https://doi.org/10.26749/rstpp.102.25

DEVELOPMENT AND GROWTH OF THE SOUTHERN ELEPHANT SEAL (MIROUNGA LEONINA) (LINN.)

A review of the literature with some further observations

By

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Communicated by Dr W. Bryden

(With three plates and one text figure)

ABSTRACT

A study of development and growth of the Southern Elephant Seal was carried out at Macquarie Island (54°S, 159°E) while the author was a member of the Australian National Antarctic Research Expeditions, 1964-1966.

HISTORY

Until recently very little was known of the natural history and physiology of the Southern Elephant Seal, although its economic significance has been realised and the species has been exploited commercially since early in the nineteenth century. The inaccessibility of the habitat of the animal has been largely responsible, although relatively little work has been done on the closely related Northern Elephant Seal (*Mirounga angustirostris* (Gill), which is much more accessible. The mass slaughter of elephant seals, both northern and southern species, for their valuable oil in the nineteenth century and the early part of the present century, is well known, and it is thought that the total world population of Northern Elephant Seals may have been as low as 20 during the nineteenth century (Bartholomew and Hubbs, 1960). Apathy, and a general ignorance of the biology of these species, almost caused their complete extinction. It was not until results of a large scale study by Dr R. M. Laws at the Falkland Islands Dependencies in the late 1940's became available that slaughter of elephant seals at South Georgia was put on a sound scientific footing, in order to prevent any repetition of the mass slaughter and decimation of the species which had occurred during the previous century.

Soon after the discovery of Macquarie Island in 1810, sealers began exploiting the elephant seal and in 1826 and 1827 over 1,000 tons of oil were procured (Carrick, 1956). The island was quickly depleted of its stock, breeding cows, young animals, surplus bachelor bulls and breeding bulls being taken. Intermittent killing continued in the same reckless way, and it was after a great deal of publicity concerning the danger of indiscriminate killing of seals, initiated by Sir Douglas Mawson following his journey to Antarctica in 1911-1913, that the Tasmanian Government in 1919 discontinued issuing licences for the killing of elephant seals at the island. The success of this move was soon evident, for, when the "Discovery" called at Macquarie Island in 1930, it was found that large numbers of elephant seals were again breeding there (Mawson, 1932).

The study of the Southern Elephant Seal is difficult due to its inaccessibility, and more importantly to the fact that less than half of its life is spent ashore, where observation is possible. Virtually nothing is known about the life of the animal at sea, and any form of controlled experimentation is difficult due to its amphibious habits.

Two major ecological studies have been made on the species, one by Laws (1953a, 1956a, 1956b) on the Falkland Islands Dependencies populations, the other at Macquarie Island (Carrick and Ingham, 1962a, b and c; Carrick Csordas and Ingham, 1962; Carrick, Csordas, Ingham and Keith, 1962). These major works have expanded and correlated earlier observations performed by a number of other workers (Murphy, 1914; Ring, 1923; Matthews, 1929; Sorenson, 1950; Aretas, 1951; Paulian, 1953, 1957; Angot, 1954; Gibbney, 1953, 1957) and provided the first quantitative data on various aspects of the biology of the Southern Elephant Seal. These studies have rendered the Southern Elephant Seal a well-known animal insofar as its distribution and annual cycle on land, its breeding ecology and physiology, and its numbers are concerned. The detailed study of moulting and the integument of this species made by Ling (1965a, b) has added to our knowledge of the animal.

Some work on the postnatal growth of *Mirounga leonina* has been reported, but it is limited to observations on growth of body length and weight of seals during early postnatal life, and body length changes in later life (Laws, 1953a; Carrick, Csordas and Ingham, 1962). These studies have revealed an interesting and unusual growth pattern in this species. Sivertson (1941) reported a study of growth and changes in gross body composition (blubber and carcass) during early postnatal life in the harp seal (*Phoca groenlandica*), and Scheffer and Wilke (1953) studied relative growth (changes

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in body length, body weight, flipper measurements and skull dimensions with growth) in the Northern Fur Seal, *Callorhinus ursinus*. However, no detailed systematic study of development and growth in the Pinnipedia has been attempted.

REVIEW OF DEVELOPMENT AND GROWTH

Differential growth of the constituent parts of an animal's body has been recognised for centuries as being necessary in order to give rise to the animal's inherent shape. It was known to Xephenon (400 B.C.) and reported by Markham (1617), that one could predict the ultimate size of a horse from the measurement of its shin bone. " For in all quadrupeds the shanks increase but little in size as time goes on, whereas the rest of the body grows to them, so as to be in the right proportion " (Marchant, 1925). Systematic quantitative studies on postnatal development in animals were commenced by Lawes and Gilbert (1859, 1861).

Several authors have proposed definitions of growth and development, each of which has certain advantages and disadvantages. The definitions furnished by Brody (1945) appear adequate for the study of development and growth in the elephant seal. He defined (1) *development* as the directive co-ordination of the diverse processes into an adult—into an " organised heterogeneity " (Needham, 1933); (2) *growth* as biologic synthesis, production of new biochemical units. It is the aspect of development concerned with increase in living substance or protoplasm, and includes one or all of three processes: (i) cell multiplication, (ii) cell enlargement, and (iii) incorporation of material taken from the environment.

