STUDIES ON THE SOUTHERN ELEPHANT SEAL, *MIROUNGA LEONINA* (L.)

V. POPULATION DYNAMICS AND UTILIZATION

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[*Manuscript received June* 22, 1962]

Summary

The breeding population of *Mirounga leonina* (L.) at Macquarie Island is stable at about 36,000 cows and 3500–4000 bulls, with an annual maximum of the order of 110,000. Survival of branded weaned pups to the fourth year of life is over 40% in both sexes: 20% of females survive to the eighth year of life, but few may live more than 12 years: 15% of males survive to the eighth year of life, but the small number of breeding males may contain individuals 20 years old. Important factors limiting the world population are the number of possible breeding places in the zone of maximum food supply near the Antarctic Convergence, and the amount of food immediately around them. The logistic and biological merits of harvesting large bulls and fat weaned pups are compared: the latter merits experimental investigation, which should always precede commercial operations.

I. Introduction

Study of the population dynamics and related economic aspects of pinnipeds is somewhat impeded by the fact that most present-day populations of these gregarious species on which basic information is desirable have been seriously depleted in the past. They are still either being harvested or in process of recovery, so that data on entirely natural populations are not obtainable. The seals are a classic example of a natural resource that has been ignorantly exploited for immediate profits, frequently to the point where all or most of the capital stock has been taken. There is little or no quantitative research on normal populations to provide data on natural productivity which are the basis of rational harvesting and perhaps of advantageous manipulation of population numbers and structure. Scientific intervention has, however, radically improved commercial practices in industries based on, for example, the northern fur seal, *Callorhinus ursinus* (L.), in Alaska and the southern elephant seal, *Mirounga leonina* (L.), at South Georgia. Numbers of the former species have regained their natural ceiling through selective culling of immature bulls in place of the former indiscriminate slaughter ashore and at sea, and extensive marking (Kenyon, Scheffer, and Chapman 1954) has enabled population trends to be critically estimated (Chapman 1961). In the latter species, research leading to limitation of the annual catch and respite for one-quarter of the island each year is enabling the South Georgia population to hold its own numerically (Laws 1953, 1960; Bonner 1958). The methods and levels of exploitation of the Cape fur seal, *Arctocephalus pusillus* (Schreber), and

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the harp seal, *Pagophilus groenlandicus* (Erxleben), have been constructively criticized by Rand (1954) and Fisher (1955) respectively, to cite only two further scientific contributions towards improved utilization of pinniped stocks.

Estimates of the size of pinniped populations are quoted by Scheffer (1958). The current recuperation of *Mirounga angustirostris* (Gill) in California is being documented by Bartholomew and Hubbs (1960). The breeding populations of *M. leonina* are listed by Laws (1960), who gives tentative life-tables for exploited and natural populations of the species. Annual survival and population turnover in *C. ursinus* are discussed by Kenyon, Scheffer, and Chapman (1954) and by Chapman (1961).

Though the underlying principles are the same, the very variable life histories and habits of pinnipeds, and the different objectives and methods of exploitation, make the approach to the study of population dynamics, and the resultant advice on practices, a highly specific matter. The gregarious and polygynous fur seals and elephant seals lend themselves to population counts and marking of large samples of young, and the commercial removal of "surplus" males without impairment of breeding rate. Whether the valuable product is the natal fur of the harp seal pup, the pelt of the older fur seal, the stored blubber of the elephant seal, or the tusks of the walrus, *Odobenus rosmarus* (L.), the two requirements necessary to put commercial operations on a sound permanent footing are the study of normal population size, productivity, and turnover, followed by equally accurate study and large-scale experimentation on the effects of exploitation. The empirical methods now in use reflect the difficulty of approaching this ideal, and the unique merit of the present study of *M. leonina* at Macquarie and Heard Islands is that good data can be obtained from these large, balanced, and now undisturbed populations for comparison with South Georgia and as the basis for field experiments on optimal yield.

In this paper the natural survival of pups of *M. leonina*, branded by members of the Australian National Research Expeditions at Macquarie Island during 1951–1961, is discussed and other implications for commercial sealing are considered.

