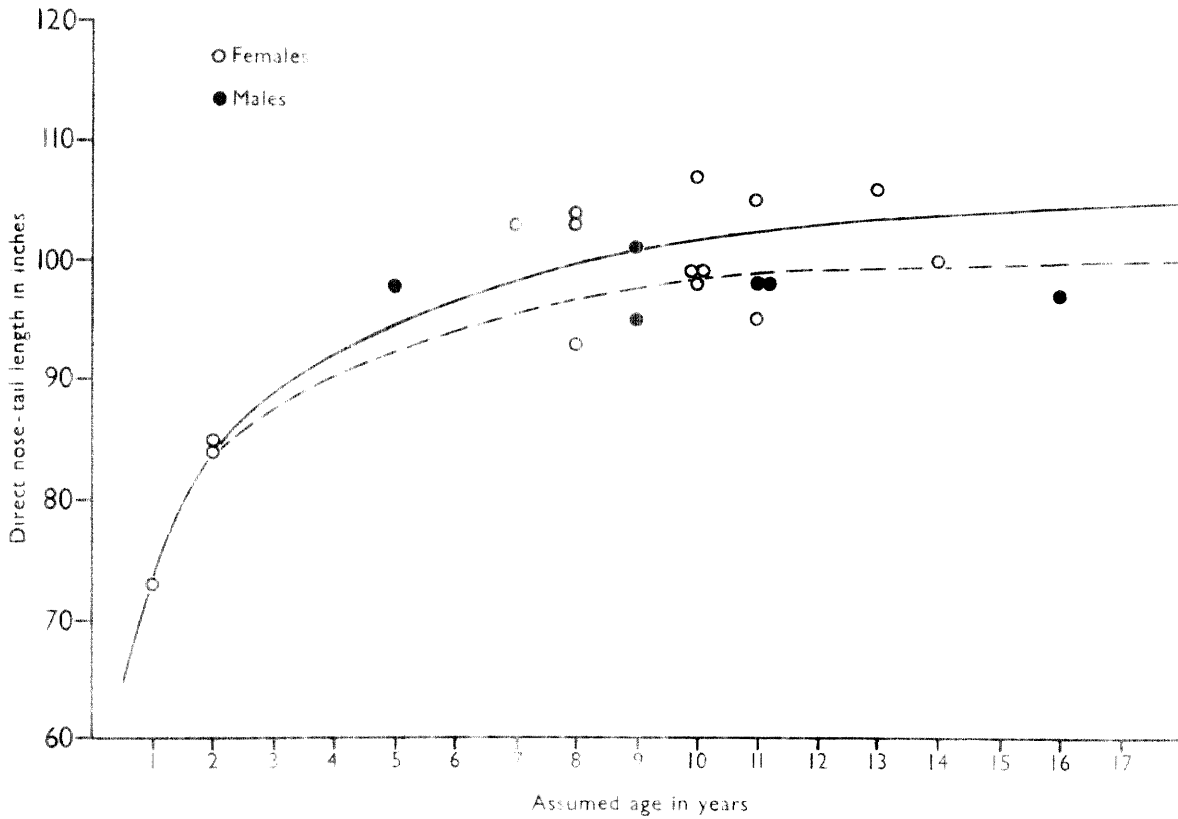


FIGURE 14. Probable growth curves for small series of Weddell seals taken at South Orkneys in 1952.



developed in the left ovary, whilst the right uterus contained the full-term foetus, and it is assumed that in this case trans-uterine migration of the embryo occurred.

From the assumed age-composition of the series of breeding cows (Fig. 14), it appears that the average life is nine years. Assuming that impregnation occurs early in the third year, and allowing for one missed pregnancy (see Bertram, 1940, p. 65), each cow can be expected to bear six pups in a lifetime; this compares with the figure of seven pups for the southern elephant seal (Laws, 1953c).

## B. THE NORMAL OVARIAN CYCLE

### 1. Oestrus

It was originally intended that a representative series of ovarian and other reproductive material covering the whole of the lactation period should be selected from the population of breeding cows on the west coast of Signy Island during 1952. Unfortunately, the sudden break-up of the fast ice resulted in the dispersal of the rookery, and only a small series of specimens was obtained. Marking of female seals was continued in Stygian Cove, and in the Paal Harbour and Outer Islet rookeries, and the series was finally extended to cover the period from minus one to plus twenty-one days, relative to parturition. Enough female seals were marked to enable the series to be extended to plus fifty days, but circumstances prevented any field work being done for nearly a month, and the marked seals were never recovered.

The measurements and numbers of follicles, *corpora lutea* and *corpora albicantia* in the ovaries of the seals taken are given in Table III. These data are represented graphically in Fig. 12 a, in which curves for the assumed regression of the *corpus luteum* after parturition and for the growth of the follicle destined to ovulate are given.

According to Bertram (1940) ovulation does not take place until the end of the lactation period, but then it follows quickly. Lindsey (1937) has found that the average duration of the lactation period is fifty days; assuming that the follicle destined to ovulate at the end of this period continues to increase in mean diameter as suggested in Fig. 12 a, it would reach a mature size of 14 to 15 mm. This compares with an average diameter of the order of 13 mm. for the mature follicles of antarctic seals in early November (Harrison *et al.*, 1952). The maximum size for mature follicles in the southern elephant seal has been found to be 15 mm. (Laws, 1953a), though, in this species, the *corpus luteum* of pregnancy is not known to develop to a greater average diameter than 23 mm., as compared with 28 mm. for the Weddell seal.

In the mature cow during oestrus, ovulation occurs in the ovary opposite to the one which contained the recently functional *corpus luteum* (Figs. 12 a & b). In the ovary which will control the next pregnancy there is a tendency for the number of follicles of mean diameter greater than 6 mm. to increase during the first half of the lactation period (see Table III and Fig. 12 b). This is accompanied by a corresponding increase in the number of follicles in the size range 3–6 mm. The majority of the larger follicles are already atretic, and the follicle destined to ovulate is able to grow whilst the remainder regress still further.

In the other ovary, in spite of the comparatively large size of the *corpus luteum* at parturition, the average diameter of the largest follicle is of the order of 3 mm.; an apparent increase in average follicle size to 5 mm. is found half-way through the lactation period, but it is assumed that little more follicular growth occurs after this. However, the initial controlling effect of the *corpus luteum* on the growth of follicles is clear, for an average of only one follicle in this ovary grows to be larger than 3 mm. Half-way through the lactation period, the effect of the old *corpus luteum* is decreasing, and only then are follicles larger than 6 mm. present (two follicles 8 mm. in diameter in H1030 at plus twenty-one days relative to parturition; see Fig. 12 b). Suppression of follicular growth may be effected partly mechanically, but this internal ovarian pressure is probably not the only controlling factor.

No oocytes are present in the cortex of the mature ovaries, but small numbers of primary follicles occur below the sub-surface crypts. In most sections, the oocytes rarely number more than 2 or 3 per mm. (measured parallel to the surface of the cortex), and are usually clustered in small nests of granulosa cells. In specimens later in the post-partum series, there is a tendency for the primary follicles to enlarge, and then cytolysis invariably occurs. The single layer of granulosa cells tends to remain complete, though in one specimen several granulosa cells can be seen in the cytoplasm of a degenerating oocyte.

Deeply staining basophilic and acidophilic bodies 20–30  $\mu$  in diameter occur in the sections of many mature ovaries; these are apparently concretions and are surrounded by a flattened layer of epithelial cells (Plate III a). These bodies have a close association with the sub-surface crypts; in some specimens the

epithelium of the crypts is continuous with the cells surrounding the concretion, but in others, the body, either with or without its covering of epithelial cells, appears to be free in the lumen of the crypt. A possible explanation of this association is considered in Section IV, B3. Harrison *et al.* (1952) mention a virgin female fur seal (*Callorhinus ursinus*) taken on 27th July, 1949 in which, "scattered irregularly throughout the interstitial tissue in the form of irregular clumps some 30  $\mu$  in diameter, are masses of amorphous basophil material. Histo-chemical tests have shown that these masses contain calcium salts, but their exact nature is not yet clear." Similar tests for calcium using Alizarin Red S were made on sections of ovaries in the present series, but no positive results were obtained.

The presence of precociously developing oocytes, usually relatively deep in the cortex, and sometimes in the medulla, have been noted by Harrison *et al.* (1952). A few of these oocytes appear in a yearling female, H1006/2 and each one is degenerate. The zona pellucida is much distorted and persists after the cytoplasm and the nucleus of the oocyte have disintegrated. These oocytes are surrounded by interstitial cells which invade the medulla up to 1 mm. from the surface of the ovary.

The small numbers of healthy maturing follicles can be distinguished in macroscopic sections by their translucent appearance; the *liquor folliculi* is homogeneous or finely granular, and does not show the coarser granulations found in follicles undergoing atresia. In a 3 mm. follicle in the right ovary of H1010, taken on 18th August, 1952, the layer of granulosa cells is 9 to 15 cells deep in places and averages 100  $\mu$  in thickness (Plate III b). The *theca interna* is composed of several layers of oval or polyhedral cells with nuclei 7-8  $\mu$  in diameter, and is surrounded by a *theca externa* of fibrous cells with crescentic nuclei; the combined thickness of the thecae is approximately 50  $\mu$ . In the later stages of growth, the granulosa develops lobes which project into the cavity of the follicle. In female H1018, in the ovary destined to ovulate, a small portion of an advanced follicle shows two pronounced lobes, each containing a large blood vessel at the inner extremity; much of the remainder of the lobe is occupied by large *theca interna* cells with deeply-staining nuclei, closely resembling luteal cells. The few fibrous cells in the centre of each lobe are probably formed from the *theca externa*, and are well supplied with arterioles. The supporting walls which occasionally divide the cavities of the larger follicles are evidently derived from the extensions of these lobes. In the present series of ovaries these walls have been seen more often in atretic than in healthy follicles, and are then reduced to thin fibrous septa with degenerating granulosa cells.

Most of the follicles of all sizes are atretic, and these appear opaque in macroscopic sections. Follicles with a diameter greater than 1 mm. usually undergo a characteristic type of cystic atresia in which the thecae become fibrous, and the *liquor folliculi* is retained. The first signs of degeneration occur in the granulosa layer, particularly in the *discus proligerus*; vacuoles are formed between the cells, and the granulosa tends to break away in layers. In follicles in later stages of atresia, the granulosa is reduced to a single layer, which soon begins to fragment. The cells, which contain deeply staining particles of chromatin, shrink and become rounded and float freely in the *liquor folliculi*. Rapid breakdown of these cells occurs, for the liquid becomes granular in appearance, and few of the cell remains are to be seen. Both the *thecae interna* and *externa* gradually become fibrous, and soon any distinction between the layers is lost. Gradual resorption of the liquid, or fibroblast invasion then occurs, although in one cystic follicle the thecae have ruptured, and some of the liquid has escaped into the surrounding interstitial tissue.

Not all atretic follicles undergo cystic atresia, and some may collapse after resorption or sudden release of the *liquor folliculi*. In specimens H1010/2b and H1027/1c, the follicles have collapsed in this way, and the wall has been thrown into a star-shaped series of deep folds. The granulosa cells are much larger, measuring 10 to 12  $\mu$ , with deeply staining nuclei 7 to 8  $\mu$  in diameter. The nuclei in the basal layer of cells are confined to the proximal half of the cytoplasm, forming a distinct line of nuclei which helps to accentuate the adjacent basement membrane. The *theca interna* cells have grown much larger and have become luteinised; they range in size from 12 to 18  $\mu$ , with nuclei 7 to 8  $\mu$  in diameter, though a few cells may grow as large as 25  $\mu$ . Fibroblasts and blood vessels occupy the central portion of each fold (Plate III c).

## 2. The Corpus Luteum

In the majority of mammals, the *corpus luteum* develops rapidly after successful fertilisation, and the maximum size is reached within one or two weeks, but in the Pinnipedia, in which delayed implantation is such a characteristic feature of the reproductive cycle, the development of the *corpus luteum* differs to some extent. Initially it grows quickly in the typical mammalian manner, but at the time when the blastocyst

reaches the uterus, the gland has not reached a stage of development similar to that in other mammals. During the delay in implantation, the *corpus luteum* maintains this appearance of retarded development; just before implantation it reaches its maximum activity, and this is maintained during the first month of embryonic development (Harrison *et al.*, 1952). This pattern of development may be general amongst the *Phocidae*, and is supported by detailed histological examination of the cycle in the southern elephant seal (Laws, 1953a).

It is apparent from all the data surveyed, that the actual diameter of the *corpus luteum* does not necessarily reflect its activity. In the Weddell seal, the average diameter is about 25 mm. and this size is maintained throughout pregnancy, that is for seven to eight months after the gland has reached its peak of secretory activity. No young *corpora lutea* were available in the present series of specimens, but their development has been described in detail by Harrison *et al.* (1952). For comparison with the old *corpora lutea* in the post-partum females, the *corpus luteum* of an adult female leopard seal (*Hydrurga leptonyx*) has been examined; the vacuolated luteal cells and lack of connective tissue show that the gland is not yet completely active, and this is in accord with the general statement that maturity of the *corpus luteum* is not attained until implantation occurs.

Only one specimen, H376, taken on 13th February, 1950, is available from the post-implantation period. A foetus of 23 cm. crown-rump length in the left uterine cornu was associated with a *corpus luteum* of mean diameter 24 mm. The appearance of the gland suggests that a phase of maximum activity has recently been reached, for all the luteal cells are large with densely staining cytoplasm and few vacuoles, and the amount of connective tissue is still surprisingly small in comparison with the condition of the gland found in post-partum females (Plate III e).

