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THE ELEPHANT SEAL

(Mirounga leonina Linn.)

I. GROWTH AND AGE

By

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and Department of Zoology, Cambridge

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(Manuscript received March 1953)

CONTENTS

I. INTRODUCTION

THIS paper is the first of a number on the biology of the southern elephant seal (*Mirounga leonina* Linn.). The field work which forms the basis of the study was carried out in the years 1948 to 1951, in the Falkland Islands Dependencies. From February 1948 to February 1950 the studies were made in the South Orkney Islands, from a base on the east coast of Signy Island, in lat. 60°40′ S. and long. 45°36′ W. In the following year from March 1951 to December 1951 the field base was at King Edward Point, East Cumberland Bay, South Georgia, in lat. 54°18′ S. and long. 36°30′ W. In addition a few observations were made in the Falkland Islands during February and March 1951.

Nomenclature

The elephant seal was called the Sea-Lyon by Lord Anson who brought the original specimen to England from Juan Fernandez and on the description and figure given by Walter (1748) Linnaeus founded his species *Phoca leonina*. After the dismemberment of the Linnaean genus *Phoca* by Nilsson in 1820, F. Cuvier (1824) removed the elephant seal from the genus *Phoca* and made it the type of a special genus "Macrorhine", which he first used in the classical form *Macrorhinus*, in 1826. The vernacular name "Macrorhine" is untenable, and *Macrorhinus* is preoccupied for a coleopteran by Latreille (1825).

In 1827 Gray proposed the genus *Mirounga* to include the elephant seal and the hooded seal. The latter had already been made the type of the genus *Cystophora* by Nilsson (1820) and the elephant seal becomes the type of *Mirounga* by restriction (Gray, 1847).

The three specific names most often applied to the southern elephant seal are, *leonina* (*Phoca leonina* Linn. 1758), *elephantina* (*Phoca elephantina* Molina, 1782) and *proboscidea* (*Phoca proboscidea* Peron, 1816). The former has priority and is convenient.

Until more detailed comparative work has been done there is no justification for the recognition of more than one species of elephant seal in the Southern Hemisphere, although several have been proposed. A recent statistical analysis of a series of skulls collected by the Australian National Antarctic Research Expedition (private communication) indicates that there are probably subspecific differences between the elephant seals of Heard and Macquarie Islands. It seems possible that there are at least three subspecifically distinct groups in the Southern Ocean.

But the northern elephant seal (*Mirounga angustirostris* Gill) is undoubtedly specifically distinct from *leonina* although in his description Gill (1866) compared the skull of a probably full grown female northern elephant seal with the figure of a two thirds grown male skull of the southern form (Gray, 1844).

Previous Knowledge of the Species

The first description and figure of the elephant seal appears in the account of Lord Anson's voyage (Walter, 1748), and it was Anson who brought the first specimens of the "Sea-Lyon" to England, in 1744. Picturesque accounts are given by other early voyagers, among them that of Pernetty (1770) being outstanding, although he does not always differentiate between the sea-lion and the elephant seal.

The anatomy is incompletely described by Turner (1887) and Holz and Zukowsky (1926). Wilson (1907) contributes a description of the external appearance and dentition. There are several papers on the skull characters, of which those by Flower (1881), Lydekker (1909) and Lönnberg (1910) are the most useful. Doran (1878) contributes a paper on the auditory ossicles; Mitchell (1916) and Sonntag (1923) deal incidentally with aspects of the anatomy of the species.

Allen (1905) gives a detailed synonymy and a brief history of commercial exploitation by American sealers.

It is not until 1914, in a paper by Murphy, that we have the first reliable account of the habits of the elephant seal, then Ring (1923), made further contributions in an interesting paper. Harrison-Matthews (1929) published the most comprehensive account of the life history and habits of the species, but it is based solely upon field observations. In recent years there has been a revival of interest and the United Kingdom, Australian, New Zealand, South African and French governments have all financed investigations. At the time of writing the present paper there are only two published accounts of this work, one based on original observations by Sorensen (1950) and the other by Aretas (1951).

Of special interest is the excellent account by Bartholomew (1952) of the behaviour of the northern elephant seal (*Mirounga augustirostris*).

General Description of Life and Habits

At the present day the elephant seal is mainly subantarctic in distribution. It is a gregarious but not a sociable animal, hauling out to form large concentrations in favoured areas during the breeding season in the spring, and in the summer months when it moults the hair coat. In both periods it undergoes prolonged fasting. For a few months between the breeding season and the moult, and throughout the winter months, it is pelagic in distribution, feeding mainly on fish and cuttlefish.

The elephant seal is the largest of the pinnipeds; the length of a large bull may be more than twenty feet and the weight over three tons. The name is derived from the great size of the animal and from its trunk-like proboscis. The cows are rarely more than twelve feet in total length and weigh up to a ton. The colour of the animal is a bluish grey, lighter ventrally, but the coat rapidly becomes browner with weathering and more or less discoloured with faeces and mud during the annual moult. The species is quite unafraid of man and may be approached closely except in the breeding season, at which time both sexes are very pugnacious. After the annual moult the animals leave the land and lead a pelagic life throughout the winter, probably in the vicinity of the edge of the pack-ice, though stragglers reach the coasts of South Africa, Australia and New Zealand. At the southern limits of their range the adult males may keep open breathing holes in the sea-ice for a few weeks in the autumn, and in the spring.

Although the period of gestation is a little less than a year, implantation of the blastocyst is delayed for over four months so that active development of the embryo takes seven-and-a-half months. In the spring the males take up stations on land, or fast-ice, and the cows, which begin to haul out a few days later, collect into harems. Social behaviour is highly developed in the breeding season and sexual fights between the bulls are a feature of this period. Bulls may have harems of up to 100 cows, but in an undisturbed population the number is between ten and thirty. The pups are born on land or fast-ice and twins are rare. At birth the pup is about four feet long and weighs about a 100 pounds, increasing to over 400 pounds when weaning takes place at the age of twenty-three days and it is deserted by its mother. It then spends about a month on land before taking to the water. During this period it lives on the reserves of blubber laid down during the suckling period. The pup is born with a black woolly coat, which is moulted within three or four weeks. It begins to feed on crustacea and then on the adult diet of fish and cuttlefish. In the first few months the young do not remain for long away from land and frequently haul out to sleep.

The cows have their first pregnancy in the second year and bear their first pup when they are three years old. Pupping takes place a week later each year. The bulls are sexually mature at four years but, owing to the selection imposed by the harem system, they do not normally breed on land until they are seven years old. The cows produce on an average seven pups in their lifetime and have one "missed pregnancy"; their average length of life is twelve years but they may live as long as seventeen years. Bulls may live up to twenty years, more usually about twelve, and at South Georgia, owing to the sealing operations, rarely longer than ten years.

II. COLLECTING METHODS

A. General

THE collecting methods described below are the result of personal experience and experiment in the field. Standard routines were developed primarily in connection with the elephant seal (*M. leonina*) but field work on weddell seals (*Leptonychotes weddelli*), crabeater seals (*Lobodon carcinophaga*), leopard seals (*Hydrurga leptonyx*) and southern sea-lions (*Otaria byronia*) was also carried out. These collecting methods are generally applicable to large mammals.

Ethical considerations and the precarious position of the breeding population of elephant seals in the South Orkneys prevented the killing of a large series of seals on Signy Island. Unfortunately in the absence of dogs, the carcasses could be put to but limited use. The animals to be killed were, therefore, selected so as to give a representative series. At South Georgia, on the other hand, it was possible to obtain data on a large number of male elephant seals by accompanying the sealing boats; the cows were carefully selected to fill in the gaps in the previous work. Except when working with the sealers, when time was limited, a full examination was made of every seal killed.

A great deal of the work was done without assistance and the collecting procedure was standardised so as to be as economical as possible. Special conditions for collecting, which have to be taken into account, are the low temperatures and frequent adverse weather conditions, and it was necessary to concentrate on certain lines of research, such as the reproductive cycle, to the exclusion of other less important aspects.

The importance of a standard routine is very apparent when working at low temperatures in a blizzard, possibly soaked to the waist in sea water. It is often necessary to stop and swing the arms to restore the circulation and a single post-mortem examination may take as long as three hours. The amount of equipment has to be limited to what can conveniently be carried on the back.

B. Equipment

After much experiment the equipment finally adopted was as follows:

Light B.S.A. sporting rifle, .22 calibre, with long rifle, high velocity ammunition, and five-shot magazine.
Flensing knife (Eskilstuna) with blade 11½ ins. by 2 ins., in a wooden sheath with 9½ in. blubber hook and steel attached. This combination has been developed by the sealers at South Georgia (Laws, 1953).
Small knife with 5 in. blade.
Hacksaw and spare blades.
Dissecting instruments.
Carborundum stone.
Surveyor's linen tape (33 feet).
Printed paper specimen labels.
Numbered metal labels.
One-pound Kilner jars half full of Bouin's *picro-formol-acetic* fixative.
Special fixatives (see next section).
Specimen tubes, 3 ins. by 1 in.
Squares of butter muslin, 6 ins.
Fuse wire.
Seal data sheets.

All these items were packed in a "Venesta" box with a hinged lid, divided into compartments and attached to an "Everest" tubular steel carrying frame so that it could be carried on the back. The data sheets were fixed by a clip to the inside of the lid, and a pencil attached to the box by a string.

C. Procedure

1. *Recording*

For the purpose of identifying the specimens each seal killed was given a staion number, the position of which (latitude, longtitude and description) was entered in the Station List kept at base. All stations were plotted on large scale maps. The individual specimens collected from each seal such as skull, *os penis*, claws, and organs fixed for histological examination were given serial numbers. Each station number is preceded by the base letter ("H" = Signy Island, "M" = South Georgia, "J.B." = RRS "*John Biscoe*"). Thus the reference M6.11 means South Georgia, station 6, specimen 11.

Details of the specimens collected were entered on the seal data sheets in the field, clean copies being made at base. Details were also entered in the Biological Register for the appropriate F.I.D.S. Base.

2. *Killing*

Of the 226 elephant seals subjected to post mortem examination ninety-seven had been killed by sealers at South Georgia. They were shot in the head by using a Winchester or Krag rifle, and soft-nosed ammunition.

The remaining 128 male and female elephant seals were selected and killed by the writer, at Signy Island and South Georgia. The elephant seal, in common with the other species of seal is very tenacious of life and must be shot in the head so that the bullet strikes the brain. Initially, soft-nosed .303 ammunition was used for killing, but death is not certain unless the bullet is placed through the skull which is, as a consequence, shattered and its value as a specimen greatly reduced. After the first season's experience a .22 rifle, firing high velocity ammunition, was used and proved most effective except when dealing with very large bulls. In that case .22 bullets did not have enough power to penetrate the heavily ossified skull and a .303 rifle was used. The best shot is from the side about one or two inches behind the eye, but oblique shots from in front, just behind and above the eye or from above on a line joining the ear holes, are effective. With experience the seal may be killed from almost any position. It is the shock effect of the first shot which is important. If it is wrongly placed several other shots, each of which would normally be sufficient to kill the animal, are required.

Immediately after the seal was shot, it was stabbed in the heart and/or the carotid arteries were cut, to ensure that it was dead and to restrict as far as possible the flow of blood to the thorax and exterior. A sure sign of death is the relaxation of both pupils and the bleaching of the retina to a brilliant emerald green. The reflexes after death are frequently startling.

3. *External Measurements*

Immediately after killing, the sex was recorded and the animal measured from the tip of the snout or proboscis to the tip of the tail along the curve of the back (figure 1). For this purpose a surveyor's linen tape measure was used. This measurement was chosen instead of the more usual measurement in a straight line because it is easier to accomplish single handed. Furthermore, on rough ground a measurement in a straight line is inaccurate and a large elephant seal cannot be straightened out easily. Measurements taken along the curve of the back have the disadvantage that seasonal variations in fatness are accompanied by proportionate variations in length (this is shown in figure 19).

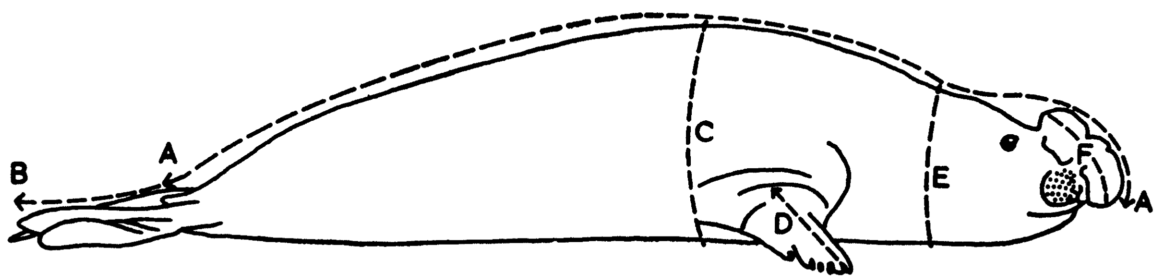


FIGURE 1. Male elephant seal showing external body measurements.
A–A = Standard length, or nose–tail length.
A–B = Nose–flipper length.
C = Axillary or greatest girth.
D = Length of fore-flipper.
E = Neck girth.
F = Length of proboscis.

The other measurements taken were:

(a) The overall length from nose to tip of the hind flippers.
(b) The axillary girth, measured just behind the fore-flippers.
(c) The length of the fore-flipper, measured from the axilla to the tip of the first digit.

In some cases extra measurements were taken such as neck girth, length of the proboscis, position of the genital opening, etc., the measurements were recorded to the nearest inch although the amount of error in the length measurements of a large male is of the order of $\pm$ 3 to 6 inches.

Except in the case of pup seals, direct measurements could only be made on dead animals. However, a photographic method of measuring the length of living animals (primarily breeding cows at Signy Island), proved very successful and extended the series of measured animals considerably. It is based on the fact that the dimensions of objects photographed at a given range with the same lens will be directly comparable. In a Leica camera with a coupled rangefinder the superposition of two images determines the distance from the object to be photographed. The rangefinder was set at seven metres for photographing cows, and ten metres for males, because of their larger size.The rangefinder has a short base and is therefore not highly accurate, but by standardising the procedure satisfactory results were obtained. Owing to the short base of the rangefinder there is a region about ten inches deep within which the two images are coincident. In practice this difficulty was overcome by approaching the animal to be photographed at right angles to its long axis until the images in the rangefinder just coincided. The animal, which had to be lying prone so as to give a true length, was then photographed. For calibration purposes a horizontal graduated rod was photographed in the same way from distances of seven and ten metres.

The resulting negatives were all enlarged to an equal magnification and measurements taken from them, using a strip of card marked to scale from the calibration photograph. The measurements of fifty-eight breeding cows, of known date of pupping and of sixteen individually marked bulls were obtained in this way. Comparison of lengths measured photographically with the lengths measured directly on dead animals showed that the difference is negligible. Scale photographs give an indication of the condition, amount of scarring and the relative development of different parts of the body, as well as providing a means of measuring large numbers of living animals. It is, of course, essential that the animal should be motionless and lying naturally at full length, and because of its lethargic and fearless nature the elephant seal is an ideal subject.

For future work a special rangefinder could be made for the direct reading of measurements in the field without the intermediary of photographs.

4. *Other Measurements*

In addition to the external body dimensions the blubber thickness and certain internal organs were measured.

The blubber thickness at the level of the chin, chest and anus was usually recorded. The measurements were made along the mid-ventral incision with a metal ruler. Because it is difficult to see where the skin ends and blubber begins, the thickness of the blubber was measured from the epidermis to the fascia of the underlying muscle. The thickness of blubber on the "chin" was taken at the level of the angle of the lower jaw, that of the chest over the xiphisternum, and the "anus" measurement about three inches anterior to the vent.

The length of the intestine from pyloris to rectum was measured in eighty-seven individuals. For this purpose the intestine was cut free from the mesentery and measured soon after death. The degree of stretching was slight. At first a tape measure was used but to save time was soon discarded in favour of an approximate method assuming an arm stretch of six feet. Comparison of lengths measured in both ways showed an error in the latter of ± 1 per cent. In view of the surprising length of the intestine (662 feet in one male), this was considered satisfactory.

In the male, measurements of the greatest length and breadth of the right testis were taken with a steel ruler.

The measurements taken of female genitalia are shown in figure 2, they were:

(a) Greatest length of each ovary } after removal of capsule.
(b) Greatest breadth of each ovary }
(c) Length of fallopian tube (straightened).
(d) Length of each cornu of the uterus (straightened).
(e) Length of the common uterus.
(f) Length of part of uterus protruding into the vagina.
(g) Length of vagina.
(h) Height of hymeneal ridge.
(i) Length of vestibule.
(j) Length of clitoris.

These measurements were taken, as time permitted, with a steel ruler. (a) and (b) were usually obtained with calipers, on fixed, sliced specimens. In some cases the measurements were taken after laboratory dissection of genitalia preserved in salt.

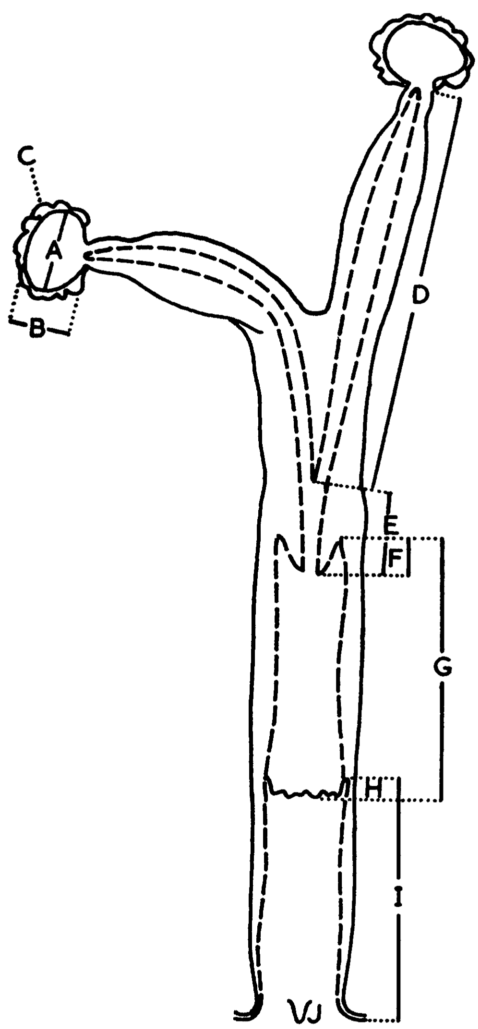


FIGURE 2. Female genital tract showing measurements taken. Explanation in the text.

5. *General Observations*

In addition to the measurements detailed above, the following general observations were made as time permitted:

(a) The sex was invariably noted immediately after killing.

(b) If the animal was a marked seal, the mark was noted (Red "O", Yellow "I", etc.).

(c) The habit of the specimen: whether it was freshly hauled out, or had been on land for some time; located inland or on the beach, solitary or gregarious.

(d) Its condition: whether fat or emaciated, looking healthy or not; the appearance of the mouth and gums (bloody, dirty or clean); the appearance of sores or wounds on the body (clean or suppurating).

(e) Its colour and the state of the hair were noted. If in moult, the stage of the moult process was recorded; if not it was noted as in either pre- or post-moult condition.

(f) The extent, location and type of scars.

(g) If a male, the state of development of the proboscis was noted.

(h) The presence of distinct bands on the claws.

(i) Any aberrations in the dentition.

Interesting conditions of the internal anatomy were also noted such as:

(j) Pathological conditions.

(k) Parasites, internal and external; type, location and numbers.

(l) Gross appearance of the genitalia. Presence of vesicles on the fallopian tube or ovarian capsule; *os clitoris*; presence or absence of embryo, aborted foetuses; appearance of the uterine fluid. The presence of areas of hyalinised blood vessels in the wall of the uterus, marking the site of a previous implantation, and the appearance of the vulva were also noted.

(m) The stomach contents; the type and estimated amount of food; the presence of sand and/or stones.

(n) The body temperature was recorded by inserting a 5 cm. immersion thermometer into the thorax immediately after death.

(o) As time and weather permitted field dissections to elucidate the structure of various organs or systems were made.

6. *Specimens Collected*

(a) *Gross Material*

In the male the *os penis* was removed by cutting posteriorly from the genital aperture in the mid-line. The bone can be felt through the skin and blubber. It was roughly cleaned in the field, and the remaining tissue removed later by boiling.

In both sexes the skull was removed by cutting through the soft tissues of the neck (all round) just behind the skull. The connective tissue below the *foramen magnum* (between the occipital condyles and the axis bone) was severed and the head bent downwards; the cut was then continued round the condyles until the head was freed. The skull was roughly cleaned of flesh and skin and the brains removed so far as possible with a small knife, taking care not to injure the inside of the cranium. In the early stages of the work the skulls were boiled until the remaining flesh could easily be removed, they were then dried. Large skulls prepared in this way are impregnated with oil and after the first season the skulls were cleaned through the intermediary of marine amphipods. The skulls, after preliminary cleaning, were attached to strong wire and allowed to lie on the sea floor, just offshore for about a week; they were then dried. All skulls have been presented to the British Museum (Natural History).

At South Georgia only the lower canine teeth were collected, for the purpose of age determination by a newly evolved method (Laws, 1952b, 1953b). The top part of the canine was required for this purpose, and the majority were sawn off at the level of the alveolar bone, using a hacksaw with a medium grade blade.

The claws together with the distal phalanges were removed from the right fore-flipper of a number of individuals and cleaned by boiling.

(b) *Histological Material* (*Fixation*)

Immediately after the appropriate external measurements had been taken the seal was turned over onto its back and a longitudinal ventral incision was made so as to open the body cavity. The blubber thickness was measured, and then, before making further notes or measurements, the organs or parts of organs required for histological investigation were taken as quickly as possible to ensure good fixation. In the case of females it was, of course, necessary to measure the genitalia before fixation.

As a general routine, pieces of material up to 1 cm. thick were fixed in *Bouin's picro-formol-acetic*, which is simple to use and requires no involved post-fixation technique. It is most suitable for field work of this nature and the fixation secured was in general very good. For comparative purposes, and to bring out details of cell structure which are not well defined in *Bouin*, thin slices were fixed in *Heidenhain's Susa* fixative left for up to twenty-four hours before changing to iodine alcohol, and stored in 80% alcohol.

For the secretory cycle of certain glands, especially the *corpus luteum*, small tissue slices, 2 mm. thick were placed in *Zenker-formol* (*Helly*) fixative (Romeis, 1948, pp. 74–75), made up just before use by adding 5 cc. of 40% formol to 100 cc. of *Zenker* stock solution. It was left for six hours and then washed for twenty-four hours in running tap-water (or when camping, by frequent changes of distilled water). After washing, the specimens were post-osmicated with 2% Osmic acid for twenty-four hours and then washed in tap or distilled water for twenty-four hours. After taking the specimens up through the alcohols they were treated with iodine in 80% alcohol, to dissolve the mercuric salts, and stored in 80% alcohol.

McClung (1950) states that with picro-formol-acetic combinations the optimum temperature is in the range 35°C to 40°C, and low temperatures slow down the penetration and cause variations in the fixation of individual cell structures. For *Zenker* the optimum temperature is about 0°C. The elephant seal material collected was fixed at temperatures ranging from –15°C to +6°C and fixation is good with all three combinations.

LOCALITY	Skull	Tooth	Claws	R. ovary	L. ovary	R. cornu	L. cornu	Common uterus	Fallopian tube	Utero-tubal junction	Vagina	Embryo	Corpus luteum (OsO_4)	Placenta	Mammary Gland	Pituitary	Thyroid	Adrenal	Skin	Parasites
SIGNY ISLAND	29	—	17	28	28	28	28	11	—	—	28	2	—	1	4	1	—	—	23	4
SOUTH GEORGIA	—	55	—	55	55	51	52	26	2	2	49	9	12	4	2	20	50	2	—	2
TOTAL	29	55	17	83	83	79	80	37	2	2	77	11	12	5	6	21	50	2	23	6

TABLE I. ♀ Material: Figures show number of specimens represented in the material.

LOCALITY	Skull	Tooth	Claws	Os penis	Testis	Epididymis	Pituitary	Thyroid	Skin	Proboscis	Small intestine	Rectum	Stomach	Parasites
SIGNY ISLAND	42	—	15	42	38	38	—	—	37	1	1	1	1	6
SOUTH GEORGIA	—	100	1	23	50	50	1	1	1	—	—	—	—	2
TOTAL	42	100	16	65	88	88	1	1	38	1	1	1	1	8

TABLE II. ♂ Material: Figures show number of specimens represented in the material.

(c) *Histological Material* (*Tissues Collected*)

In the female the genitalia were exposed by the median ventral incision, but it was necessary to cut the ligament of the pubic symphysis to expose the vagina. As an invariable rule both ovaries were removed, incompletely split to ensure penetration of the fixative and, with a section of each uterine horn and of the common uterus and vagina, were fixed in *Bouin*. Each specimen was placed separately with the appropriate label on a square of muslin, the corners of which were drawn up to form a bag and tied with fuse wire. Usually all the specimens from one individual were put into a 1 lb. Kilner jar containing *Bouin*.

Foetuses if under 3 inches crown-rump length were fixed in *Bouin*; if over 3 inches they were fixed in 30% alcohol and moved to 70% alcohol after twelve hours. Very small embryos, and specially fixed material, were placed in a specimen tube. Placenta, mammary gland, fallopian tube, etc., were also collected when possible.

Tissue slices of *corpus luteum* were fixed in *Helly* and post-osmicated.

In some specimens the remainder of the genitalia were removed and stored in salt for later dissection.

In the male, the testes are exposed by cutting obliquely forwards from the base of the hind flipper towards the mid-ventral line about 6 inches in front of the anus. Portions of the testis (including the medulla) and epididymis were fixed in *Bouin* and occasionally in *Heidenhain's Susa*. A portion of the proboscis of one bull was fixed in *Bouin*.

From both sexes a 1 inch square of skin from the hind flipper was fixed in *Bouin*, and occasionally pieces of skin illustrating the moult process were fixed in the same way. The pituitary, thyroid, parathyroids and adrenals, pieces of gut and lymph glands were fixed in *Bouin* or *Susa*.

Parasites were fixed in *Bouin*.

Altogether 1126 specimens were collected from a total of 226 elephant seals (84 female, 142 male), and their distribution is shown in tables I and II.

III. PHYSICAL CHARACTERS

A. General

THE colour of a freshly moulted adult male is a uniform dark grey with a bluish cast, lighter ventrally. The new coat of the cow is usually darker and more brown; young animals are noticeably lighter.