The inclusion of non-protoplasmic substances such as fat, blood plasma, cartilage, &c., is an increase by incorporation of material from the environment. Such increase is not regarded as " true growth " by this definition, yet operationally, from the standpoint of quantitative measurement of growth of the organism as a whole we must consider these non-protoplasmic inclusions as parts of the growth process. It is difficult in practice to separate " true growth " and accretion, or increase in amount of non-living structural matter, since the parameter used most in the study of growth is body weight. Elsley, McDonald and Fowler (1964) have pointed out some of the inaccuracies of using total body weight increase as a measure of growth. They showed that fat is a unique tissue with functions very different from those of the other major tissues, and fat deposition is not closely related to the growth of the fat-free body mass. Nalbandov (1963) produced evidence which indicated that reduced growth rate and eventual growth stasis in the growing animal could be attributed to a steady reduction in the amount of available growth hormone per unit of fat-free body weight, but fat deposition was not related to the growth of the fat-free body mass from this point of view.

The use of body weight increase as a measure of growth can never be done away with completely, in spite of the shortcomings, since a vast amount of work is involved to divide the animal body, either by anatomical or biochemical means in the dead animal, or by more recent *in vivo* techniques which have been reviewed by Brozek (1963), Panaretto (1963), and Kirton (1963, 1964), into its component parts.

In some animals, including many aquatic species, certain linear measurements are more useful than body weight to define growth operationally in terms of time relations. The body length is a useful means of estimating growth in terms of chronological time in seals (Scheffer and Wilke, 1953), since body length gives a better indication of body size than does body weight—weight depends on both size and " condition ". However any linear measurement can measure growth in only one dimension, whereas it is obvious that growth is three-dimensional, as defined above.

The regular changes which take place in the body composition and conformation of animals during development and growth from birth to maturity were studied by Huxley (1932), who showed that the allometry equation, $y = bx^k$ (where y = size of organ, x = size of rest of body, k = growth coefficient of organ) gave a useful quantitative description of many of these changes. A valuable characteristic of this allometry equation is that it can be transformed into:

$$\text{Log } y = \log b + k \log x$$

to give, generally a straight line. This transformation accentuates the three-dimensional and multiplicative nature of the growth process.

The theory associated with Huxley's formula and its logarithmic transformation implied that the form of an animal depends solely on its absolute size and not on the length of time taken to reach that size. The concept of physiological age (Brody, 1937, 1945) also implies this basic relationship, although in a less direct way. Huxley showed that this relationship applied over a wide range of species and environmental conditions, but pointed out that it may be influenced by some external conditions such as extremes of nutrition and temperature. Severe undernutrition associated with loss of body weight has been shown by Widdowson, Dickerson and McCance (1960), and Wilson and Osbourne (1960), to affect this relationship. Mendes and Waterlow (1958) demonstrated that even when animals were held at an almost constant weight by undernutrition, some growth took place in tissues such as bones and collagen, which have good structural stability. McCance, Ford and Brown (1961) showed that dental development, although delayed by undernutrition, was more closely linked to the animal's chronological age than that of other tissues. Nerve cells in the central nervous system which have already made most of their growth do not regress in size, but the cells in the skeletal muscles do (Widdowson, Dickerson and McCance, 1960).

Extremes of temperature have been shown to affect the relationship, as Huxley predicted. Barnett (1959) observed that mice reared at − 3°C reduced their heat loss by developing shorter tails and longer hair. The relationship of tail length to body weight in rats was altered in a hot environment (Harrison, Morton and Weiner, 1959). However, for animals growing on a normal plane of nutrition, Huxley's equation is a most useful empirical formula for the study of growth gradients (Medawar, 1945; Richards and Kavanagh, 1945; Needham, 1950).

Huxley examined growth gradients in a wide variety of species through application of the allometric equation. His results and those of other workers were reviewed by Palsson (1955), who described a centripetal pattern of postnatal growth. At birth the head, limbs and forequarters are relatively well-developed, the skeleton relatively better developed than the musculature. Developmental changes in the skeleton were attributed to a primary wave of growth beginning at the head and passing down to the nose and lower jaw, and caudally towards the lumbar region; and to a secondary wave from the lower parts of the trunk and limbs ending in the lumbar region. The lumbar region was described as the last part of the body to attain maximum growth rate and was therefore the latest maturing part of the body. Growth in length of the long bones takes place earlier than growth in thickness. A similar centripetal pattern of growth was described for the musculature, but some of the details of this have been challenged by Butterfield and Berg (1966), who showed that although there was evidence of centripetal growth in the limbs of cattle, development did not terminate in the lumbar region. Differential growth also occurs in the major tissues and organs which attain their maximum rate of growth in a definite order with age: broadly, nervous tissue, bone, muscle and fat. Allometric growth of individual organs appears to be primarily functional: brain, eyes, kidneys and heart, for example, being early maturing organs. Those organs of most physiological significance to the animal are relatively well developed at birth, as distinct from those organs which have little functional importance until some time after birth.