Although in late pregnancy and at parturition the *corpus luteum* is still at its maximum size, it is evident that secretory activity has been reduced to a minimum. The healthy lutein cells range in size from 25 to 35  $\mu$ , and have finely granular cytoplasm and large nuclei 7 to 10  $\mu$  in diameter. The greater majority of the cells are vacuolated, and usually show an increase in size up to 45 to 50  $\mu$ ; this must be an important factor in maintaining the size of the *corpus luteum*. In contrast, in the southern elephant seal the largest vacuolated luteal cells reach a diameter of 60 to 80  $\mu$ , and yet the *corpus luteum* slowly regresses in size in the later months of pregnancy, apparently as a result of the greater shrinkage of the inner luteal cells in this species (Laws, 1953a). The vacuoles may be small, and sufficiently numerous at the periphery of the cytoplasm to give a frothy appearance to the cell contents. Most luteal cells, however, contain one or more large vacuoles and the nuclei are usually degenerate and eccentric. Though it has been impossible to carry out histo-chemical tests on the fixed material, the vacuoles would be expected to contain the products of fatty degeneration of the cytoplasm. At this stage of regression, small clusters of luteal cells are separated off by a network of fibrous interstitial tissue, and this is well shown in sections treated with Mallory's Triple Stain (Plate III d).

In the second and third weeks after parturition the development of interstitial tissue increases rapidly, and the proportion of highly vacuolated luteal cells increases still further. At the end of the third week, the amount of fibrous tissue may be greater than the degenerating luteal tissue, and the whole *corpus luteum* has shrunk to nearly half its original diameter. The luteal cells at this stage are either shrunken and irregular in shape, or highly vacuolated with broken-down nuclei. Little change takes place in the deeper blood supply during this period, for capillaries and arterioles are present throughout the luteal tissue in all the specimens. Large blood vessels occur at the periphery of the *corpus luteum* in the fibrous trabeculae which divide it into lobes. In the second week after parturition the *tunica adventitia* of these blood vessels becomes more fibrous, and the lumen of the vessels decreases in diameter.

Further regression of the *corpus luteum* into a compact fibrous *corpus albicans* varies somewhat in different species and in individual animals. Reference to Table III shows that in each of the specimens H1016, H1018, H1023, H1027 and H1030, an ovary contains a *corpus albicans* of the previous pregnancy of mean diameter 10 mm. or more; in one of these ovaries there are five recognisable *corpora albicantia*, the largest of which has a mean diameter of 15.5 mm.

In the crabeater seal, the *corpora albicantia* are similarly persistent, and Harrison *et al.* (1952) note that each of three specimens collected at Hope Bay, Graham Land, in early February contained a *corpus albicans* of mean diameter 13 mm. In the elephant seal, the *corpus albicans* does not persist so long, and at parturition, the *corpus albicans* resulting from the previous year's pregnancy has regressed to 5 mm. or less. During the following breeding season it may be completely resorbed (Laws, 1953a).

STATION NO. Date taken, or age in days relative to parturition		*FOLLICLES						Largest healthy follicle	Size of <i>Corpus Luteum</i>	No. of <i>Corpora Albicantia</i>	OVARY		Remarks
		< 3 mm.		3-6 mm.		> 6 mm.					Volume in cc.	Length × Breadth in mm.	
		A	H	A	H	A	H						
H1001 3 May	R †	0	0	0	0	0	0	—	—	—	2.5	27 × 15	
	L †	0	0	0	0	0	0	—	—	—	3.6	27 × 23	
H1006 23 July	R	0	0	0	0	0	0	—	—	—	1.5	23 × 18	No follicles visible No follicles visible
	L	0	0	0	0	0	0	—	—	—	2.0	26 × 17	
H1007 6 August	R	11	10	1	3	0	1	9 × 7	—	—	5.0	30 × 24	
	L	13	16	0	3	0	1	7 × 4	—	—	5.0	29 × 21	
H1010 18 August	R	2	0	0	1	0	1	8 × 6	28 × 20	1	7.1	37 × 30	Largest healthy follicle collapsed and luteinising.
	L	6	2	1	6	1	1	7 × 4	—	1	9.5	36 × 26	
H1020 minus one	R	24	0	0	1	0	0	5 × 3	—	4	10.5	43 × 25	<i>C. Alb.</i> 10 × 6 mm., 7 × 6, 6 × 6, 5 × 3. <i>C. Alb.</i> 11 × 4 mm., 4 × 3
	L	10	0	1	0	0	1	6 × 2	26 × 21	2	20.1	49 × 34	
H1018 plus one	R	6	0	0	0	0	0	2 × 2	30 × 23	—	16.0	65 × 36	<i>C. Alb.</i> 18 × 13 mm., 16 × 14, 8 × 6, 8 × 6, 6 × 4
	L	46	0	0	0	0	1	7 × 5	—	5	11.2	49 × 24	
H1016 plus three	R	0	1	0	1	0	0	5 × 3	25 × 20	2	10.5	49 × 28	†one <i>C. Alb.</i> 11 × 9 mm.
	L	39	14	1	7	3	0	10 × 7	—	3	8.8	40 × 26	
H1012 plus five	R	44	2	2	1	0	0	6 × 4	—	—	6.7	46 × 23	
	L	3	1	1	0	0	0	5 × 1	33 × 22	—	14.0	46 × 34	
H1015 plus five	R	20	5	3	2	1	0	10 × 9	—	5	6.2	44 × 19	
	L	3	0	1	1	0	0	3 × 2	23 × 19	—	8.5	36 × 23	
H1017 plus seven	R	8	2	0	2	0	1	8 × 5	18 × 11	—	8.0	39 × 19	
	L	12	6	5	4	0	0	5 × 4	—	—	8.7	42 × 21	
H1014 plus nine	R	15	10	5	1	2	0	7 × 5	—	—	6.3	38 × 23	
	L	9	3	6	4	0	0	6 × 4	14 × 11	1	6.8	38 × 20	
H1023 plus eleven	R	0	0	1	0	0	0	3 × 2	19 × 16	1	5.8	32 × 22	<i>C. Alb.</i> 11 × 9 mm. <i>C. Alb.</i> 14 × 9 mm., 14 × 8
	L	17	3	1	0	0	1	7 × 7	—	2	6.4	35 × 22	
H1027 plus fifteen	R	5	0	0	2	1	4	11 × 10	—	—	6.5	38 × 20	<i>C. Alb.</i> 15 × 8 mm.
	L	3	0	0	0	0	0	2 × 1	18 × 15	1	7.8	39 × 28	
H1030 plus twenty-one	R	12	3	5	2	0	7	11 × 6	—	2	11.3	42 × 28	<i>C. Alb.</i> 18 × 19 mm., 17 × 7, 12 × 5, 9 × 8.
	L	1	0	1	0	0	2	9 × 6	19 × 18	4	—	40 × 19	
H376 13 February	R	2	0	3	0	1	0	6 × 5	—	3	—	41 × 23	<i>C. Alb.</i> 10 × 9 mm., 6 × 5, 6 × 4. <i>C. Alb.</i> 11 × 8 mm., 6 × 4
	L	0	0	4	0	5	0	11 × 8	27 × 21	2	—	48 × 28	

TABLE III. Numbers and sizes of follicles, *corpora lutea* and *corpora albicantia* in the ovaries of the Signy Island series of Weddell Seals.

Explanation of abbreviations:

\* Numbers of follicles grouped according to mean diameter. A=atretic, H=healthy.

† R=right ovary, L=left ovary

‡ *C. Alb.*=*corpus albicans*.

Bertram (1940) concluded that the *corpora albicantia* in the Weddell seal persisted for many years, probably throughout the life of the animal, and that the ovaries held a record of all the pregnancies undergone. From all the evidence at present available it seems likely that although the *corpora albicantia* may persist for a time, they do not remain easily visible throughout the whole of the animal's life. The method of age determination based on annual incremental layers in the dentine of the canine teeth has been applied to the limited number of specimens available (see p. 38) and in each animal the age as estimated from the number of *corpora albicantia* present (see Bertram, 1940) averages four years less than that determined from the tooth rings. Bertram's counts of *corpora albicantia* were made on macroscopic sections up to 5 mm. thick, but microscopic examination has sometimes revealed traces of *corpora albicantia* which would not be detected in the macroscopic sections. However, some of these smaller masses of scar tissue are probably the remains of *corpora lutea atretica* formed after involution of the larger follicles.

In a large series of Weddell seal ovaries collected in Graham Land during the period 1934 to 1937, Bertram (1940) found that 16 per cent of all females over 90 inches in length (direct nose to tail measurement) had missed pregnancies. On the assumption that the Weddell seal is monoestrous, this percentage does not greatly reduce the accuracy of the method of age determination based on counts of *corpora lutea*. However, recent work on the southern elephant seal (Laws, 1953a) has shown that a similar percentage of missed pregnancies occurs each year in this species (approximately 14 per cent), and that females which do not become impregnated are able to ovulate again; this is supported by examination of six female elephant seals taken in May and August (all of which contained regressing *corpora lutea* and were in various stages of pseudo-pregnancy), and thus agrees with the findings of Hamilton (1939) for the southern sea lion (*Otaria byronia*).

The present series of ovaries indicates that ovulation occurs in the ovary opposite to that containing the *corpus luteum* of the recent pregnancy, as in several other species of antarctic seals. If it is assumed that the *corpora lutea* persist as small masses of fibrous tissue throughout the life of the animal, then the numbers found in each ovary should not differ by more than one, or possibly two in the case of a female missing a pregnancy. Reference to Table III shows that in two pairs of ovaries there is a difference of four *corpora lutea* (H1015 and H1018), but this difference may easily be explained if a polyoestrous cycle is assumed to operate when successful mating is not achieved.

### 3. Sub-surface Crypts

In a recent paper, Harrison *et al.* (1952) have described in some detail the sub-surface crypts in the phocids and otariids examined, and have established that the formation of crypts varies during the reproductive cycle. In the antarctic seals, the peak of extension of the crypts and proliferation of the lining epithelium occurs in November, and for the remainder of the year their growth is much diminished; the seals from the northern oceans show a similar activity at the corresponding age in the reproductive cycle. Detailed work on the southern elephant seal by Laws (1953a) revealed that in pregnant females the crypts are first observed at the time when the blastocyst is about to implant, and that maximum activity is reached towards the end of pregnancy. During the lactation period, the crypts decrease in numbers, and are absent from ovaries collected during December, January and February.

Histological examination of all the Weddell seal ovaries in the present collection has been carried out, and the following is a summary of the data obtained. In the adolescent females H1001, H1006, H1007 and H123 the crypts are often very complex (Plate III f), and their deeper extensions are associated with numerous nests of from 5 to 10 primary oocytes surrounded by pre-granulosa cells; there may be as many as 25 oocytes per mm. of cortex. Many of the small concretionary bodies described in a previous section are found in the cortex of these young ovaries, and there is often a close association between these bodies and the crypts; the bodies may also be free in the lumen of the crypts.

During the last few weeks of pregnancy and the first half of the lactation period, the crypts in both ovaries are well developed and may reach a length of nearly 2 mm. They are usually simple and lie parallel to the surface of the ovary with occasional vertical branches opening to the exterior; complex crypts are found only infrequently, and then they are not extensive. In most ovaries there is little proliferation of the epithelial cells lining the crypts, for mitotic figures are rare, and the germinal epithelium on the surface of the ovary is fragmentary, the cells containing pyknotic nuclei. The cortex is usually thick and fibrous (Plates III g & IV a), and is divided into lobes by prolongations of the long horizontal crypts which reach to

the surface of the ovary. The layer of epithelial cells lining the outer walls of the crypts invariably becomes degenerate and fragmentary, whilst the inner epithelium appears quite healthy, and the cells are elongate and crowded together. Serial sections show that in places the whole outside of the cortex breaks away, leaving a new epithelial surface on a much thinner cortex. This may account for the absence of the crypts at certain times of the year, and it also affords a means of ridding the ovary of the concretionary bodies which have come to lie in the lumen of the crypts (Plates IV b & d).

The possible causes and effects of the shedding of the outer layer of fibrous cortex are a matter of speculation but it is certain that a thick hard covering surrounding the ovary would be a hindrance to successful ovulation and subsequent development of the *corpus luteum*. Activity is apparently at a minimum in the summer months, though even then differential proliferation of the inner and outer epithelial layers of the crypts is noticed, and the germinal epithelium forming the outer covering of the cortex may begin to degenerate. From this evidence, it is tentatively suggested that crypt formation may be correlated with both the production of mature follicles which are relatively large compared with the ovary, and the functional properties of the cortex.

Harrison *et al.* (1952) state that "there is some evidence that crypt formation can be induced by experimental injection of gonadotrophic and oestrogenic substances into ferrets, an animal the ovary of which does not usually exhibit marked crypt formation. It is therefore possible that the germinal epithelium responds to hormonal stimulation to form extensive crypts as a normal occurrence in . . . Pinnipeds and certain other Carnivores." In the present series of specimens, the differential proliferation of the epithelium lining the outer and inner walls of the crypts, suggests that, as the follicle destined to ovulate nears maturity, the crypts will eventually merge leaving the outer part of the cortex to break away, and allowing the follicle to reach its full size.

### C. THE UTERUS

#### 1. *Immature Seals*

The histological appearance of the uterus of foetal, young and adult seals, and the cyclical changes occurring after maturity have been described in detail by Harrison *et al.* (1952). As the majority of their young specimens were common seals (*Phoca vitulina*), the following description of the uterus of an immature Weddell seal is included for comparison. This specimen, H1006, taken on 23rd August, 1952, measured 73 inches in a direct line nose to tail, and was undoubtedly a yearling.