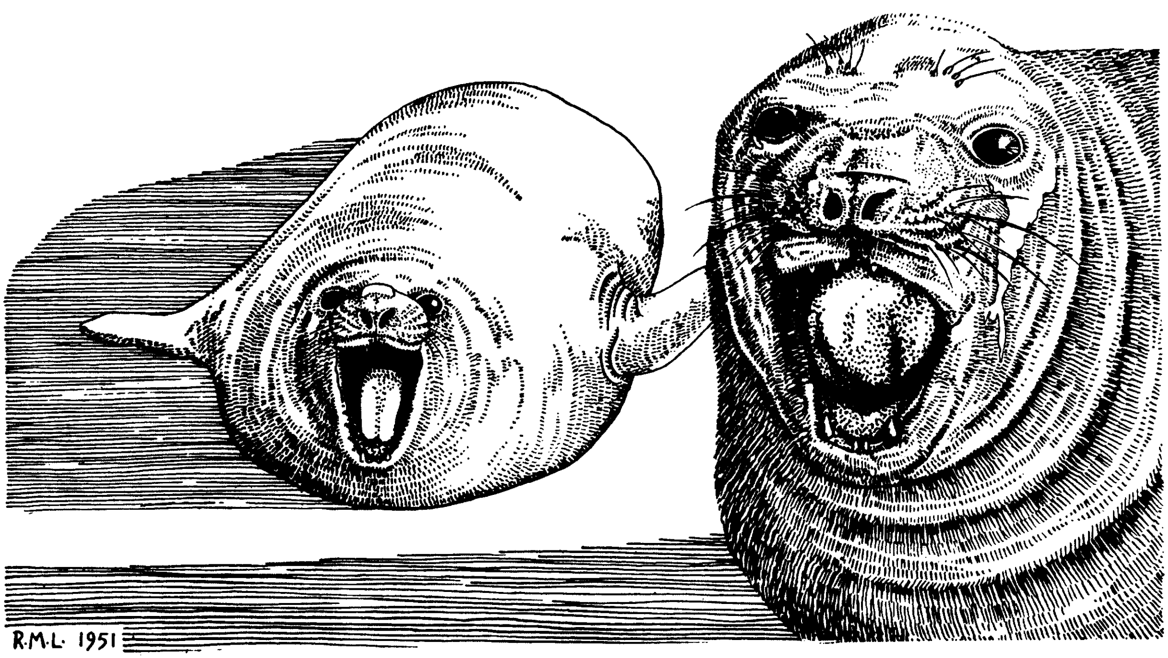


FIGURE 3. Adult female elephant seals.

According to the length of time after moulting the coat assumes various shades of brown, usually darker in the autumn and fading with time, so that in the male, prior to the moult, it is rust brown or even straw-yellow in colour. Rarely is the coat of the cow so light. The colour is uniform without any mottling and the hair is very harsh and stiff. During the moult the hair is sloughed off in large patches, held together by the old epidermis so that the roots project about 1 mm. and in older animals there is some delay before the new hair makes its appearance. Owing to the contrast between the patches of old hair of rusty-brown colour and the new grey coat the animal assumes a patchy appearance. Old males usually bear numerous light coloured scars around the underside of the neck—the "integumentary shield", and the older cows have a light coloured yoke owing to the many small white scars on the neck, caused by the bull biting the cow during copulation. There are no records of albinos in this species.

One specialisation, the nasal sac or proboscis, it has in common with the hooded seal (*Cystophora cristata*) alone. All the other characters are modifications or exaggerations of seal-like characters shared by other species. The fusiform shape of the body is enhanced by the inclusion of the elbow and knee within the general body contour. Bodily proportions and stature change considerably with age and there are marked sexual differences. The average twelve-year-old male is about six feet longer than the average female of that age, and the largest male measured (240 inches) is about eight feet longer than the largest female (145 inches). References to bulls of up to 25 feet are not uncommon in the literature and Peron (1816) gives a length of even 30 feet. Although there is a natural tendency to overestimate size, it is possible that formerly the male elephant seal reached a greater size than at present.

Part	Weight in lbs.	% of total weight
Skin	265	6.10
Blubber	1469	33.70
Meat	923	21.19
Bone	688	15.79
Flippers, fore*	174	3.98
Flippers, hind	70	1.61
Head	114	2.62
Heart	20	0.46
Liver	110	2.53
Spleen	25	0.58
Lungs	90	2.06
Kidneys	14	0.32
Stomach†	72	1.65
Intestines†	90	2.06
Tongue	15	0.35
Blood (Calculated)	218	5.00
Entire animal	4357	100.00

TABLE III. Weight of bull elephant seal, 160 inches long. *The fore flippers include shoulder blade. †Stomach and intestines were quite empty.

The only definite information about the weight of the adult elephant seal comes from the weighing of an animal in pieces. It was carried out by Messrs. Christian Salvesen and Co. at Leith Harbour, South Georgia (Hamilton, 1949). The animal, a male, was 13 feet 4 inches in length, presumably nose to tail. Details of the weights of different parts are given in table 3, and the total weight was 4357 pounds, or nearly two tons. It was a medium sized bull and, in the absence of further data, it is reasonable to believe that a large bull may weigh anything up to four or five tons. The average adult cow probably weighs about 1500 pounds. Table III shows that the blubber weighs over one third of the total body weight. This is a layer of fat and connective tissue lying immediately beneath the skin, which acts as a food reserve and as insulation. According to the season it varies in thickness from 1 to 3 inches in a small individual to 3 to 6 inches in a large male. In 1933 when the blubber was very thick it averaged about 7 inches and in one bull was 8 inches thick.

The area of the fore flippers is small and they are little used in swimming but assist in terrestrial locomotion, especially in the male. They are larger in relation to body size in old males than in younger males or females. The hind flippers are webbed, emarginate and fan-like when spread out. The first and fifth toes are longer than the others and approximately equal in length. The fore flipper is deeply notched between the fourth and fifth digits and bears strong nails, but they are vestigial on the hind flipper (figure 6). The fore limb is very mobile and can be used to scratch almost any part of the body, even the nose. The hind flippers are often stretched and rubbed together, but they are never flexed in the elephant seal as in other species.

Figures 3, 5, 12, and 22 to 27 illustrate the general appearance of elephant seal of both sexes, and the changes in size and appearance with age are described in a later section.

The vibrissae are dark brown-black in colour, flattened and with constrictions about 2 mm. apart. In older animals the bristles are worn and lighter coloured towards the tip. The eye is large—up to 3 inches in diameter—with a deep chestnut-brown iris, and the cornea with a network of blood vessels giving

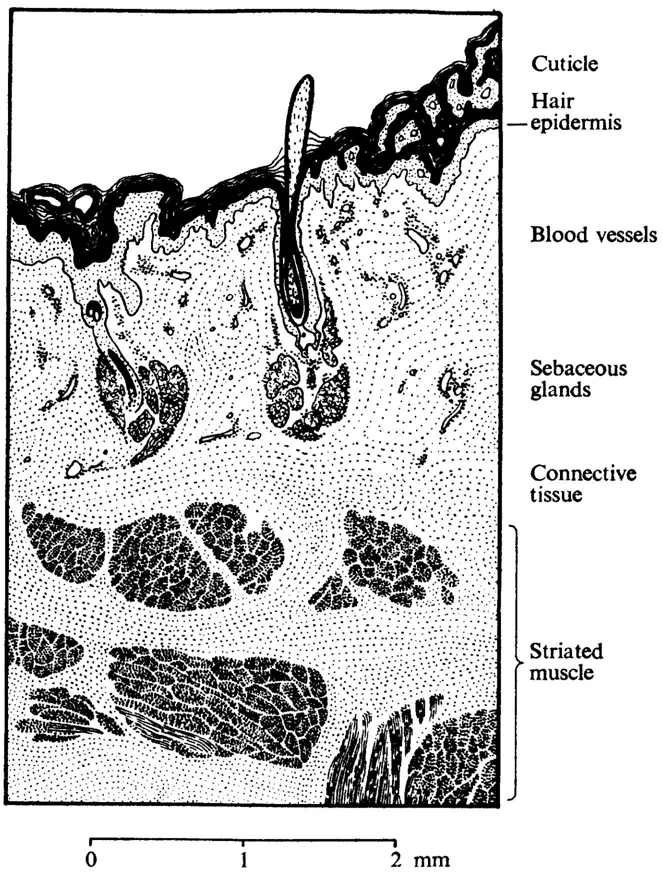


FIGURE 4. Diagram to show the histology of the wall of the proboscis in a breeding bull.

it a bloodshot appearance. The pupil is oval, vertical and about 2.5 x 1.0 cm. when expanded. The external meatus of the ear is about 5 cm. behind the external canthus of the eye in a medium sized male.

Apart from size, the presence of two or rarely four nipples on the abdomen of the female, and a penile opening in the male, the most obvious sexual difference is the proboscis borne by the bulls. There has been considerable controversy as to whether it is inflated by air pressure, or erected by muscles and blood pressure. Lesson (1822, p. 418) states more or less correctly that, " . . . cette trompe érectile manque à la femelle et parait s'éffacer peu à peu lorsque la saison de rut est passée. C'est un tissue cellulaire du nez qui semble ainsi se gorger de sang et s'allonger . . . ". Moseley (1892) believed the enlargement was brought about by inflation with air combined with contraction of the muscles at the side of the nose. Murphy (1914, p. 75) corrected the statement of other earlier writers that the proboscis is inflatable; "the upper and outer walls of the nostrils are composed of excessively developed dermal muscles the arrangement of which does not differ fundamentally from that of the nasal muscles in the harbor seal (*Phoca*). This heavy muscle layer is remarkably vascular, and is, to all appearances, true erectile tissue capable of being voluntarily charged with blood. Eliminating the inflation theory such a great expansion of the snout . . . can hardly be explained on any other hypothesis than that of erection by blood pressure. There are two or more blind vesicles leading upward from the nares at the middle of the lateral ethmoid cartilages, but they are far too small to permit appreciable inflation of the upper snout." Since then several contradictory statements have been made in the literature and Bartholomew (1952) supports Huey's statement that limited inflation occurs in the proboscis of the northern elephant seal (*M. angustirostris*). Several probosces were dissected in the present study and one was examined histologically. The findings confirm Murphy's (1914) statement but histological examination does not reveal any true erectile tissue. The small size of the two blind vesicles leading upward from the nares would not allow great expansion of the proboscis, and it is the opinion of the writer that muscular action and to a certain extent blood pressure

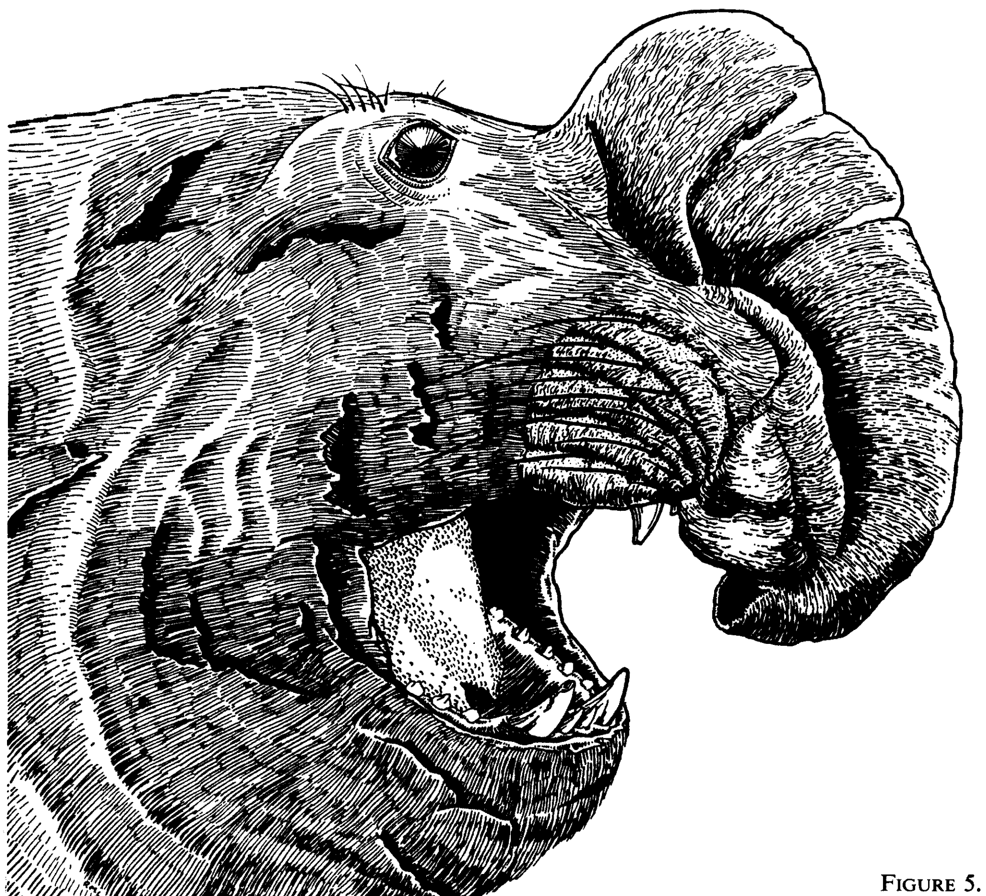


FIGURE 5. Head of harem bull H322. Proboscis fully erected.

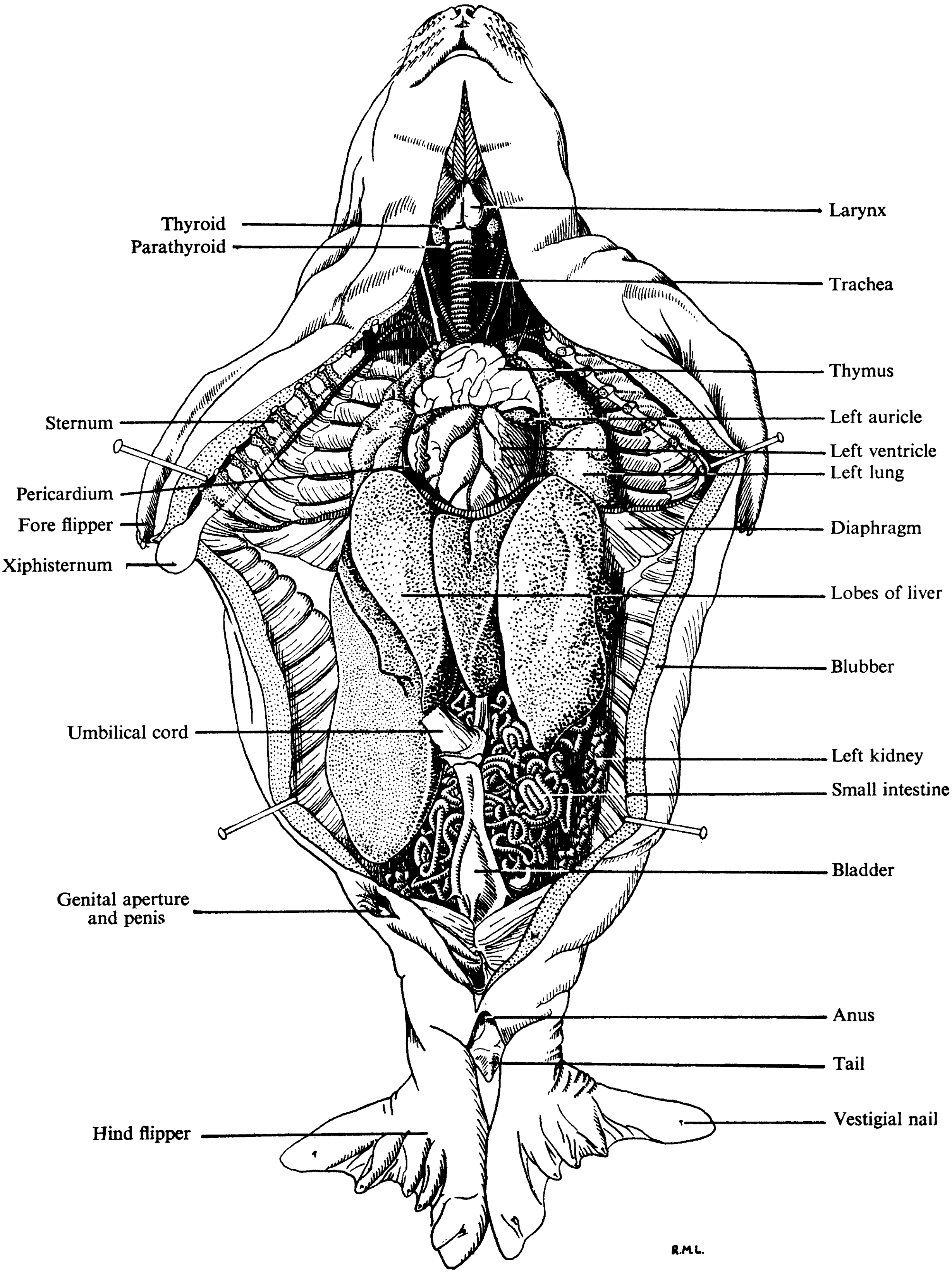


FIGURE 6. General dissection of foetal male elephant seal M78.

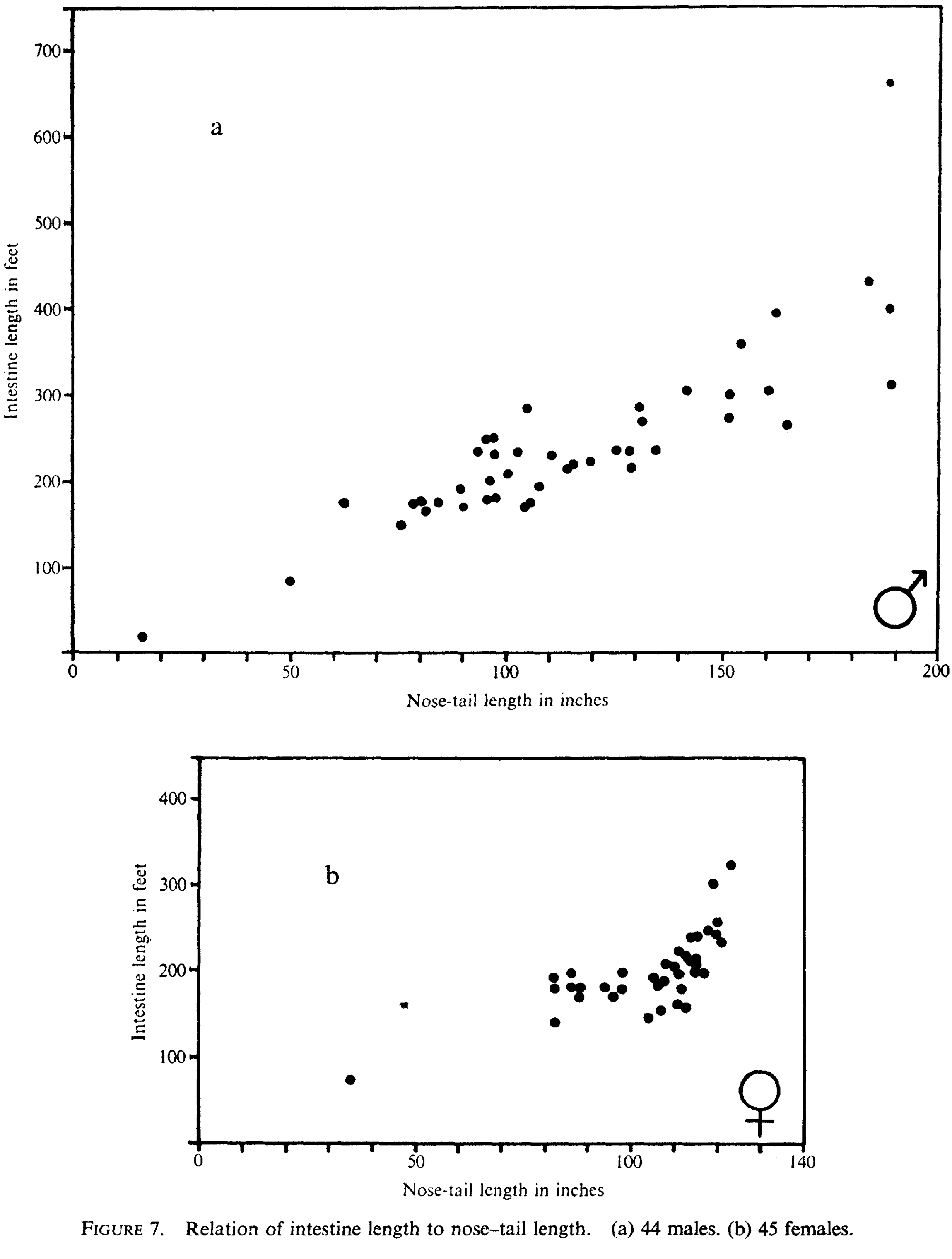


FIGURE 7. Relation of intestine length to nose-tail length. (a) 44 males. (b) 45 females.

bring about the erection of the proboscis when the animal is excited, but that there is no true erectile tissue. During forcible expiration the rush of air supplements the muscular action and causes the proboscis to vibrate so that one might suppose the proboscis to be inflated. It is interesting to note that animals which have lost a large part of their proboscis, including the air chambers, are still able to erect the remainder when excited. Bartholomew (1952, p. 400) has drawn attention to the role of the proboscis in reproductive behaviour but, in the southern species at least, it is the diverticula of the proboscis, not the mouth, which acts as a resonating chamber. The growth and development of the proboscis during the life of the animal is considered in a later section of this paper. Lesson was correct in stating that the size of the proboscis declines after the breeding season.

Turner (1887) and Miller (1887) have described the osteology and myology of the elephant seal, which is but little modified as compared with the organisation of *Phoca* described in detail by Howell (1929). Other writers have contributed notes on the morphology, notably Holz and Zukowsky (1926), and it is proposed only to figure the gross internal anatomy here (figure 6) and to discuss one of the most interesting anatomical features, the great length of the small intestine. The anatomy of the reproductive systems and of certain ductless glands will be described in a later paper.

The intestinal tract of seals is characterised by its simplicity, the great length of the small intestine, relative shortness of the hind gut, the reduction of the caecum and a single suspension from a continuous mesentery. In the elephant seal the junction of the duodenum and small intestine is not sharply defined and the small intestine is of even diameter (1 to 1.5 cm.) and thrown into numerous folds which almost surround an oval expanse of mesentery. Measurements of the length of the small intestine of eighty-nine elephant seals are set out in tables IV and V, and illustrated in figure 7. Although there is great individual range and variation, the growth of the small intestine relative to the body appears to be heterogonic. The intestine length of adults varies from twenty to twenty-five times the body length, and in H.303, with an intestine 662 feet long, the ratio is forty-two times the body length.

As a rule carnivores have short intestines and herbivores have long ones. This is largely due to the fact that cellulose is broken down by fermentative bacteria in the small intestine and caecum. Elephant seals feed mainly on cephalopods, which have hard parts of a chitinous material, structurally similar to cellulose, and it may be that the small intestine of the elephant seal is long because of the necessity of harbouring a bacterial fauna to break down the chitin. The fact that the leopard seal (*H. leptonyx*) which feeds mainly on penguins, has an intestine of larger diameter and much shorter length is perhaps significant. Sea birds (e.g. *Priocella antarctica*) feeding on cuttlefish have long intestines. Mitchell (1916) says the lengthening of Meckel's tract is best explained as an adaptation to diet. Alternatively the length of the intestine may be related to the water balance of a marine animal.

No.	Intestine length (feet)	Body length (ins.)	No.	Intestine length (feet)	Body length (ins.)
F.M73	18	16	H343	195	108
F.H	85	50	H331	230	111
H296	175	63	H332	215	115
*	176	81	H327	220	116
H370	150	76	H312	220	120
H369	175	79	H325	235	126
H358	170	82	H340	215	129
H306	176	85	H350	235	129
H309	170	90	H344	285	131
JB2	190	90	A2	270	132
H378	235	94	H326	235	135
H361	180	96	H308	305	142
M72	250	96	H355	300	152
H335	250	97	H337	275	152
H360	200	97	M77	360	155
H334	180	98	H353	304	161
H377	230	98	H302	396	163
H356	210	101	†	264	165
H357	235	103	H304	429	184
H311	170	105	H354	310	189
H359	285	105	H303	662	189
H330	175	106	H322	400	189

TABLE IV. Intestine length of forty-four male elephant seals arranged in order of increasing body length. * Mitchell (1916). † Murphy (1914).

No.	Intestine length (feet)	Body length (ins.)	No.	Intestine length (feet)	Body length (ins.)
M83.F	76	34	H320	205	110
H294	140	82	M67	200	111
M14	190	82	M74	160	111
M66	180	82	M75	225	111
M5	150	83	M70	180	112
H298	198	86	M16	220	113
M19	180	86	M83	160	113
M12	170	88	H289	216	114
M73	180	88	H372	240	114
H379	170	92	H368	240	114
M32	180	94	H363	215	115
M11	170	96	M69	215	115
H362	180	98	M81	205	115
M15	200	98	H352	200	117
H375	200	103	M13	250	118
H341	145	104	H297	306	119
H307	187	106	H300	258	120
M18	190	106	H301	244	120
M80	190	106	M76	235	121
H346	155	107	JB1	235	122
M17	210	108	H299	323	123
H373	210	109	H374	285	127
M6	230	109			

TABLE V. Intestine length of forty-five female elephant seals arranged in order of increasing body length

B. DENTITION

The milk dentition is but feebly developed in all seals. In the eared seals and the walrus the milk teeth are visible for a while after birth but in the True seals they are usually resorbed or shed during pregnancy, the foetus at full-term possessing the permanent dentition in a more or less functional condition.

Bertram has shown by X-ray examination that in both the Weddell seal (*Leptonychotes weddelli*) and the crabeater seal (*Lobodon carcinophaga*), the milk dentition reaches its maximum development in the fourth month of pregnancy when the foetus is slightly more than 30 cm. long. It is then resorbed and the permanent dentition which appears in the fourth month is beginning to erupt at the time of birth. He is able to state that, "X-ray examination shows that of the five permanent post-canines three only are preceded by milk-teeth, so that the last two post-canines should be considered as true molars". (1940, p. 129).