II. Population Size

The elephant seal population of Macquarie Island remained stable during 1950–1960. This is shown by the counts of bulls (including both breeding bulls and bachelors), cows, and pups made in the Isthmus Study Area in ten breeding seasons (Table 1) and on the northern beaches in four seasons (Table 2). These figures are reasonably good and consistent, and based on large enough samples to be considered reliable. Some low numbers are attributable to early dates for the counts, but the high bull count in 1959 was caused by an unusually large attendance of the youngest bachelor bulls.

A pup count between October 25 and November 8 is near to the total number of pups weaned in the area. A bull count made on October 10 is about 80% of the maximum reached in early November: a cow count on the same date is about 95% of the mid-October maximum, which is still slightly less than the total number breeding in the area, since some cows have left and others are still to come. The total numbers of bulls and cows breeding in the Isthmus Study Area are estimated at about 650 and 5500 respectively.

TABLE 1
BREEDING SEASON COUNTS OF ELEPHANT SEALS IN ISTHMUS STUDY AREA, MACQUARIE ISLAND

Year	Adults				Pups	
	Date	Bulls	Cows	Cow/Bull Ratio	Date	Number
1950	Oct. 5–7	465	4283	9·2	Oct. 19*	3854
1951	Oct. 9	414	4668	11·3	Oct. 9*	3260
1952	Oct. 9	464	4995	10·8	Oct. 30	3894
1953	†	†	†	†	†	†
1954	Oct. 10	512	5848	11·4	Nov. 7–9	4752
1955	Sept. 16*	394	†	†	Oct. 22	4092
1956	Oct. 12	506	5364	10·6	†	†
1957	Oct. 10	469	4630	9·9	Nov. 5	5116
1958	Oct. 10	502	5389	10·7	Oct. 26	4131
1959	Oct. 9	705	4316	6·1	Nov. 6	4127
1960	Oct. 10	412	5271	12·8	†	†

* Date too early for number to be comparable with others.
† No count.

Three counts have been made round the whole island. On November 15–22, 1949, there were 40,447 pups, a total that seems high by comparison with the others: it is possible that some 14-month old seals were included. On November 5–12, 1952, there were 33,730 pups; on October 5–17, 1959, 35,441 cows and 4753 bulls. The 1952 pup count and 1953 cow count are consistent, if a mortality of between 5 and 10% of pups is assumed, with a provisional total of 36,000–37,000 breeding cows. If the bull/cow ratio is the same over the whole island as on the Northern

TABLE 2
BREEDING SEASON COUNTS OF ELEPHANT SEALS ON NORTHERN BEACHES, MACQUARIE ISLAND

Year	Adults				Pups	
	Date	Bulls	Cows	Cow/Bull Ratio	Date	Number
1955	—	—	—	—	Oct. 22–27	8186
1956	Oct. 12	991	10243	10·3	—	—
1957	Oct. 10–11	872	9966	11·4	Nov. 5–6	9709
1958	Oct. 10	993	10304	10·4	Oct. 26	8600
1959	Oct. 5–11	1237	9169	7·4	Nov. 6–8	9232

Beaches, in a normal year as in 1959, the normal number of bulls on October 10 is about 3350 and the normal maximum number of bulls is about 4000.

These figures are higher than those given (Carrick and Ingham 1960) before the 1959 counts were available. The provisional total population of 110,000 seals in November must be regarded as a minimum figure.

The breeding population of Heard Island is estimated at 23,000 cows and 2000 bulls, on the basis of six annual counts of the Four Bays Study Area; a reliable count of 1451 bulls, 17,688 cows, and 17,664 pups in the area containing 90% of the island's seals, on October 27–29, 1949; and a whole-island count of 13,279 pups in early December 1951 (when they were already leaving the island).

TABLE 3

SURVIVAL OF BRANDED ELEPHANT SEALS TO 8 YEARS OLD, MACQUARIE ISLAND

The most reliable figures are in bold type: those obviously too low, owing to inadequate search for branded seals in some years, are in brackets

Age (Years)	Group	Survival			
		Males		Females	
		Number	Percentage	Number	Percentage
2	MF+MJ	234	(39·5)	226	(42·0)
3	MD	73	(22·5)	98	(33·5)
4	MA	101	**40·1**	115	**46·5**
5	MA	80	31·7	107	43·1
6	MA	67	**26·5**	99	**39·5**
7	No data				
8	MA	39	**14·0**	51	**20·5**

The total population at the end of the breeding season is thought to be of the order of 85,000 (Carrick and Ingham 1960).