The cross-section, taken from the centre of the right cornu, is flattened dorso-ventrally, and measures 8 by 4.5 mm. The lumen is cross-shaped, and the maximum width of one of the branches is 250  $\mu$ . The mucosa averages 600  $\mu$  in thickness, and is surmounted by an epithelium consisting of a single layer of cuboidal cells 10  $\mu$  in height with spherical dark-staining nuclei 7  $\mu$  in diameter, though in places where the cells are crowded they appear to be pseudo-stratified, and the nuclei are more ovate or elongate. In some regions of the epithelium the cytoplasm of the cells is pale, but in many areas the outer parts of the cells have become mucilaginous, and here the cytoplasm is darker in its staining properties. Scattered throughout the epithelial cells are other smaller cells with elongate dark-staining nuclei and clear hyaline cytoplasm; these are evidently lymphocytes from the sub-epithelial layer. The uterine glands are generally short, straight or slightly coiled, and simple. They average 200  $\mu$  in length with an external diameter of 35  $\mu$ , and their epithelium consists of low cuboidal or columnar cells with pale-staining cytoplasm and spherical nuclei 7 to 8  $\mu$  in diameter. The stroma between the lumen of the uterus and the layer of circular muscles is compact, and well supplied with capillaries and arterioles. The inner layer of muscles consists of a circular arrangement of fibres some 150  $\mu$  thick with pronounced dark-staining nuclei. The outer layer of longitudinal muscles is divided into bundles of from 5 to 40 fibres, and the two layers are separated by a zone of connective tissue well supplied with capillaries and small blood vessels. This immature condition of the uterus is also found in H1001, which was taken on 3rd May, 1952 and is assumed to be in its second year.

H1007 represents a stage only three months later than H1001 in the development of the adolescent seal, yet the conditions are markedly changed (Plates IV b & c). Here the lumen of each cornu has become star-shaped with clefts 2 mm. deep. The pseudo-stratified epithelium is 25  $\mu$  high and two types of cell can be distinguished. The majority are tall columnar cells with pale-staining, elongate nuclei and pale cytoplasm, the apical part of which is mucilaginous. The remainder are wedge-shaped cells, narrower at the base, with

very dark nuclei; it is not known whether these are secretory cells, or normal epithelial cells which have been strongly compressed. A stratum compactum containing aggregations of lymphocytes and polymorphonuclear leucocytes has appeared under the epithelium, and the vascularisation of this layer has markedly increased. The glands have increased both in number and activity, and the epithelial cells are tall columnar,  $15\ \mu$  in height, though occasionally they may be pseudo-stratified. These cells have long oval nuclei, and the apical cytoplasm is highly vacuolated. In some smaller glands, this extensive vacuolation has resulted in the lumen becoming filled with a foamy mass of cytoplasm, but there is only a small amount of secretion (Plate IV e). These extensive changes are accompanied by other changes in the deeper layers, for the circular muscles surrounding the mucosa have increased to  $800\ \mu$  in width.

## 2. *The Uterus in Adult Seals*

Evidence for alternation in function of the ovaries has already been given, and a comparison of uterine histology is best carried out on the basis of this cycle of change.

In the uterine cornu in which the blastocyst will eventually implant, the post-partum changes are relatively simple. In H1018, taken on the first day after parturition, the mucosa is 2.5 to 3 cm. thick, with clefts extending down to 2 mm. from the surface. The epithelium is thrown into numerous small folds and consists of a single layer of cuboidal or low columnar cells, 12 to  $15\ \mu$  high, with spherical nuclei, and supra-nuclear vacuoles in the cytoplasm; occasionally an area of pseudo-stratified cells occurs, but there is no crowding. The sub-epithelial layer of the mucosa is thinly cellular and highly oedematous and hyperaemic and contains moderate numbers of lymphocytes and a few leucocytes. This layer and the remainder of the mucosa is well supplied with blood vessels and capillaries. The glands are few in number, and appear to be simple and slightly coiled. They average  $80\ \mu$  in diameter, and penetrate the mucosa to a depth of 1.5 mm. The epithelium consists of cuboidal or low columnar cells  $15\ \mu$  high, with spherical nuclei, and occasionally a mucilaginous apical border; there is a small amount of secretion in the glands.

In H1016, taken three days after pupping, marked changes are already occurring. The mucosa is 1.5 mm. thick, and there is a reduction in the folding of the epithelium. The epithelial cells are cuboidal or low columnar, 12 to  $15\ \mu$  high, with large spherical or oval nuclei. In some places, the long axis of the nucleus lies parallel to the epithelial surface and suggests local growth of the underlying stroma. Local aggregates of lymphocytes occur in the stroma, particularly in the sub-epithelial layer, and the connective tissue is becoming invaded with numerous fibroblasts. There is no change in the glands and glandular epithelium as yet.

In H1015, taken five days after parturition, there is a slight recrudescence of secretory activity in both the uterine and glandular epithelia, but otherwise there is little change from the previous specimen. The sub-epithelial layer is still oedematous, and contains large numbers of lymphocytes, and in the deeper stroma are the hyaline remains of a few blood-vessels. In H1017, taken seven days after parturition, the glands are generally much smaller in diameter, averaging only  $40\ \mu$ , and there is little secretion present. The epithelial cells are 7 to  $8\ \mu$  high with oval nuclei, and all contain deeply staining basophil granules. The sub-epithelial layer is still slightly oedematous, whilst the deeper stroma is becoming increasingly fibrous, and contains many more sclerotised blood vessels.

The picture of increasing development of the connective tissue and slight activity of the glands is also found in H1014, nine days post-partum; the mucosa is still oedematous, particularly in the sub-epithelial layer, and there are increasing numbers of sclerotised blood vessels nearer the surface. The final specimen in the series, H1027, fifteen days post-partum, shows the progressive development of the stromal tissue, and there are now signs of an increasing though slight activity of the glands. The cells of the glandular epithelium are tall columnar,  $15\ \mu$  high, with oval or rounded nuclei, and in many cells the apical cytoplasm is mucilaginous. Some of the smaller glands are filled with a granular secretion which appears to be continuous with the outer surface of the epithelial cells. The uterine epithelium consists of either a single layer of large columnar cells  $16\ \mu$  high with round nuclei and basophil granules in the cytoplasm, or a pseudo-stratified layer of smaller cells with darkly staining nuclei; a few mitoses are visible (see Plate IV g).

In the uterine cornu in which the foetus has just developed, the specimens are all taken from the para-placental zone. In H1018, taken on the first day after parturition, the highly folded mucosa is at least 6 mm. high, and is thinly cellular, highly oedematous and very well vascularised (Plate IV f). The uterine epithelium is characterised by large columnar cells  $20\ \mu$  high, with darkly staining cytoplasm and large oval nuclei, and there is some secretory activity. The glands are coiled, and do not extend deeper than 1 mm. from the

surface, and though their columnar epithelium may be only  $15\ \mu$  high, it is indistinguishable in appearance from the surface epithelium; there is slight secretory activity.

In H1016, at three days post-partum, the highly folded oedematous mucosa persists, and there is little evidence of growth of connective tissue. The uterine epithelium is columnar or pseudo-stratified,  $15$  to  $18\ \mu$  high, and a large proportion of the cells have absorbed yellowish-brown pigment granules resulting from the breakdown of red blood cells. Similar granules are present in the upper epithelial cells of the glands; in the lower part of the glands the cells show little secretory activity (Plate IV h). H1015, five days post-partum, is quite different from all the other specimens in the series, for the outer 2 mm. of the mucosa consists of a highly complex system of glands. Many are septate, and are formed by the coalescence of ten or more simple glands, whilst in others these divisions have broken down and cystlike structures have formed (Plate V a). The largest has a mean diameter of over 1 mm., and is surrounded by a pseudo-stratified columnar epithelium which is still secreting in parts. Where two large composite glands are close together, the thin lamella separating them is well supplied with connective tissue cells and capillaries; the lumina of the glands are filled with secretory products, and clumps of epithelial cells and red blood corpuscles.\*

In H1017, taken seven days after parturition, the appearance of the mucosa is similar to that of H1016 except that the complex folds no longer exist, being replaced by a fairly even epithelium only occasionally broken by the openings of the glands. In H1014, representing a stage two days later than this, there is a noticeable change. The mucosa is still highly oedematous and hyperaemic, but there are now large numbers of oval and elongate nuclei and many lymphocytes, particularly in the sub-epithelial layer. The uterine epithelium is pseudo-stratified and up to  $25\ \mu$  high, with many elongate dark-staining nuclei, and occasional lymphocytes moving through into the lumen. There is a slight decrease both in number and activity of the glands in the mucosa, but there is no change in the appearance of the columnar cells (Plate V b). In H1027, taken fifteen days after parturition, the epithelia of the glands and uterine lumen are pseudo-stratified, and are evidently proliferating actively, for the nuclei are crowded, and only very few are pyknotic. The sub-epithelial layer is oedematous, and contains moderate numbers of lymphocytes and a few leucocytes, whilst the remainder of the mucosa is becoming increasingly fibrous with more occluded blood vessels.

Only one specimen was taken in the winter months, and this had evidently aborted its foetus. This female, H1010, was taken on 18th August, 1952, and it is interesting to compare its condition with that of the parturient and post-partum seals. The placental zone was distinct and 5 cm. wide, and this would correspond to a foetal length of about 10 cm.; abortion must have occurred in March or early April.

In the sterile cornu of this specimen, the epithelium presents a varied appearance. In most places the cells are columnar or pseudo-stratified and may occasionally be crowded. The nuclei of many cells are pyknotic, and in one place the epithelium has broken down, and there is an invasion of leucocytes into the main lumen. There is little secretion, and the lumen contains only this mucus and remains of erythrocytes and leucocytes. The uterine glands are few in number and are mostly flask-shaped, narrowing from  $100\ \mu$  in diameter at the base to  $40\ \mu$  at the neck. The epithelial cells vary in appearance; those at the neck of the glands are evidently actively secreting, having basal nuclei and mucilaginous apical cytoplasm, while many of the epithelial cells lower in the glands contain the granular remains of red blood cells. The fibrous stroma of the endometrium is moderately oedematous. In the cornu from which the foetus has aborted, the histological picture is much the same except that the glands are not secreting. The sub-epithelial tissue is moderately oedematous, and contains many leucocytes, most of which are polymorphonucleate.

It has already been noted (see p. 21) that in immature cows about to be impregnated for the first time, there is marked follicular activity even in the first week of August, and it is thought that this may indicate that the virgin cows are served by the bulls earlier in the season than the cows which have pupped. The increased secretory activity of the uterine glands gives further support to this idea, and probably indicates that oestrogens are being produced in small quantities. This picture of increased follicular and uterine activity is also found in the mature cow H1010, taken on 18th August, 1952, which had apparently aborted its foetus in March or early April.

In the ovaries of mature seals immediately after pupping, there are few large healthy follicles (see Figs. 12 a & b), and secretory activity of the uterine glands is reduced to a minimum. In the second and third weeks after parturition, there is a small but marked proliferation of both uterine and glandular epithelial cells, and it is probable that the rapidly growing follicles in the ovary opposite to that containing the recent *corpus luteum* are producing enough oestrogens to promote this new proliferative phase.

\* This section is close to the placental zone and includes typical labyrinthine glands.



## D. THE VAGINA

1. *Histological Appearance in Immature Seals*

In the yearling female H1006, taken on 23rd July, 1952, the mucosa presents an inactive appearance. Folds between 3 and 4 mm. in height are present, but the surface is only slightly irregular, and occasionally small clefts may penetrate down to  $300\ \mu$  into the stroma. The epithelium consists of a basal layer of columnar cells  $10\ \mu$  high, with oval and occasionally pyknotic nuclei, and this is overlain in places by a further one or two layers of cells with dark-staining oval or round nuclei and dark granular cytoplasm. The outer layer of cells is fragmentary in some places, but is represented by a single layer of horizontal cells with pyknotic nuclei. The whole epithelium is between 30 and  $40\ \mu$  in thickness. In the small clefts, there appears to be active proliferation in the intermediate layer, and the epithelium may consist of up to ten layers of cells, some  $50\ \mu$  to  $60\ \mu$  in thickness. The rest of the mucosa consists of a fairly dense connective tissue well supplied with blood vessels, and a marked sub-epithelial layer containing numerous small cells with dark-staining oval nuclei. Many of these are lymphocytes which actively penetrate the epithelium in some places, and there is one large concentration of these cells extending to 1.5 mm. below the basal layer of the epithelium.

This immature condition of the mucosa is also found in H1001, taken on 3rd May, 1952, and assumed to be 20 months old. The basal layer of the epithelium is not always easily definable owing to the increased concentration of cells in the sub-epithelial layer, and the superficial layer of flattened cells with pyknotic nuclei is absent. A feature not found in H1006 is the presence of small open flask-shaped structures scattered along the epithelium at intervals of about a millimetre, and filled with fluid. The largest is  $110\ \mu$  deep and  $80\ \mu$  wide, narrowing to  $45\ \mu$  at the neck, and is lined with a single layer of low cuboidal or very flattened cells (Plate V c). The function of these structures is unknown, and they have not been observed in any other section examined. A cleft 1.5 mm. deep, with branches  $300\ \mu$  long, is present in the sections, and is partly filled with a liquid containing scattered pyknotic nuclei and leucocytes, and some red blood cells.

In H1007, an adolescent seal approaching maturity, the development of the mucosa is greatly advanced. The epithelium is now prolonged into clefts up to 3 mm. from the surface, and these may bear further branches up to 1 mm. in length. The basal layer of the luminal epithelium consists of a row of tightly packed cells  $10\ \mu$  high, with elongate nuclei and occasional supra-nuclear vacuoles. An intermediate layer is not always present, but when it occurs, it is represented by one or two rows of small cells with pale-staining nuclei and sometimes large vacuoles. The superficial layer is a single row of narrow cells  $12\ \mu$  high with elongate club-shaped nuclei; in places the cells are bent over and appear almost as a squamous layer. Along much of the mucosal surface the epithelium is fragmentary, and consists of a basal layer of flattened cells overlain by one or two layers of elongate cells with pyknotic nuclei; these cells are also bent over to give a squamous appearance to the epithelium. In the long clefts in the mucosa, the epithelial cells are well developed and not crowded. The basal layer consists of a single row of low columnar cells with small oval dark-staining nuclei  $5$  to  $7\ \mu$  in diameter. The intermediate layer contains one to three rows of large cells with pale nuclei and cytoplasm, scattered lymphocytes and a few polymorphonuclear leucocytes. The cells in the superficial layer are large and columnar with oval nuclei, and the whole epithelium is  $40\ \mu$  thick (Plates V d & e). At the outer ends of the clefts there is much elongation of the epithelial cells, and the nuclei in the superficial layer become pyknotic and break away into the lumen. The remainder of the mucosa appears much the same as in the yearling females, with a compact and slightly fibrous tissue underlying the well defined sub-epithelial layer.