Owing to the difficulty of obtaining pregnant female elephant seals during the winter months when they are pelagic in distribution only seven large foetuses have been collected and there is a gap in the series between specimens of length 49 cm. and 89 cm. Thus, although the series illustrates the development of the milk dentition it throws little light on the early growth of the permanent teeth. X-ray photographs of the material available (plates I and II) show that the formula for the milk dentition is 1, $\frac{2}{1}$; C $\frac{1}{1}$; Pc $\frac{3}{3}$ and that it makes its first appearance when the embryo is about 18 cm. long and 4–6 weeks after implantation. It reaches its maximum development when the foetus is about 50 cm. long, three months after implantation of the blastocyst. The results have been summarised in table VI. The order of appearance of the milk teeth is: lower canines, upper canines, upper and lower incisors, lower and upper post-canines. The permanent canines do not appear until the milk dentition is complete, and reabsorption of the milk precursors of the canines and incisors begins before the milk post-canines reach their full size. The first upper incisors are small and generally indistinct.

Flower (1881) describes an 11 inch foetus (nose-flipper) in these words, "The jaws contained a set of very minute calcified teeth, viz: I $\frac{2}{1}$, C $\frac{1}{1}$, M $\frac{3}{3}$, on each side, being the complete number of milk teeth which the species would have for the incisors and canines would be of the same number as the permanent set,

Station No.	Approx. Age (months)	Nose-tail length (mm.)	TEETH			
			Milk		Permanent	
			Upper	Lower	Upper	Lower
H307	1–1½	186	—	C	—	—
M68	1–1½	192	C	C	—	—
M32	1½–2	248	I_2C	IC	—	—
M76	1¾–2½	282	I_1I_2CPc1	IC	—	—
M73	2¼–3¼	410	$I_1I_2CPc1–2$	ICPc1–3	C	C
M78	2½–3½	490	$I_1I_2CPc1–3$	ICPc1–3	C	C
M83.F	5–6	890	$I_1I_2CPc1–3$	ICPc1–3	$I_1I_2CPc1–5$	ICPc1–5

TABLE VI. Development of milk dentition in foetal elephant seals. Age of foetus in months post-implantation.

and the milk molars of all seals, . . ., are $\frac{3}{3}$, corresponding to the second, third and fourth premolars of the second dentition. There was in addition, in the upper jaw a small cap of dentine, in the situation of the apex of the first permanent premolar—a tooth which, in its development, is almost coeval with the milk teeth and has no predecessor". His specimen is intermediate in size between M32 and M76 but in the state of development of the teeth it is almost equivalent to M73. Possibly the discrepancy can be explained by

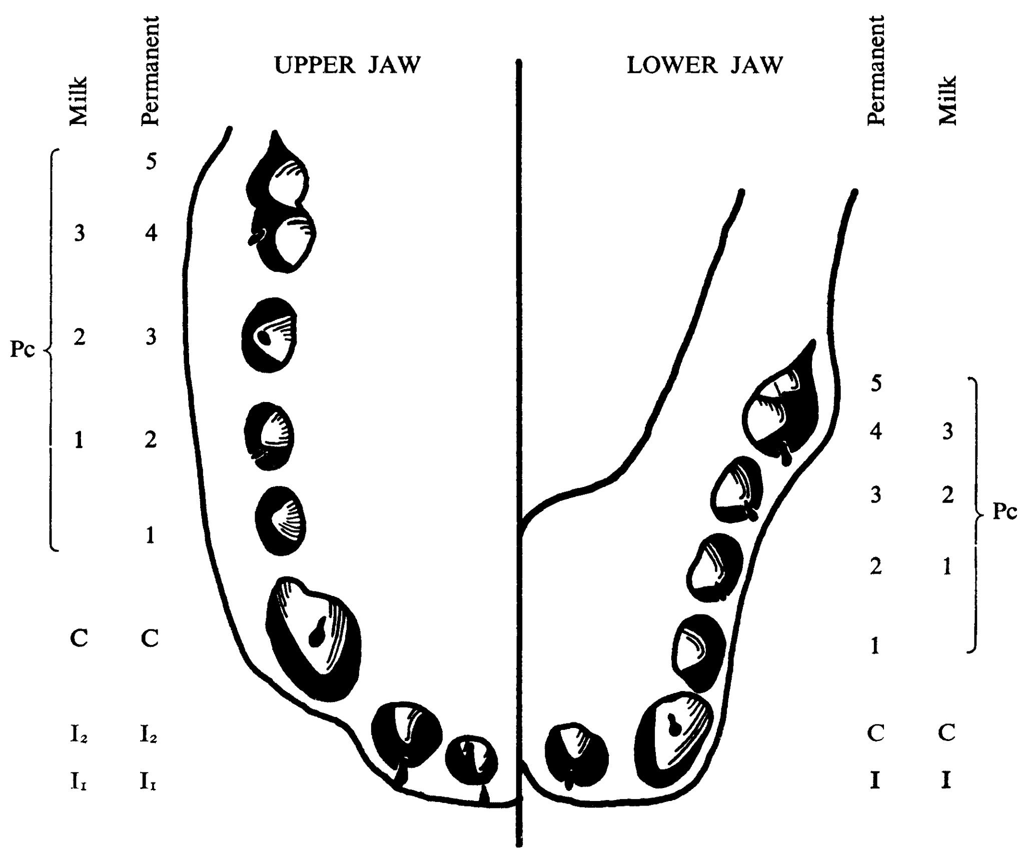


FIGURE 8. Diagram of milk and permanent dentition of elephant seal foetus M83.F, 21.viii.51.

assuming that Flower's specimen had undergone considerable shrinkage before he was able to examine it, and that his length (11 inches) is therefore too small. Moreover, he does not state whether the measurement was made in a straight line or along the curve of the back.

Bertram believes that Tims' (1923, p. 416) statement that "the first premolar has no predecessor either in this animal [*Otaria*] or in the Phocidae", requires to be modified for the Weddell and crabeater seals, and that in these species the three milk post-canines are the precursors of the *first three* permanent post-canines, making the adult dentition $I\,\frac{2}{1}$, $C\,\frac{1}{1}$, $Pm\,\frac{3}{3}$, $M\,\frac{2}{2}$. Figure 8 illustrates the result of a dissection of

Pup No.	Incisors			Canines		Post-canines									
	Upper		Lower	Upper	Lower	Upper					Lower				
	1	2				1	2	3	4	5	1	2	3	4	5
22	>38	35	>38	24	22	>38	>38>	38	>38	24	26	30	30	38	35
7	>25	11	>25	7	0	>25	>25	>25	>25	>25	>25	>25	>25	>25	25
43	20	5 & 9	20	3	5	>24	>24	>24	>24	16	16	24	24	24	24
45	34	1	14	1	0	34	34	34	34	34	16	27	18	28	28
46			3												
50			4												
44				2	2										
41	>13	13	7	>13	>13	>13	>13	>13	>13	>13	>13	>13>	13	>13	>13
54	>26	26	26	26	26	>26	>26	>26	>26	>26	>26	>26	>26	>26	>26
59	>27	22	22	22	22	>27	>27	>27	>27	22	>27	27	27	27	22
34	22	22	22	22	1	>27	>27	>27	>27	>27	27	27	27	27	27
57	>24	>24	>24	>24	24	>24	>24	>24	>24	>24	>24	>24	>24	>24	>24
6					1										
8				2	2										
1		1													
19	27	0	0	0	4	27	>33	27	27	33	4	28	28	>33	28
29	>21	6	21	0	0	>21	>21	>21	>21	>21	15	>21	>21	>21	>21
51	>24	>24	>24	24	24	>24	>24	>24	>24	24	>24	>24	>24	>24	>24
52		8		0	0										
11	>20	9	20	1	1	>20	>20	>20	>20	>20	20	20	20	>20	>20
47	>17	17	11	0	0	>17	>17	>17	>17	>17	17	>17	>17	>17	>17
Av.	>24	>14	>17	>10	>8	>24	>25	>24	>24	>23	>20	>24	>23	>25	>24

TABLE VII. Eruption of the permanent dentiton of twenty-one elephant seal pups, 1948, 1949. (Figures give age in days at which teeth appeared). A number of pups were carried out to sea when the ice broke up so that observations are incomplete. For the individuals shown in the table the age at which the last tooth is shown to erupt, was the age at which observations were discontinued. Pups not shown in the table and which were under observation still had no teeth showing at ages of 18, 12, 11, 11, 10, 9, 6, 5, and 3 days.

the dentition of specimen M83.F, a near term foetus 35 inches (890 mm.) in length. The post-canine milk teeth correspond to the permanent post-canines 2–4, confirming Flower's description quoted above. In both jaws the fourth and fifth permanent post-canines occupy a common socket and in the upper jaw the sockets of the canine and first post-canine are confluent within the jaw. Furthermore, on the right side of the upper jaw there are three incisors, the two inner ones occupying a common socket.

At Signy Island observations were made on the dentition of thirty marked pups of known age, but of these, owing to the break-up of the sea-ice, only thirteen sets of records are at all extensive. The observations are summarised in table VII. It will be remarked that the acquisition of the permanent dentition is extremely variable. Of the pups examined only six (or 20%) had any teeth erupted at birth. Typically, in the pups for which data is available, the lower canines are the first to appear at an average age of just about eight days (0–26 days). The upper canines follow at 0–26 days averaging about ten days. At an average age of more than fourteen days (0–35 days) the upper outer incisors appear but the upper inner incisors do not erupt until over twenty-four days after birth (20–38 days). The lower incisors appear at an average age of more than seventeen days (0–38 days).

The age at which the post-canines pierce the gums is very variable, as might be expected in view of their vestigial character. The first lower post-canine is usually visible at 4–27 days of age, averaging more than twenty days. Then the upper last post-canine appears at an average age of over twenty-three days (16–34 days), and the other post-canines erupt at greater ages.

The typical formula at weaning, twenty-three days after birth, is therefore I $\frac{\text{outer pair only}}{1\text{–}1}$, C $\frac{1\text{–}1}{1\text{–}1}$, Pc $\frac{0}{\text{first pair}}$. The appearance of the full set of teeth in the lower jaw comes in advance of the upper, as Lindsey (1937) observed to be the case in the Weddell seal (*Leptonychotes weddelli*). The last teeth to appear are the first four upper post-canines. One pup had the full adult dentition at thirty-four days of age, which is probably somewhere near the average age. The acquisition of a full set of functional teeth is thus not completed in the elephant seal until about eleven days after weaning. Possibly the delay is correlated with the behaviour of the young animal, which does not usually enter the water and therefore does not feed for about a month after weaning. In comparison, the Weddell seal has a longer suckling period (about fifty days) but the young enter the water even before they are deserted by their parent. Their average age on attaining a complete dentition is thirty-four days, which corresponds well with the elephant seal. It is interesting that elephant seal pups which had undergone a pre-natal moult showed no precocity in the eruption of the teeth. There is a tendency for pups born later in the season to develop the teeth at an earlier age than those born at the beginning of the season, but fuller data might not confirm this.

The complete adult dentition is I $\frac{2}{1}$, C $\frac{1}{1}$, Pm $\frac{4}{4}$, M $\frac{1}{1}$, totalling thirty. Wilson (1907) as a result of his work on Antarctic seals, came to the conclusion that in all the seals, with few exceptions, the variation in the dentition is excessive. But the leopard seal (*Hydrurga leptonyx*) and the crabeater seal (*Lobodon carcinophaga*) show no variations from the normal type with Pc5/5. Of 130 skulls of the Weddell seal (*Leptonychotes weddelli*) which have been examined, about 7 per cent had aberrant dentition, the variation taking the form of an extra post-canine on one or both sides of the upper jaw (Wilson, 1907; Bertram, 1940). In the elephant seal, on the other hand, the tendency is to lose one or more post-canines, usually the upper fifth molar, although on one skull examined the right side of the lower jaw bears only four post-canines. In the skull of specimen M71, in addition to five post-canines, there was a small cap of enamel piercing the gum just posterior and lateral to the lower left canine. H360 has four canines on the left side of the lower jaw.

There is some variation in the size and arrangement of the inner incisors of the upper jaw, and their milk precursors are very much smaller than the second milk incisors. Attention has already been drawn to the presence of a small third permanent incisor at one side of the upper jaw of a near term foetus (M83.F), and the basic original number of incisors found in seals is three. One would suppose that all the incisors are becoming vestigial for, with the exception of the second upper incisor they are so reduced as to have no function.

The pinnipeds as a group exhibit a wide range of adaptive radiation in the form of the teeth, correlated with the diversity of the feeding habits, but the form of the canines is always a simple conoid. The canine teeth of the elephant seal have marked sexual differences; in the female they are used mainly for feeding and to a negligible extent in defence. They grow in width as well as in length during adolescence and develop four longitudinal flutings which give the teeth a more or less rhomboidal cross section. A lower canine from a thirteen-year-old cow has an enamel crown of length 11–13 mm. (there has been some attrition), and the rest of the tooth is 59–62 mm. in length, measured in a straight line. The average diameter of the tooth at the level of the alveolar bone is 15 mm.

Correlated with their use during the breeding season in fights with other males, the canines of the males, especially in the upper jaw, are larger and better developed than in the female. They continue to grow in width, as well as in length, until the attainment of sexual maturity and are further enlarged by the deposition of a thick layer of cement on the outer surface of the root. The pulp cavity does not close (up to 18–20 years at least) and the enamel crown apparently grows during life, so that there must be a persistent enamel organ which is a unique occurrence among mammals. A well worn canine from a fourteen-year-old bull has an enamel crown 13–19 mm. high, and a root measuring 104–115 mm. The mean diameter of the tooth at the level of the alveolar bone is 32 mm. The skull of one adult male had only one lower canine, and no socket was visible on that side of the lower jaw; another had five lower canines. Other bulls frequently have the canines badly chipped or even completely smashed during sexual fighting.

The post-canines are small peg-like structures which are almost functionless, but are used to a limited extent to crunch large fish. "The crowns, when young, present traces only of the division into pointed cusps or lobes, so characteristic of the molars of most seals—mere grooves upon the surface, becoming deeper towards the apex, to which they converge, and marking off rudimentary cusps, more distinct on the outer than on the inner surface of the tooth. The fifth molar in both upper and lower jaws is of more simple character than the others, often only a simple cone". (Flower, 1881, p. 152).

IV. GROWTH AND AGE

A. General

THE problems presented by a study of the growth rates and age composition of wild populations of mammals are such that a detailed knowledge of this aspect of the life of only a few species is available. The seals and whales, largely owing to their commercial value as fur-bearing or oil-producing animals, have probably received more attention than other mammals. For this reason knowledge of the growth rates and ages, both average and maximal, of the valuable northern fur seal (*Callorhinus ursinus*) is far advanced. Rand (1950) has made an interesting study of the cape fur seal (*Arctocephalus pusillus*), but it will be many years before the long term branding experiments come to fruition. Hamilton (1939) has studied these problems in the Falkland sea lion (*Otaria byronia*), another economically important species.

Lindsey (1937) was the first to publish detailed work on the growth and age of a species of true seal, and Bertram (1940) who worked on the same species, the Weddell seal (*Leptonychotes weddelli*), has given the most complete account of growth rates and age composition of a population of Phocids. Sivertsen (1941) has given a detailed description of the harp seal (*Phoca groenlandica*), based on the commercial catch. This is one of the few species of True seals which is exploited commercially. Hamilton's (1939) conclusions for the age groups of the leopard seal (*Hydrurga leptonyx*) require revision in the light of recent developments in techniques of age determination.

Lindsey, Sivertsen, and Amoroso and Matthews (1950) are responsible for the only detailed published papers on the growth and development of the young Phocid during suckling.

It is believed that the present study of the southern elephant seal is the most detailed for any Phocid yet to appear. This is largely due to the discovery of a new and accurate method of determining age.

In order to obtain some idea of the age composition of a population it is necessary to be able to distinguish between the sexes, and to have some means of estimating individual ages fairly accurately.

Except in the first two years differences in the gross external appearance clearly distinguish the sexes of the elephant seal. When there is some doubt, the form of the canine teeth usually provides adequate confirmation, but in the first two year groups the sexes can only be distinguished by inspecting the ventral surface.

In some mammals the division into age classes is relatively simple, at least in the younger year groups. The general appearance, size, colour, form of the antlers or horns, complement of teeth and their attrition, and even the behaviour, may be distinctive for different age groups. In most mammals, however, after the first year the best that can be done on general grounds alone is to differentiate between mature and immature. There is usually a considerable overlap between the successive age groups caused by great individual variations, or by the small size of the samples available for comparison.

The method now used for the determination of the age of elephant seals has already been described (Laws, 1953b), and for the sake of completeness other methods of age grouping which have been investigated are described below. One very important factor in the lives of seals which greatly simplifies ageing and makes for a remarkable degree of accuracy, is the shortness of the pupping season. Since, all elephant seal pups are born within a short season of about eight weeks each year with a pronounced peak period, it follows that the age of any individual is always a known number of months plus an exact multiple of twelve. So that, as Bertram (1940) has pointed out, all individuals killed within the same month in any year will be either the same age or separated by an exact number of years. This fact must be borne in mind in the ensuing discussion. The elephant seal material obtained by the writer was collected over three-quarters of the year, extending over the months, August to May; age grouping by some of the methods presented below would be more successful if the animals had all been killed within the same short period of each year.

B. Possible Methods of Age Grouping

1. *Marking*

The most satisfactory means of studying the growth of an animal is by marking large numbers of the young in some permanent way, so that when they are examined at a later date the age is known. It also provides a useful check on any method of ageing which may be developed. It is, however, a long term policy and in an animal living to twenty years or more, full results would not be available until this period had elapsed. Furthermore, in view of the high mortality rates, a large number of animals have to be marked initially to ensure success. At the beginning of the field work on the elephant seal experiments in various types of permanent marking were carried out. Three methods presented themselves for investigation; branding by means of heat, branding with caustic, and tagging with non-corroding metal marks. Scheffer (1949) has given an excellent review of current marking methods.

Hot iron branding produces the most satisfactory results, but is time consuming and with an animal as large as the elephant seal (the pups of which weigh as much as 400 to 450 pounds at the stage when suitable for marking) requires a number of assistants to hold the animal down when the iron is applied. For these reasons branding was soon discontinued. "Some hundreds of pups" were branded yearly at South Georgia from 1921 to 1925 (Matthews, 1929, p. 243). Only three were seen later, in 1925, and all had been branded the previous season. One of them was seen on King Edward Point, Cumberland Bay, twelve months after branding; the wound of the brand was not healed and it was suppurating slightly. No branded seals were seen in the period 1948 to 1951.

Experiments in branding with sticks of caustic soda were made, after a method described for marking cattle (*Farmer and Stockbreeder* 1947) but proved unsuccessful and impracticable in the Antarctic. The procedure was to shave the area to be marked, and to draw in the symbol required, using a well-wrapped stick of caustic, but contact with water within twenty-four hours of application reduces its effectiveness. Moreover, the prevalent low temperature may well have weakened the action of the caustic.

A number of clips were made from metal alloy strips used for making identification rings for penguins. They had a locking overlap similar to a large bird ring, and were stamped with serial numbers and the inscription, "Inform F.I.D.S. Colonial Office London" both inside and outside. In order to attach the clip a small incision was made in the web of the hind flipper using a scalpel, but the pups did not appear to feel any pain. One man held the pup while another attached the clip to the hind flipper, and in this way sixty-three elephant seals and seventy-nine Weddell seals were marked at Signy Island. So far no marked animals over six months old have been recovered, but the tags facilitated a detailed study of the early growth history of the elephant seal.

The permanent marking of pups at Signy Island would have been of little value in assessing the later stages of growth because of the small size of the breeding population and low percentage of recoveries which could be expected. Less than 100 pups are born annually at Signy Island, and when work on the larger population at South Georgia began, a reliable method by which to determine the age of dead animals had been discovered and the lack of assistance made permanent marking a physical impossibility.

2. *Tooth Rings*

The yearly cycle of the elephant seal is remarkable for the occurrence of two periods of complete or partial fasting corresponding to the breeding season and the moulting period. Working on the assumption that these periods would result in a discontinuity in growth, the structure of the various hard parts of the body was investigated. The method of determining age which was finally adopted (Laws, 1953b) depends upon the occurrence of concentric rings of dentine of varying density visible in cross sections of the canine teeth. Subsequent work on material from South Georgia confirms the value of this method and the ages of 226 elephant seal in all have been determined. The validity of other methods of ageing have been checked by comparison with ages determined from the teeth.

3. *Body Length*

The lengths of 302 elephant seals (160 ♂, 142 ♀) have been recorded in the present investigation. Of these sixteen males and fifty-eight females were measured photographically, and other data relating to them is purely descriptive of external characters and behaviour. However, the ages of 226 (142 ♂, 84 ♀) are known from counts of tooth rings, and more or less complete anatomical and histological data is available.

In Bertram's opinion the length of a Weddell seal (*Leptonychotes weddelli*) cannot be measured with greater accuracy than $\pm$ 2 inches (1940, p. 37). In a large elephant seal the accuracy is no better than $\pm$ 6 inches, for variations in the size of the proboscis add to the uncertainty. Furthermore, seasonal variation in fatness may affect the measurements to the extent of 12 to 15 inches. (See figure 19.)

Lindsey (1937) has made a special study of the growth of the Weddell seal based on the killing of 233 seals in a short period of just over five weeks. He was able to define the first three annual groups in terms of size, and writes that, "Since all the young are born within about one month and the period during which we measured seals was similarly restricted, these frequency distribution charts show a drop to or toward the base line between adjacent annual age groups" (p. 199).

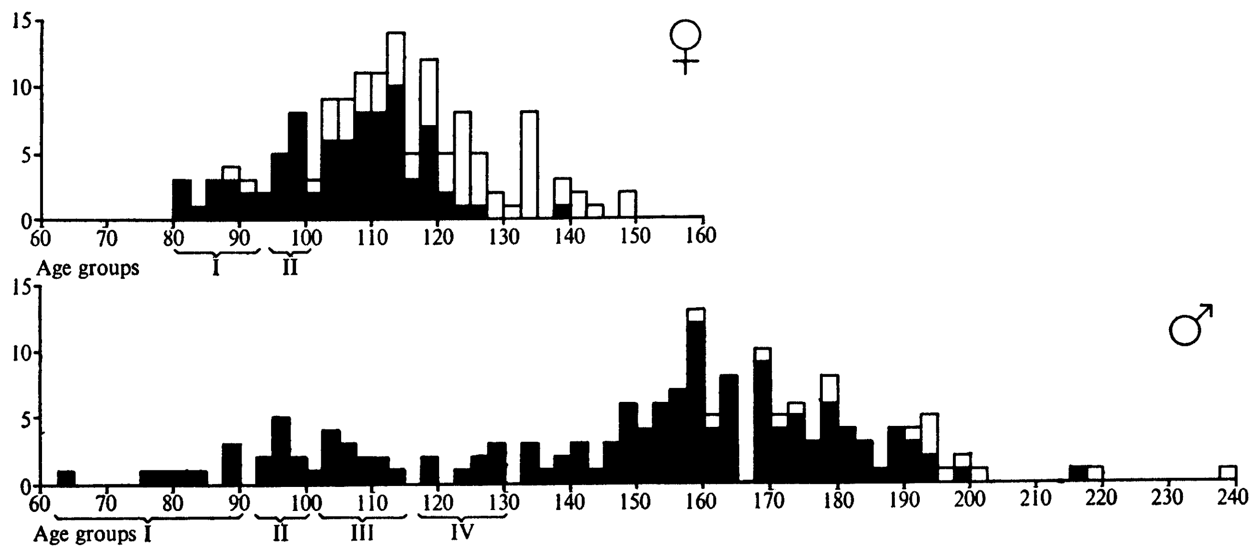


FIGURE 9. Length frequency diagrams for 142 female and 160 male elephant seals. Lengths in inches.

The number of elephant seals measured is greater but they are spread over several months and over several years. In figure 9 the frequency distribution of length is set out. The tendency for the animals measured photographically to be larger than the remainder is explained by the fact that all photographic measurements were made during the breeding season when only the older age groups were ashore. It seems that the first two female age groups and the first three male age groups are indicated by the frequency distribution of nose-tail length. If there were more measurements it is possible that a fourth age group would also be distinct. Though the early groups are apparently distinct, the ages from the teeth belie the length frequency groupings, and show that there is an extensive overlap.

4. *Claws*

Plehanov (1933) has drawn attention to the presence of growth ridges on the claws of the harp seal (*Phoca groenlandica*) and claims to be able to estimate the ages of individuals up to thirteen years by means of them. He gives no proof of their validity. Doutt (1942) describes and figures "annulations or growth rings" on the claws of the fore-flipper of the ringed seal (*Phoca hispida*) and of the banded seal (*P. fasciata*) and the bearded seal (*Erignathus barbatus*). He remarks that since wear at the tip of the claws removes some of the rings, under normal conditions it is not possible to tell the age beyond four to five years.

Clearly such a means of age determination would be of great value because it would mean that animals could be aged in the field without killing them.

The elephant seal has large strong claws on the fore-flippers which usually, but not invariably, display more or less conspicuous growth zones. They take the form of light bands on the dark grey-brown claw, about 3–4 mm. in thickness, but are not raised as ridges on the surface of the claw. Text figure 10a and plate V, figure d, give some idea of the conspicuous appearance which the claw bands sometimes assume. However, the elephant seal annually spends two or three months on land and the claws are subject to great wear, though less so in the female than in the male. The rings on the claws of the fore-flipper when they occur, afford a means of estimating the age only up to the fourth or fifth year, and unfortunately there are no visible claws on the hind flipper where they would not be subjected to wear. Since, with experience, it is possible to estimate the age of male elephant seals in the field (from general appearance), up to five or six years with considerable accuracy, the value of the claws as indicators of age is slight. In the female, however, it is only possible to estimate the age from general characters up to about four years, and claw bands would be useful in fixing a minimum age for certain individuals.

5. *Skull Characters*

Doutt (1942) has given an excellent account of possible methods of age grouping and concludes that in the harbour seal (*Phoca vitulina*), the degree of suture closure is the most reliable character for this purpose. Rand (1949, a, b,) used suture closures as a basis for class grouping of the Cape fur seal (*Arctocephalus pusillus*). He was able to grade the skulls in his collection into a continuous series showing advancing age, but the existence of well-defined age groups is not always apparent and he does not claim that suture groups in older animals represent annual or similar age groups. The method gives only a relative age for individual skulls within the series. Bertram (1940) found closure of certain sutures of little value as measures of absolute age, although in conjunction with other physical characters they were useful. Doutt has also suggested that weight and specific gravity of skulls may be of value in ageing.

Skull measurements, together with tooth wear, and body size and appearance were of primary importance in Hamilton's (1934, 1939) grouping of the Falkland sea lion (*Otaria byronia*) into definite annual classes, but Rand concludes that skull measurements are unreliable and that tooth wear is not a valid indicator of age.