III. Survival in the Macquarie Island Population

The sex-ratio of 5202 pups branded at Macquarie Island is 53·2% males to 46·8% females: that of 1486 branded at Heard Island is 52·7% males to 47·3% females. The slight excess of males in these weaned pups may be due to a greater pre-weaning mortality of the smaller and lighter females, acting on a sex-ratio at birth of 50 : 50.

Table 3 gives the percentage survival, up to the eighth year, of Macquarie Island seals, based on records of branded seals, especially the oldest (MA) group. Observations in 1959 necessitate revision of earlier figures (Carrick and Ingham 1960). The most reliable figures are those in bold type, though these are still subject to confirmation or revision. The number of individuals seen in any year in the study area is lower than the number surviving; searches during the next 2–3 years reveal others of the same year group and so increase the calculated survival. Since there are few records from 1960 and 1961, the eighth-year survival (based on 1959 records) may be higher than that calculated.

Survival to the second and third years of life appears low, because most records are made in the Isthmus Study Area whereas these young seals are dispersed round the island and abroad (Paper III). In the third year, the apparent survival of females, which are approaching maturity and returning towards their birthplace, is higher than that of males, which still have at least three immature years.

Provisionally, mortality is likely to be 40–50% in both sexes in the first year of life: in females it is low from the fourth to the sixth or seventh years but may increase thereafter: in males it is constant, but higher than in females, from the fourth to at least the eighth year. A much longer period of thorough observation is needed to complete the data on survival, especially in males.

IV. Causes of Mortality

Deaths of pups are caused by: stillbirth (rare); starvation after separation from the cow (probably the most frequent cause); trampling and crushing by bulls; drowning when large harems are invaded by high seas; after weaning, molestation by bachelor bulls (Paper IV). Pups in crowded harems develop skin disease, but this is not fatal. The mortality rate varies widely, being greatest in large harems on narrow beaches and least in small harems: the overall rate at Macquarie Island is probably 5–10%.

In the first year there is some mortality from malnutrition in inefficient food-finders. During July–November 1957, 16 yearlings, with no reserves of blubber, were found dead in the Isthmus Study Area: dissection of one showed no obvious cause of death. Two branded 1-year olds (MK AX and MK MR) are known to have died in this way.

The killer whale, *Orcinus orca* (L.), is an important predator of the species. Seals from 6–7 ft long to males 11–12 ft long haul out bearing fresh wounds or tooth marks, in a curving pattern 3 ft or more across (Plates 2 and 3). Wounded yearlings are rarely, if ever, seen, and as the newly independent animal is the most vulnerable to predators, it seems that they are unable to escape at all. Breeding bulls are not seen with fresh wounds, being presumably too large or too swift for attack.

The elephant seal can recover from an extensive wound if it does not penetrate through the blubber. A seal 6–7 ft long (Plate 2, Figs. 1–3) had a fresh wound estimated at 1 ft by 10 in., and 3 in. deep, with accessory tooth marks; three months later it had completely healed. Damage to the fore-flipper (Plate 3, Fig. 2), which is not used in the water, is not serious: another seal had the right fore-flipper completely bitten off, but was in fair condition with the wound partly healed. Injury to the hind-flippers, the organ of propulsion, can be fatal, as shown by the emaciated condition of a seal which had lost part of both flippers (Plate 3, Fig. 1).

In two breeding seasons, mortality of cows in the Isthmus Study Area was 0·15% and 0·10%, and that of bulls 1·3% and 1·5%. Two of seven cows dying were unable to regain the water after weaning their pups, the others died in prolonged labour. One of these had a mispresentation, the head of the pup having entered the pelvic canal, but in a blind end of the uterus. Corpses have been washed ashore of cows which had drowned after labour had begun at sea. Rarely, cows are killed during attempted copulation by inexperienced bulls, which bite the head instead of the neck and crush the skull (Plate, 1 Fig. 2). Another cow may have been crushed by a bull, as the abdominal cavity and organs were full of blood, and there was no foetus.