2. *Post-Partum Changes in Mature Females*

In H1018, taken on the day following parturition, the epithelium is markedly folded, forming branching clefts up to 6 mm. deep, and numerous papillae project from the epithelium into the underlying tissue; the average height of the epithelium is between 60 and  $70\ \mu$ , whereas the papillae may measure up to  $300\ \mu$ . The basal layer consists of a single row of cells  $10\ \mu$  high with conspicuous oval nuclei, closely associated with large numbers of leucocytes. Two layers of large cuboidal or polyhedral cells  $20\ \mu$  in diameter with large vesicular nuclei and pale-staining cytoplasm overlie the basal layer, and the superficial cells have foamy, highly granular basophilic cytoplasm with dark-staining elongate nuclei; there are numerous leucocytes in both these layers. Deep in the clefts, the numerous papillae result in much cell crowding, and

nearly all the cells in the epithelium show some attenuation (Plates V f & g). The three types of cell so far described are found in the papillae in the same sequence as in the epithelium, but the large pale-staining cells may proliferate to form up to fifteen layers. Many of the papillae along the surface epithelium have central cavities, and these are usually filled with the highly basophilic cytoplasm of the superficial layer of cells. Deeper in the clefts of the mucosa, these superficial cells occasionally give an acidophilic reaction. The sub-mucosa is highly oedematous, and scattered throughout the connective tissue are numerous lymphocytes with small round deeply staining nuclei, and occasional polymorphonuclear leucocytes. A third type of cell with a pale-staining oval nucleus  $10\ \mu$  in length is also present. A marked sub-epithelial layer is formed by the aggregation of these scattered cells beneath the basal cells of the epithelium. The lumen of the clefts is filled with blood, and a few lymphocytes and some cell debris.

In H1016, three days after parturition, the epithelium has decreased in thickness; the basal layer of small cells is retained, but their nuclei are now no longer densely staining. The large polyhedral cells of the intermediate layer are generally replaced by a row of columnar cells with pale cytoplasm and oval nuclei. The superficial layer consists of tall columnar cells, often  $30\ \mu$  high, with dark-staining basal nuclei, and mucified and usually basophilic cytoplasm. The papillae are less numerous and are much smaller in size than in the previous specimen, for they contain fewer layers of the large polyhedral cells (Plate VI a).

At five days post-partum, in H1012, a further reduction in the number and size of the papillae is found, and the largest recorded in any section measures only  $100\ \mu$  in depth (Plate VI b); the mucosa is still oedematous, chiefly in the sub-epithelial layer. This appearance of the mucosa is retained in H1017, seven days after parturition, though by now the mucified cytoplasm of the superficial epithelial cells has broken away, and only the basal pyknotic nuclei are left (Plate VI d).

In H1014, nine days post-partum, the epithelium shows signs of increased activity. The basal layer consists of pseudo-stratified cells  $15\ \mu$  high, with conspicuous oval nuclei, and is overlain by up to five layers of long cells, attenuated at either end, with round nuclei  $10\ \mu$  in diameter. The luminal layer of cells has slightly smaller oval nuclei, most of which lie with their long axes parallel to the surface of the epithelium; the whole epithelium is from  $60$  to  $70\ \mu$  in thickness. In the clefts, many of the cells of the intermediate layer increase in size, and become polyhedral, and a large proportion of these are highly vacuolated. This may be a post-fixation phenomenon, but it is of interest to note that many of these vacuoles contain one or two apparently normal red blood cells. The sub-mucosa is slightly oedematous, and appears more fibrous, and there is a marked reduction of the lymphocytes, particularly in the sub-epithelial layer; there are few lymphocytes in the epithelium (Plate VI c).

The somewhat varied post-partum development of the vagina is emphasised in H1023, taken eleven days after parturition, for the whole appearance of the mucosa suggests a much younger stage than that found in H1014. There is, however, little oedema in the sub-mucosa. In the final specimen in the series, H1027, taken fifteen days after parturition, the appearance of the mucosa suggests little development beyond the stage represented by H1017, seven days post-partum, though there is less oedema and fewer lymphocytes, and the sub-mucosa is more fibrous.

In H1010, taken on 18th August, 1952, the only non-pregnant mature cow in the series, the surface epithelium consists of a basal layer of pseudo-stratified crowded cells  $11$ – $12\ \mu$  high, with deeply staining elongate nuclei. In the intermediate layer, there are five to six rows of columnar cells, attenuated at each end, with elongate oval nuclei, and these cells merge into a further four or five rows of large polyhedral cells with round or oval nuclei. The superficial layer consists of up to five layers of squamous cells, cornified in places, and sometimes breaking away into the lumen. The epithelium varies in depth from  $70\ \mu$ , to  $180\ \mu$  in the papillae. The sub-mucosa is well supplied with blood vessels, and is densely cellular with many oval and elongate nuclei; there is no marked aggregation of lymphocytes and other cells in the sub-epithelial layer (Plate VI f).

In the discussion on the development of the uterus it was noted that, in the immature female H1007, the condition of the uterine glands suggested that oestrogens were being produced in small quantities by the rapidly expanding follicles. Although the appearance of the vaginal epithelium is one of low activity, it has been shown by Allen *et al.* (1939) that oestrogens at a sub-threshold value for cornification can cause mucification of the vaginal epithelium in rodents, and this may have occurred in H1007.

The vagina of the post-partum cow is characterised by much oedema and lymphocytic invasion of the sub-mucosa, particularly directly below the epithelium, together with mucification of the superficial layer of cells. There seems no reason to doubt that with rapid growth of the follicles, and sufficient production

of oestrogens, the epithelium of the vagina would develop into a stratified, squamous layer with cornified outer cells as in H1010. Harrison *et al.* (1952) found only relatively slight changes in the vaginal epithelium of post-partum cows, and they correlated this with the few noticeable signs of any oestrus behaviour. This assumption was based on insufficient evidence, however, and Laws (1953a), in a more detailed study, has shown that in the southern elephant seal normal oestrus changes do occur in the vagina, and are accompanied by definite behaviour patterns.

Station No.	Date	Nose-tail length (in.)	Assumed age in years
MALES			
H1009	16. 8.52	105	5
H1011	27. 8.52	105	9
H1021	16. 9.52	102	11
H1022	23. 9.52	104	16
H1024	28. 9.52	109	9
H1033	11.11.52	105	11
FEMALES			
H123	20. 4.48	71	8 months
H376	13. 2.50	102	11 years
H1001	3. 5.52	90	20 months
H1006	27. 7.52	78	10 months
H1007	6. 8.52	91	23 months
H1010	18. 8.52	106	10 years
H1012	7. 9.52	100	8
H1014	8. 9.52	111	7
H1015	8. 9.52	106	10
H1016	9. 9.52	115	10
H1017	11. 9.52	108	14
H1018	12. 9.52	112	8
H1020	15. 9.52	114	13
H1023	26. 9.52	111	8
H1027	30. 9.52	105	10
H1031	4.10.52	113	11

TABLE IV. Male and female Weddell seals collected at the South Orkneys. Nose-tail measurements are taken along the curve of the back; approximately 7 per cent should be deducted to give an equivalent direct length.

## Section V

### THE MALE REPRODUCTIVE CYCLE

THE series consists of seven mature Weddell bulls, six of which were taken in August and September; the specimens taken amplify the results obtained by Harrison *et al.* (1952), and in Fig. 15 the measurements of tubule diameters are compared with similar measurements obtained by these authors. Measurements of the epididymis have also been taken, and these are set down, together with an estimate of the amount of sperm present, in Table V.

The *bacula* of all the adult bulls were also collected, but no correlations were found between their shape and length and the length of the animal. The *baculum* of a three-day-old pup (born of female H1016) is included in the series, and is shown in Fig. 11 a together with the *baculum* most representative of the adult collection, H1022.

Tissues were fixed in the same way as the female material, and sections of testis and epididymis stained well with Heidenhain's Iron Haematoxylin and Eosin.

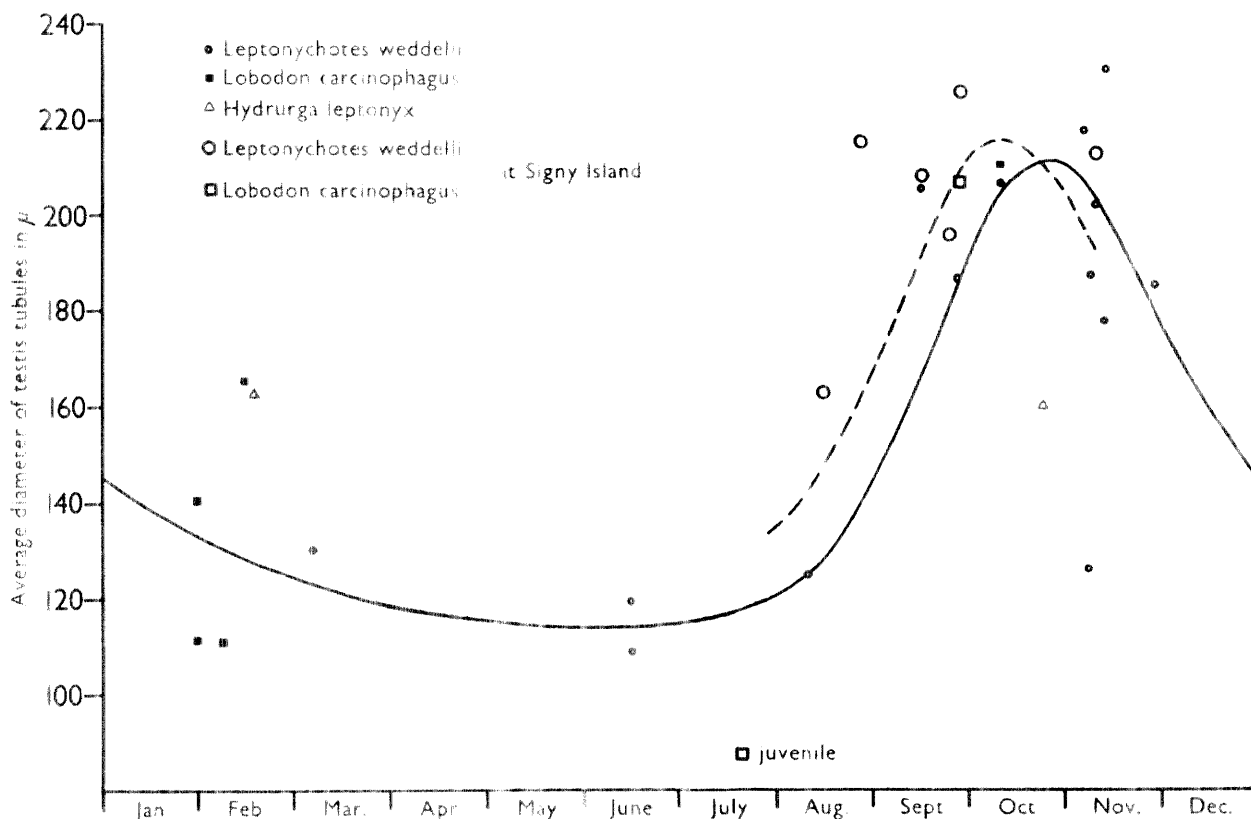


FIGURE 15. Testicular activity of seals taken at Signy Island (broken line), compared with the testicular cycle of antarctic seals, after Harrison, Matthews and Roberts (1952, figure 4).

Station No.	Date	Assumed age in years	Length of baculum in mm.	TESTIS TUBULES			EPIDIDYMIS			Remarks
				average diam. in $\mu$	Ht. of Epith. in $\mu$	*Types of Tubule. I, II, III	average diam. in $\mu$	Ht. of Epith.	†Percentage of sperm.	
H1009	16/8	5	—	162	33 $\mu$	mostly †	182	—	3	Very poor fixation
H1011	27/8	9	196	215	83	6.1.3.	245	60	30	
H1021	16/9	11	215	207	55	2.1.7.	240	48	15	
H1022	23/9	16	190	195	55	2.0.8.	260	60	10	
H1024	28/9	9	192	225	60	4.1.5.	272	55	30	
H1033	11/11	11	214	212	46	7.2.1.	254	52	33	Many spermatids together with spermatozoa
H1016 (pup)	3 days old		55							

TABLE V. Histological summary of male Weddell seal material.

\* Numbers refer to proportions of ten random tubules showing types I, II, III as illustrated in Fig. 16.

† Average amount of sperm calculated from ten random tubules.

## A. HISTOLOGICAL CHANGES IN THE TESTIS

The first adult Weddell seal in the series, H1009, was taken on 16th August, 1952. Unfortunately the specimen was badly preserved, but some idea of the histology of the seminiferous tubules can be obtained. In most tubules a small number of spermatids are present, and occasionally groups of spermatozoa are seen attached to the terminal portions of Sertoli cells. All of the tubules are patent, though as yet they contain no free spermatids or spermatozoa. In H1011, taken on 16th September, 1952, the tubules are lined with spermatogonia and Sertoli cells and up to four layers of primary and secondary spermatocytes, in all of which cell divisions are occurring. Spermatids are numerous, and the majority of tubules contain developing spermatozoa. In this testis, and in the remainder of the specimens taken in September and November, the degree of spermatogenesis is variable, and three stages can usually be recognised. There is no sharp demarcation between them, however, for it is evident that successive stages of development occur throughout the length of each tubule. These recurring phases of the mature testicular cycle are illustrated in Fig. 16, and their occurrence in the present series of specimens is recorded in Table V.