Most mammals on which detailed systematic growth and development studies have been made have been domestic species. Growth and development have been studied in several wild mammalian species, but most of these studies have only involved body weight changes where possible, and more often, external changes in form in terms of linear measurements, and have not considered the relative growth of the body tissues and organs. A problem met with in studying growth in many wild species is the absence of any reliable method of ageing.

EXPERIMENTAL

(a) Introduction

A systematic study of development and growth of *Mirounga leonina* was attempted, on the assumption that such a study might reveal interesting comparisons with growth and developmental patterns in other mammals. The mammals on which detailed studies of this nature have been made exhibit external forms and ecological patterns markedly different from those of the seal. It was felt that the unusual pattern of postnatal growth in the elephant seal could possibly provide details of some facets of the growth process not revealed by studies of growth in domestic mammals, and clarify some of the hitherto misunderstood aspects of mammalian growth. In particular it was considered that the period of accelerated growth which is known to occur soon after birth (Laws, 1953a; Carrick, Csordas and Ingham, 1962) may be illuminating due to the exaggeration of all the physiological processes involved with growth at this time.

In planning the present study, knowledge of the seasonal movements of the Southern Elephant Seal at Macquarie Island furnished by Carrick, Csordas, Ingham and Keith (1962) was invaluable. Immediately after birth the elephant seal undergoes a 23-day suckling period on land, during which time growth is extremely rapid (see Plate 1), followed by a five- to seven-week postweaning fast while the animal becomes adapted for a life at sea. After the attainment of nutritional independence, individuals spend most of their lives at sea, but from time to time they haul out on land where they undergo a complete fast lasting up to two months, and suffer dramatic body weight losses in some instances. Following puberty, a very marked discrepancy in size develops between males and females (Plate 2).

(b) Materials and Methods

A description of the anatomical methods used in, and the results obtained from, this work have been submitted for publication elsewhere (Bryden, 1967a). In brief, seals of both sexes from birth to maturity were dissected anatomically into skin, fat and connective tissue, and individual muscles, bones and organs. A total of 96 animals was dissected.

Seals could only be studied during their periods on land, and the numbers of animals of the different age groups ashore at Macquarie Island during the year are illustrated in Figure 1. Growth was studied in most detail during the early postnatal period, from birth of the pup to the time of its departure to the sea, which meant that a very large portion of the work was concentrated in the breeding season, from mid-September to mid-November, 1965; adult females were studied during their annual moult period in January and February; immature seals of both sexes were studied from April to August when they appeared at the island for winter "rest periods"; and breeding bulls ashore for the breeding season were studied during the latter half of August and the first half of September, up to the beginning of the breeding season.

Foetal growth was not considered in any detail in this study owing to the lack of material. Pregnant females spend the entire gestation following implantation of the blastocyst at sea, and only the occasional straggler returns to land during winter. An attempt was made to keep six pregnant females in captivity during the winter months in a large enclosure in which a swimming tank was provided (Plate 3), but the many hours spent on attempts at feeding the animals were unfruitful. Suggestions for encouragement of feeding this and closely related species (Bullier, 1954; Pournelle, 1962 and personal communication) were observed, but with no success. Subsequent discussions with Dr C. R. Schroeder, Director of the San Diego Zoo, California, U.S.A., have revealed that for all practical purposes, it is impossible to train adult elephant seals to eat in

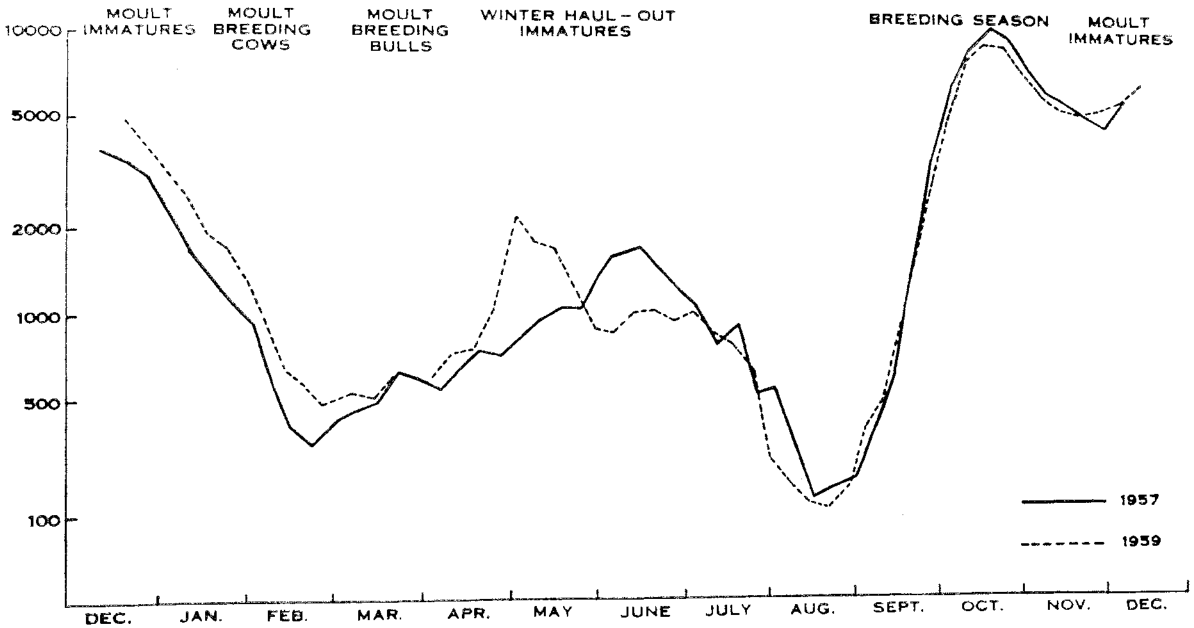

FIG. 1.—Total number of elephant seals in the Isthmus Study area, Macquarie Island, each week during 1957 and 1959 (from Carrick, Csordas and Ingham, 1962).