Nearly all the bulls which die in the breeding season are bachelors, apparently in good condition and without visible external injury. One had a deep wound in the back, doubtless inflicted by a larger bull. Fights between evenly matched bulls rarely result in more than superficial injuries to proboscis (Plate 1, Fig. 3), head, neck, or back (Plate 1, Fig. 4), and sometimes the loss of an eye. Broken teeth are more serious, as infection of the jaws with inability to feed may follow, as in emaciated bulls dissected by Gourin at Macquarie Island and Paulian (1957) at Amsterdam Island.

Little is known of diseases of elephant seals. An 11-ft male had a 68·5 lb tumour originating in a thoracic vertebra. Csordas noted four seals suffering from skin diseases (Plate 1, Figs. 5 and 6), one of which had lost hair and epidermis from an area of about 3 by $1\frac{1}{2}$ ft.

V. Discussion

The evidence given in this and preceding papers of the series enables a reasonably clear picture of the population ecology of *M. leonina*, especially at Macquarie Island, to be obtained. Survival and breeding are optimal in a circumpolar zone in the region of the Antarctic Convergence, owing to the large biomass of zooplankton that is seasonally constant but descends to deeper levels in winter (Foxton 1956). Beaches suitable for harem formation are scarce in this zone, and breeding is restricted to scattered islands which probably support more or less self-contained demes. The breeding population of small or heavily glaciated islands near the Convergence is limited by the beaches, so that Heard Island has a smaller population than Macquarie Island though both are in the same zone, while the small and precipitous Bouvetoya can accommodate only a few seals. Where there is adequate beach space, as at Macquarie Island, the breeding population is limited to the number of males and females that the adjacent feeding zone will allow to come ashore in peak physical condition for the strain of the breeding fast. It is this which limits the population of islands such as Campbell Island and Gough Island, which are otherwise suitable but are on the margins of the optimal feeding zone. The wide dispersal during the winter will, despite predation, ensure survival of a large non-breeding population that cannot gain entry to the feeding zone adjacent to the island where competition is greatest. There follows a considerable deferment of breeding beyond the age of puberty, so that both the natural population size and productivity are limited by insufficient breeding places in the zone near the Convergence. The aquatic part of this picture is inferred from terrestrial data on breeding and dispersal.

Breeding rate and success are relatively high, and survival of pups branded after weaning shows that at least 40% of each sex survive into the fourth year. In the male, there follows a rapid fall to about 25% in the sixth year and about 15% in the eighth; fighting during the testing years of adolescence would explain this. Successful males, with secure social status and immune from killer whales, then appear to survive with a much slower mortality rate to 20 or more years old. In the female, on the other hand, there is a 40% survival to the sixth year, the age of maximum breeding, and a fall to 20% in the eighth year, with probably a steady decline thereafter so that the average breeding female is unlikely to live more than 10 years. These figures differ from the provisional life-tables given by Laws (1960).

In this system there are two surpluses that could be harvested without detriment to the breeding stock and rate. About half of each sex succumb during the first year, and a further quarter or more of the males play no part in reproduction. At what age and in what manner can these surpluses be taken so as to ensure the maximum yield of blubber with minimum disturbance, especially to breeding, and without adverse long-term effects on the population? In addition to the quantitative aspects of relative numbers in each age-group and total amount of blubber obtainable from each, there are behavioural factors that cannot be ignored without loss, especially if breeding cows are disturbed. (Rand (1954) describes adverse effects of sealing operations on breeding cows, even where none are killed.) Also different regimes of harvesting require quite different logistic arrangements.