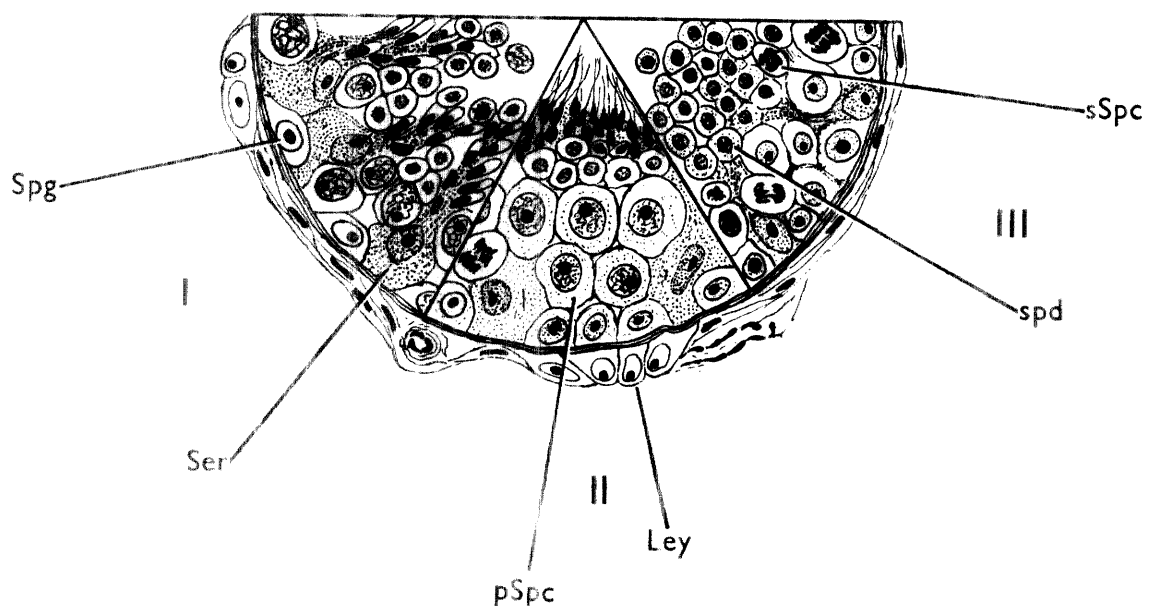


FIGURE 16. Diagram illustrating the three phases of development observed in the testis tubules of the South Orkney series of Weddell seals: spg=*spermatogonium*, Ser=*Sertoli cell*, pSpc=*primary spermatocyte*, Ley.=*Leydig cell*, spd.=*spermatid*, sSpc.=*secondary spermatocyte*.

## B. THE EPIDIDYMIS

In the adult Weddell seals there is no discernible variation between the individual males, other than in the height of the epithelium, and it will suffice to describe the condition found in H1011. The epithelium consists of tall columnar cells up to  $60\ \mu$  high with oval or round nuclei  $8\text{--}10\ \mu$  in diameter. The position of the nucleus varies in the cells, but in some parts of the tubules all the nuclei may be basal; usually, however, the nuclei in any one section appear at different levels, and a pseudo-stratified epithelium results. Cilia up to  $15\ \mu$  in length are present on most cells, and they are often twisted together into a point. Scattered amongst the bases of the columnar cells are small polygonal cells with round or oval nuclei  $7\text{--}8\ \mu$  in diameter, and in some sections the cells are numerous enough to form a distinct layer below the columnar epithelium. The total amount of spermatozoa and spermatids present in the epididymis is very variable, and the estimates are shown in Table V.

Though the data are so limited, the comparison of the present series with the material examined by Harrison *et al.* (1952) suggests that the breeding bulls at the South Orkneys come into rut one or two weeks earlier than those inhabiting the coasts of Graham Land. In view of the comparatively early pupping season

in the South Orkneys, this appears to be reasonable. It is unfortunate that no information concerning the development of the interstitial tissue is available for the male taken earliest in the season. However, only a small amount of sperm is present in the epididymis, and it seems certain that the males seen fighting on 7th August, 1948 (see p. 19), were in a very early condition of rut.

The first bull in breeding condition is H1011, taken on 27th August, 1952, and there is much sperm present in the epididymis. Comparison with H1021 and H1022, taken on 16th and 23rd September respectively, shows that the amount of sperm present in mature bulls during this month is very variable. It is assumed, however, that the bulls impregnate the virgin and non-pregnant mature cows in the latter half of September and early October, and then, after the break-up of the rookeries, the cows which have recently pupped are ready to be impregnated.

## Section VI

### GROWTH AND AGE

#### A. INTRODUCTION AND METHODS

THE first serious attempt to find a method of determining the age of the Weddell seal was made by Lindsey (1937) with specimens collected during the Second Byrd Antarctic Expedition (1933-5). The frequency distribution of nose-tail lengths of 93 adult and adolescent males and 124 females showed several well defined groups; these Lindsey interpreted as annual age groups, and supplemented the measurements by skull data and field observations.

Bertram (1940) was able to make another large collection of over 200 Weddell seals from Graham Land, though the killings were spread over many more months of the year than were Lindsey's specimens. For comparison with Lindsey's figures, the measurements of 81 young and adult seals of both sexes killed between 8th March and 21st April in two separate years were set down in a similar fashion. From these data, and skull measurements on all the seals, Bertram concluded that it was impossible to determine the age groups of the Weddell seal after the first two years of life.

Laws (1953b) has shown that in the southern elephant seal, growth layers occurring in the dentine of the teeth may be correlated with the yearly cycle, and thus the age of any specimen may be determined to within a month. Similarly Scheffer (1950), from examination of the canine teeth of Alaskan fur seals, has found that the number of growth ridges formed by differential deposition of dentine on the roots of the canine teeth corresponds with the known ages of marked seals.

Laws has also shown that concentric rings in the dentine occur in at least fourteen other species of pinnipeds, though in many species the pulp cavity of the teeth may become closed shortly after maturity is reached, and further deposition of dentine is considerably reduced or ceases altogether. Thus while the method is of great value in estimating the ages of species which possess canine teeth with open roots, particularly the polygynous species which show marked sexual dimorphism, it has limited application to other pinniped species in which the teeth are apparently fully grown after reaching sexual maturity.

For the present study, which mostly concerns mature seals, it was assumed from Bertram's observations that measurements of skulls would be of little value in determining age, and only the canine teeth were collected.

In the Weddell seal the roots of the canine teeth are nearly closed at maturity, but dentine deposition still occurs inside the pulp cavity; examination of ground sections of teeth shows that many concentric rings are visible in the dentine, and an attempt has been made to correlate these with the supposed age of the seals. The validity of age determinations from tooth-rings cannot be proved for the small series of Weddell seals examined. Marked differences do occur in the numbers of rings in the dentine of different individuals, and it is suggested that these rings are analagous with those found in the southern elephant seal for which this method of ageing has been proved satisfactory. The validity of age determinations based on counts of *corpora lutea* has already been questioned, and it is considered that the present method provides a more accurate estimate of the age of the Weddell seal.

For a description of the methods employed in preparing sections of teeth, and a discussion of the structure and growth of the dentine, the detailed account by Laws (1953b) should be referred to. In many of the Weddell seal teeth examined there appeared to be only slight evidence of concentric rings of "columnar" and "marbled" dentine, but by viewing the sections between crossed polarising filters under an ordinary microscope, the rings usually became clearly defined. Eventually all the sections were examined by this method, and consistent results were obtained.

#### B. MACROSCOPIC AND MICROSCOPIC APPEARANCE OF THE TEETH

In H1006, the youngest Weddell seal in the series, the width of the dentine in a cross-section of the canine tooth is 2.3 mm. and the dentine is divided into two clearly defined concentric rings. The outer ring is 1.3 mm. wide, and is very well calcified. This is the "mantle" dentine of Schourr and Massler (1942) and is a constant feature of both immature and adult teeth; it probably represents the growth during foetal life and up to the end of lactation. The inner ring is composed entirely of marbled dentine, and there is a clear transition between the zones (Plate VI e). In the southern elephant seal the zones of marbled dentine correspond to the periods of feeding at sea, and it is assumed that this applies also to the Weddell seal.

In H1007, assumed from its nose-tail length to be in its second year, the layer of mantle dentine is 1.0 mm. thick, and is clearly separated from the inner zone of marbled dentine. This inner zone is 2.6 to 3.0 mm. thick, and contains two thin rings in which the marbled dentine is noticeably more fused. The cross-section of the tooth of H1001 has a very similar structure to that of H1007, and it is assumed that in spite of the immature appearance of the gonads, the seal is in its second year.

In the adult seals, the pulp cavity is very much reduced, but is never entirely obliterated. From comparison with the two seals assumed to be in their second year, it is possible to see how much growth has occurred after maturity has been reached. This is illustrated diagrammatically in Fig. 17, and the rings in the adult

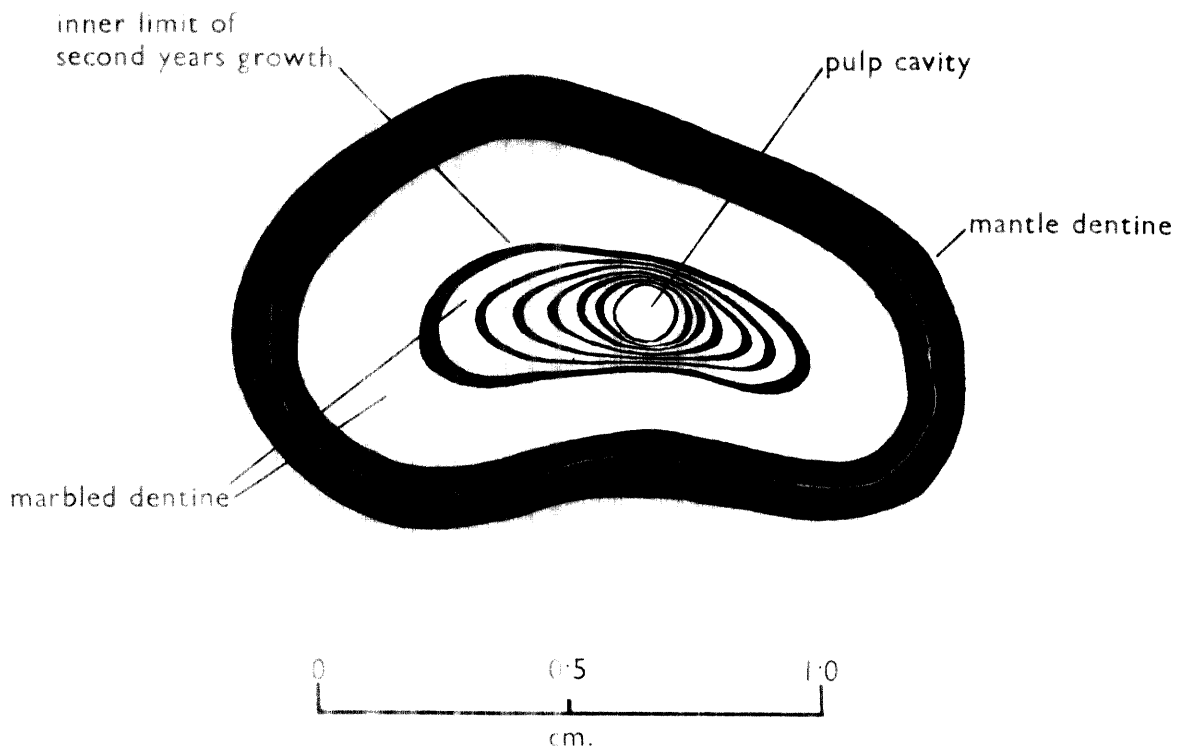


FIGURE 17. Diagrammatic transverse section of the canine tooth of an adult female Weddell seal assumed to be eight years old.

dentine are shown. On microscopic examination the rings are seen to consist of a dense outer zone of columnar dentine, and a lighter inner zone of large marbled dentine. The width of each ring is variable, being 70–100  $\mu$  in thickness laterally, and up to 450  $\mu$  in thickness at the anterior and posterior ends of the section (Plate VI g). In the majority of sections examined marbled dentine is being formed next to the pulp cavity, and it is evidently laid down during the winter feeding and right up to the time of parturition. This sudden change from marbled to columnar dentine evidently reflects a change in the metabolism of the animal and the columnar dentine is assumed to represent the period of fasting during the pupping season and the irregular feeding during the summer moult. This differs from the conditions found in the elephant seal for which the fasting periods during the pupping season and then during the time of moult are represented by two distinct rings of columnar dentine.

For further comparison, the canine teeth of ten specimens of the southern fur seal (*Arctocephalus australis*) were examined macroscopically, and in the older specimens in which the pulp cavity was almost occluded, a similar pattern of alternate light and dark rings of dentine was found. As in the Weddell seal a pair of these rings was assumed to represent one year of the life cycle, and the specimens were aged on this basis; the age determined in this way was found to agree within a year with the age determined by the number of external ridges on the teeth. These ridges are well marked, and the teeth resemble those of the Alaskan fur seal for which the method has been proved valid.

The assumed ages of the Weddell seals in the present series are set down in Fig. 14, and a suggested growth curve is drawn for both sexes. The absence of three-, four- and six-year-old seals of either sex must either be attributed to the limited nature of the collection, or to reflect some difference in the habits of the younger seals.

### C. TOOTH WEAR

Observations made in the south of Graham Land, and in the Ross Sea at the Bay of Whales and McMurdo Sound, show that a large proportion, if not the whole of the Weddell seal population winters beneath the fast ice, in which breathing holes are maintained.

The method by which the seals keep the holes clear has been accurately described by Lindsey (1937). "Swinging the entire head from side to side, with the mouth held open at an angle of about 150 degrees, they cut a double groove by use of the canines (and perhaps incisors also) of both jaws. In one case, a seal in the water rasped away the margin of the exit hole, without those of the lower jaw touching the ice."

It is clear that ice-sawing is responsible for excessive wear often leading to extensive damage of the anterior teeth in so many adult seals, and Bertram (1940) considers this to be "a very potent factor in the mortality of the species". He also states "that one might surmise that the chief mortality is among the pups, that then for a number of years the adults suffer rather few losses, and that finally most deaths occur under the winter ice by reason of the seals failing to keep open the necessary breathing holes. In this last process, any breakage or rotting of the teeth may be a severe handicap, and lead directly to the failure of the animal to maintain itself."