Of the earlier methods of age grouping, skull characters have in general proved of most value. In view of the controversial nature of the literature it will be interesting to check the value of skull characters of elephant seals with the ages determined from growth layers in the teeth. A representative series of seventy-one elephant seal skulls were collected and have been deposited in the British Museum (Natural History) but they have not yet been examined in detail.

6. *Tympanic Bulla*

The tympanic bulla in the Phocidae is generally large and well rounded in contrast to the shrunken condition of the bulla in the Otariidae. The bulla of the elephant seal increases in size considerably during life and examination of thin sections shows it to have a layered appearance (figure 10b). The layers are from 1 to 2.7 mm. in thickness and plainly visible on polished surfaces. Their definition is improved by staining with a dye such as eosin.

Shipley (1929) has remarked that "bone instead of being almost completely stable is one of the most labile tissues of the body". . . . Thin undecalcified sections of the bullae of several elephant seals present an appearance which suggests that the bone is not greatly reconstructed internally as a result of growth, and that ossification proceeds by layered increments, rather than in the usual manner by resorption and re-deposition. The layers are separated by spaces 300 μ to 500 μ in diameter containing blood vessels of circumferential arrangement which arise as branches from vessels in radial spaces 600 μ to 800 μ in diameter. In view of this structure there can be no question of the layered appearance being a manifestation of Leisegang rings, and the structure of the bulla would repay further study in regard to ageing. Comparison of the number of layers with the age determined from the teeth suggests that in the development of the bulla there may be two discontinuities in growth each year.

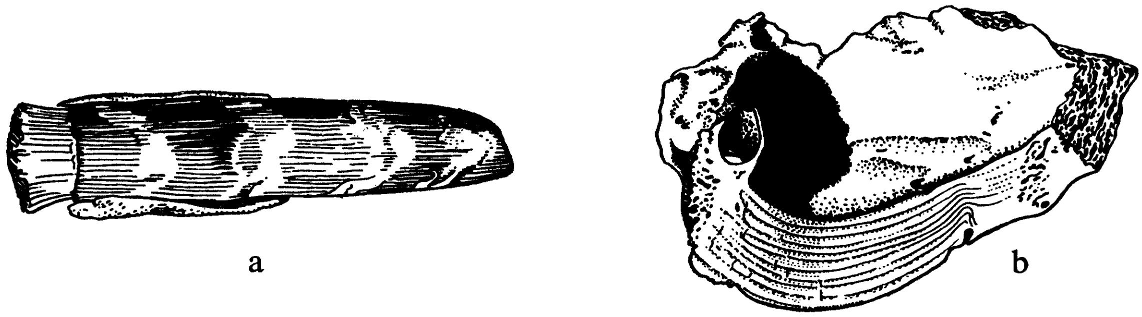


FIGURE 10. (a) Dorsal view of claw from fore-flipper of male H131, age five years (from tooth rings). (b) Saggital section of left tympanic bulla of a male elephant seal showing supposed growth layers.

7. *Os Penis or Bacula*

The *os penis* of most seals grows throughout life but there are often variations in the rate of growth. Havinga (1933, p. 81) was apparently the first to recognise the value of this bone as an indicator of age in seals. In the harbour seal (*Phoca vitulina*) sexual maturity is attained in the third year when the weight of the *baculum* increases from 0.001 to 0.005 per cent of the body weight. Similarly Hamilton (1939a) has demonstrated a rapid enlargement of the *baculum* in the three-year-old leopard seal (*Hydrurga leptonyx*). Rand (1949b) found that in the Cape fur seal (*Arctocephalus pusillus*) the increase was most noticeable in two to three-year-old animals; he concluded that it was of no absolute value as a criterion of age but that, in conjunction with cranial features, it emphasises important developmental changes. The method is only applicable to the male, since the presence of an *os clitoris* is unusual.

In the elephant seal there is a more rapid rate of growth of the *os penis* during the fourth year, than immediately before or after.This is related to the onset of sexual maturity of the species, but may bear a merely heterogonic relationship to general body size (p. 66, and figure 21). The size of the bone is thus of some value in determining whether an individual is sexually mature or not, but again this can usually be done as easily by consideration of the external appearance of the living animal. Rand (private communication) mentions that he has observed annulations on the *bacula* of elephant seals from Marion Island, which he believes may have some significance in determining age. However, few of the penis bones from the Falkland Islands Dependencies which have been examined have clear annulations. In cross section they have a medulla of typical spongy bone with a cortex of compact bone; there is no trace of any layering. Scheffer (1950b) has examined the *os penis* of the northern fur seal (*Callorhinus ursinus*) but was unable to distinguish any growth lines.

8. *Ovaries*

A method of ageing which is applicable only to the females was developed by Bertram (1940). By examining the structure of the ovaries of Weddell seals (*Leptonychotes weddelli*) from Graham Land, he was able to make important deductions regarding the age of individual animals. From his study of the frequency distribution of the numbers of old *corpora lutea* (*corpora albicantia*) in this species, Bertram concludes that the corpora persist throughout the adult life of the individual. All the ovulations in the life of the individual female are believed to be permanently recorded in the ovaries by the corresponding *corpora albicantia* and as it is probable that each seal ovulates only once a year, "the number of *corpora lutea* persisting in each pair of ovaries is a direct measure of the number of pregnancies undergone. The individual age is therefore this number plus the two pre-adult years" (Bertram, 1940, p. 56). In the absence of branded animals as a check there is no absolute proof of this conclusion, and in recent years doubt has been cast on the deductions made from the studies of whale ovaries, for which the method was first employed. Furthermore, in seals allowance must be made for "missed pregnancies" which are not represented by persistent *corpora albicantia.* It is hoped to undertake counts of the tooth rings of individuals in Bertram's material in order to verify the truth of his conclusions based upon the ovaries.

He postulates a similar condition in the crabeater seal (*Lobodon carcinophaga*), although the material available for examination was much less.

Hamilton (1939b, p. 135) writing of the sea lion in the Falkland Islands states, "Corpora lutea disappear fairly rapidly; in the whole series two are present in but six cases and in only three others can the traces of a third be found". The ovaries of the elephant seal present a similar appearance; the old *corpora lutea* are generally completely resorbed within a year and rarely are there distinctive traces of more than two *corpora lutea* in one pair of ovaries. The presence and appearance of *corpora lutea* can only be used for confirming the age of primiparous females, or females at the beginning of their second pregnancy.

C. The Development of the Pup

1. *General*

The detailed studies of pup growth were all made at Signy Island in 1948 and 1949, although work on other aspects of development was carried out there and also in 1951, at South Georgia.

Three manifestations of growth were studied—the weight changes, and the variations in girth and in length. The elephant seal normally breeds on land in huge rookeries and the cows and pups are collected together into local concentrations, the harems, each of which is controlled by a single bull. Harems may include over 100 cows at South Georgia, but at Signy Island the largest harem contained thirty cows. At South Georgia, owing to the crowded state of the beaches, measurement of the growth of the pups during suckling would have been virually impossible, and even at Signy Island the work was difficult and exhausting. There, however, the scattered location of the harems and, in 1949, the fact that all were situated on the level fast-ice, ensured that it was not too dangerous.

In developing a technique for weighing and measuring the pups four factors had to be taken into account before the measurements could be made. The disturbance to the harem must be minimal; the pups must be individually marked for recognition and ageing, and they have to be removed from the mother, and conveyed out of the territory of the bull.

During the 1948 season, while a technique was being developed, nine pups were weighed at two to three

FIGURE 11. Weighing procedure at Signy Island in 1949. Sledging pup to tripod, and weighing.

day intervals until they were seventeen days of age and weighed over 300 pounds. Length and girth measurements were made on a greater number up to age thirty-seven days. This season's work was carried out on the harem at Drying Point, Signy Island, with the help of two companions. In 1949, with the assistance of three men, six pups were weighed and measured at two to three day intervals up to thirty days of age, and a weight of nearly 400 pounds.

Originally a portable tripod made of bamboo, with legs in three sections for easy transport, was used. It was soon found to be unsuitable for weighing any but the smallest pups, for they are much heavier at birth than had been expected, and grow very rapidly. Both for these reasons and so that it might stand up to the bulls when they threw their weight about, a heavier tripod was constructed. It was made from 15 foot lengths of 1¼ inch galvanised steel piping, but even so the legs were bent when it was knocked down by the bulls in their rushes. The weight of the tripod and the difficulty of transport restricted weighing to a single harem each season, though measurements and general observations were carried out on the pups in several harems.

A three-pulley block and tackle system was attached to the apex of the tripod and onto the lower block was hung a spring balance for measuring the weight. Lindsey (1937) to whom we owe the only detailed study of the early growth history of an Antarctic pinniped, used a similar apparatus for weighing Weddell seal (*Leptonychotes weddelli*) pups, hoisting them up in a rope net. Various types of canvas sling were used for the elephant seal pups, and for some days (until smashed by the bull in one of his rushes) a stretcher, on which the pups were carried to the tripod. Later a wooden sledge with two webbing straps which could be tightened so as to hold the animal in position, was employed.

The routine eventually practised was for two men to grab the pup to be measured, roll it onto the sledge, strap it down and sledge it to the tripod which was set up ten to thirty yards from the harem. Meanwhile, the two other men distracted the attention of the mother and of the harem bull with sticks or a whip. The older pups are very strong and lively and have to be taken by surprise; administration of chloroform, owing to its absorption by the large fat-stores, had little effect in quietening them. Furthermore, they were usually lying among the cows of the harem and, as well as being arduous, the work was dangerous. Four men are much less than the ideal number for handling these animals. Frequently it was not possible to prevent the bull from rushing the tripod or a particularly maternal cow would follow her pup and interfere with the operation. On one occasion, in an attempt to minimise the interference, the bull and a cow were lassoed, but the cow had to be freed because it was choking, and there was no fixed rock near enough or large enough to provide anchorage for the bull.

Owing to these practical difficulties only seven male and eight female pups were weighed regularly and even to accomplish this meant several hours of strenuous work each weighing day.

After weighing, the pups were measured to the nearest inch with a surveyor's linen tape* the dentition was inspected and the state of the wool coat was noted. In a number of pups up to two weeks old the rectal temperature was recorded with a 5 cm. immersion thermometer. Pups over this age struggled too violently to permit temperature taking.

When all the necessary data had been obtained the animal was sledged back to its mother and the next pup selected, strapped down and carried away.

2. *Appearance of the Pup at Birth*

The young are born at Signy Island, on an average, five days after the cows haul out, and at South Georgia seven days after the haul out. The pup bears a black fur coat, weighs about 100 pounds, and measures about 50 inches from nose to tail. During suckling, which lasts just over three weeks, it deposits a thick layer of blubber, increasing in weight fourfold, and undergoes a moult of the natal *fur* so that, at an age of about four to five weeks, it has a perfect silver-grey *hair* coat.

At birth the appearance is rather ludicrous; a huge head, too heavy for the neck muscles to support, large shoulder girdle and fore limbs, and a body tailing off disproportionately behind. It is very weak and helpless, its movements uncoordinated and sprawling, a travesty of the rhythmic locomotory movement of the adult. Yet within a day or two it has a great access of strength and the forelimbs especially exhibit an unexpected mobility. The digits are capable of flexion almost like a human hand and the pup can scratch almost any part of its body with ease. The eyes open ten to fifteen minutes after birth and the pup has a querulous high-pitched bark which deepens with age. The muzzle is black and more or less shiny, and when

* The tape was frequently tested for stretching.

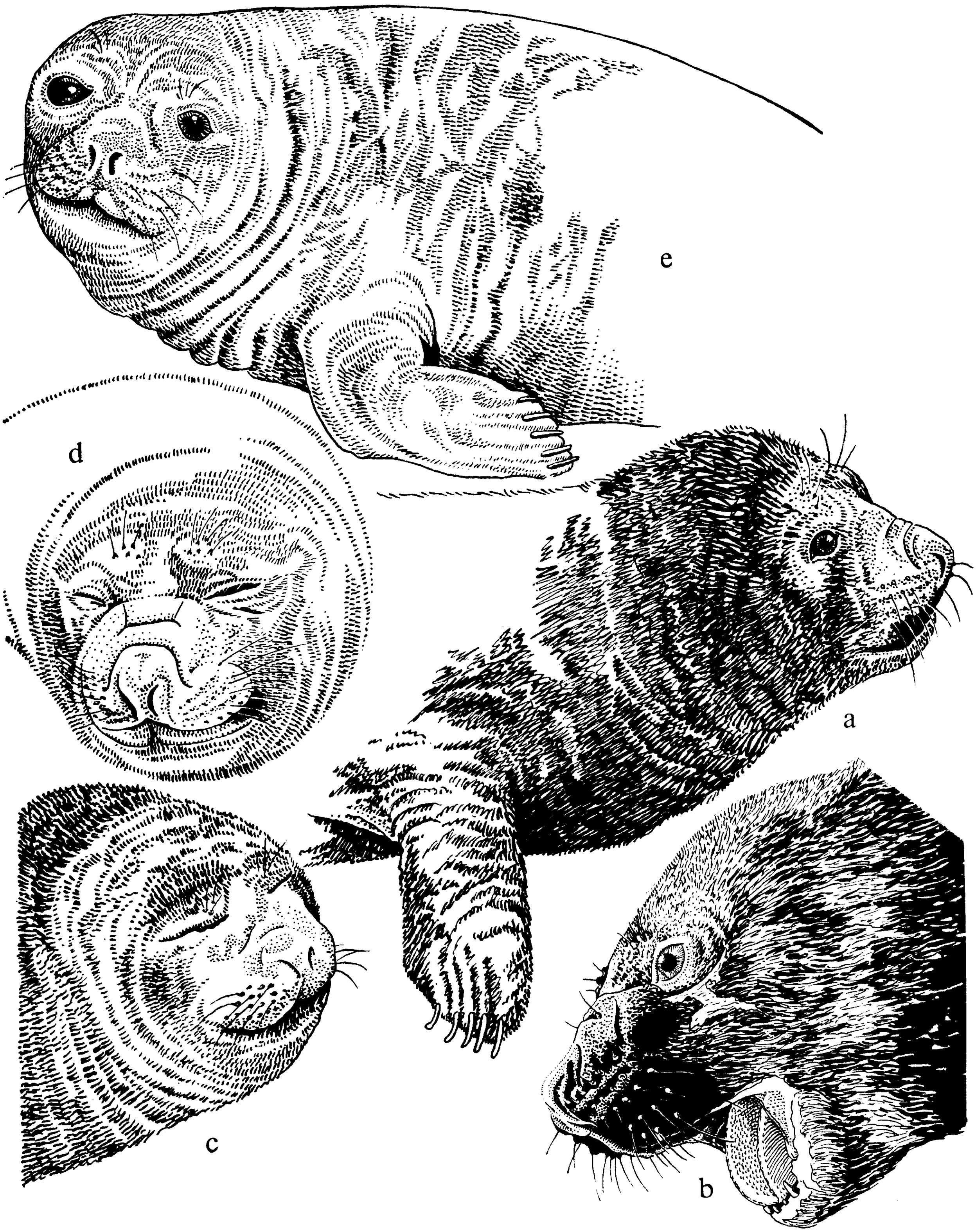


FIGURE 12. Pup elephant seals. (a) New born; (b) 1 week old; (c) 2 weeks old; (d) 4 weeks old; (e) 8 weeks old.

Pup No.	Age at weaning	Moult stage			Length of moult	Cord shed	Entered water
		a	b	c			
22	22		13	38			
7	20	pre-natal		2		9	31
43	23		15	30			36?
45	23		5	34			36
56			7	>25			
50			12			8	
44			7				
41			10				
55			12				
54	27		13	>27			
59	23						
34	23						
57	23						
8			12			10	
49			12			9	
1			11			8	
37			11			8	
40			10			7	
2			9	>23			
R/l						10	
R/n						8	
19	24	4	14	34		10	
29	24	4	10			6	
51	22	4		>24		7	
52		4	8			6	
11	23	3	9			7	
47	21	2	6			7	
Average	23	3.5	10.3	c. 34	c. 24	8	34

TABLE VII. Early post-natal history of twenty-seven marked pups. Ages in days.
Moult stage (a) Hair pulls out easily.
(b) Hair falling out.
(c) Moult complete.

excited the vibrissae are erected and small papillae of a bright pink colour are conspicuous at their bases. Usually there is a thick layer of mucus at the nostrils.

The claws are long (4 cm.) and curved, of a delicate slate-grey colour shading to ivory-white at the tips.

Usually there are not any external sexual differences except for the presence of a penile opening in the male. However, in a proportion of male pups the muzzle is large, like a roman nose in profile, and it can be erected to some extent when they are excited. This precocious development was seen in about 5 per cent of male pups at Signy Island but was never observed in the females.

Out of 1500 pups under close observation, colour varieties were recorded in only three individuals. In one there was a dirty yellowish-white patch on the breast, about 8 inches by 6 inches in area and almost rectangular. In another the patch was about 8 inches by 2 inches surrounding the navel. The third was a mottled greenish grey, with slight silvery cast. More commonly there were individuals with scattered white hairs in the general black coat, giving it a grizzled appearance. The pre-natal moult is dealt with below.

The intact umbilical cord is about 3 feet long. Just after the pup is born a weak spot is noticeable which appears redder than the rest. The mother breaks the cord at the weak point by suddenly swinging round through 90°. The pup is then left with some 8 to 14 inches of the cord still attached. This part is much tougher than the remainder. Except for the proximal 3 inches which are black, the appearance is fleshy and red in colour. As it dries it becomes darker and is sloughed off after six to ten days (average for fifteen pups was eight days) leaving a small reddish scar which quickly heals.

In September 1951 a pair of "siamese twins" was born in South Georgia. The monster was collected by sealers of the S/F "Diaz" in New Fortuna Bay. It had been still-born, and the size was rather more than normal, the nose-tail lengths being 51.5 and 52 inches. The twins, which were male, were joined ventrally from the umbilicus forwards; the hind parts were normal in appearance and there were eight limbs. When opened up putrefaction was found to be far advanced and permitted only a cursory examination. Moreover, it had to be examined in the field. Each of the bodies had a separate organisation except in the head region, where the two crania were joined anteriorly so that there were no lower jaws and there were two *foramina magna*. A common oesophagus and trachea branched in the neck, and there were two hearts, four lungs and two sets of all abdominal viscera. The circulations were separate except in the head region, but complicated in the umbilical region where there was a hernia. The monster's appearance is illustrated in figure 13, although in the specimen there was no eye; it had been removed by birds.

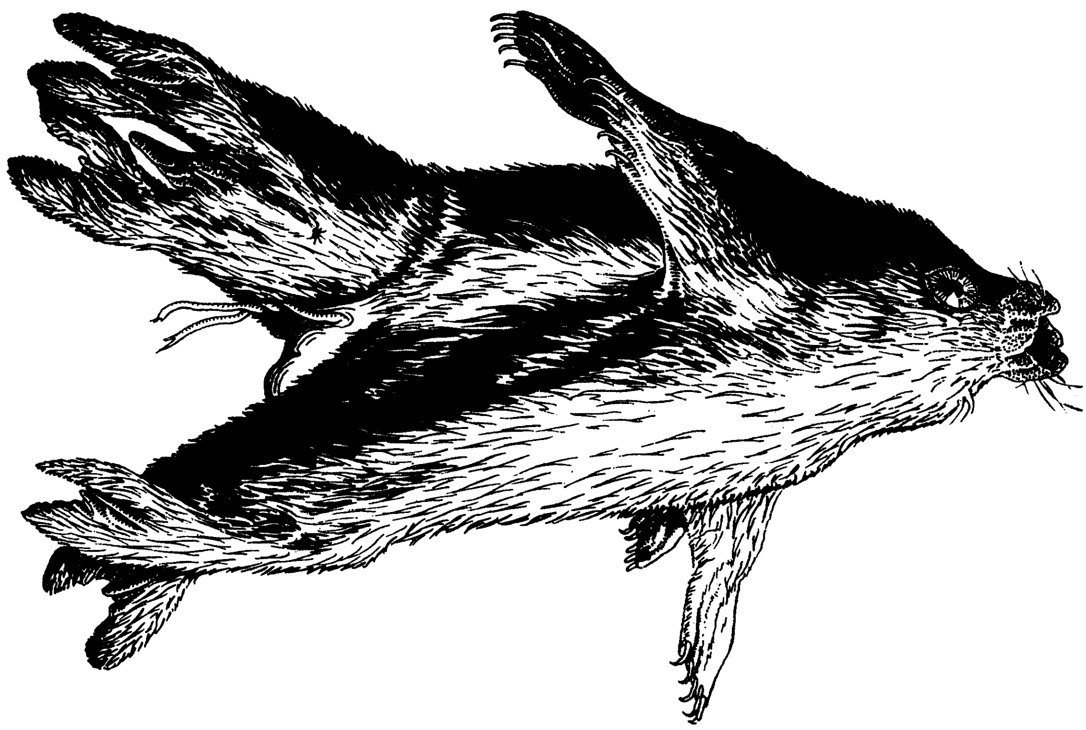


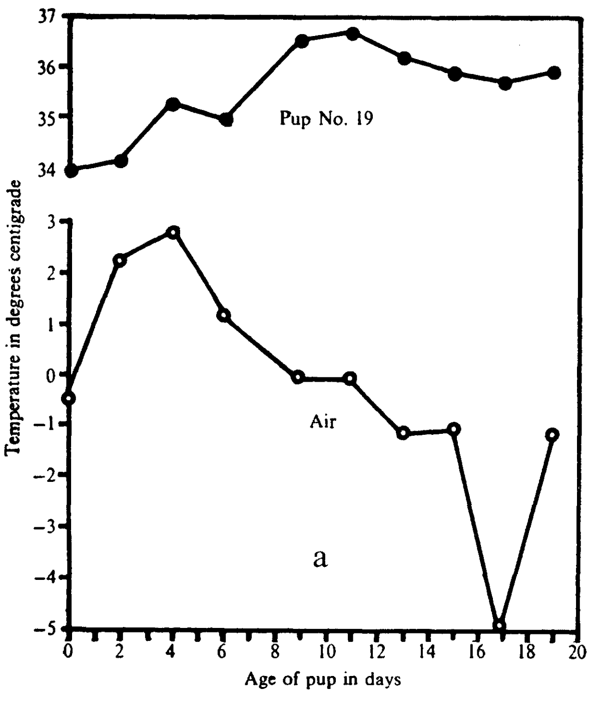
FIGURE 13. Siamese twins of elephant seal at South Georgia.

3. *The Moult*

At birth the natal coat, wet with amniotic fluid, is smooth and glossy, the hairs measuring from 22 to 30 mm. in length. The diameter of the individual hair is .08 x .05 mm. and only the distal third is jet black, the remainder being brownish-black in colour. The general colour is therefore jet black at birth, browner ventrally, and becomes increasingly brown with age. Very shortly after birth the fur dries and the individual hairs become curly, so that a hair 23 mm. long when stretched will have as many as ten curves or bends, and the actual thickness of the hair coat is about 15 mm. to 20 mm. The insulating properties of a coat composed of curly hairs are clearly better than those of a coat of long silky hairs. The Weddell seal (*Leptonychotes weddelli*) which is subject to lower air temperatures at birth has a woolly coat consisting of two varieties of hair, one long, fine and almost straight, the other shorter, fine and very curly (Wilson 1907, p. 17). In the week-old harp seal (*Phoca groenlandica*) Sivertsen (1941) has described a similar division into two layers. The elephant seal has no such arrangement. Hair pulls out easily at two to four days, but it does not begin to fall out, or be rubbed off by the pup's movements until five to fifteen days after birth (average ten days) and the moult is complete at thirty to thirty-eight days (averaging about thirty-four). Thus the average duration of the moult of the natal fur in the elephant seal is about twenty-four days. This compares with thirty days for the Weddell seal and about two weeks in the harp seal.

The order of the moult is variable. Usually bare patches appear first on the fore and hind flippers, then on the face and neck, the dorsal surface of the body, and lastly on the rump and in a line along the mid-ventral surface. This is so despite the fact that the ventral surface is subject to most wear. Sorensen's (1950) statement that, " . . . shedding commences first on the belly and sides, and . . . the lower back and rump clears last of all", would seem to conflict, but there is considerable individual variation. The hairless skin on the muzzle appears to slough off also, the muzzle assuming a grey-brown colour; the pink papillae darkening. The hair coat which succeeds the natal fur is stiff and bristly, the individual hairs being 7 to 8 mm. long and 0.14 x 0.05 mm. in diameter and orientated with the broadest diameter at right angles to the axis of the body.

Some 3 per cent of the pups born at Signy Island underwent a complete prenatal moult, and a few others were born with the moult already begun. Pup No. 7, which had undergone an almost complete prenatal moult was born with, "black face and flippers, black dorsal surface and a longitudinal band of black ventrally, tailing off in front of the umbilical cord. In such cases tufts of natal fur persist in the black areas. The rest of the coat is light silvery-buff in colour and the hairs are short and springy. . . . The shed tufts of natal hair in the amnion are a sooty brown in colour" (from field notebook). Weaning is precocious in pre-natally



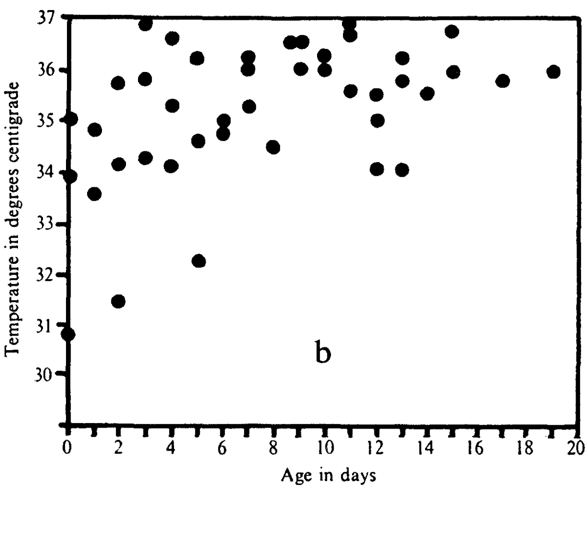


FIGURE 14. (a) Rectal temperatures of pup No. 19 from 0 to 19 days with air temperatures for comparison. (b) Rectal temperatures of 6 elephant seal pups.

moulted young. At South Georgia no individuals which had undergone a pre-natal moult were seen.