It is convenient to consider first the practice of removing a quota of adult males above a stated length. Limitation of the kill to an annual number that keeps the male population stable is not difficult, but sealers naturally take the largest animals and so reduce the average age and size, as at South Georgia. It seems biologically undesirable to eliminate the older bulls altogether, in view of their greater proficiency as beachmasters. The younger bulls are physiologically potent, though there is some doubt whether they are quite as adequate throughout the copulation period as older bulls; but removal of the males most experienced in copulation and harem management (skills acquired after puberty) must surely reduce reproductive efficiency. These bulls have to be taken as they haul out laden with blubber either to breed in September–October or to moult in March–April. If they are taken in or near harems it is difficult to see how disturbance of pregnant and parturient cows can be avoided; apart from the risk of immediate loss of pups and perhaps of cows, a breeding colony reacts to interference at this phase by moving elsewhere, as has happened at South Georgia (Laws 1960). It would appear that there are logistic or other difficulties in the way of autumn operations, but these would still not ensure retention of old bulls. Owing to their less synchronized haul-out habits, and intermixing with other ages and with cows, it is not feasible to select younger bulls.

Harvesting of fat weaned pups as they leave the harems deserves serious consideration. It can be entirely safe from both numerical and behavioural viewpoints. The cow–pup bond is broken and the former has returned to sea. The pups are very fat and, pending experimental evidence, it might be possible to take up to 80% of male and up to 50% of female weaned pups without affecting future breeding stocks and success. The normal age-range of each sex would be maintained, but reduction of the youngest males to nearer their eventual breeding number could make part of their food resources available to cows and enable the latter to breed at puberty or even to increase their survival rate. The enhanced breeding rate would increase the harvest of pups, which in turn would maintain population size at the optimum density for maximum breeding. Good comparative data on production of blubber, bone, and meat from weaned pups and bulls are now required, but a rough estimate, along with other practical considerations, warrants exploration of this proposal. The taking of newly weaned mammals and newly fledged birds is proven practice, and the elephant seal offers an unusual opportunity because of its gregarious and synchronized seasonal breeding, the rapid growth and fat condition of the pup, and the large surplus of males.

These tentative figures may exceed the maximum permissible take if the causes of juvenile mortality during the first few months of free life are not approximately density-dependent. For example, intrinsic weaknesses that prevent some individuals from learning in time how to live would cause the same proportion of losses, and even predation might exert something like its usual toll until the first-year seals had dispersed from inshore waters. Imponderables such as these mean that large-scale field trials are necessary before firm advice on levels and methods of harvesting is possible, and the Heard Island population would be an appropriate one for them. Assessment of the effects of commercial operations should be continued permanently, as at South Georgia, using the observations of inspectors, data on numbers taken, counts of breeding adults, and teeth samples to determine changes in population structure.

VI. Acknowledgments

The observations for this study were made by members of the Australian National Antarctic Research Expeditions: those responsible are listed in Paper I of this series. The section on causes of mortality is based on observations and dissections by Drs. S. E. Csordas, A. A. Gourin, A. M. Gwynn, and Z. Soucek. Dr. Csordas also took the photographs, except for Plate 1, Figure 2, which is by K. Keith.

VII. References

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Explanation of Plates 1–3

Plate 1

Injuries and Disease in Elephant Seals

Fig. 1.—Stillborn pup, still in foetal sac. Stillbirths are less than 1% of all births.

Fig. 2.—Head of cow killed during attempted copulation. The marks of the bull's canine teeth are visible behind her eyes.

Fig. 3.—Head of breeding bull with torn and nectrotic proboscis, the result of a fight.

Fig. 4.—Scars on a bull's back, caused by the bite of a stronger bull which had defeated it.

Fig. 5.—Immature male with an unusual spotted coat, apparently caused by skin disease.

Fig. 6.—Immature female with skin disease: the epidermis has sloughed off over an area of 3 by 1½ ft.

Plate 2

Injuries to Elephant Seals 2–5 Years Old, Caused by Predators

Figs. 1 and 2.—Male 6–7 ft long with fresh superficial wound on back, caused by killer whale.

Fig. 3.—The same seal a week later, the wound healing. Three months later it had healed completely.

Fig. 4.—Young male in good condition with a suppurating wound of unknown origin.

Figs. 5 and 6.—Head of an immature seal with suppurating wounds caused by killer whale.