In the South Orkneys, where fast ice remains to the south of the group for an average of three and a half months in the winter and early spring (Fig. 2 b), few Weddell seals show more than slight tooth wear. Of the eighteen males and females whose teeth have been examined, fourteen have unworn or only slightly worn teeth. The remaining four seals show varying degrees of damage to the dentition:

H1014. Upper canines and outer incisors worn down a quarter of an inch.

H1017. Upper left outer incisor worn down to expose pulp cavity, no obvious necrosis.

H1022. Right upper and lower canines broken or worn down nearly to pulp cavities, right upper outer incisor also worn.

H1033. Slightly worn dentition, upper left outer incisor broken off at gum.

The variable and usually unstable ice conditions on the north coasts of the South Orkneys have already been discussed, and it seems certain that a large part of the population spends the winter there. Thus the need for ice-sawing would be small, and tooth wear would not become a potent factor in mortality.



## SUMMARY

1. Factors affecting the hauling-out habits of the breeding population of Weddell seals at the South Orkney Islands are discussed, and the wide variations in ice conditions from year to year are correlated with observed fluctuations in the population.

2. The breeding behaviour of the pregnant cows and cows which have pupped is examined in detail, and a description of the birth of a pup is included.

3. Variations in the colour and marking of pup coats have been observed, and an analysis of these, together with an estimate of the sex ratio is given. The locomotion of young pups shows ancestral traits, though co-ordination of the limbs and the resultant adult type of locomotion develops quickly. Many pups show precocious swimming habits. Observations on these are compared with the findings of other authors. The factors affecting the mortality of the pups are considered.

4. A series of specimens from female seals taken relative to parturition provides the basis for the discussions of the ovarian cycle, and of changes in the uterus and vagina.

The follicular cycle for the three weeks following parturition, and changes in the *corpus luteum* of the recent pregnancy are described. The validity of the method of age determination based on counts of *corpora lutea* is discussed, and possible explanation of the function of the sub-surface crypts is given. The histological change in the uterus and vagina of young and mature seals is described.

5. Histological changes in the testis tubules and epididymis are described, and fighting and rut in the male seals are correlated with the testicular cycle.

6. The canine teeth have been examined microscopically. By analogy with several species of *Pinnipedia* in which age can be determined from incremental zones in the dentine, the ages of the individual seals in the present series have been estimated. Finally, tooth wear is discussed in relation to local ice conditions.

## ACKNOWLEDGEMENTS

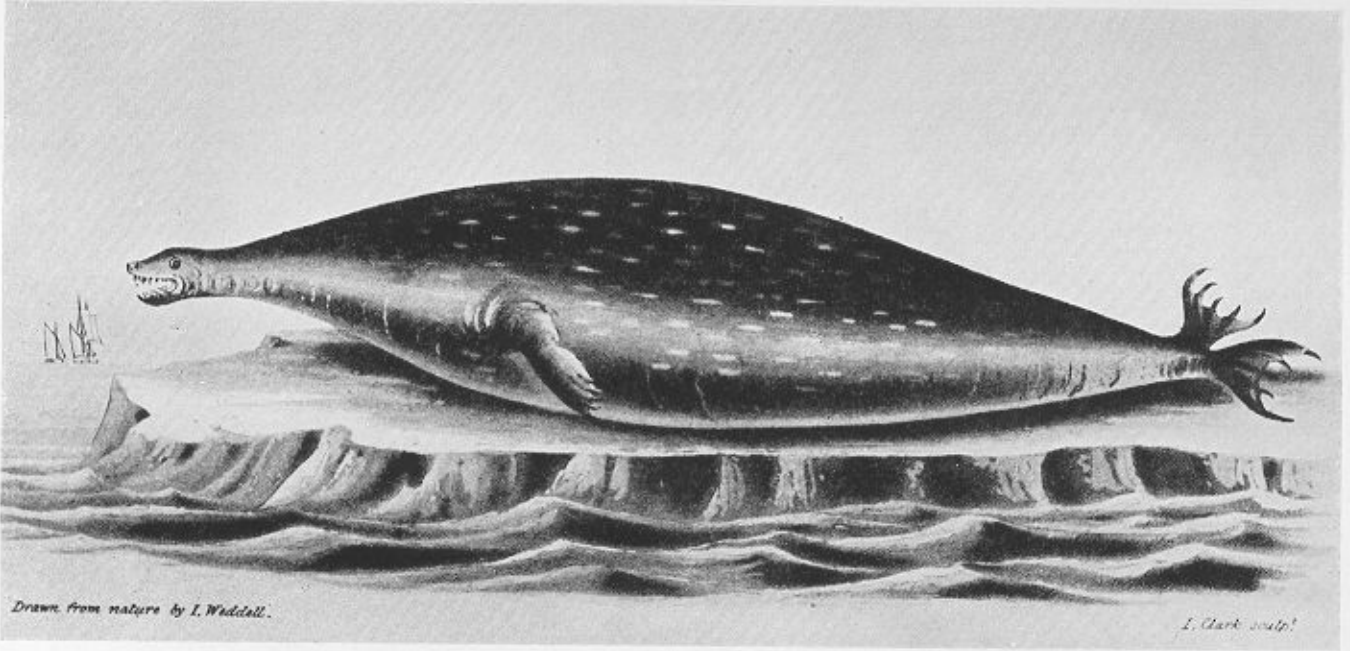
I AM INDEBTED to R. M. Laws of the Falkland Islands Dependencies Survey and now of the National Institute of Oceanography for teaching me the basic techniques whilst at South Georgia, and for allowing me to use his original field observations, and to make reference to unpublished work on the reproductive cycle of the southern elephant seal.\* My thanks are due to G. de Q. Robin and T. G. Owen for other observations which appear in the text, and particularly to F. L. Johnson who gave me great assistance in the field.

I also wish to thank Dr. L. Harrison Matthews for permission to use an original illustration (see Harrison, Matthews and Roberts, 1952; fig. 4); Dr. Elspeth McConnachie for valuable criticism and correction of the manuscript, and Dr. L. E. R. Picken and F. Lemmon for advice on microscopical and histological techniques.

\* Now published as F.I.D.S. Scientific Report No. 15.

## BIBLIOGRAPHY

- ALLEN, J. A. 1905. The mammalia of Southern Patagonia. *Rep. Princeton Univ. Exped. to Patagonia, 1896-9*, 3, 1-120.
- ALLEN, E. *et al.* 1939. *Sex and Internal Secretions*. Bailliere, Tindall & Cox, London, 475 pp.
- AMOROSO, E. C. and L. H. MATTHEWS. 1950. The growth of the grey seal (*Halichoerus grypus* (Fabricius)) from birth to weaning. *J. Anat. Lond.*, 85, 427.
- BERTRAM, G. C. L. 1940. The biology of the Weddell and crabeater seals: with a study of the comparative behaviour of the Pinnipedia. *Sci. Rep. Brit. Graham Land Exped., 1934-7*, 1, 1-139.
- BROWN, R. N. R. 1913. The seals of the Weddell sea: notes on their habits and distribution. *Rep. Scot. nat. antarct. Exped., 1902-4*, 4, 185-98.
- BROWN, R. N. R., R. C. MOSSMAN and J. H. H. PIRIE. 1906. *The Voyage of the Scotia*. Blackwood & Sons, London.
- CANDOLIN, Y. 1953. "Seal finger." *Acta Chirurgica Scandinavica*, Suppl. 77.
- CHEAL, J. J. (Unpublished.) Base H, Sea ice Report, 1951. F.I.D. Scientific Bureau.
- CHOYCE, M. A. (Unpublished.) Base C, Biological Report, 1946; Seals. F.I.D. Scientific Bureau.
- DAVIES, J. L. 1949. Observations on the grey seal (*Halichoerus grypus*) at Ramsey Island, Pembrokeshire. *Proc. zool. Soc. Lond.*, 119, 673-92.
- HAMILTON, J. E. 1939. A second report on the southern sea lion, *Otaria byronia* (De Blainville), "Discovery" *Rep.*, 19, 121-64.
- HARRISON, R. J., L. H. MATTHEWS and M. ROBERTS. 1952. Reproduction in some Pinnipedia. *Trans. zool. Soc. Lond.*, 27, 437-540.
- JOHNSON, F. L. (Unpublished.) Base H, Sea ice Report, 1952. F.I.D. Scientific Bureau.
- LAWSON, R. M. (Unpublished.) Base H, Biological Reports, 1948; Seals. F.I.D. Scientific Bureau.
- (Unpublished.) Base H, Biological Report, 1949; Seals. F.I.D. Scientific Bureau.
- (1953a, Unpublished.) The reproduction of the southern elephant seal (*Mirounga leonina* Linn.). *Dissertation submitted for the degree of Doctor of Philosophy at the University of Cambridge*.
- 1953b. A new method of age determination in mammals with special reference to the elephant seal (*Mirounga leonina* Linn.). *Falkland Islands Dependencies Survey Scientific Reports*. No. 2, 11 pp.
- 1953c. The elephant seal (*Mirounga leonina* Linn.). 1. Growth and age. *Falkland Islands Dependencies Survey Scientific Reports*. No. 8, 62 pp.
- LINDSEY, A. A. 1937. The Weddell seal in the Bay of Whales. *J. Mammal.*, 18, 127-44.
- MACKINTOSH, N. A. and H. F. P. HERDMAN. 1940. Distribution of pack ice in the southern ocean. "Discovery" *Rep.*, 19, 285-96.
- MARR, J. W. S. 1935. The South Orkney Islands. "Discovery" *Rep.*, 10, 283-382.
- MATTHEWS, L. H. 1929. Natural history of the elephant seal. "Discovery" *Rep.*, 1, 233-56.
- OWEN, T. G. (Unpublished.) Base H, Biological Report, 1953; Seals. F.I.D. Scientific Bureau.
- ROBIN, G. de Q. (Unpublished.) Bases C & H, Biological Reports, 1947; Seals. F.I.D. Scientific Bureau.
- SAPIN-JALOUSTRE, J. 1952. Les phoques de Terre Adélie. *Mammalia*, 16, 179-212.
- SCHEFFER, V. B. 1949. The clitoris bone in two pinnipeds. *J. Mammal.*, 30, 269.
- 1950. Growth layers on the teeth of Pinnipedia as an indication of age. *Science*, 112, No. 2907, 309-11.
- SCHOOUR, I. and M. MASSLER, 1942. *The Rat in Laboratory Investigation*. Edited by Griffith and Farris. J. B. Lippincott Co., London.
- SIVERTSEN, E. 1941. On the biology of the harp seal, *Phoca groenlandica* Erxl. *Hvalrødets Skrifter*, 26, 1-166.
- SKILLING, C. (Unpublished.) Base H, Sea ice Report, 1949. F.I.D. Scientific Bureau.
- TINBERGEN, N. 1951. *The Study of Instinct*. Oxford University Press.
- WEDDELL, J. 1825. *A Voyage towards the South Pole performed in the years 1822-24*. Longmans, London.
- WILSON, E. A. 1907. Mammalia (Whales and Seals). *British National Antarctic Expedition 1901-04, Nat. Hist.*, 2, 1-66.
- WILSON, J. I. (Unpublished.) Report by the stipendiary magistrate on sealing operations conducted at South Georgia during the season ended 30 September 1914. *Enclosure to Falkland Islands despatch No. 146*.

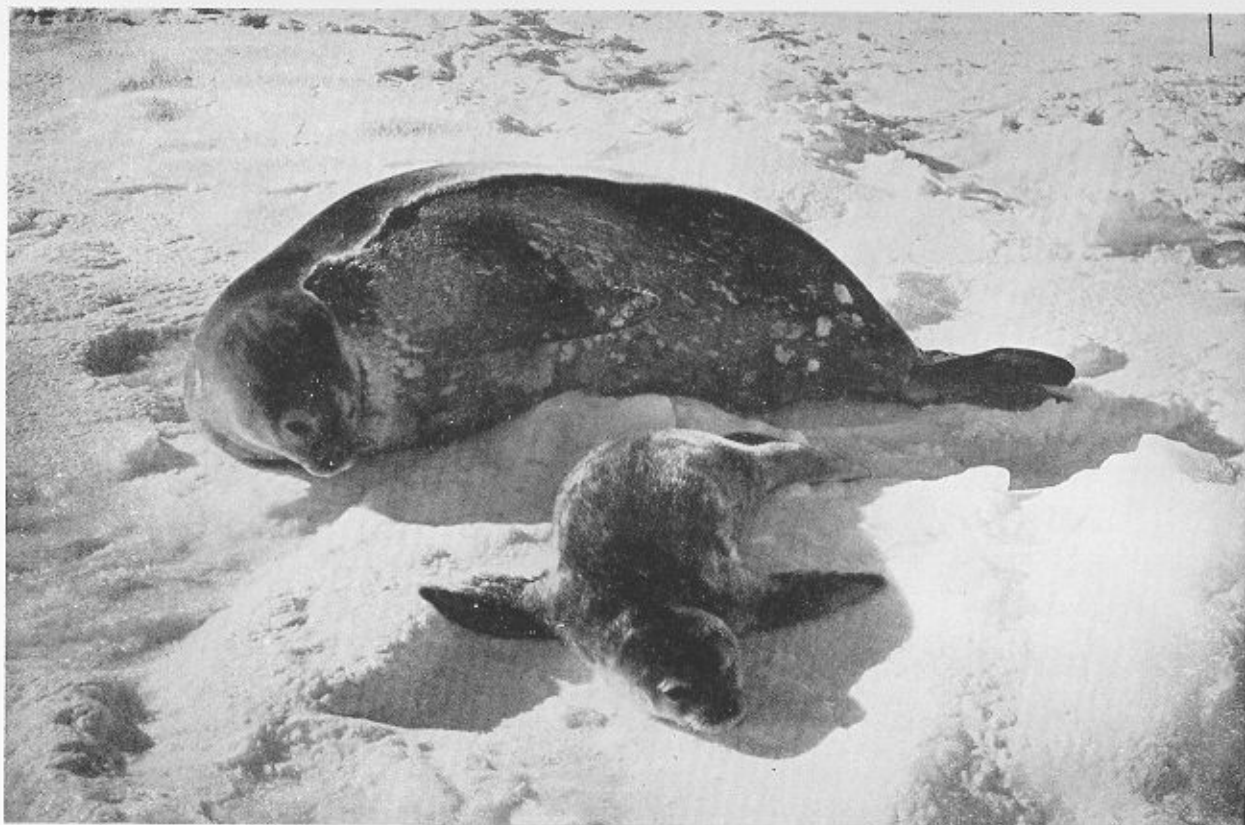


a



b

- a. Reproduction of a lithograph entitled *Sea Leopard of South Orkneys* from James Weddell's book *A Voyage towards the South Pole*.
- b. A female Weddell seal emerging from a hole in the fast ice.