The temperature records (figure 14) suggest that the pup is to some extent poikilothermic at birth, but acquires an efficient temperature regulating mechanism, associated with deposition of blubber, before the thick pup fur with its insulating properties is shed. At birth the subcutaneous fat is about 0.5 cm. thick and a natal fur is essential for insulation from the low temperatures. The blubber layer is no thicker in those individuals which have had a pre-natal moult than average, and they were invariably seen to be shivering when the sun was not shining—in marked contrast to the pups which bore the usual thick natal coat. It is surprising that a pre-natal moult should take place, on occasion, at the southern limit of the species' breeding range, and never, so far as is known, at South Georgia where the air temperatures are so much higher.

On completion of the moult the young are clothed in a beautiful silver-grey hair coat, soft and velvety in texture, the hairs about 1 cm. long. With increasing age the hair round the mouth becomes progressively stained yellow-brown, and the entire coat gradually loses the cold bluish cast, and fades to a warmer colour.

Pups were first seen to enter the water voluntarily at an average age of thirty-four days, but the data is limited to observations of only three individuals. Even so it does show a correspondence with the age at which the moult is completed.

4. *Growth*

Girth measurements were taken of thirty-one marked pups of known age up to thirty-four days. In

Age in days	Girth in inches			No. of measts.	Age in days	Girth in inches			No. of measts.
	Max.	Min.	Av.			Max.	Min.	Av.	
0	39	35	36.8	6	18	63	55	59.8	3
1	40	38	38.7	11	19	64	60	62.0	2
2	43	36	39.5	12	20	65	61	62.2	4
3	45	37	40.3	11	21	65	55	60.0	2
4	44	38	41.1	10	22	66	60	63.0	3
5	44	41	42.2	5	23	65	59	61.2	5
6	46	40	42.7	9	24	67	62	64.4	2
7	48	42	44.3	9	25	62	61	61.5	2
8	48	42	45.1	8	26	68	59	63.0	5
9	48	42	45.8	6	27	—	—	63.0	1
10	53	42	47.4	5	28	64	59	61.0	3
11	52	44	49.1	8	29	61	59	60.0	2
12	53	49	50.6	3	30	—	—	65.0	1
13	55	46	52.3	8	31	—	—	—	0
14	53	50	52.0	3	32	63	50	55.0	2
15	55	47	53.0	5	33	—	—	57.0	1
16	58	53	55.6	3	34	60	51	55.5	2
17	61	53	57.6	3					

TABLE IX. Girth measurements of thirty-one marked pups of known age.

Table IX the combined data for 1948 and 1949 are set out; no distinction has been made between the sexes. The apparent anomalies in the table are caused by the fact that any two or three consecutive days are represented by different groups of pups. The animals were born at different dates and measurements were made, not daily, but every second or third day. However, when the average figures are plotted graphically (figure 15) a simple curve can be fitted to them.

The average girth increases from 36.8 inches to a maximum of 63.5 inches at twenty-three to twenty-four days and then decreases almost as rapidly. The peak corresponds with the observed age of weaning of thirteen marked pups, which was twenty-three days (range twenty–twenty-seven days). Variations in girth are, of course, a measure of variations in the degree of fatness and of the weight of the animals.

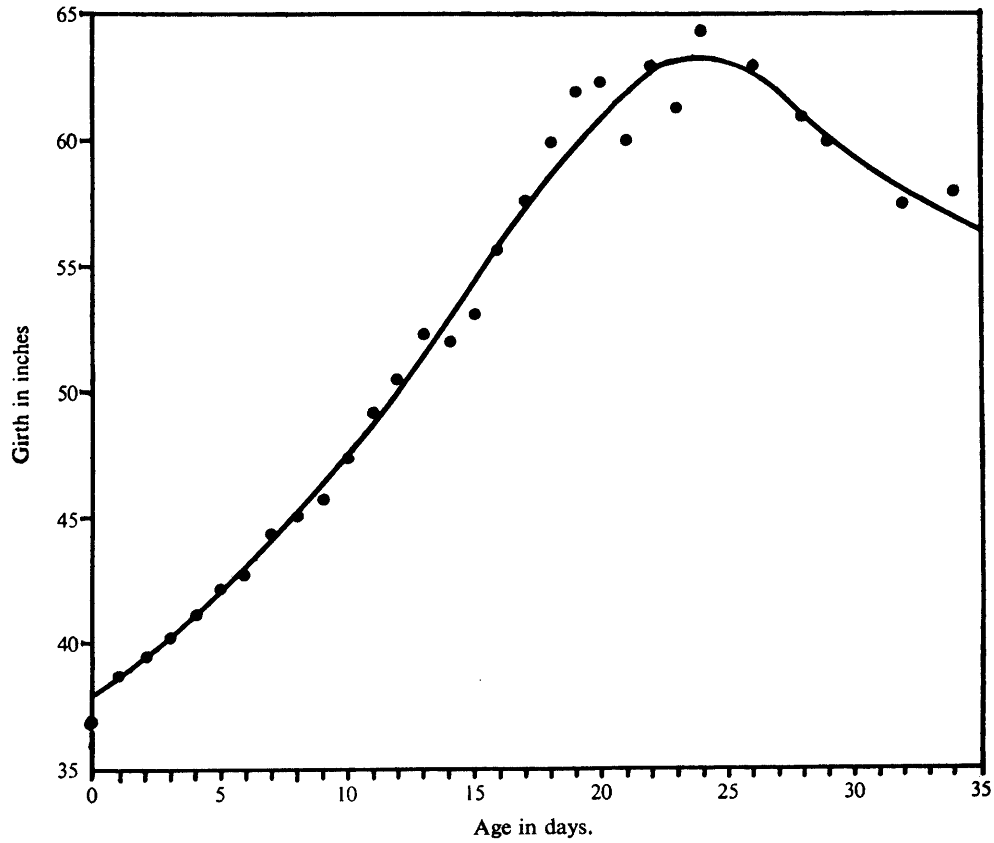


FIGURE 15. Change of girth with age. Average of 31 marked pups.

In 1948 the lengths of fourteen pups were measured in connection with weighing. Owing to the difficulty of holding the animals still it is not possible to measure their length in a direct line from nose to tail, so they were measured along the curve of the back. The length measurements represent, not only variations in length, but also reflect changes in fatness, though not to the same extent as do the girth measurements, and their value is doubtful. When the daily averages were plotted graphically they showed an increase from about 50 inches at birth to 68 inches at weaning. About half of this increase can be accounted for by increased corpulency.

At Signy Island fifteen elephant seal pups were weighed at regular intervals over periods of ten to thirty-four days. The results are set out in tables X and XI, and shown graphically in figures 16–18.

The average weight of eight female pups at birth was 101.1 pounds and of seven male pups 108.1 pounds. Thus, for the individuals studied, the males are on an average seven pounds heavier at birth than the females, and have a slightly faster rate of growth for the first two days. Afterwards, they grow at the same rate

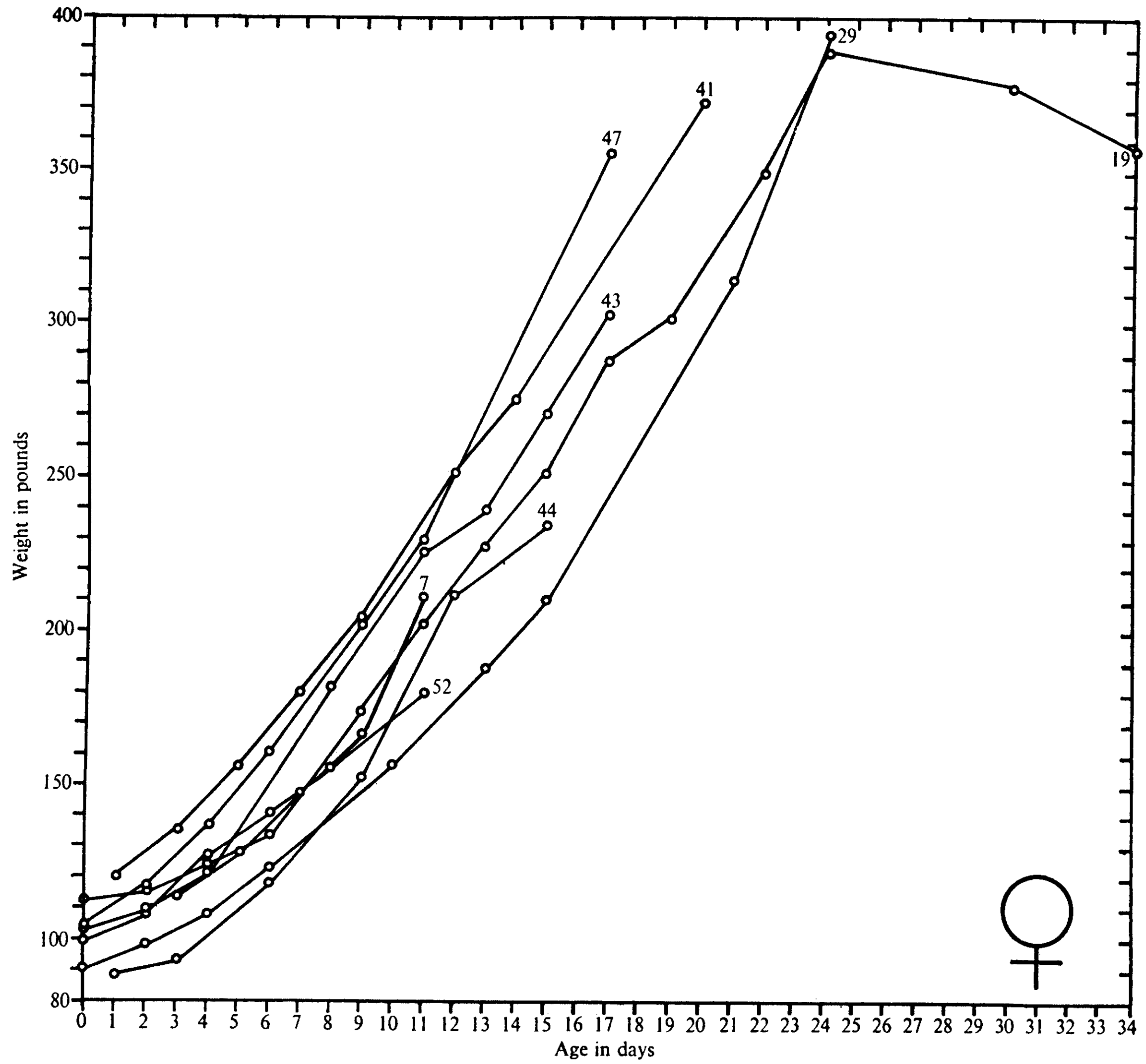


FIGURE 16. Individual weight increases of 8 female pup elephant seals.

as the females, so that at five days they are 10.7 pounds heavier, and at ten days weigh 10.8 pounds more than the females. The individual growth curves have been drawn in figures 16 and 17, and by extrapolation and interpolation from these curves, tables X and XI, and figure 18, have been drawn up. In the latter the averages have been plotted only when observations from more than four pups are available; the upper part of the curves have been adjusted by reference to the trends of growth of individual pups, in figures 16 and 17.

Both male and female pups increase their weight by 50 per cent during the first week and double their weight at birth in eleven days. The females treble it in seventeen days and the males in eighteen days, and they quadruple it at twenty-one and twenty-two days respectively. If the increase in weight during suckling is converted into the percentage increase in each five-day period (figure 18) the animals are found to increase in weight by about 40 per cent in each of the three five-day periods from five to twenty days of age. In the first five days the daily increase is from two to nine pounds for the female pup and from five to nine pounds for the male. In the second five days it is from nine to thirteen pounds for the female and nine to fourteen days for the male. From the eleventh to the nineteenth day the daily increase ranges from thirteen to twenty-three pounds per day in the female and from thirteen to eighteen pounds in the male. The highest individual daily gain was one of twenty-six pounds between the twenty-third and twenty-fourth day for pup No. 29, a female.

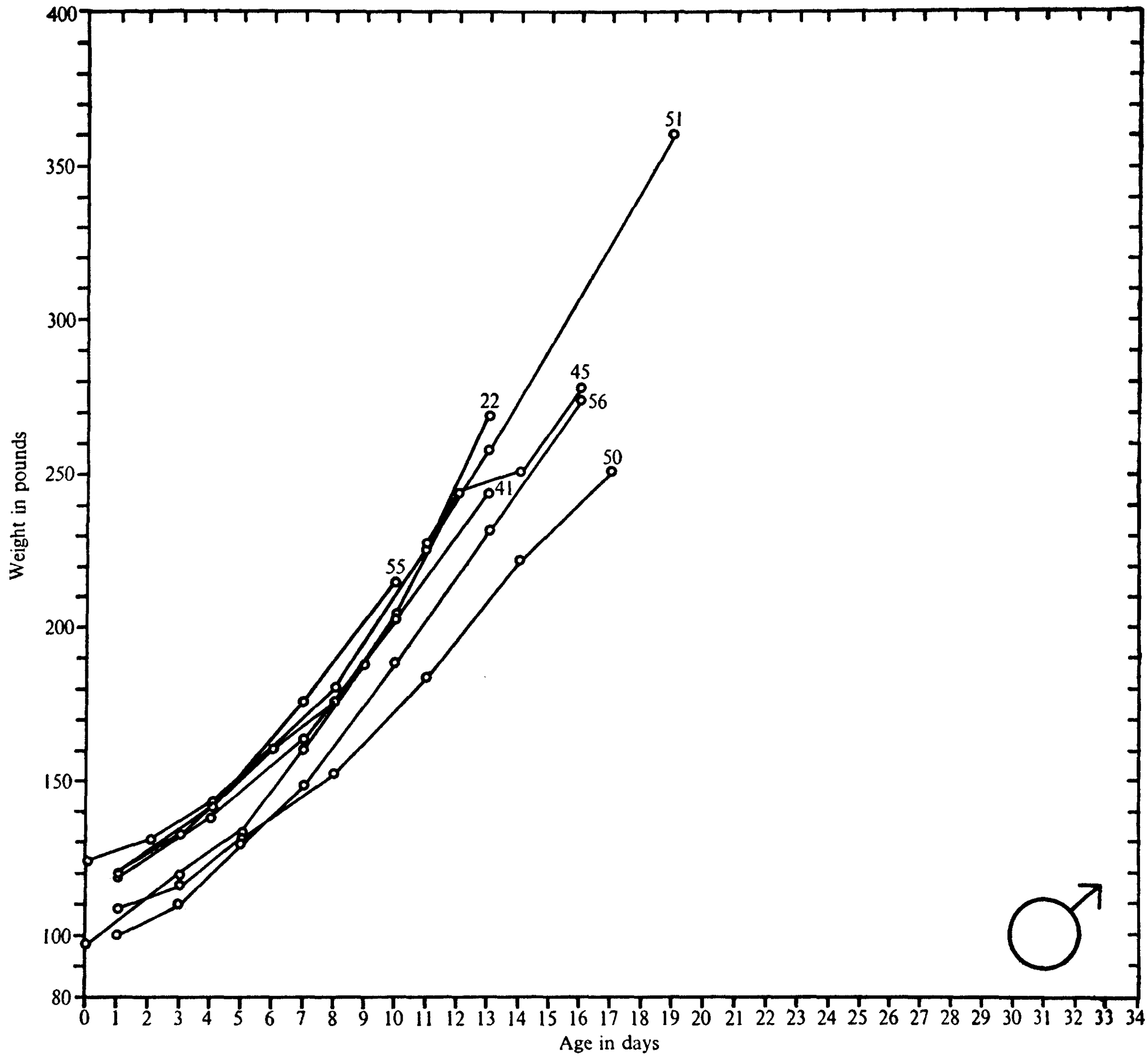


FIGURE 17. Individual weight increases of 7 male pup elephant seals.

It is interesting to compare these figures with the growth rates of other species of phocids. In the harp seal (*Phoca groenlandica*) weaning takes place when they are ten to twelve days old and the young, which weighs on an average 11.8 kg. (twenty-six pounds) at birth, doubles its weight in four to five days and trebles it in nine to ten days (Sivertsen, 1941, p. 105). The Weddell seal (*Leptonychotes weddelli*) has a suckling period of fifty days, over twice as long as the elephant seal and although the weight at birth is only sixty-four pounds, it shows a slower rate of growth, both absolute and relative, than the latter. Its weight is doubled at two weeks, trebled at four weeks and almost quadrupled at six weeks. It is evident that the elephant seal has an exceptionally rapid rate of growth during suckling.

This weight increase has come directly from the assimilation of the mother's milk, and since the cow does not feed during the period, a gain in weight of 300 to 350 pounds probably represents over 700 pounds loss in weight for the mother.

Amoroso and Matthews (1950) made some interesting observations on a captive adult female grey seal (*Halichoerus grypus*) and her pup. They showed that the average daily gain in weight of the pup was 3.3 pounds, and the average daily loss in weight of the female was 6.3 pounds. In other words the transfer from cow to pup is over 52 per cent effective, assuming that weight changes were unaffected by the condition of captivity.

Age in days	WEIGHT IN POUNDS								
	Pup No. 19	29	52	41	47	43	7	44	Average
0	**112**	**90**	**99**	112	**104**	**103**	103	86	101.1
1	113	94	102	**120**	110	105	105	**88**	104.6
2	**115**	**98**	**107**	127	**117**	**109**	109	90	106.7
3	120	103	116	**135**	127	114	**114**	**93**	115.2
4	**124**	**108**	**127**	146	**137**	**121**	120	100	123.0
5	129	116	134	**156**	149	135	**128**	109	132.0
6	**134**	**123**	**141**	167	**161**	151	137	**118**	141.5
7	148	132	149	**180**	175	166	**147**	129	153.2
8	161	140	**156**	192	188	**182**	157	140	164.5
9	**184**	148	164	**205**	**202**	197	**167**	**153**	176.2
10	188	**157**	172	220	216	211	188	165	189.6
11	**202**	167	**180**	237	**230**	**226**	**211**	178	204.0
12	215	177		**252**	250	233		**192**	219.8
13	**228**	**188**		265	271	**240**		206	233.0
14	240	199		**276**	292	256		220	247.1
15	**252**	**210**		292	314	**271**		**235**	262.3
16	270	227		308	334	286			285.0
17	**288**	244		324	**357**	**303**			303.2
18	295	262		340					299.0
19	**302**	280		356					312.7
20	318	297		**372**					329.0
21	334	**315**							324.5
22	**350**	341							345.5
23	370	367							368.5
24	**389**	**395**							392.0

TABLE X. Weights, in pounds, of eight female elephant seal pups of known age. Heavy figures —actual weights measured; light figures—taken from curves in figure 16.

Two samples of elephant seal milk were collected at Signy Island, but owing to refrigerator troubles did not survive the long voyage through the tropics. However, Sivertsen (1914) has analysed the milk of the harp and hooded seals (*Cystophora cristata*) of the Arctic, the latter species being closely related to the elephant seal. He discusses the composition of seal and whale milk and compares them with the milk of other mammals. "If we take the most familiar of these kinds of milk, cow milk and compare it with seal milk we see what an enormous difference there is between them. Whilst cow milk only contains 34‰ fat, seal milk contains 427‰, i.e., more than twelve times as much. Also the amount of protein is very different,

Age in days	WEIGHT IN POUNDS							
	Pup No. 51	22	45	56	50	41	55	Average
0	**124**	**97**	114	95	105	110	112	108.1
1	128	105	**120**	**100**	**109**	**119**	**120**	114.4
2	**131**	112	126	105	112	124	127	119.6
3	137	**120**	**133**	**110**	**116**	131	134	126.0
4	**143**	126	142	120	123	**138**	**142**	133.4
5	152	**134**	151	**130**	**132**	147	152	142.7
6	162	146	**161**	140	138	155	163	152.1
7	171	**161**	168	**149**	145	**164**	**176**	162.0
8	**181**	173	**176**	163	**153**	177	188	173.0
9	196	**188**	190	177	163	189	201	186.3
10	212	206	**205**	**189**	173	**203**	**215**	200.4
11	**226**	**226**	224	204	**184**	216		213.3
12	243	246	**244**	218	197	230		229.7
13	**258**	**269**	247	**232**	210	**244**		243.3
14	275		**251**	246	**222**			248.0
15	292		264	260	232			262.0
16	308		**278**	**274**	241			275.2
17	326				**251**			288.5
18	342							342.0
19	**360**							360.0

TABLE XI. Weights of seven male elephant seal pups of known age. Heavy figures—actual weights measured; Light figures—taken from curves in figure 17.

three-four times greater in seal milk" (Sivertsen, 1941, p. 95). The transfer of over 300 pounds weight during the very short suckling period of the elephant seal is only possible because the milk is so rich in fat and protein. The milk fat is similar to seal blubber fats, but has a higher palmitic acid content than any seal blubber fats on record.

Both Lindsey and Sivertsen regard weaning as a gradual process. "At about the seventh week the rate of gain diminishes rapidly until there is a cessation of weight increase, and a pronounced loss occurs. For example, a seal that weighs 300 pounds at fifty-two days lost seventeen pounds in the next seventeen days . . . and another weighing 283 pounds at thirty-six days weighed 245 pounds at fifty-nine days". (Lindsey, 1937, p. 136). Owing to the break-up of the fast-ice and the scattering or death of the pups, it was not possible to study the weight changes of the elephant seal for more than two to five weeks and only two individuals were followed through weaning. In these two seals there was no gradual slowing down of the rate of increase in weight. In fact the gain for the two days before weaning was thirty-nine pounds in pup No. 19, and in pup No. 29, for the three days prior to weaning, eighty pounds. These figures represent average daily gains of 19.5 pounds and twenty-six pounds, just before weaning. Moreover, the rates of growth of these two pups were below the average of all the female pups.

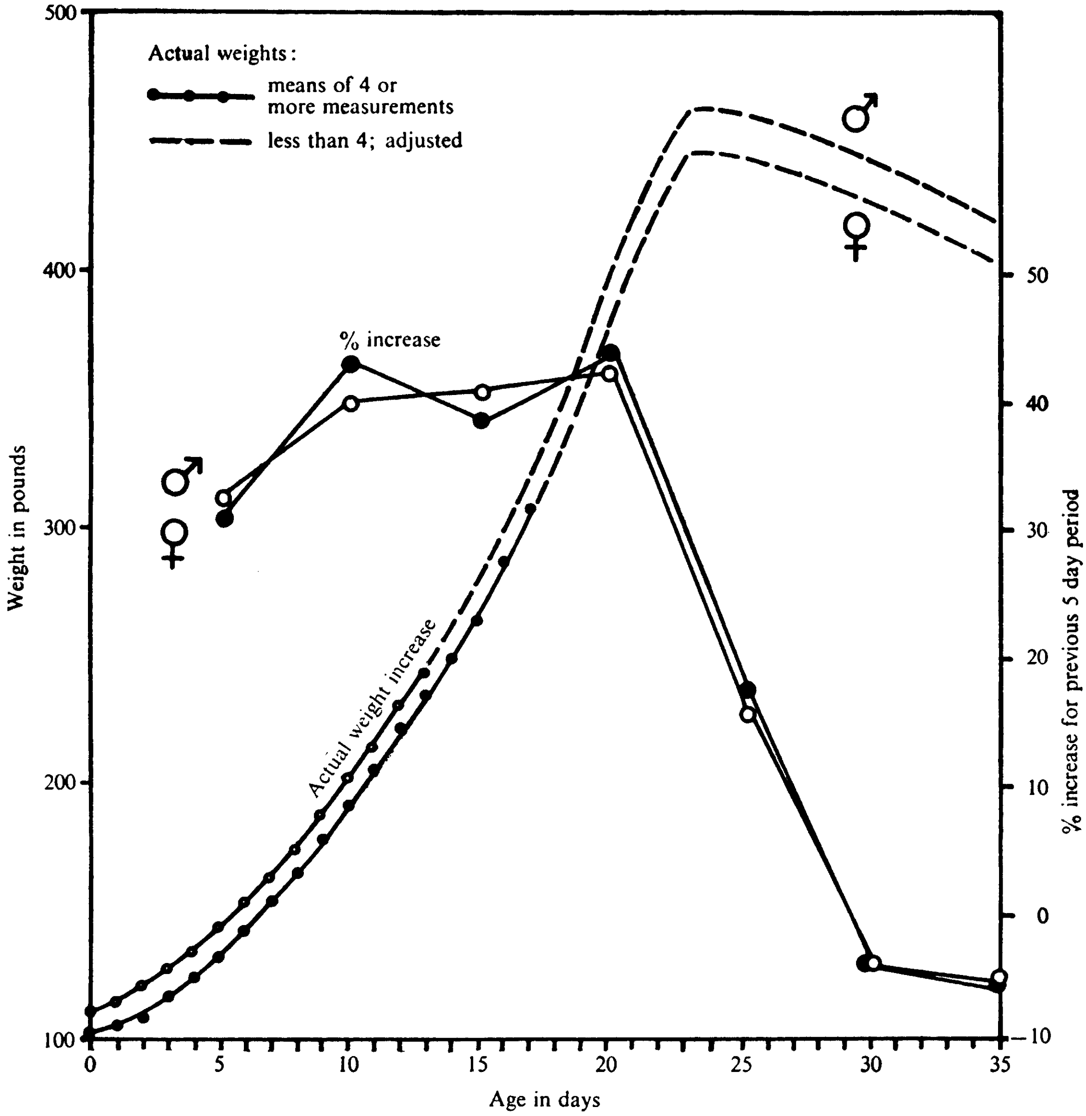


FIGURE 18. Average curves for the increase in weight of both sexes, from 0 to 35 days of age. The percentage increase for the previous five-day period is also plotted.

Constituents	*Phoca groenlandica* I	*Phoca groenlandica* II	*Cystophora cristata*	*Halichoerus grypus*
Water	453.3	437.9	498.5	—
Fat	426.5	428.2	404.3	522.0
Protein	104.5	119.8	66.5	112.0
Sugar	0.0	0.0	0.0	26.0
Ash	8.0	9.14	8.64	7.0

TABLE XII. Composition of seal milk in grammes per 1000 g. of milk. Data for *P. groenlandica* and *C. cristata* from Sivertsen (1941); *H. grypus* from Amoroso and Matthews (1950).

Pup No. 19 was weighed six days after weaning, during which period it had lost eleven pounds, and four days later at the age of thirty-four days, it had lost a further twenty pounds. The weights of two pups over eight weeks old were recorded. One was a marked pup, sixty-one days old, and the other, unmarked, was estimated to be fifty-seven days old. Both showed a considerable decrease in weight as compared with the weight at weaning. The marked pup, sixty-one days old, weighed 245 pounds, and had lost in thirty-eight days, 165 pounds, representing a minimum daily loss of 4.3 pounds.