captivity. All of the elephant seals (*Mirounga angustirostris*) which have been kept successfully at the San Diego Zoo have been introduced at an immature stage, and the most successful have been recently-weaned pups.

Measurements of six elephant seal foetuses collected at Macquarie Island in 1956 by Mr K. Keith were kindly made available by Dr R. Carrick, Mawson Institute for Antarctic Research, Adelaide, and measurements of these plus the one foetus collected in 1965, were included in this study as they were the only foetal measurements available to the author.

(c) **Results and Discussion**

Development and growth of the elephant seal were considered along two main channels of thought, first the aspects of development (which, by the definition given earlier, includes growth) associated with the ecology of the species, and secondly the changes in form which are similar to those in other animals.

The ecology of the species, so very different from that of other mammalian species on which detailed studies of development have been made, has resulted in alterations to many of the postnatal developmental processes within the body and has exaggerated some of the physiological mechanisms associated with development. Brody (1945) stated " aquatic animals are not forced to change much in form with increasing weight because their weight is counterpoised by the displaced water ". This statement was based on earlier observations of Hecht (see Jackson, 1928) in fish, whose form was shown to change little with increasing weight, and whose ultimate size was not an important factor in the growth process. The form of the elephant seal must alter with increasing weight because, although most of its life is spent at sea, it is still subjected to the effects of gravity during its haul-out times. This study has revealed that the control of ultimate size in the elephant seal is of great importance, particularly in the male (which is very much larger than the female), due to the periodic influence of gravity during times when animals are ashore (Bryden, 1967b). Thus it differs from a totally aquatic mammalian group such as the whales, whose development does not need to allow for the effects of gravity.

The change in form of the elephant seal during growth is quite marked, and was illustrated by a quotation of Charles Eyre, cited by Sorenson (1950): " Over a big hill which separated us from the next bay some of the party had seen, the previous day, a huge sea-elephant . . . The first thing which caught our eye when we reached the bay was a small seal of the sort I had never seen before. Its eyes were about the size of a five-shilling piece and something awful to look at ". The latter was later identified as a young elephant seal. The early development of the eyes of the elephant seal is very obvious, as this observation illustrates, and in this and certain respects differential growth in this species is similar to other mammals studied. However in other respects the pattern of differential growth has been shown to be different from domestic mammals. For example, postnatal development of the subcutaneous fat in the elephant seal occurs much earlier than does the fat in terrestrial mammals; considerable relative postnatal growth of the blood occurs in the seal, and relative growth within the muscular and skeletal systems in elephant seals, showing patterns different from those in domestic mammals, occurs. Details of these observations have been submitted for publication elsewhere (Bryden, 1967a).

In an anatomical study of this kind, in which animals were dissected and measured at different stages of postnatal growth, it is clearly impossible to take measurements on the same animal at different stages of growth. In similar studies with other animals, it has been possible to utilise identical twins (Bonnier and Hansson, 1945-46; Walker, 1961; Taylor, 1958, 1962) or littermates (Cuthbertson and Pomeroy, 1962) in order to minimise the errors involved by comparing different animals at successive stages of growth. This is virtually impossible in any wild species since one cannot be certain of recapturing any particular animal after it becomes nutritionally independent. Multiple births are extremely rare in the elephant seal (Bryden, 1966), which rendered impossible the use of closely related seals, even at the suckling stage. The only means of overcoming these difficulties was to use a large number of animals, which made time the limiting factor. Sufficient numbers of animals were dissected to study developmental changes during early postnatal growth, before the establishment of nutritional independence, in considerable detail, but further dissections of animals during the time of life at sea are required to gauge more accurately the differential changes which take place in the body during this phase of growth. In particular, a more detailed study of the developmental changes in the male just before and just after it reaches sexual maturity would reveal more clearly changes which have been only briefly dealt with in the present work.

One of the difficulties involved with a study of this nature is that one has no means of knowing whether immature animals which haul-out during winter are truly representative of their age group. Possibly only the smaller, weaker seals haul-out at this time, or it could be that the more dominant animals which do not have to travel so far from land to feed successfully are the ones seen resting on the beaches. However the shapes of the growth curves, which exhibit the characteristic sigmoid shape (see Carrick, Csordas and Ingham, 1962), indicate that animals of the earlier age groups, most of them measured during winter haul-out, are representative of their respective age groups. The uncertainty again exists with foetuses, whether these foetuses are representative of growth of the elephant seal foetus at a particular stage, or whether only weak cows, with retarded foetuses, haul-out during the winter. However this is not likely to have affected most of the foetuses considered in this work, in the light of the observations of Barcroft (1946), who states that environmental retardation does not occur in the foetus until during the final quarter, or less, of pregnancy. All but one of the elephant seal foetuses were at an earlier stage than that.