a

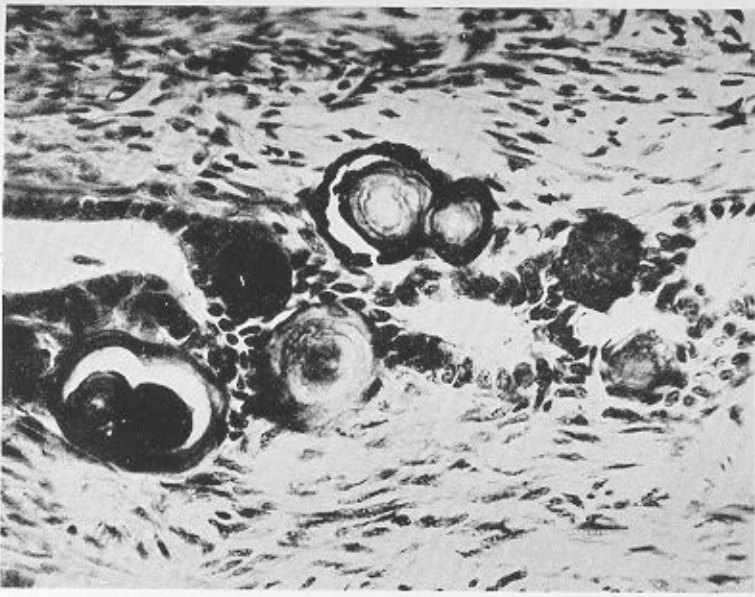


b

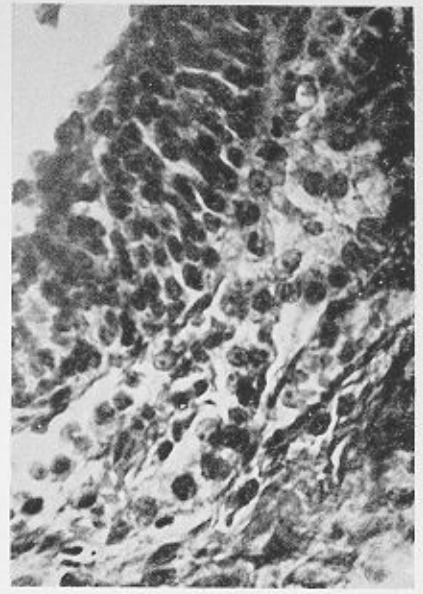
- a. Female Weddell seal and pup.
- b. View of Signy Island from Wave Peak, Coronation Island (3271 feet), taken ten days after break-up of the fast ice along the north-west coast. Fast ice still remains in Borge Bay and Paal Harbour, and consolidated pack ice extends to the horizon, sixty miles distant.

PLATE III

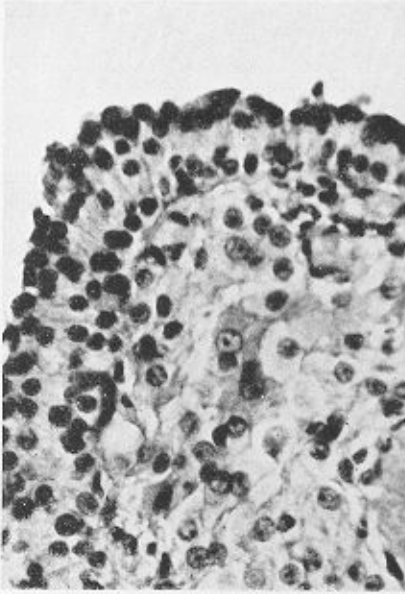
- a. "Concretionary follicles" associated with sub-surface crypts in the right ovary of H1014, plus nine days relative to parturition. ( $\times 400$ .)
- b. and c. Granulosa and luteinised *theca interna* cells in a collapsed follicle in the left ovary of H1010, taken on 18th August, 1952. ( $\times 500$ .)
- d. *Corpus luteum* of H1018, plus one day relative to parturition; the section is stained with Mallory's Triple Stain to show the development of fibrous tissue. ( $\times 400$ .)
- e. *Corpus luteum* from the left ovary of H376, taken on 13th February, 1950. ( $\times 400$ .)
- f. Cortex of the left ovary of H123, taken on 20th April, 1948. ( $\times 500$ .)
- g. Cortex of the left ovary of H1027, plus fifteen days relative to parturition. ( $\times 100$ .)



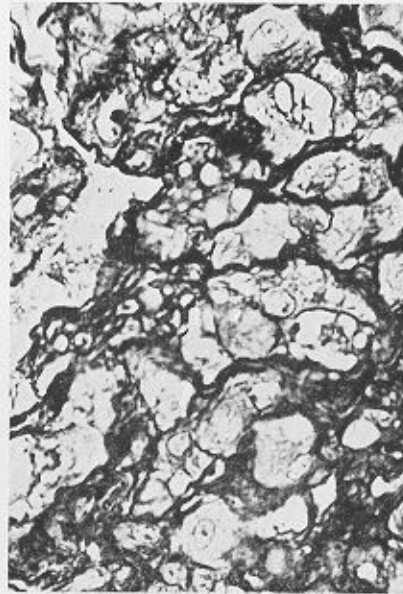
a



b



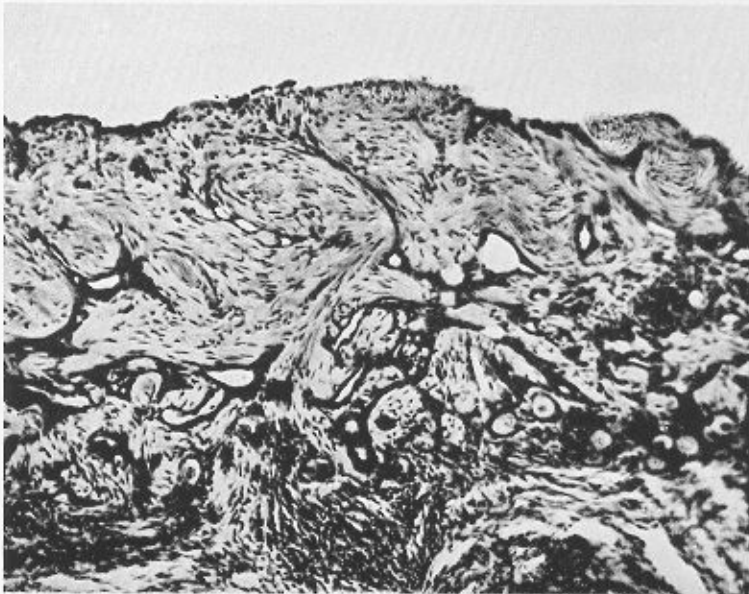
c



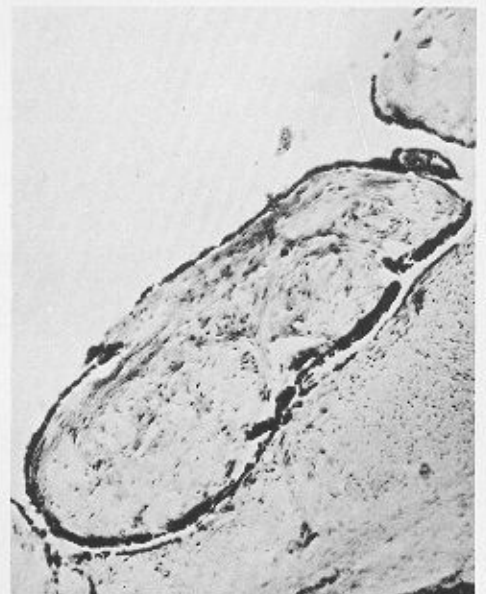
d



e



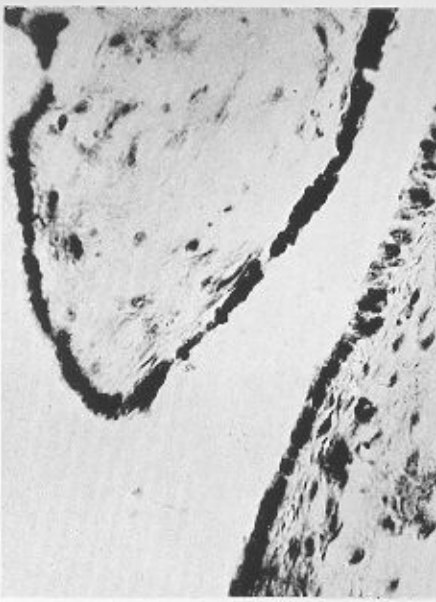
f



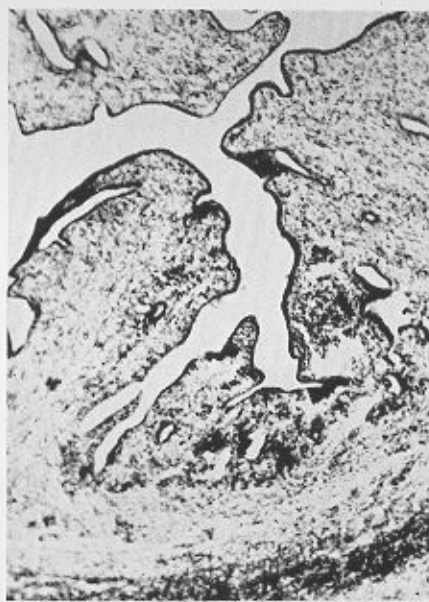
g

PLATE IV

- a. Cortex of the left ovary of H1027; the lobe in the upper part of the picture is breaking away from the remainder of the cortex. ( $\times 400$ .)
- b. Uterine mucosa of H1006, taken on 23rd July, 1952. ( $\times 65$ .)
- c. Uterine mucosa H1007, taken on 6th August, 1952. ( $\times 65$ .)
- d. Uterine mucosa of H1006. ( $\times 300$ .)
- e. Uterine mucosa of H1007. ( $\times 400$ .)
- f. Uterine epithelium in the sterile cornu of H1018, plus one day relative to parturition. ( $\times 400$ .)
- g. Uterine epithelium in the sterile cornu of H1027, plus fifteen days relative to parturition. ( $\times 500$ .)
- h. Uterine epithelium in the cornu of recent pregnancy of H1016, plus three days relative to parturition. ( $\times 100$ .)