D. Growth after the Establishment of Nutritional Independence

1. *Data Relating Body Length and Age*

Tables XIII and XIV give the lengths of 142 male and 84 female elephant seals and their individual ages determined from tooth rings. In figure 19 this information is presented as a scatter diagram.

Station No.	Date	Age in months	Nose-tail length (ins.)	Year
H370	8.i.50	1	76	1st
H369	8.i.50	2	79	
H296	23.ii.49	4	63	
H306	7.iv.49	5	85	
H133	12.v.48	7	89	
H334	17.xii.49	14	98	2nd
H358	4.i.50	14	82	
JB2	24.ii.50	16	90	
H287	16.ii.49	16	96	
H295	23.ii.49	16	93	
H378	16.ii.50	16	94	
H309	13.iv.49	18	90	
H335	17.xii.49	26	97	3rd
H356	4.i.50	26	101	
H359	5.i.50	26	105	
H360	5.i.50	26	97	
H361	5.i.50	26	96	
H377	15.ii.50	28	98	
M22*	31.iii.51	29	120	
M47*	12.iv.51	30	108	
H311	25.iv.49	30	105	
M72	4.v.51	31	96	
H327	6.xii.49	37	104	4th
H330	16.xii.49	38	106	
H331	16.xii.49	38	111	
H357	4.i.50	38	103	
H343	20.xii.49	38	108	
M10	17.iii.51	41	107	
M21*	31.iii.51	41	129	
M45*	12.iv.51	42	111	
H312	26.iv.49	42	120	
M71	1.v.51	43	126	
H129	3.v.48	43	124	
H332	10.xi.49	49	115	5th
M157*	12.xi.51	49	157	
H340	20.xii.49	50	129	
M33*	24.iii.51	53	148	
M53*	3.iv.51	53	153	
M56*	5.iv.51	53	134	
M57*	5.iv.51	53	137	
M61*	5.iv.51	53	138	

Table XIII (continued on p. 39).

Station No.	Date	Age in months	Nose-tail length (ins.)	Year
H308	13.iv.49	54	142	5th
M80*	10.viii.51	58	106	
M88*	8.ix.51	59	160	
M95*	8.ix.51	59	150	
M100*	8.ix.51	59	159	
M113*	10.ix.51	59	165	
H325	4.xii.49	61	126	6th
M155*	12.xi.51	61	152	
M158*	12.xi.51	61	144	
M159*	12.xi.51	61	141	
M163*	15.xi.51	61	135	
M164*	15.xi.51	61	159	
H350	30.xii.49	62	129	
M49*	24.iii.51	65	160	
M20*	31.iii.51	65	159	
M23*	31.iii.51	65	148	
M51*	2.iv.51	65	146	
M58*	5.iv.51	65	149	
M64*	6.iv.51	65	156	
M65*	6.iv.51	65	162	
H131	11.v.48	67	147	
M98*	8.ix.51	71	175	
M106*	10.ix.51	71	159	
M109	10.ix.51	71	178	
M110*	10.ix.51	71	173	
M122*	11.ix.51	71	170	
M150*	11.xi.51	73	168	7th
M153*	11.xi.51	73	153	
H326	6.xii.49	73	135	
H353	2.i.50	74	161	
M34*	24.iii.51	77	157	
M35*	24.iii.51	77	156	
M42*	24.iii.51	77	159	
M43*	24.iii.51	77	172	
M46*	24.iii.51	77	151	
M54*	3.iv.51	77	156	
M62*	6.iv.51	77	142	
M77	23.v.51	79	155	
M84	31.viii.51	83	171	
M86*	7.ix.51	83	168	
M89*	8.ix.51	83	163	
M91*	8.ix.51	83	182	
M94*	8.ix.51	83	177	
M97*	8.ix.51	83	168	
M101*	8.ix.51	83	172	
M108*	10.ix.51	83	172	
M114*	10.ix.51	83	177	
M115*	10.ix.51	83	175	
M117*	10.ix.51	83	169	
M119*	11.ix.51	83	184	
M120*	11.ix.51	83	182	
M151*	11.xi.51	85	168	8th
M152*	11.xi.51	85	179	
M154*	12.xi.51	85	180	
M156*	12.xi.51	85	163	
M162*	15.xi.51	85	153	
M167*	15.xi.51	85	178	
H337	19.xii.49	86	152	
H355	3.i.50	86	152	
M25*	31.iii.51	89	150	
M27*	4.iv.51	89	175	
M31*	4.iv.51	89	154	
M38*	24.iii.51	89	192	

TABLE XIII (continued on p. 40).

Station No.	Date	Age in months	Nose-tail length (ins.)	Year
M40*	24.iii.51	89	170	8th
M41*	24.iii.51	89	159	
M50*	2.iv.51	89	173	
M55*	5.iv.51	89	140	
M59*	5.iv.51	89	146	
M60*	5.iv.51	89	158	
M92*	8.ix.51	95	163	
M103*	10.ix.51	95	169	
M104*	10.ix.51	95	189	
M105*	10.ix.51	95	165	
M116*	10.ix.51	95	179	
M118*	10.ix.51	95	181	
M161*	15.xi.51	96	184	
M165*	15.xi.51	96	153	
H354	2.i.50	98	189	9th
H302	12.iii.49	101	163	
M36*	24.iii.51	101	159	
M39*	24.iii.51	101	163	
M48*	24.iii.51	101	194	
M24*	31.iii.51	101	161	
M30*	4.iv.51	101	149	
M90*	8.ix.51	107	194	
M93*	8.ix.51	107	177	
M96*	8.ix.51	107	164	
M102*	8.ix.51	107	181	
M107*	10.ix.51	107	192	
M111*	10.ix.51	107	198	
M121*	11.ix.51	107	192	
M44*	24.iii.51	113	217	10th
M26*	31.iii.51	113	158	
M29*	4.iv.51	113	170	
M160*	15.xi.51	121	187	11th
M166*	15.xi.51	121	162	
H304	13.iii.49	125	184	
M52*	2.iv.51	125	180	
M28*	4.iv.51	125	157	
H322	16.xi.49	132	189	
H303	13.iii.49	137	189	12th

TABLE XIII. Age and length of 142 male elephant seals with date of collection. Prefix to Station Numbers: H = South Orkneys; M = South Georgia; JB = R.R.S. "John Biscoe". * Indicates killed by sealers.

Station No.	Date	Age in months	Nose-tail length (ins.)	Year
H294	23.ii.49	4	82	1st
H298	4.iii.49	4	86	
M5	17.iii.51	5	83	
M12	19.iii.51	5	88	
M14	19.iii.51	5	82	
M19	29.iii.51	5	86	
H132	12.v.48	7	86	
M66	24.iv.51	7	82	
M79	28.v.51	19	96	2nd
M130	4.x.51	24	99	

TABLE XIV (continued on p. 41).

Station No.	Date	Age in months	Nose-tail length (ins.)	Year
H341	20.xii.49	26	104	3rd
H362	6.i.50	27	98	
H307	7.iv.49	29	106	
M32	10.iv.51	29	94	
M78	28.v.51	31	106	
M138	9.x.51	36	100	
M137	9.x.51	36	99	
M132	5.x.51	36	103	
M136	9.x.51	36	100	
M143	12.x.51	36	96	
M141	11.x.51	36	100	
M147	12.x.51	36	90	
M146	12.x.51	36	101	
M129	4.x.51	36	94	
M135	6.x51	36	92	
M133	5.x.51	36	96	
M124	30.ix.51	36	109	
M126	2.x.51	36	105	
M123	29.ix.51	36	102	
H346	21.xii.49	38	107	4th
M2	26.ii.51	40	99	
M11	19.iii.51	41	99	
M15	19.iii.51	41	98	
M73	10.v.51	43	88	
M134	6.x.51	48	106	
M144	12.x.51	48	97	
H288	16.ii.49	52	104	5th
H379	18.ii.50	52	92	
M80	10.viii.51	58	106	
H375	11.ii.50	64	103	6th
M18	21.iii.51	65	106	
M139	9.x.51	72	115	
M125	30.ix.51	72	112	
H285	27.i.49	75	105	7th
H292	19.ii.49	76	111	
M74	12.v.51	79	111	
M75	16.v.51	79	111	
M142	11.x.51	84	118	
M148	12.x.51	84	138	
M145	12.x.51	84	100	
H305	24.iii.49	89	110	8th
H293	19.ii.49	88	118	
H282	16.ii.49	88	108	
M69	1.v.51	91	115	
M128	4.x.51	96	111	
H300	4.iii.49	100	120	9th
M83	21.viii.51	106	113	
M140	9.x.51	108	116	
H352	1.i.50	111	117	10th
H291	19.ii.49	112	116	
M6	17.iii.51	113	109	
M16	19.iii.51	113	113	
M76	16.v.51	115	121	
H363	6.i.50	123	115	11th
H372	27.i.50	123	114	
M3	26.ii.51	124	112	
M13	19.iii.51	125	118	

TABLE XIV (continued on p. 42).

Station No.	Date	Age in months	Nose-tail length (ins.)	Year
H376	28.i.50	135	109	12th
M4	28.ii.51	136	116	
H289	19.ii.49	136	114	
H290	19.ii.49	136	119	
M9	17.iii.51	137	112	
H297	4.iii.49	137	119	
H299	4.iii.49	137	123	
H301	11.iii.49	137	120	
M68	28.iv.51	138	109	
M70	1.v.51	139	112	
M67	25.iv.51	139	111	
M127	3.x.51	144	114	
M81	10.viii.51	166	115	14th
H374	3.ii.50	172	127	15th
H368	7.i.50	183	114	16th
M17	21.iii.51	185	108	
H320	4.xi.49	205	110	17th

TABLE XIV. Age and length of 84 female elephant seals with date of collection. Prefix to station numbers: H = South Orkneys; M = South Georgia; JB = R.R.S. "John Biscoe".

Year group	Average age (mths.)	Length (ins.)			No. of indivs.
		Max.	Min.	Av.	
I	5.3	89	63	79.0	3
II	15.7	98	82	92.0	7
III	27.8	120	96	102.3	10
IV	40.0	129	103	113.5	11
V	55.7	165	106	142.3	14
VI	64.7	178	126	153.4	20
VII	79.6	184	135	165.0	25
VIII	89.7	192	140	166.5	26
IX	103.8	198	149	177.0	14
X	113.0	217	158	181.7	3
XI	124.8	189	157	176.5	6
XII	137.0	—	—	189.0	1

TABLE XV. Average, maximum and minimum lengths of year groups I to XII of male elephant seals collected.

Year group	Average age (mths.)	Length (ins.)			No. of indivs.
		Max.	Min.	Av.	
I	5.2	88	82	84.3	8
II	21.5	99	96	97.5	2
III	34.0	109	90	99.7	19
IV	42.7	107	88	98.7	7
V	54.0	106	92	101.0	3
VI	68.2	115	103	109.0	4
VII	80.1	138	100	113.4	7
VIII	90.4	118	108	112.4	5
IX	104.7	120	113	116.3	3
X	112 8	121	109	115.2	5
XI	123.7	118	112	114.7	4
XII	137.6	123	109	114.8	12

TABLE XVI. Average, maximum and minimum lengths of year groups I to XII of female elephant seals collected.

It is at once evident that there are great individual variations which, as examination of the length frequencies has shown (p. 36) preclude differentiation between all except the first two age groups on the basis of body length alone. Some of the variables which have to be taken into account in drawing up average growth curves are:

(a) Inaccuracies in individual measurements. The accurate measurement of a large mammal is always difficult; the living seal shows surprising apparent changes in body length when moving over land or ice, and the length when dead is likewise variable, though to a lesser degree. Thus the position of the killing shot, the attitude in which the seal was lying when killed and the delay between killing and measuring, all affect the measurement to some extent.

(b) Seasonal changes in the physical condition (especially in blubber thickness) affect the measurements.

(c) There are variations in the size of individuals of the same age born in the same year.

(d) There are variations in the size of animals of the same age born in different years.

(e) The collection of material was spread over three years, over several months of the year, and over different localities.

(f) For obvious reasons the sealers tend to select the larger animals for killing.

Since the sample is not random and there are so many variables it is not feasible to treat it statistically But it is thought necessary for the description of the age groups to have some approximate figures for average length, and the average curves have, therefore, been drawn by eye. In drawing the trend lines specialist advice was sought, as regards the growth of the male in the fourth year of age, and field impressions confirming the sudden increase in size at this age were drawn upon. It is thought that the growth rates bear a fairly close relationship to the average curves which have been drawn, but they must be used with caution, especially that representing the growth of the male. It is not claimed that the average lengths at different ages which are used below are accurate to within even 10 inches and these reservations should be borne in mind when the characteristics of the age groups are discussed below.

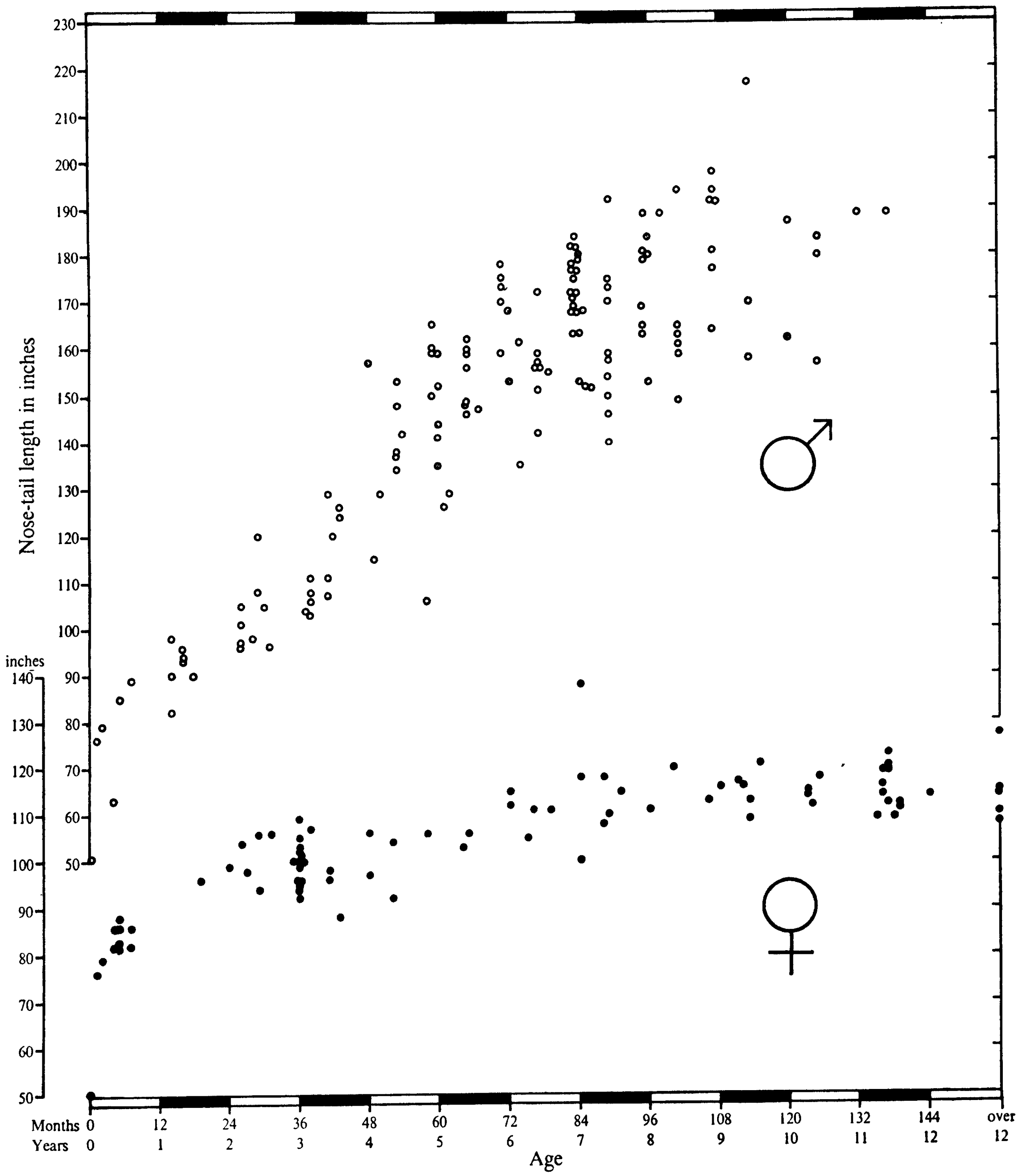


FIGURE 19. Scatter diagram of relation of body length to age (determined from tooth rings); 142 male, 84 female elephant seal.

2. *The Degree of Fatness*

Smirnov (1923) made use of the relationship between girth and length in determining what he called the degree of fatness of the harp seal (*Phoca groenlandica*). He gives the simplified formula: degree of fatness $= \frac{\text{maximum girth x 100}}{\text{total length}}$. As the length depends only upon the size of the animal and the girth is dependent upon size and fatness, the size will enter into both numerator and denominator in the equation and introduce a correction for the size of the animal. The degree of fatness calculated for different individuals will, therefore, be directly comparable. Sivertsen (1941, p. 117) also calculated the degree of fatness for harp seals and compared his results with Smirnov's figures. He appears to have used, not total length but nose-tail length, so that his figures are presumably not directly comparable with those of Smirnov.

In the calculations of the degree of fatness for the elephant seal the measurements of sixteen pups, thirty-eight males, and twenty-seven females from Signy Island have been considered. The resulting figures for the degree of fatness are not directly comparable with either Smirnov's or Sivertsen's figures, because the length (from nose to tail) is measured along the curve of the back. Consequently the figures are relatively smaller than those for the harp seal. Nevertheless they are thought to be comparable within the series of seventy-two animals measured. They have been set out graphically in figure 20, where the degree of fatness has been plotted against age (determined from the teeth).

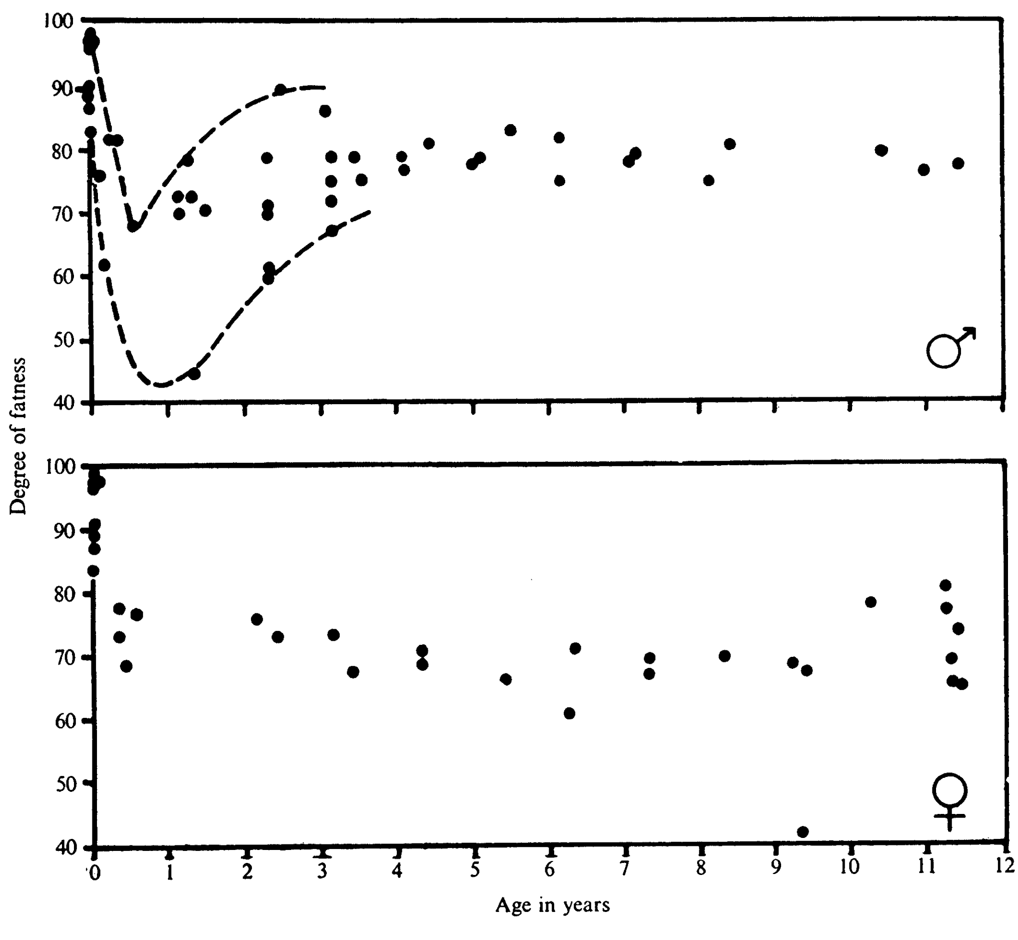


FIGURE 20. Degree of fatness of male and female elephant seal of different ages.

It is at once apparent that the females in the sample are much less fat than the males. The average degree of fatness of thirty-one males in the sample which were over two years old is 76 per cent, while for the twenty-three females older than two years it is 68.5 per cent, a difference of 7.5 per cent. This is thought to be a reflection of the difference in hauling out habits of the sexes. The females haul out only for the moult and lie much further inland, fasting completely, while the males remain on or near the beaches and occasionally go to sea, possibly to feed. The difference in fatness between the two sexes of moulting seal is quite apparent in the field. Thus interpretation of the figure is complicated.

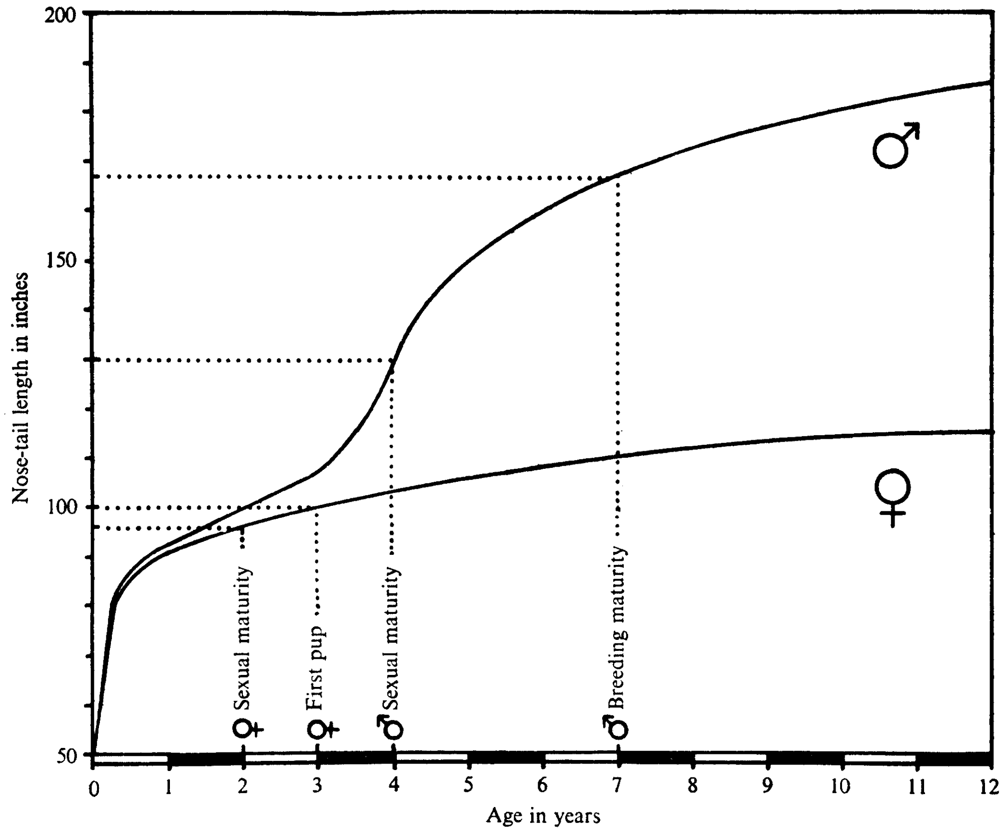


FIGURE 21. The average curves for the rate of growth in body length of both sexes of the elephant seal. The age and length at sexual maturity and breeding maturity are indicated.

3. *The Age Classes: Descriptive*

Elephant seals spend the winter months at sea when they are quite inaccessible and rarely seen. The descriptions of the age groups which follow are naturally based upon the appearance and dimensions of the species when on land. Moreover, when hauled out on land the elephant seal undergoes a fast. Thus the animals studied are not representative of the species as a whole, but only of about half of the annual cycle. The age range of the material is given in brackets after the age of the class.

(a) *The Male*

Class I, age four to twelve months (material four to seven months).

The average length of animals in this age group ranges from 82 inches at four months to 92 inches at one year of age.

The appearance of the pup up to and shortly after weaning has been described in an earlier section (p. 44). The rate of growth in length of the young elephant seal decreases rapidly and the girth declines progressively from weaning until the middle of the year. Growth takes the form of consolidation of the bony structures and strengthening of the muscles, and the yearlings present a much sleeker appearance than the weaned pups. It is emphasised by the data for the degree of fatness presented in figure 20. The fatness decreases from about 93 per cent in the weaned pup to about 60 per cent in the six-month-old animal and subsequently increases to about 70 per cent. Although no figures are available the average body weight of year-old animals is almost certainly less than the average weight at weaning. Figure 22b, shows the usual appearance of the yearling.

The body colour when fresh from the sea is a light grey, darker dorsally and shading to a pale yellowish tone ventrally. The coat has lost the bluish cast of the newly moulted "weaner" and there is a brown stain round the jaws. The general colour is darker when wet. According to the time of year the coat becomes progressively discoloured with mud and faecal matter; it is also bleached by the rays of the sun, owing to the oxidation of body oils and consequently all shades of light brown and grey are seen in the group.

In general they spend little time on land and do not become as weathered as the animals in older age groups. The flippers are generally darker, and the claws lose the slate-grey colour of the "weaner" owing to impregnation with mud and filth.

Scarring of the coat is unusual. In this age group sex differentiation is possible only by inspection of the ventral surface of the body when the presence of the penile opening is diagnostic of the male.

Class II, age thirteen to twenty-four months (material fourteen to eighteen months).

The average length of animals in this age group ranges from 93 inches at an age of thirteen months to 100 inches at two years.

The general impression is of increasing robustness, though individuals may become very emaciated during the moult. The degree of fatness varies between 45 per cent at the end of the moult and about 80 per cent when well fed.