As opposed to the several difficulties encountered, studies on the elephant seal have several advantages. First, the animals are very tractable and easy to handle on land. Secondly, there are relatively few hauling-out places around the Southern Ocean, so the chances of a marked animal returning to a part of the small area of coastline of Macquarie Island are high. Thirdly, animals can be aged with a considerable degree of accuracy as a result of the findings of Laws (1953b) and Carrick and Ingham (1962b).

By selecting the elephant seal as an experimental mammal in which growth processes are exaggerated during early postnatal life and are modified due to the marked alteration of environment when the animal goes to sea, it has been possible to study some aspects of growth in detail, which have been obscure up to the present time.

ACKNOWLEDGMENT

I am most grateful to the Animals and Birds Protection Board of Tasmania, who gave permission to work on the elephant seals at Macquarie Island, and to the Antarctic Division of the Department of External Affairs for its support of this project.

References

ANGOT, M. (1954).—Observations sur les mummifères marins de L'Archipel de Kerguelen, avec une étude detaillée de l'éléphant de mer, *Mirounga leonina* (L.) *Mammalia* 18: 1-111.

ARETAS, R. (1951).—L'éléphant de mer (*Mirounga leonina* Linn.)—Etude biologique de l'espèce dans les possessions francaises Australes (Archip. de Kerguelen). *Mammalia* 15: 105-117.

BARCROFT, J. (1946).—*Researches on Prenatal Life.* (Oxford: Blackwell).

BARNETT, S. A. (1959).—Skin and hair of mice living at a low environmental temperature. *Quart. J. exp. Physiol.* 44: 35-42.

BARTHOLOMEW, G. A. and HUBBS, C. L. (1960).—Population growth and seasonal movements of the Northern Elephant Seal, *Mirounga angustirostris. Mammalia* 24: 313-324.

BONNIER, G. and HANSSON, A. (1945-46).—Studies on monozygous cattle twins. V. The effect of different planes of nutrition on growth and development of dairy heifers. *Acta Agric. Suec (Stockh.)* 1: 171-205.

BRODY, S. (1937).—Relativity of physiologic time and physiologic weight. *Growth* 1: 60-123.

——— (1945).—*Bioenergetics and Growth.* (New York: Reinhold).

BROZEK, J. (Ed. 1963).—Body composition. *Ann. N.Y. Acad. Sci.* 110: 1-1018.

BRYDEN, M. M. (1966).—Twin foetuses in the Southern Elephant Seal, *Mirounga leonina* (L.). *Papers Proc. Roy Soc. Tas.* 100: 92-93.

——— (1968a).—Growth and development of the Southern Elephant Seal, *Mirounga leonina* (L.) . I to VII. *Aust. J. Biol. Sci.* (In press).

——— (1968b).—Theoretical consideration of the control of growth in two populations of elephant seals (*Mirounga leonina*, L.). *Nature.* (In press).

BULLIER, P. (1954).—Alimentation et acclimatement d'éléphants de mer (*Mirounga leonina* L.) en captivité, au parc zoologique du Bois de Vincennes. *Mammalia* 18: 272-276.

BUTTERFIELD, R. M. and BERG, R. T. (1966).—Relative growth patterns of commercially important muscle groups of cattle. *Res. Vet. Sci.* 7: 389-393.

CARRICK, R. (1956).—The wildlife of Macquarie Island. *Aust. Mus. Mag.* 12: 255-260.

CARRICK, R. and INGHAM, S. E. (1962a).—Studies on the Southern Elephant Seal, *Mirounga leonina* (L.).—I. Introduction to the series. *C.S.I.R.O. Wildl. Res.* **7**: 89-101.

——— (1962b).—Studies on the Southern Elephant Seal, *Mirounga leonina* (L.).—II. Canine tooth structure in relation to function and age determination. *C.S.I.R.O. Wildl. Res.* **7**: 102-118.

——— (1962c).—Studies on the Southern Elephant Seal *Mirounga leonina* (L.).—V. Population dynamics and utilisation. *C.S.I.R.O. Wildl. Res.* **7**: 198-206.

———, CSORDAS, S. E. and INGHAM, S. E. (1962).—Studies on the Southern Elephant Seal, *Mirounga leonina* (L.).—IV. Breeding and development. *C.S.I.R.O. Wildl. Res.* **7**: 161-197.

———, INGHAM, S E. and KEITH, K. (1962).—Studies on the Southern Elephant Seal, *Mirounga leonina* (L.).—III. The annual cycle in relation to age and sex. *C.S.I.R.O. Wildl. Res.* **7**: 119-160.

CUTHBERTSON, A. and POMEROY, R. W. (1962).—Quantitative anatomical studies of the composition of the pig at 50, 68 and 92 kg carcass weight.—I. Experimental material and methods. *J. Agri. Sci.* **59**: 207-214.