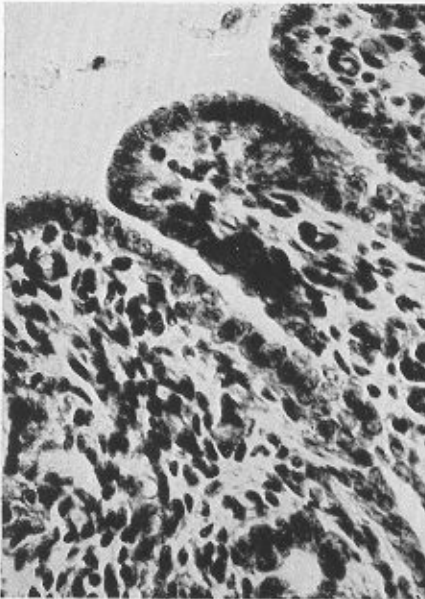
a



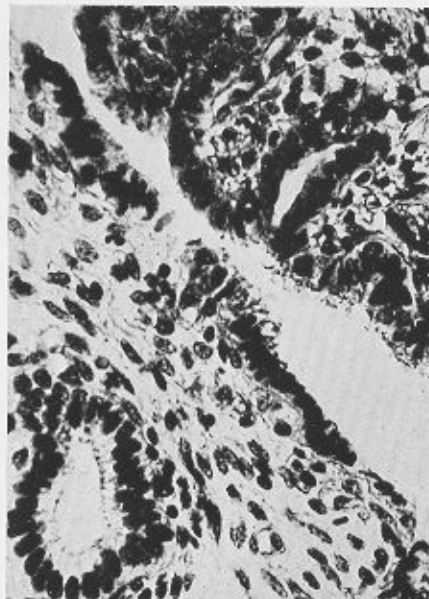
b



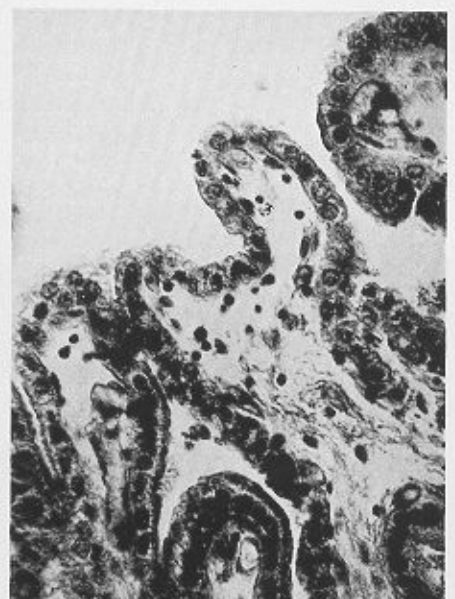
c



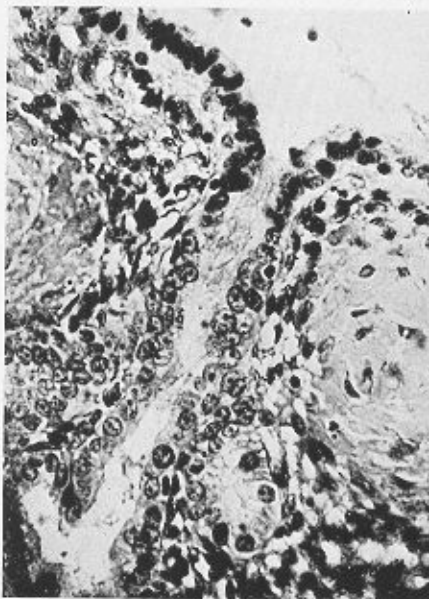
d



e



f



g

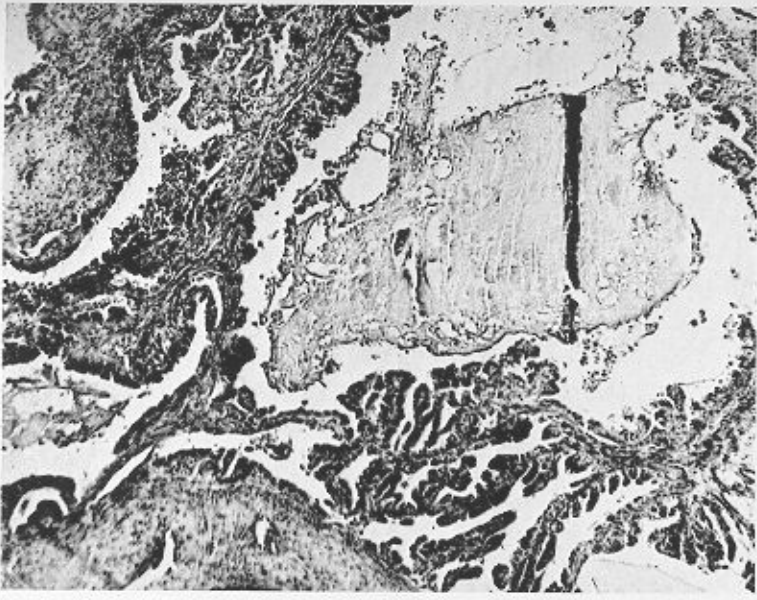


h

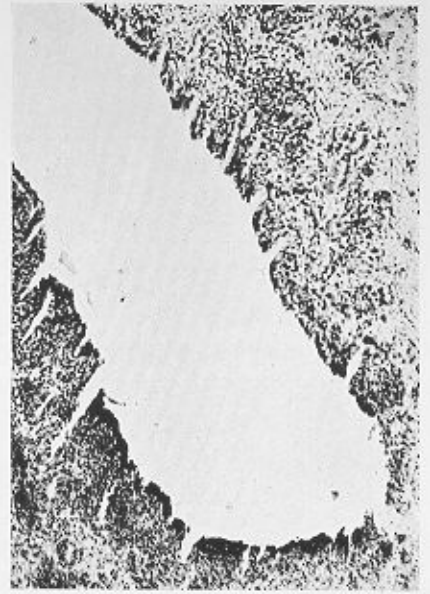


PLATE V

- a. Coalesced uterine glands in the cornu of recent pregnancy of H1015, plus five days relative to parturition; the main lumen of the uterus is at the upper left of the picture. ( $\times 75$ .)
- b. A uterine cleft in the cornu of recent pregnancy of H1014, plus nine days relative to parturition. ( $\times 75$ .)
- c. Vaginal epithelium of H1001, taken on 3rd June, 1952. ( $\times 400$ .)
- d. Epithelium in the deeper clefts of the vaginal mucosa of H1007, taken on 6th August, 1952. ( $\times 400$ .)
- e. Epithelium from the upper parts of the vaginal clefts of H1007. ( $\times 400$ .)
- f. A cleft in the vaginal mucosa of H1018, plus one day relative to parturition. ( $\times 60$ .)
- g. Terminal portion of a cleft in the vaginal mucosa of H1018; the lumen of the cleft runs diagonally from the upper right corner of the picture. ( $\times 350$ .)



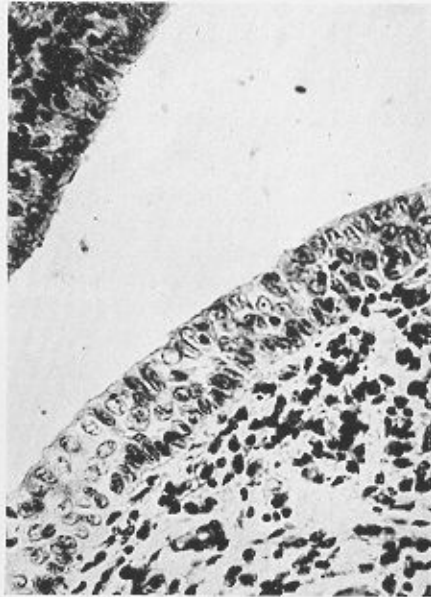
a



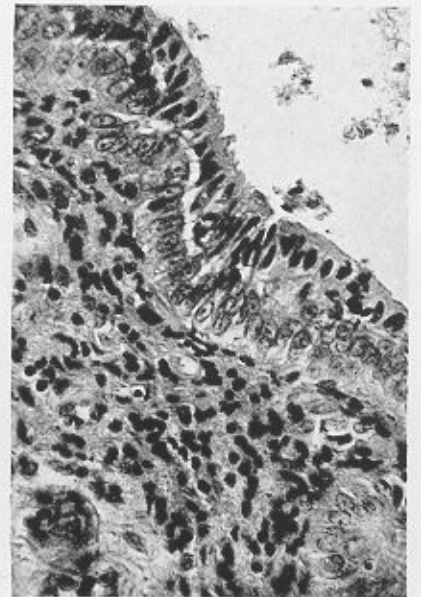
b



c



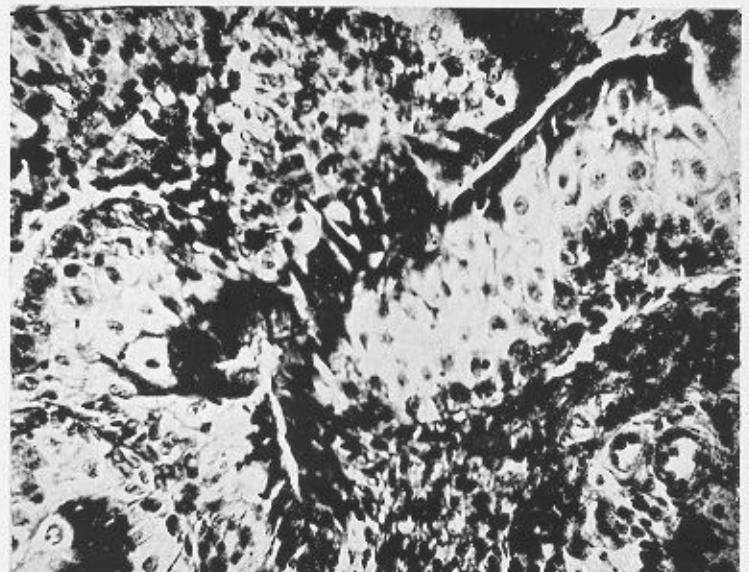
d



e



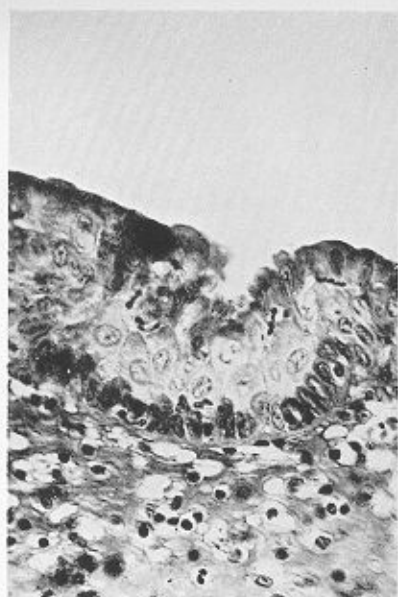
f



g

PLATE VI

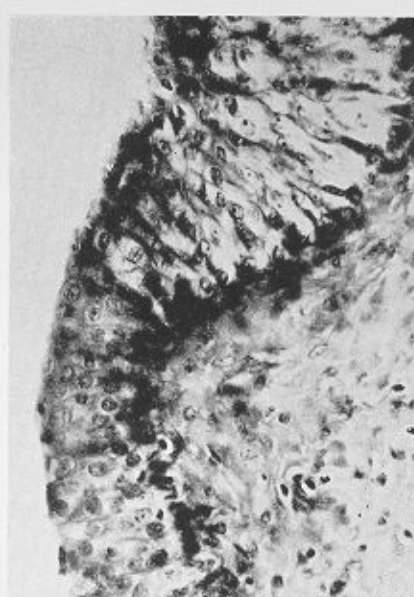
- a. Vaginal epithelium of H1016, plus three days relative to parturition. ( $\times 450$ .)
- b. Vaginal epithelium of H1012, plus five days relative to parturition. ( $\times 800$ .)
- c. Vaginal epithelium of H1014, plus nine days relative to parturition. ( $\times 350$ .)
- d. Vaginal epithelium of H1017, plus seven days relative to parturition. ( $\times 550$ .)
- e. Microscopic appearance of a thin ground section of the canine tooth of a young female Weddell seal, H1006; the light zone marks the transition from columnar to marbled dentine. ( $\times 75$ .)
- f. Vaginal epithelium of H1010, taken on 18th August, 1952. ( $\times 300$ .)
- g. Microscopic appearance of a thin ground section of the canine tooth of an adult female Weddell Seal, H1027, showing four pairs of growth rings. ( $\times 75$ .)



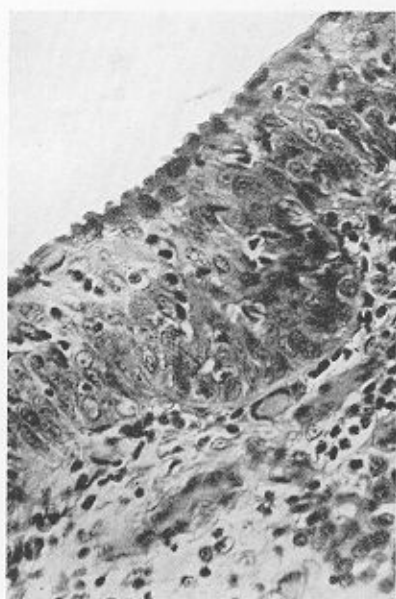
a



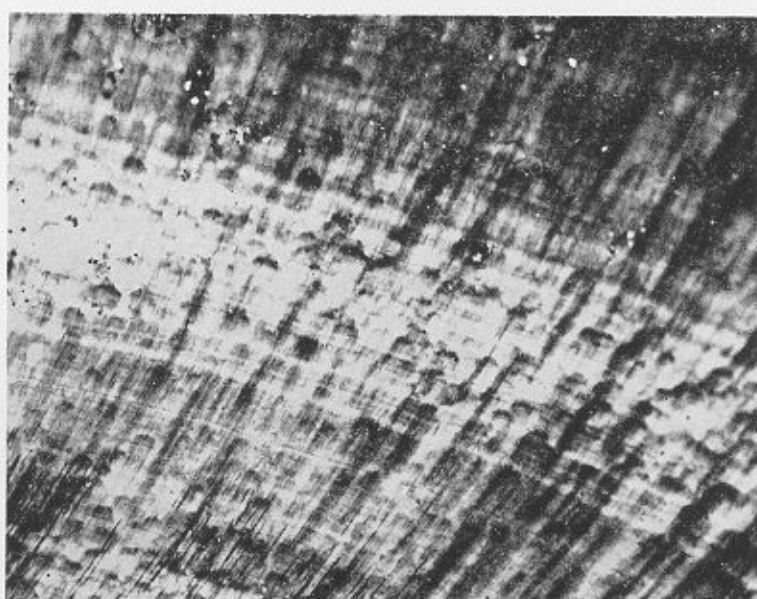
b



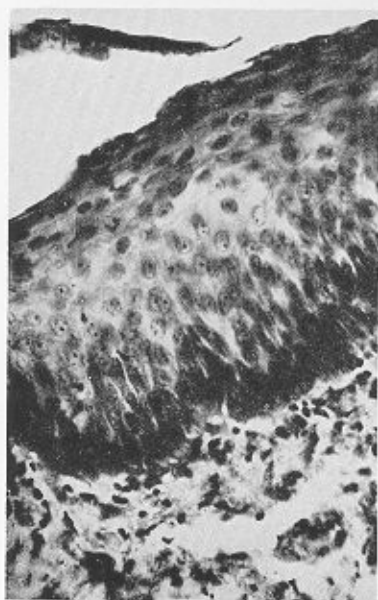
c



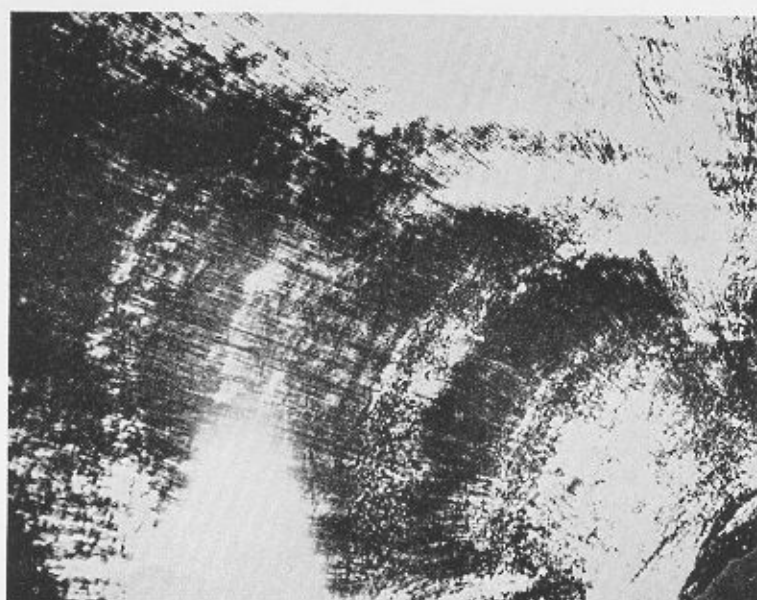
d



e



f



g