The proportions of the head have begun to alter, becoming broader and rather "square" in appearance, and sexual distinction is more apparent. The first stage in the development of the proboscis is seen to take the form of a puckering of the dorsal surface of the muzzle which forms one or two transverse sulci (figure 24a). These characters in the male are in some cases sufficient for distinction between the sexes. The degree of development of the canine teeth is a much more certain diagnostic character; towards the end of the second year they are very much larger and less pointed than the canines of the females, and are of a smooth conical shape, not fluted.

The remarks about the colour of class I animals apply in general to the second year animals except that the colour is slightly darker and the weathering is more advanced, resulting in a browner coloration.

Class III, age twenty-five to thirty-six months (material twenty-six to thirty-one months).

The average length of the third year seal ranges from about 100 inches at twenty-five months to 107 inches at three years of age.

The tendency towards increased robustness continues, the degree of fatness of the sample varying between 58 per cent and 90 per cent according to the time of year. Owing to a thickening of the neck and shoulder regions the profile of the animal changes (figure 22c) and when it is excited the proboscis may be enlarged to a much greater extent than in younger individuals, showing two transverse sulci (figure 24b). There is a marked increase in the length and especially in the diameter of the canine teeth. With few exceptions sex distinction is plainly apparent to an observer.

Though darker than in the younger age groups, the body colour remains light especially during and after the moult. Wounds are inflicted by opponents during mock battles between the young males which are a feature of this and subsequent age groups. These result in small patches of scar tissue, chiefly in the neck region.

Class IV, age thirty-seven to forty-eight months (material thirty-seven to forty-three months).

The average body length of male elephant seals in the fourth year increases from 108 inches at thirty-seven months to 130 inches at four years. It is probable that this is the steepest part of the growth curve (see above p. 43) and marks the change from immature to adult, for sexual maturity is attained at about forty-seven months.*

The general coarsening of the physical characters continues during the fourth year and the development of the thoracic and neck regions progresses. The degree of fatness varies from 65 per cent to 85 per cent or more, according to the season

The colour is more or less the same as in the third year animals, but darker, especially on the ventral surface. Scarring of the neck is more extensive and wear of the claws on the fore-flippers may remove the distal light coloured band.

Class V, age forty-nine to sixty months (material forty-nine to fifty-nine months).

Class VI, age sixty-one to seventy-two months (material sixty-one to seventy-one months):

The average length of fifth year animals increases from 131 inches at four years of age to 150 inches at five years. In the following year the average body length increases to 160 inches at six years of age. These year groups are sexually mature but are usually prevented from breeding by the presence of older and

* The evidence for the age of sexual maturity will be presented in a later paper in this series.

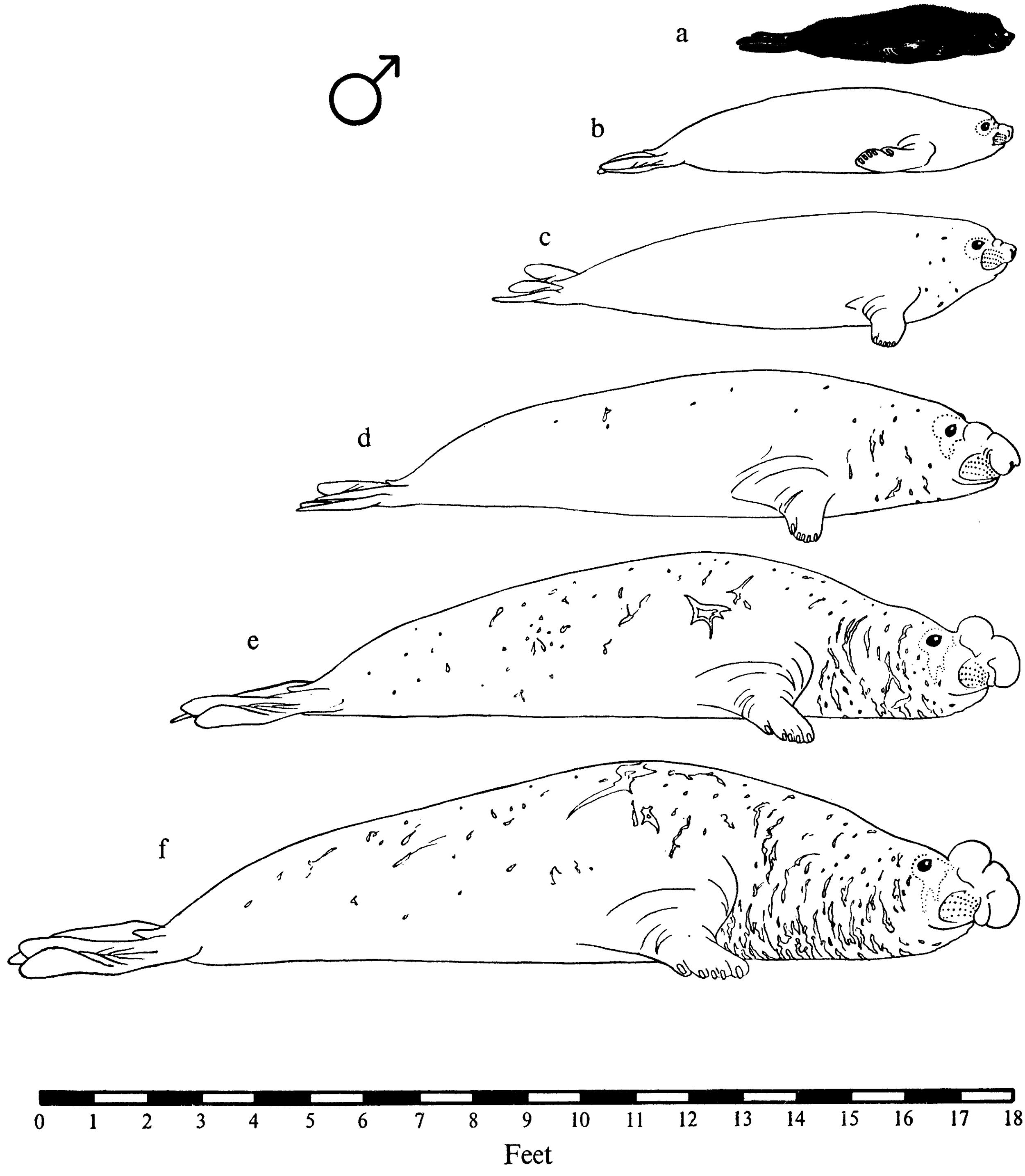


FIGURE 22. Characteristic size, proportions and appearance of male elephant seals of various ages. (a) New born; (b) 1-year old; (c) 3-year old; (d) 6-year old, sub adult; (e) 9-year old, harem bull; (f) Large harem bull, about 16 years old. Scale in feet.

stronger bulls. They may conveniently be called sub-adults. The animals of classes V and VI are similar in appearance and there is no constant distinction between them.

Figure 22d illustrates the bulky forequarters and the massive head and neck. The skull is now quite massive and low occipital and saggital crests make their first appearance to provide insertions for the enlarging

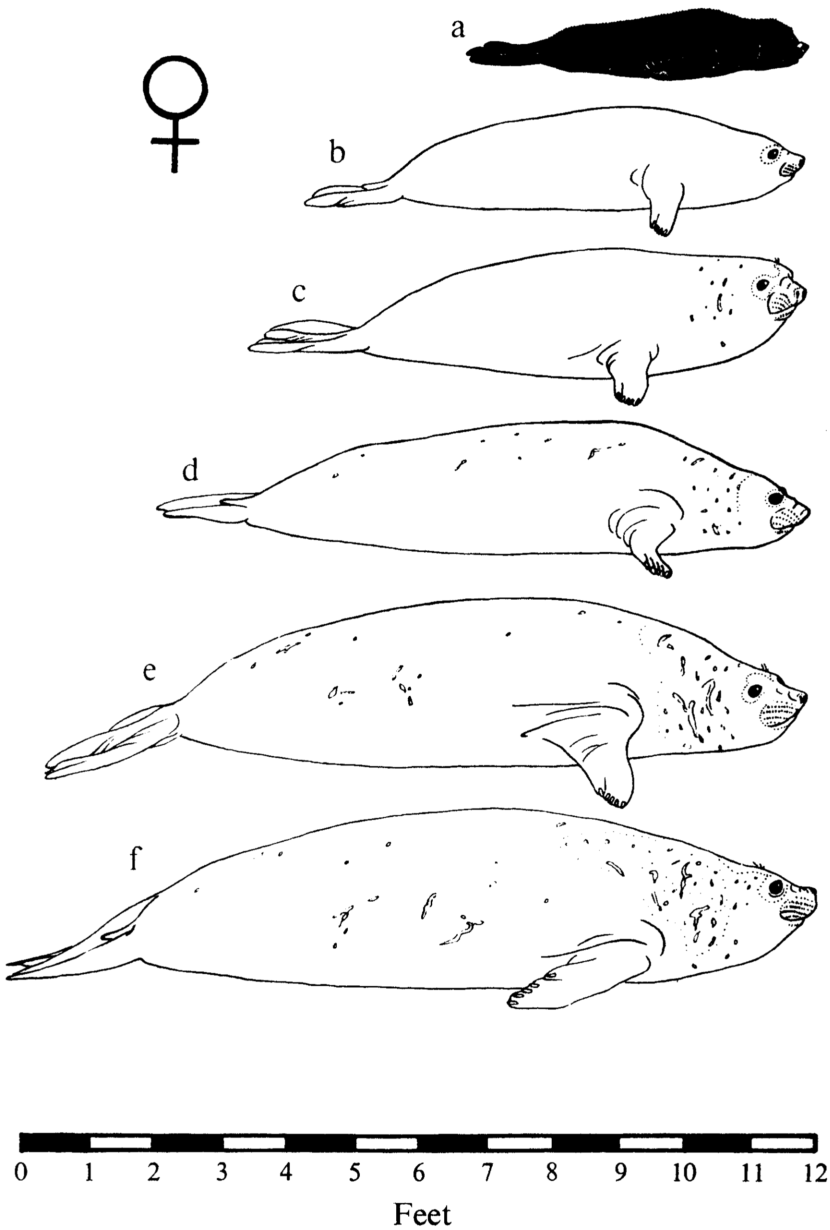


FIGURE 23. Characteristic size, proportions and appearance of female elephant seals of various ages. (a) New born; (b) 6-months old; (c) 3-year old, pre-parturient; (d) 6-year old, post-oestrus; (e) 12-year old, pregnant; (f) 16-year old, pregnant. Scale in feet.

neck and jaw muscles. In the sixth year especially, the great thoracic development and the disproportionately rapid tailing off of the hinder parts becomes very noticeable. The degree of fatness is not so variable as in the younger groups, ranging from about 75 per cent to 85 per cent in the fifth and subsequent years.

The proboscis is in process of assuming the adult form and in some sixth year individuals it does reach full development. More usually it is of the shape and size shown in figure 24d, the external nares opening downwards when in the relaxed position, but opening forwards and downwards when the proboscis is erected. The profile of the head is still rather pointed, more so when excited than at rest.

As in all year groups the colour varies both between individual animals at any one time, and in the same individual with the season. Before the moult the colour may be straw-yellow, golden-brown, chestnut,

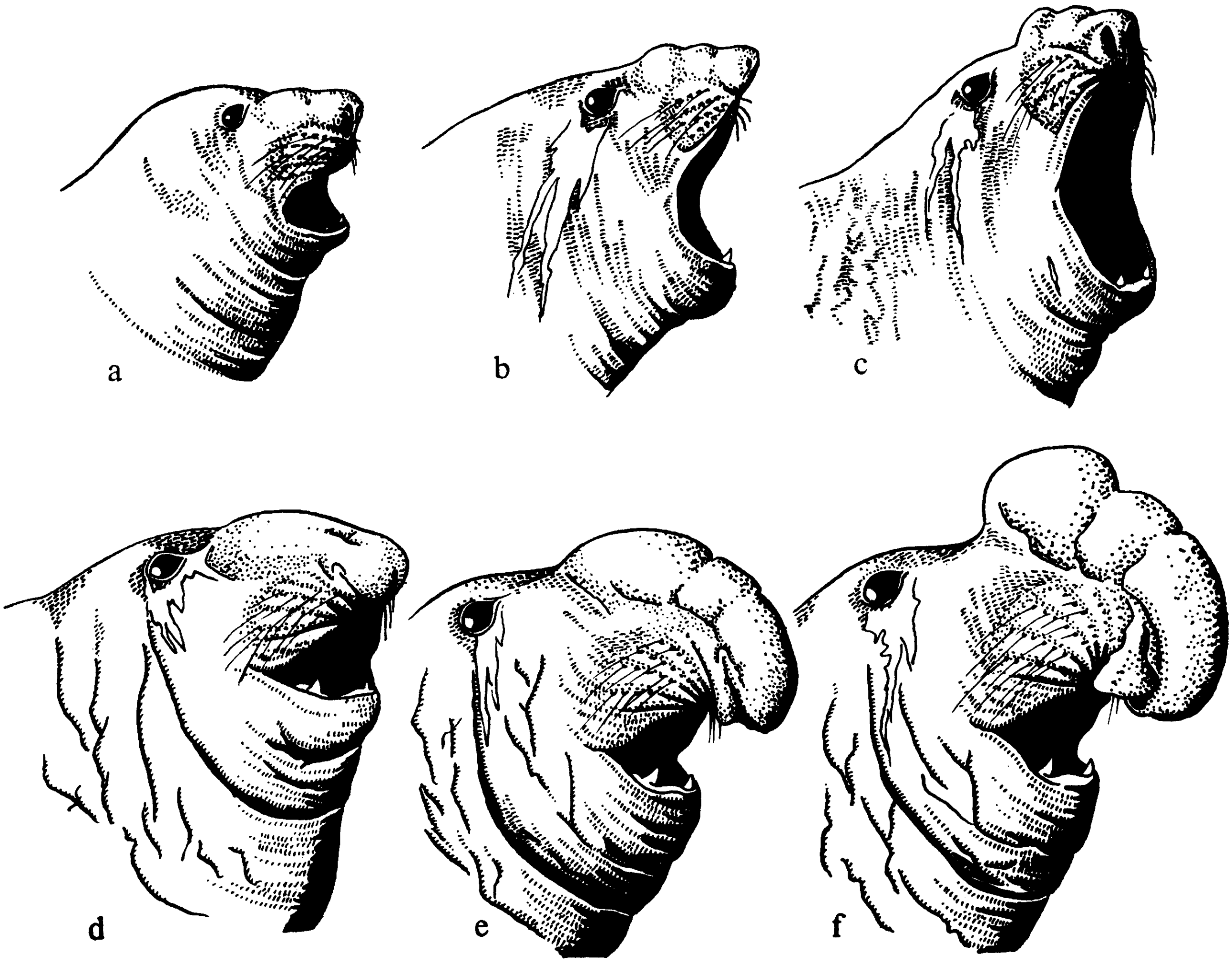


FIGURE 24. The development of the proboscis of the male elephant seal. (a) 2-year old; (b) 3-year old; (c) 4-year old; (d) 6-year old; (e) 8-year old, non-breeding; (f) 8-year old, harem bull.

blackish-brown or dark olive-brown, or intermediate shades. At the moult the old hair peels off in sheets and instead of being replaced immediately by the next coat there may be an interval of a week or ten days before the new coat makes its appearance. In this condition, which is not found in animals less than four-and-a-half years old the patches where the old hair has been shed are bare, and the colour of the new epidermis is a dark slaty-grey with a bluish cast. The new hairs, when they appear, are predominantly dark olive-grey, or blue-black, but they soon assume a warmer tone.

The amount of scarring of the body increases, especially in the neck region and individual scars are larger. In some animals there is also considerable scarring of the hinder parts; these wounds are a consequence of the greatly increased pugnacity, as compared with the sexually immature age groups.

Class VII, age seventy-three to eighty-four months (material seventy-three to eighty-three months).

Class VIII, age eighty-five to ninety-six months (material eighty-five to ninety-six months).

In general the first of these classes represents the transition from sub-adult to adult, breeding maturity being determined by sexual fighting at the beginning of the breeding season when about eighty-three months old. It may be postponed until near the end of the season or even until the next season and a few individuals never attain the status of harem bull, owing to small stature or timidity. Animals of these two classes are nearing the peak of their physical development and, owing to the range of individual variation it is not possible to distinguish between class VII and subsequent age groups using size and external appearance alone as criteria.

The average length of animals in the seventh year increases from about 161 inches at seventy-three months to 164 inches at seven years of age, and by the time they are eight years old the average length is 172 inches or just over 14 feet. The group is characterised by increased bodily stature, chiefly represented by great development of the shoulder and neck regions, with massive head and large fore flippers.

The scarring of the neck becomes extensive and owing to scar tissue the integument of the chest becomes very thick and tough. There are few mature individuals which do not carry an extensive integumentary shield, though this is not as well developed as in the northern elephant seal (*Mirounga angustirostris*), (Bartholomew, 1952, plate 51). Some large and numerous small scars are distributed all over the remainder of the body.

The proboscis, low and flaccid during the summer and autumn, is capable of impressive erection during the breeding season when it has significance in the reproductive behaviour. It may be severely lacerated

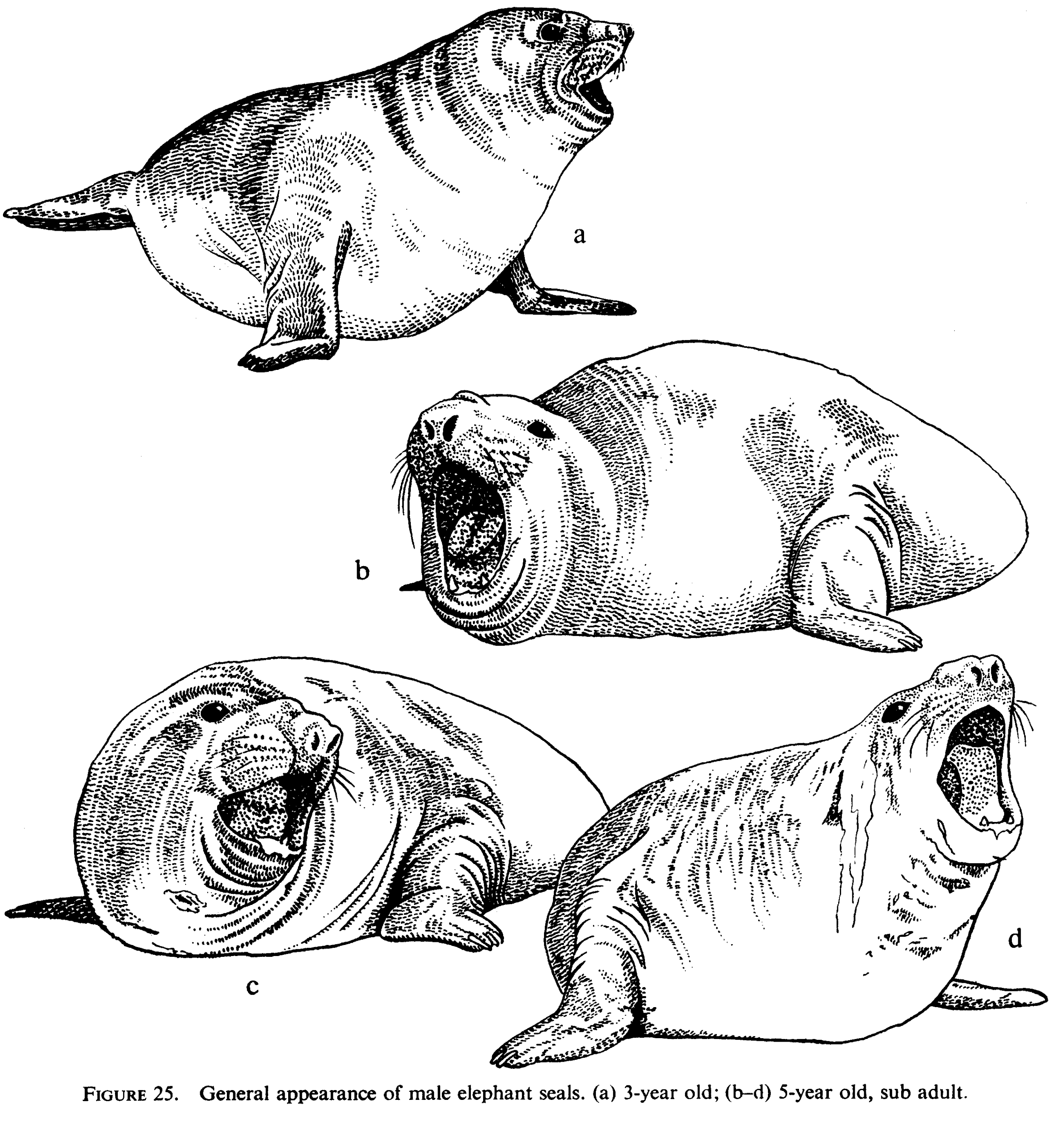


FIGURE 25. General appearance of male elephant seals. (a) 3-year old; (b–d) 5-year old, sub adult.

during the sexual fights, and occasionally the anterior projecting part may be completely torn away. The canine teeth, owing to their use in territorial fighting, begin to exhibit signs of wear. Sometimes one of them may be missing, but more usually they are cracked, or small parts are chipped off. There is some evidence that the mucous membrane of the mouth becomes congested during the breeding season and assumes a redder colour than is usual at other times of the year, but such a subjective observation must be treated with reserve.

The general body colour is predominantly a dark greyish-brown during the breeding season, becoming lighter throughout the summer until just before the moult it may be chestnut or golden-brown. The new coat after the moult is dark grey with a touch of brown. There is much individual variation and some very pale coloured animals look almost white when dry. These are seen in the spring and are usually of small size. It seems likely that the cause is similar to that which produces "isabelline" plumage of penguins, namely that the individual has missed a moult in the previous season, so that the degree of fading is at least twice as great as in normal individuals.

Classes IX to XII, age over ninety-seven months (material ninety-eight to 137 months).

In an undisturbed population the animals in this class provide the majority of the harem bulls. They are similar in appearance to those in the previous class. Bodily size and proportions increase heterogonically with age, tending to a more and more massive appearance, and the proboscis becoming longer and higher (figure 22).

The largest animal killed (No. M44) measured 217 inches in length, and the largest measured photographically (at Signy Island) was 240 inches long, or 20 feet. Only one larger animal was observed, but unfortunately it was not measured.

(b) *The Female*

Class I, age four to twelve months (material four to seven months).

The description given for the males of this age class applies equally to the female. The only external difference observed was the presence of a penile opening in the male.

Class II, age thirteen to twenty-four months (material nineteen and twenty-four months).

The average length is presumed to be slightly less than for the class II males.

Second year females have very different habits from the males and are rarely seen on land. Only one individual is represented in the material if we except the precocious M130 which was post-parturient with an eight-day pup. It had, therefore, been impregnated the previous season when only one year old, and was sexually a year in advance of others in its year class. Sexual maturity is attained by the female elephant seal at two years of age and the first pup is normally born when the female is three years old.*

No other second year females were seen although attention was directed to them when it became apparent that they were not fully represented in the material.

M79, aged nineteen months, was shot on May 29th, 1951, just after it had hauled out. It measured 96 inches from nose to tail and at the time was thought, from its appearance, to be seven months old.

* Evidence for this will be given in a later paper.

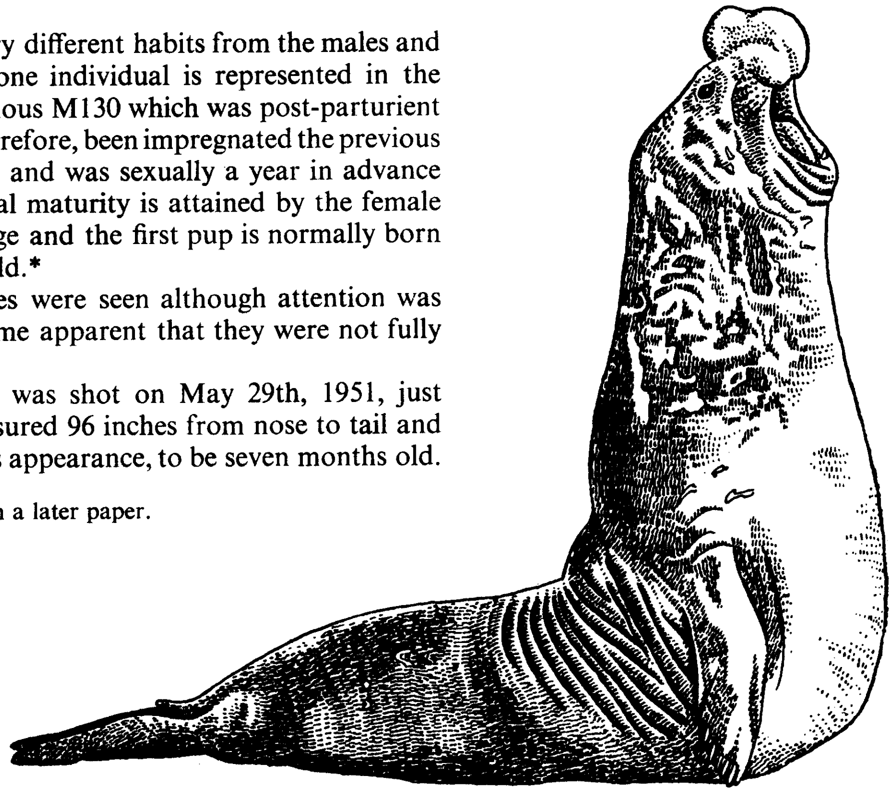


FIGURE 26. 10-year old harem bull rearing up.

Class III, age twenty-five to thirty-six months (material twenty-six to thirty-six months).

The average length of the female increases from 96 inches to 100 inches during the third year. The female is impregnated for the first time when two years old, and from the age of twenty-nine months bears a rapidly growing foetus which is delivered when the cow is three years old. As a result there is an increased robustness and corpulency about individuals near term, compared with females younger than twenty-nine months which have a free blastocyst in the uterus.

The rate of growth in length is much less than in the preceding age groups, so that the average body length of three-year-old females is 14 inches less than the average length of males at the same age. The head is smaller in proportion to the body than in a typical male and there is no alteration in the appearance of the snout. The profile is therefore more pointed than in the male. Cows of this age group show for the first time a small number of tiny white scars on the neck, which are inflicted by the male when copulation takes place. They differ in appearance from those which the third year males bear.

In colour these females differ but slightly from the males of the same age, tending in general to be rather lighter. With few exceptions sex distinction is clearly apparent to an observer.