ELSLEY, F. W. H., MCDONALD, I. and FOWLER, V. R. (1964).—The effect of plane of nutrition on the carcasses of pigs and lambs when variations in fat content are excluded. *Anim. Prod.* **6**: 141-154.

GIBBNEY, L. F. (1953).—Delayed implantation in the elephant seal. *Nature, Lond.* **172**: 590.

——— (1957).—The seasonal reproductive cycle of the female elephant seal—*Mirounga leonina* (L.)—at Heard Island. *A.N.A.R.E. Rep.* (B) **1**: 1-26.

HUXLEY, J. S. (1932).—*Problems of Relative Growth.* 1st Ed. (London: Methuen).

JACKSON, C. M. (1928).—Some aspects of form and growth. In Robins, W. J., Brody, S., Jackson, C. M., Hogan, A. G. and Green, C. W.—*Growth.* (New Haven: Yale Press).

KIRTON, A. H. (1963).—Some relations between the potassium and sodium contents of animals and their composition. Sect. 3, pp. 1-18. In *Selected Papers of Aust C.S.I.R.O. Symp. on Carcase Composition and Appraisal of Meat Animals.* (Melbourne: C.S.I.R.O.).

——— (1964).—Assessment of body composition in the live animal. *Proc. N.Z. Soc. Anim. Prod.* **24**: 77-89.

LAWES, J. B. and GILBERT, J. H. (1859).—Experimental enquiry into the composition of some of the animals fed and slaughtered as human food. *Philos. Trans.* **2**: 494-680.

——— (1861).—On the composition of oxen, sheep and pigs and of their increase whilst fattening. *J.R. Agric. Soc.* **21**: 433-488.

LAWS, R. M. (1953a).—The elephant seal (*Mirounga leonina,* Linn.). I. Growth and age. *F.I.D.S. Scientif. Rep.* **8**: 1-62.

——— (1953b).—A new method of age determination in mammals with special reference to the elephant seal (*Mirounga leonina, Linn.*). *F.I.D.S. Scientif. Rep.* **2**: 1-11.

——— (1956a).—The elephant seal (*Mirounga leonina,* Linn.). II. General, social and reproductive behaviour. *F.I.D.S. Scientif. Rep.* **13**: 1-88.

——— (1956b).—The elephant seal (*Mirounga leonina,* Linn.). III. Physiology of reproduction. *F.I.D.S. Scientif. Rep.* **15**: 1-66.

LING, J. K. (1965a).—The integument and moulting process of the Southern Elephant Seal, *Mirounga leonina* (Linn.). Ph. D. Thesis, Australian National University.

——— (1965b).—Hair growth and moulting in the Southern Elephant Seal, *Mirounga leonina* (Linn.). In *Biology of the Skin and Hair Growth.* Ed. Lyne, A. G. and Short, B. F. (New York: American Elsevier Publ. Co.).

MCCANCE, R. A., FORD, E. H. R. and BROWN, W. A. B. (1961).—Severe undernutrition in growing and adult animals. 7. Development of the skull, jaws and teeth in pigs. *Brit. J. Nutr.* **15**: 213-224.

MARCHANT, E. C. (1925).—*Xephenon: scripta minora.* English translation: Loeb Classical Library. (London: Heineman).

MARKHAM, G. (1617).—Cavalarice; Book 1, Chap. 14. Cited by McCance, R. A. (1962)—Food, growth and time. *Lancet,* ii, 621-626.

MATTHEWS, L. H. (1929).—The natural history of the elephant seal, with notes on other seals found at South Georgia. *'Discovery' Rep.* **1**: 233-256.

MAWSON, D. (1932).—The B.A.N.Z. Antarctic Research Expedition, 1929-1931. *Geograph. J.* **80**: No. 2.

MEDAWAR, P. B. (1945).—Size, shape and age. In *Essays on Growth and Form.* Ed. le Gros Clark, W. E. and Medawar, P. B. (Oxford: Clarendon Press).

MENDES, C. B. and WATERLOW, J. C. (1958).—The effect of a low protein diet, and of refeeding, on the composition of liver and muscle in the weanling rat. *Brit. J. Nutr.* **12**: 74-88.

MURPHY, R. C. (1914).—Notes on the sea elephant, *Mirounga Leonina* (Linné). *Bull. Am. Mus. Nat. Hist.* **33**: 63-79.

NALBANDOV, A. V. (1963).—Symposium on growth: endocrine causes of growth and growth stasis. *J. Anim. Sci.* **22**: 558-560.

NEEDHAM, A. E. (1950).—The form transformation of the abdomen of the female pea crab, *Pinnotheres pisum. Proc. Roy. Soc.* B, **137**: 115-136.

PALSSON, H. (1955).—Conformation and body composition. In *Progress in the Physiology of Farm Animals.* (London: Butterworths).

PANARETTO, B. A. (1963).—The estimation of body composition in living animals. In *Selected Papers of Aust. C.S.I.R.O. Symp. on Carcase Composition and Appraisal of Meat Animals.* (Melbourne: C.S.I.R.O.).

PAULIAN, P. (1953).—Pinnipèdes, cétacés, oiseaux des Iles Kerguelen et Amsterdam. *Mem Inst. Sci. Madagascar* **8**: 111-234.

——— (1957).—Note sur les phoques des Iles Amsterdam et Saint-Paul. *Mammalia* **21**: 210-215.

POURNELLE, G. H. (1962).—The Northern Elephant Seal, *Mirounga angustirostris,* Gill, in the San Diego Zoo. *Internat. Zoo Handbook* **4**: 32-33.

RICHARDS, O. W. and KAVANAGH, A. J. (1945).—The analysis of growing form. In *Essays on Growth and Form.* Ed. leGros Clark, W. E. and Medawar, P. B. (Oxford: Clarendon Press).

RING, T. P. A. (1923).—The elephant seals of Kerguelen Land. *Proc. Zool. Soc. Lond.,* 431-433.

SCHEFFER, V. B. and WILKE, F. (1953).—Relative growth in the Northern Fur Seal. *Growth* **17**: 129-145.

SIVERTSON, E. (1941).—On the biology of the harp seal, *Phoca groenlandica,* Erxl. *Hvalradets Skrifter, Oslo,* No. **26**: ix + 166 pp.

SORENSEN, J. H. (1950).—Elephant seals of Campbell Island. *Cape Exped. Ser. Bull.* No. **6**: 1-31.

TAYLOR, ST C. S. (1958).—A linear growth process in twin cattle. *Proc. 10th Int. Congr. Genet.* **2**: 291A.

——— (1962).—Identical twins and developmental stability. *Anim. Prod.* **4**: 144-164.

WALKER, D. E. (1961).—A study of the growth and development of Jersey cattle. I. A new carcass dissection technique. *N.Z. J. Agric. Res.* **5**: 190-222.

WIDDOWSON, E. M., DICKERSON, J. W. T. and MCCANCE, R. A. (1960).—Severe undernutrition in growing and adult animals. 4. The impact of severe undernutrition on the chemical composition of the soft tissues of the pig. *Brit. J. Nutr.* **14**: 457-471.

WILSON, P. N. and OSBOURNE, D. F. (1960).—Compensatory growth after undernutrition in mammals and birds. *Biol. Rev.* **35**: 324-363.

PLATE 1.—The relative size of cows and pups changes rapidly during growth of the pup, as can be seen here. Some pups are very much smaller than their mothers, whereas others appear to be almost as large as their mothers.