Class IV, age thirty-seven to forty-eight months (material thirty-eight to forty-eight months).

The average length increases from 100 inches at thirty-seven months to 103 inches when four years old.

The general appearance is similar to that of the previous age class, but the build is heavier. The colour is slightly darker with more of a brownish tinge when newly moulted and there are many more scars in

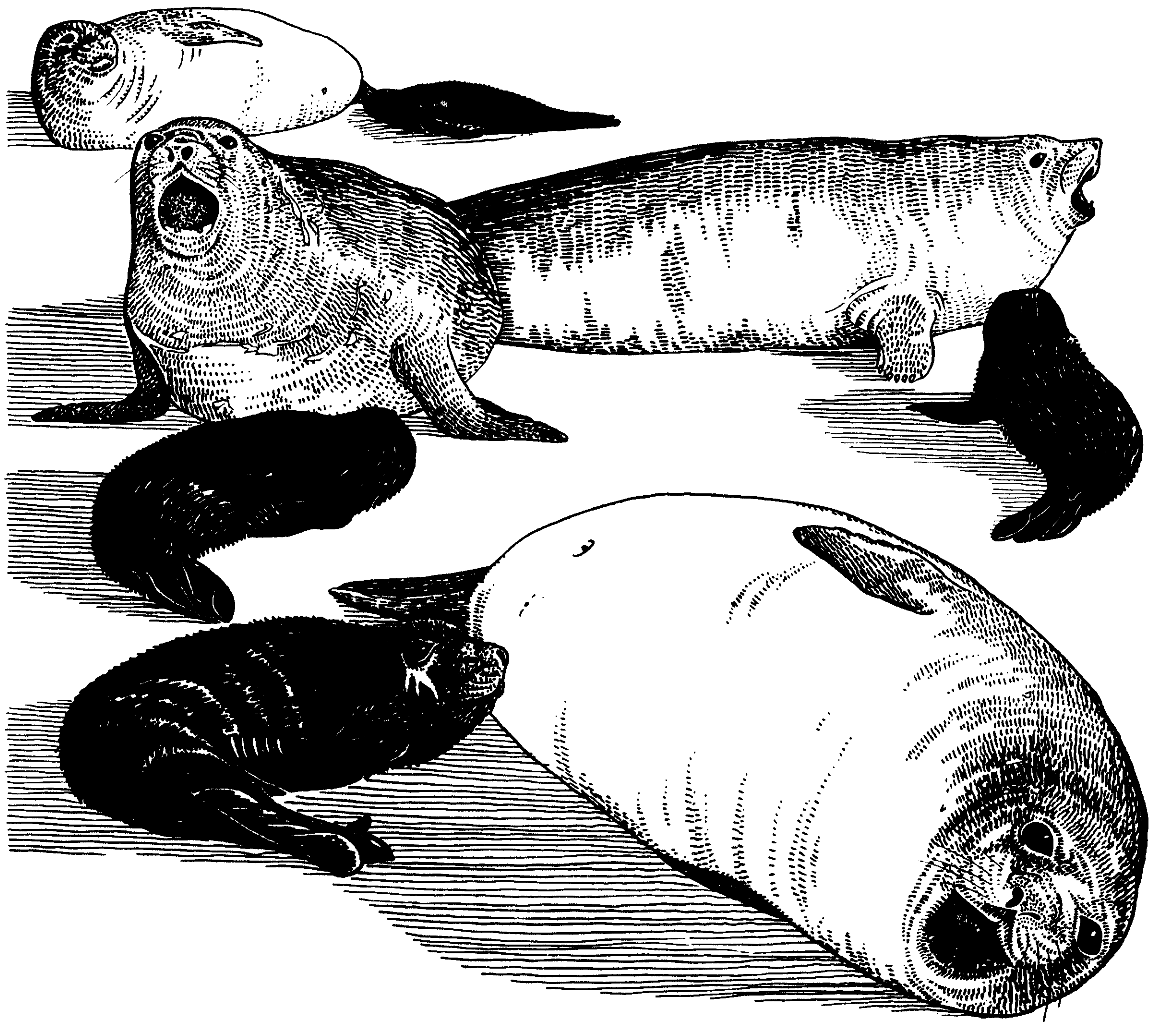


FIGURE 27. Cow elephant seals in the breeding season.

the neck region. The canine teeth are now quite different in shape from those of the male, being long, of small diameter and grooved.

Classes V to XII, age forty-nine months and over (material fifty-two to 205 months).

The average length of four-year-old females is 103 inches, five-year-old 105 inches, increasing to 115 inches at twelve years. The largest female killed was only eighty-four months old but measured 138 inches in length (M148), and the largest measured photographically, at Signy Island, was 145 inches long.

With increasing age there is a general coarsening of the bodily appearance. The head and neck appear relatively smaller in comparison with the rest of the body and a light coloured facial mask is a characteristic of the older animal. The degree of fatness varies between 80 per cent when recently hauled out and 45 per cent at the completion of the moult.

In some individuals the snout is puckered and can be erected to some extent so as to resemble the proboscis of class III males. The canine teeth become progressively longer and slightly recurved at the tip, and the grooves become more prominent.

Small scars appear on the body, which are inflicted by other cows during the breeding season, and the scarring of the neck increases in extent so that there is a lighter coloured "yoke". When the older cows haul out for parturition the recent scars are very often in an infected condition, and have a bright red colour; apparently it is due to a fungal growth which quickly dries up and disappears after the haul-out.

The general colour of the older females is drab-brown, lighter ventrally. Individuals of all shades from grey-brown to red-brown may be seen but the golden colour which is common among moulting bulls is seldom assumed. The reason is that in general, the cows when moulting tend to frequent wallows further inland and to become dirtier than the males. As a result their colour during the moulting period is usually a dark-chocolate or earthy-brown. Once the moult is completed they go to sea and seldom haul out again, but those that do are dark grey in colour. As in the other sex, some very light coloured individuals may be seen which usually have the appearance of great age.

V. MORTALITY

A. Pups

THE mortality rate during the first year of life is evidently very high, perhaps as much as 50 per cent, and mainly at sea. The death rate ashore, even among the young pups, is low.

Very few still-born pups were noted and the female elephant seal appears to experience no great difficulty at parturition. Indeed, at Signy Island, where a proportion of the cows travelled several miles over the sea ice before pupping (in one case as much as seven miles), there were only two recorded still-born pups, or about 1 per cent of the total. At South Georgia the figure is very much lower, probably less than 0.5 per cent.

The highest mortality on land occurs at the beginning of the season. There is then a deep layer of snow covering the tussac clumps and the first harems usually form some way inland. The body heat of the pups, increased by their black-body-radiation, causes the underlying snow to melt. As a result deep holes develop and the unfortunate pup is trapped in an icy prison perhaps four to six feet deep. Many die of starvation because they are unable to reach the parent which lies on the surface; others drown when the hole fills with melt water. The mortality from this cause is greatest in the tussac covered areas because there are deep pits between the adjacent clumps of tussac. At South Georgia, in 1951, 30 per cent of the pups born on the tussac area at Dartmouth Point, in the first two weeks of the breeding season, met their death in this manner. At Signy Island, only one pup is known to have died in similar circumstances. Mortality from these causes emphasises the effectiveness of the blubber layer as an insulator, for no adults sink down in this way.

In some years at South Georgia adverse weather conditions increase the mortality rate of the young. In 1939, for example, the island experienced the worst winter for many years and the death rate was very high. The severe winter weather caused snow to pile up to a height of from eight to ten feet and in consequence the seals were compelled to give birth at high water mark. At high tide many pups were washed away and drowned.

In the large rookeries a small number of pups undoubtedly die of starvation when they lose their mothers. The mother is usually able to distinguish her own pup only by smell and if the pup has wandered far she

Beaches	Number of Pups		Percentage dead
	Alive	Dead	
"Hestesletten"	947	24	2.5
Ice Fjord A	761	6	0.8
,, B	847	27	3.1
,, C	1574	24	1.5
Langestrand	235	16	6.8
,,	945	30	3.1
King Haakon Bay A	275	10	3.6
,, B	968	13	1.3
,, C	414	6	1.4
Queen Maud Bay	971	14	1.4
Total	7937	170	2.1

TABLE XVII. Count of dead pups on ten beaches at South Georgia. October 1951.

rarely finds it. The pup has no discrimination and will nose at strange cows and bulls in its search for food, expecting a response. Usually the result is a savage bite at the head or shoulders, which does not kill the pup outright. Such a bite is more common in the large rookeries, but at Signy Island, in one small group of a bull, cow and pup, the latter was killed by the bull, and bore deep tooth marks which pierced the skull.

A proportion of pups are killed or maimed by the bulls in their furious rushes. When a harem bull has roared at a rival without effect it will travel in a straight line at full speed towards the intruder, disregarding any cows or pups that may happen to be in the way. The older pups are surprisingly resilient to such treatment, especially when lying on snow, but on a pebble or boulder beach the pup is squashed by the weight of the bull. Pups are also frequently accidentally overlain by adults of both sexes and asphyxiated. Frustrated "bachelor" bulls which have been unable to get a harem of their own, occasionally attempt to pair with the older weaned pups. Matthews (1929, p. 240) believes that, "pups are sometimes killed by this misplaced affection", but the present writer has not seen any deaths resulting from such actions.

Table XVII details counts of dead pups on various beaches at South Georgia in 1951. The percentage of deaths ranges from 0.8 to 6.8 per cent, averaging 2.1 per cent. It is extremely difficult to count all the dead pups on a crowded beach and some are washed out to sea, or die in the tussac wallows and are unseen, so that in the writer's opinion 3 per cent is probably a conservative figure for the deaths prior to weaning. In some seasons, moreover, the weather conditions are much worse.

At Signy Island, in spite of the severe weather conditions the percentage of deaths from the causes outlined above is approximately equal to the figure given for South Georgia, but there is another very serious factor influencing mortality. In 1948 and 1949 the elephant seal harems were situated on the sea-ice, so that in 1948, 60 per cent of the pups were born there, and in 1949, 99 per cent. When the fast-ice broke up an estimated 80 per cent of all the pups born on the sea-ice were drowned or crushed in tide-cracks.

It seems likely that at Signy Island the freezing of the sea and the subsequent break-up of the ice during the breeding season is the major factor preventing the stock from increasing in numbers.

Although for the reasons already discussed, a proportion of pups die, there are some which survive starvation when separated from the mother. They are recognisable among the weaned pups as smaller less robust individuals, and the term "dwarf" is proposed for them. They are unusually lean, the body is small and the head and flippers appear unnaturally large. They correspond to the "starvelings" of the harp seal (*Phoca groenlandica*). In one herd of 226 weaned pups, six dwarfs were observed, corresponding to 2.6 per cent. Unfortunately no further figures are available. Clearly their chances of survival are much lower than for normally developed pups and in the older age classes dwarfs are rare. Nevertheless, several are included in tables XIII and XIV and figure 19. For instance H296 and M80 are certainly dwarfs.

B. Adults

Very few adults are seen to die from natural causes when on land. The cause of death of those which do is usually obscure. At Signy Island, when the pack-ice is inshore, the seals have to pass through a piled up mass of ice blocks in order to reach the sea and they are often seen in difficulties. One bull fell into a crack in the consolidated snow near the ice-foot in the spring, and was unable to get out; it died of exhaustion and compression. Another was lying in a confined space between two ice blocks for several days and the underlying snow melted, so that it settled in a narrow crevice from which it was unable to extricate itself. At Signy Island there may be some mortality from failure to locate breathing holes when under the sea-ice, and a number must die when making their way over the consolidated pack-ice to open water.

At the Falkland Islands, elephant seals are occasionally trapped, and drowned in wallows. On Arch Island, Falkland Sound, in February 1951, mud wallows, sounded and found to be 7–8 feet deep, contained the carcasses and bones of elephant seals, and one living seal. It was trapped in the thick mud because evaporation had lowered the surface and the sides of the wallow were too steep to allow escape.

The fighting among the males, although impressive, does not lead to many deaths. Only two such deaths were observed and one of the animals had no visible wounds. In view of the filthy state of the rookeries it is not surprising that the wounds invariably suppurate badly, though they do so even when the animals are lying out on the clean sea-ice. The bulls frequently lose part of the proboscis—sometimes more than half is torn off. Others carry huge scars on their backs, and bulls have been seen to tear from an opponent a lump of flesh and blubber nearly a foot square. Occasionally the eyes are injured in fighting and the sight is lost by inflammation. When it heals the surface of the conjunctiva is white and opaque. Injuries to the eye are more common among cows than bulls, possibly because they have somewhat sharper teeth. Sorensen (1950, p. 26) refers to one mature bull, which was blind in both eyes and, judging by appearances, had been so for some time. He was, like the others, in prime condition. So it would seem that the loss of an eye is not a very serious matter to the elephant seal.

Apart from the usual greyish suppuration of the wounds, the cows, when they haul out to pup at South Georgia, are often in a diseased condition. About the nose and eyes, the axilla and the fore and hind flippers, and in some individuals, extending down the back is a scattering of small brilliant orange-red spots. They appear to be some fungal growth and quickly dry up after the seals are on land. The condition was not observed at Signy Island.

C. Parasites

The Weddell seal (*Leptonychotes weddelli*) and the leopard seal (*Hydrurga leptonyx*) are much more heavily infested with parasites than the elephant seal although they are less gregarious in habit. On the other hand the latter is more heavily infested than the other two Antarctic seals.

Only two forms of external parasites have been observed; Sorensen (1950, p. 27) has recorded barnacles and "small tick-like animals" mainly from young seals. Barnacles (*Pedunculata*) up to 3 cm. long have been collected from elephant seals at South Georgia.

More significant to the seals' well-being are the many internal parasites, which are characteristic of the group. An acarinid parasite (*Halarachne*), is of constant occurrence in the nasal passages of all except the very young elephant seals. Large numbers of these small white parasites are found lining the mucous membrane. In some individuals they had caused an irritation which had resulted in a pathological growth of the turbinate bones. This produced nodules which partially or completely blocked the nostril.

Nematode parasites are found in great profusion in the viscera, mainly in the stomach and to a lesser extent in the heart, bronchii, and small intestine. In the male, No. H304, there were very large numbers of roundworms in the auricles, which must have impeded the circulation and sooner or later brought about death. Three species have been recorded from the elephant seal—*Contracaecum osculatum*, *Porrocaecum decipiens*, and *Anisakis similis*. It has been suggested that the purpose of the sand and shingle in the stomachs of seals is to destroy the parasites, but observations show them to be unaffected by it. A small number of the nematodes are occasionally vomited up with the stones. Moreover, the stones in the stomachs have been shown to have a different function in the elephant seal, being connected with the periods of fasting. In the older animals growths and thickening of the stomach walls are common. These are the result of local irritation by the nematode fauna.

In the small intestine a yellowish species of *Acanthocephala* of common occurrence. In one female these parasites had given rise to a pathological tumour of the gut which had almost blocked the lumen of the small intestine.

Cestodes are common in the rectum of the elephant seal, even at so early an age as seven months. In the rectum of H133, a male, were five tapeworms up to 8 inches in length, the heads attached about 6 inches forward from the anus and confined to a segment of the rectum about 1 inch broad. The bodies extended forwards. There were also many large cysticercoids in the blubber of almost every seal killed. The only species which has so far been recorded from the elephant seal is *Baylisiella tecta*, and it appears to be specific to this host (Markowski, 1952, p. 250).

A representative collection of parasites was made. It is hoped that they will be described and named in a later paper.

D. Predators

The sealers assert that the leopard seal (*Hydrurga leptonyx*) occasionally attacks adult elephant seals on land and in the water and that it kills and feeds on them, but it is difficult to accept such statements. It is established beyond doubt that *Hydrurga* attacks young seals of several species and there are five authentic records of attacks on young elephant seals at the South Orkneys and one from South Georgia. In five cases the prey had been killed and was being devoured, but at South Georgia, appropriately enough, in Sea Leopard Fjord, the leopard seal was playing with a young weaned elephant seal. The former was shot and the pup came ashore, apparently unperturbed, and was found to have dozens of deep tooth marks piercing the skin and blubber. It is rare to see *Hydrurga* take an elephant seal, and it cannot be classed as an important predator.

Aretas (1951, plate 1) has a photograph of a sub-adult male at New Amsterdam, which had been wounded by a killer whale (*Orcinus orca*), and died a few days later. Sorensen (1950, p. 25) describes wounds inflicted on elephant seals at Campbell Island by killer whales; one of the wounds, borne by a very large bull was so deep that the intestines were protruding. Only one example of the scars inflicted by killer whales came to the notice of the writer, but Matthews (1929, p. 243) gives some precise information; "One of the gunners at Leith Harbour Whaling Station shot a killer whale off South Georgia in November 1926, and when it was struck by the harpoon it vomited up the heart, liver, and a piece of blubber, about 4 feet by 2 feet in size, of an elephant seal. This gunner also told the writer he had previously seen killers attack elephant seal and cut them in two at one bite".

VI. LONGEVITY

THE longest authentic life-span of a pinniped is forty-one or forty-two years for a specimen of the grey seal (*Halichoerus grypus*) kept in Stockholm Zoo, Skansen, from 1898 or 1899 to 1940. Another grey seal lived twenty-six years and three months in captivity at Cardiff (Matheson, 1950). The longevity of pinnipeds in the wild state is less well known. In fact, only for the northern fur seal (*Callorhinus ursinus*) is there any detailed knowledge. Evidence of its maximum length of life comes from the recovery of three fur seals branded as pups in 1902, which were later seen when twenty-one years old (Scheffer, 1950a). Elsewhere Scheffer indicates that, in his opinion, twenty to twenty-five years is the life span of this species (1950b, p. 309).

Species	Length of life (in years)			
	Captivity		Wild	
	Av.	Max.	Av.	Max.
Otaria byronia	19*	23*		
Eumetopias stelleri	17*	19*		
Zalophus californianus	13½*	23†		
Callorhinus ursinus				21(3)[s]
Arctocephalus pusillus		20†		
Phoca vitulina	10¾*	19‡		
Halichoerus grypus	17	41–42[m]		
Mirounga leonina			12	♂ 20; ♀ 18(2)

TABLE XVIII. Longevity of pinnipeds. Authorities, * Flower (1931), † Bourlière (1951), ‡ Sivertsen (1941), [s] Scheffer (1950b), [m] Matheson (1950). *Mirounga*—original data, age estimated from tooth rings.

Table XVIII gives the available data on the length of life of various pinniped species, taken mainly from captive animals.

The average age of the 142 male elephant seal collected is sixty-four months, and of the eighty-four females, seventy-six months, but these figures have no significance for the elephant seal population as a whole.

In figure 28 the frequencies of the various age groups are illustrated. Figure 28a shows the age frequency distribution of ninety-five bull elephant seals killed by the sealers. It would be true to say that this is a random sample of the seals killed commercially in 1951 in the two northern divisions of South Georgia during the months when the sample was collected. Though this sample is only truly representative of the animals killed *in certain localities and during certain months of the year*, there is reason to believe that it is also representative of the total commercial kill at South Georgia. Since the sealers exercise a selection in favour of large size, only the larger, and therefore older, animals are fairly represented by the frequency distribution. In other words, we may assume that the relative proportions of the age groups from six to twelve years in the total population are represented by the proportions of those age groups in figure 28a.

At South Georgia bull elephant seals rarely attain to an age greater than eleven years. The sealing captains can still remember the time when very large bulls were not uncommon there, but apparently the last was seen about fifteen years ago.

At Signy Island, on the other hand, a selection in favour of the younger animals was unavoidable since the shortage of assistance rendered examination of the large bulls very difficult. To roll a large bull elephant seal, weighing perhaps more than four tons, onto its back is beyond the capacity of three men, without special equipment. In fact, specimens H303 and H304 had to be dismembered from the dorsal surface. Within a short time of arrival at South Georgia it was apparent that the Signy Island bulls attained a much more massive stature than those in the South Georgia population.

Thus, at South Georgia, the selection of the material was in favour of the older individuals, though the maximum age had almost certainly been lowered by forty years of commercial sealing. On the other hand, at Signy Island, owing to practical difficulties, selection was in favour of the younger age groups. It is thought that only animals killed in the breeding season were certainly representative of the Signy Island population, because the summer population is nearly thirty times larger and must be a migrant herd from South Georgia.

So far as is known at present, the maximum age which is attained by bull elephant seals in a unexploited

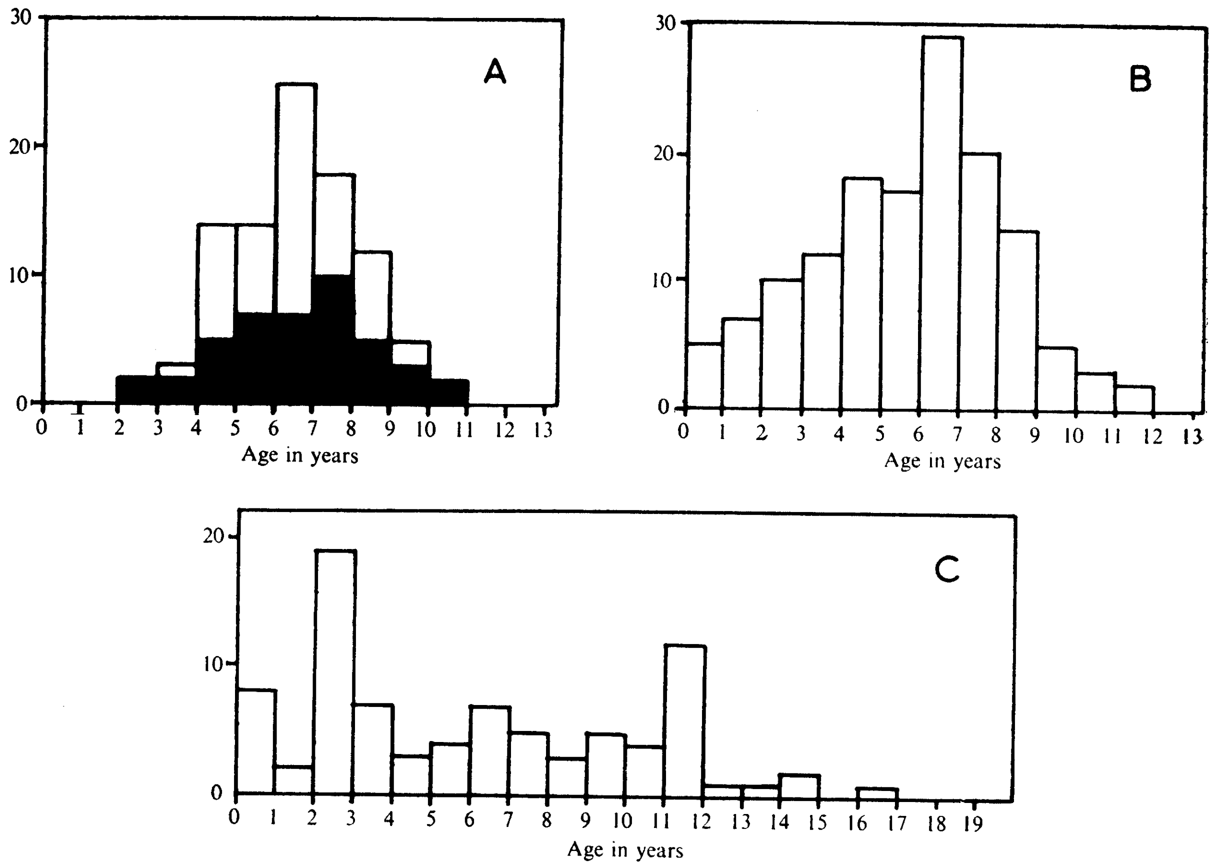


FIGURE 28. Age frequency distribution of the material collected:
(a) Killed by sealers, South Georgia, black—March–April, 1951.
(b) Total males, Signy Island and South Georgia, white—Sept.–Nov.
(c) Total females, Signy Island and South Georgia.

population is twenty years. Of two large skeletons at Signy Island, aged by counts of teeth rings, one was twenty years, and the other eighteen years old at death. In comparison with the ages that other species are known to attain (table XVII) this is an acceptable figure. In view of the small amount of material available it is clearly impossible to give a precise figure for the average longevity. In the writer's opinion it is reasonable to assume that the average age of harem bulls (the fully mature males) in an unexploited stock is somewhere between ten and twelve years.

Although the male material collected was actively selected, the mature females above three years of age were not subject to any conscious selection as regards age, but were carefully selected to obtain material covering the annual reproductive cycle. In figure 28c the age frequency distribution of the material is illustrated. If it is representative, then the proportions of the different age groups in the sample collected should roughly correspond to the proportions of the various age groups in the entire population.

The relatively large number of twelfth year females recorded is probably due to inaccuracies in age determination, which becomes difficult after ten years owing to crowding of the tooth rings, and later to the occlusion of the pulp cavity. A proportion of the twelfth year cows may, therefore, be removed to later age groups, and the frequency distribution then suggests that from the fourth to the fifteenth year the mortality rate declines, or at least remains more or less level. A discussion of probable mortality rates must be left until another paper, when the reproductive cycle, and censuses carried out at Signy Island and South Georgia have been discussed. In the writer's opinion the average expectation of life of mature females (above three years of age) is of the order of a further seven years.

VII. SUMMARY

THIS is the first of a series of papers on the biology of the southern elephant seal (*Mirounga leonina*, Linn.).

1. The nomenclature and literature are discussed and a general introductory account of the life history is given.

2. The equipment employed, and the methods and difficulties of the collection of the material are described, and the distribution of over one thousand specimens is set out in tabular form.

3. Some aspects of the gross anatomy are dealt with, and a detailed account of the acquisition of the milk and permanent dentition is included.

4. A survey of possible methods of age-grouping is given.

5. The development of the young, from birth until shortly after weaning is described and the time relations of weaning, moulting, and the rate of blubber deposition are clarified. The increase in weight is compared with other pinnipeds.

6. A still-born pair of "siamese twins" of the elephant seal are described and figured.

7. Growth of the older animals is discussed and average curves for the rate of growth in length of both sexes, from birth to twelve years of age are given. They are based on ages determined from the tooth rings of 142 males and eighty-four females.

8. The age classes of both sexes are described.

9. Various factors influencing the mortality rates are discussed, including diseases, predators and parasites. The age frequency of the material is indicated.

10. It is provisionally concluded that the average age of the harem bulls in an unexploited stock is ten to twelve years, but that they may live up to twenty years; at South Georgia bulls rarely live longer than ten years. The average expectation of life of mature females above three years of age is a further seven years.

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