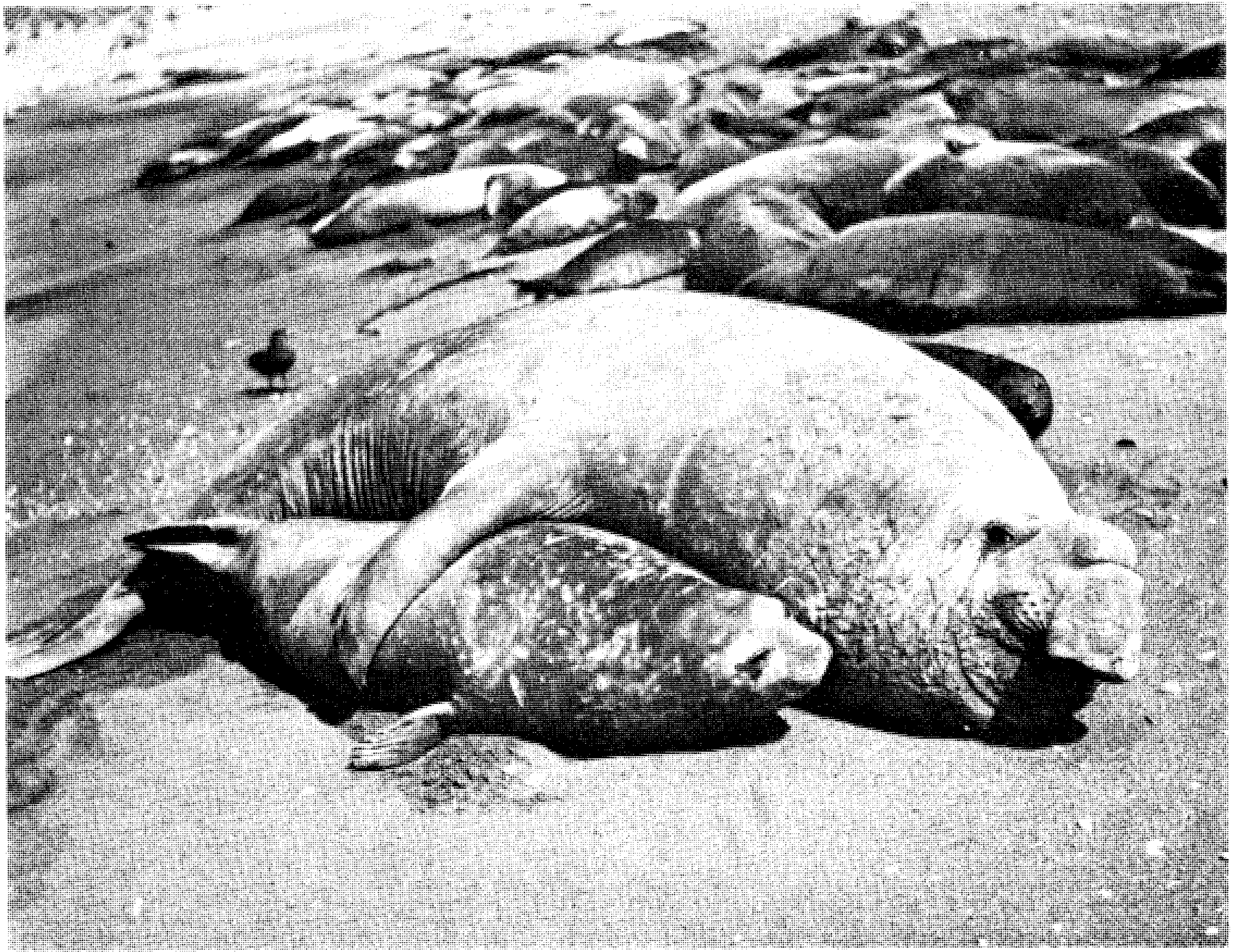

PLATE 2.—Relative size of a mature male and a mature female elephant seal at Macquarie Island. The male is approximately eight times as heavy as the female.

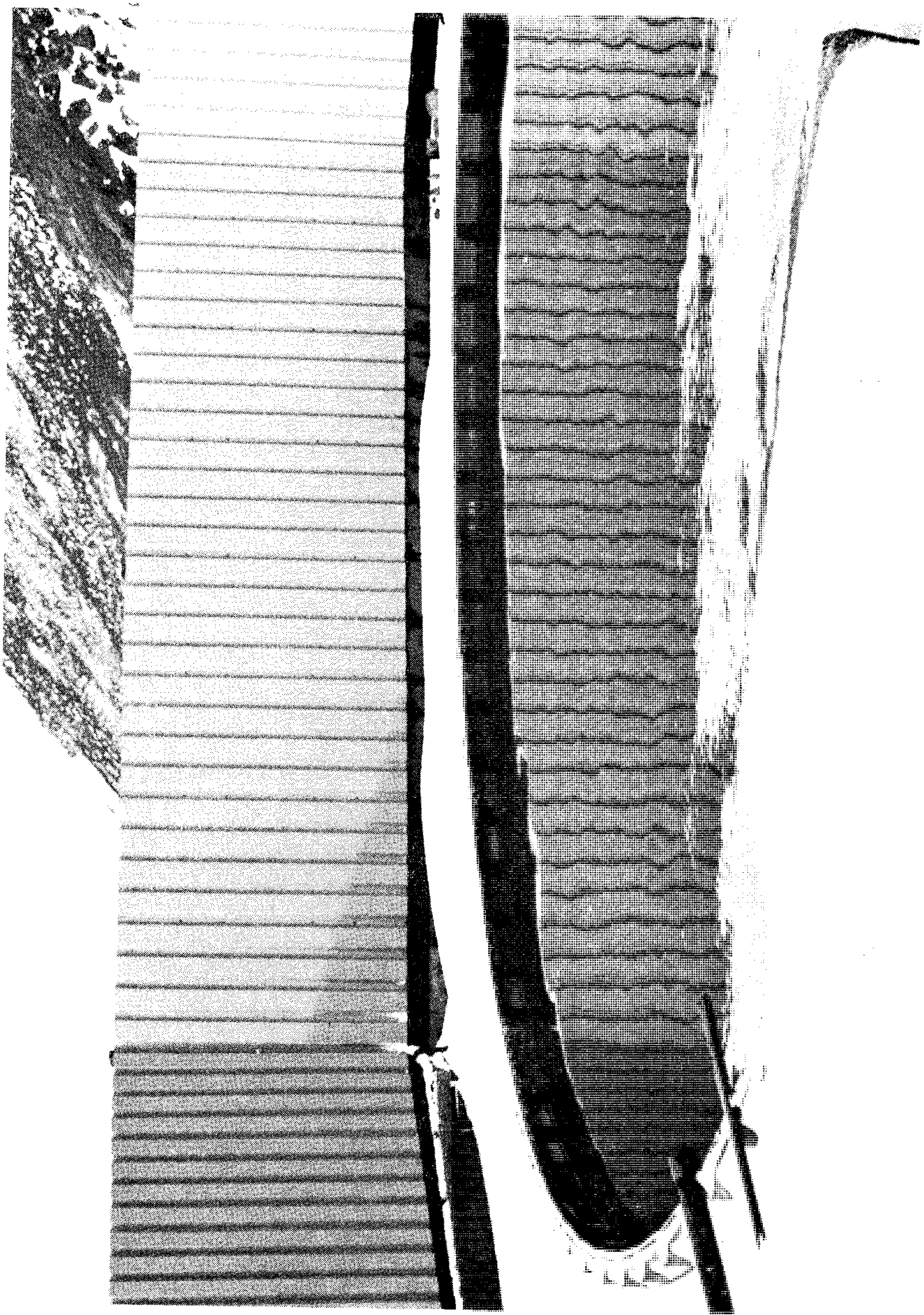

PLATE 3.—Enclosure and swimming tank for elephant seals at Macquarie Island. Photograph is taken through opened doors.