Plate 3

Injuries by Killer Whales on Male Elephant Seals 4–8 Years Old

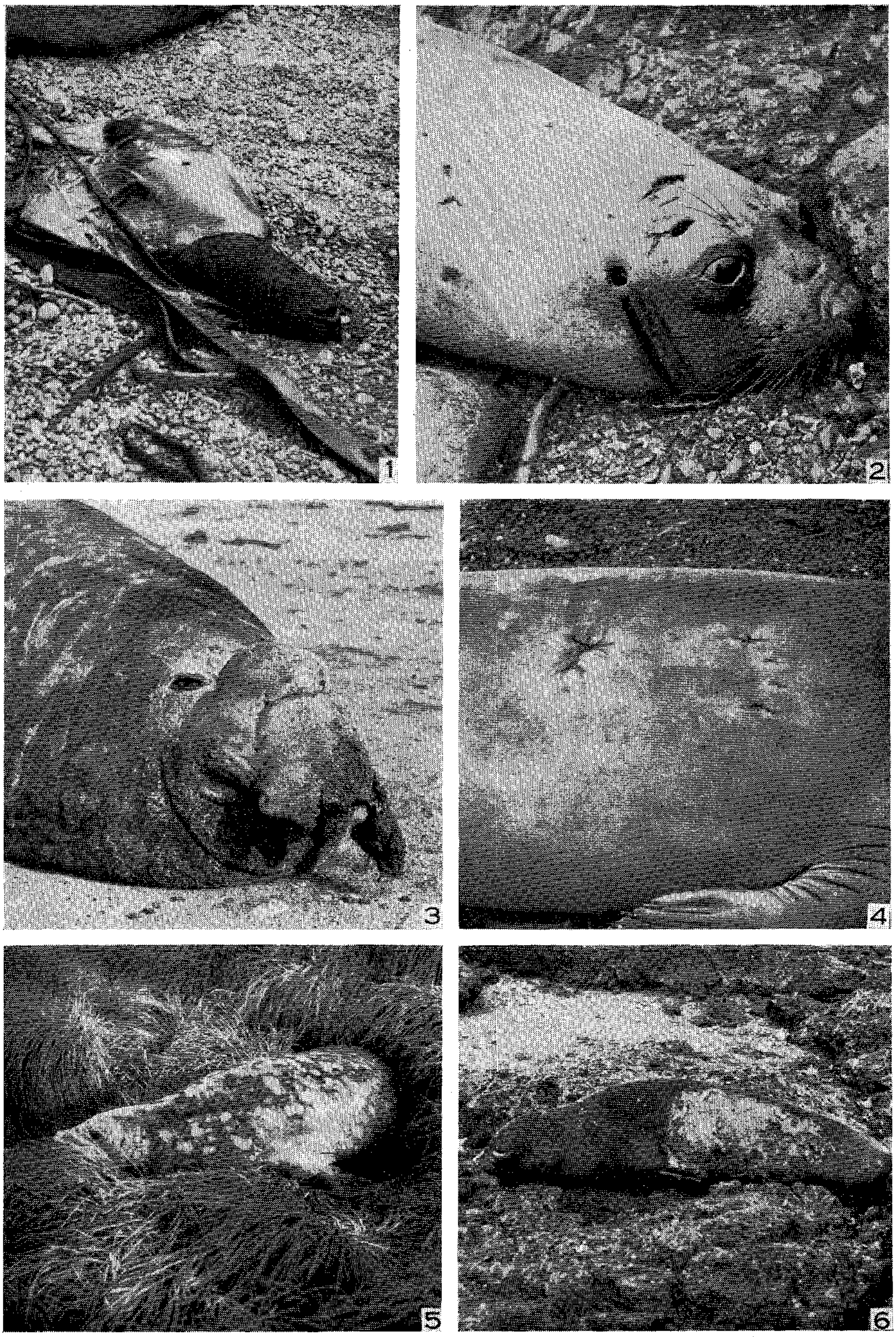
Fig. 1.—Hind quarters of emaciated and dying seal whose hind flippers have been bitten off by a killer whale, and whose swimming is seriously impaired.

Fig. 2.—Wound nearly healed on a 10-ft male.

Fig. 3.—Wounded right foreflipper of 8–9 ft male, which later recovered.

Fig. 4.—Partly healed wound on the side of a 12-ft male.

STUDIES ON THE SOUTHERN ELEPHANT SEAL. V



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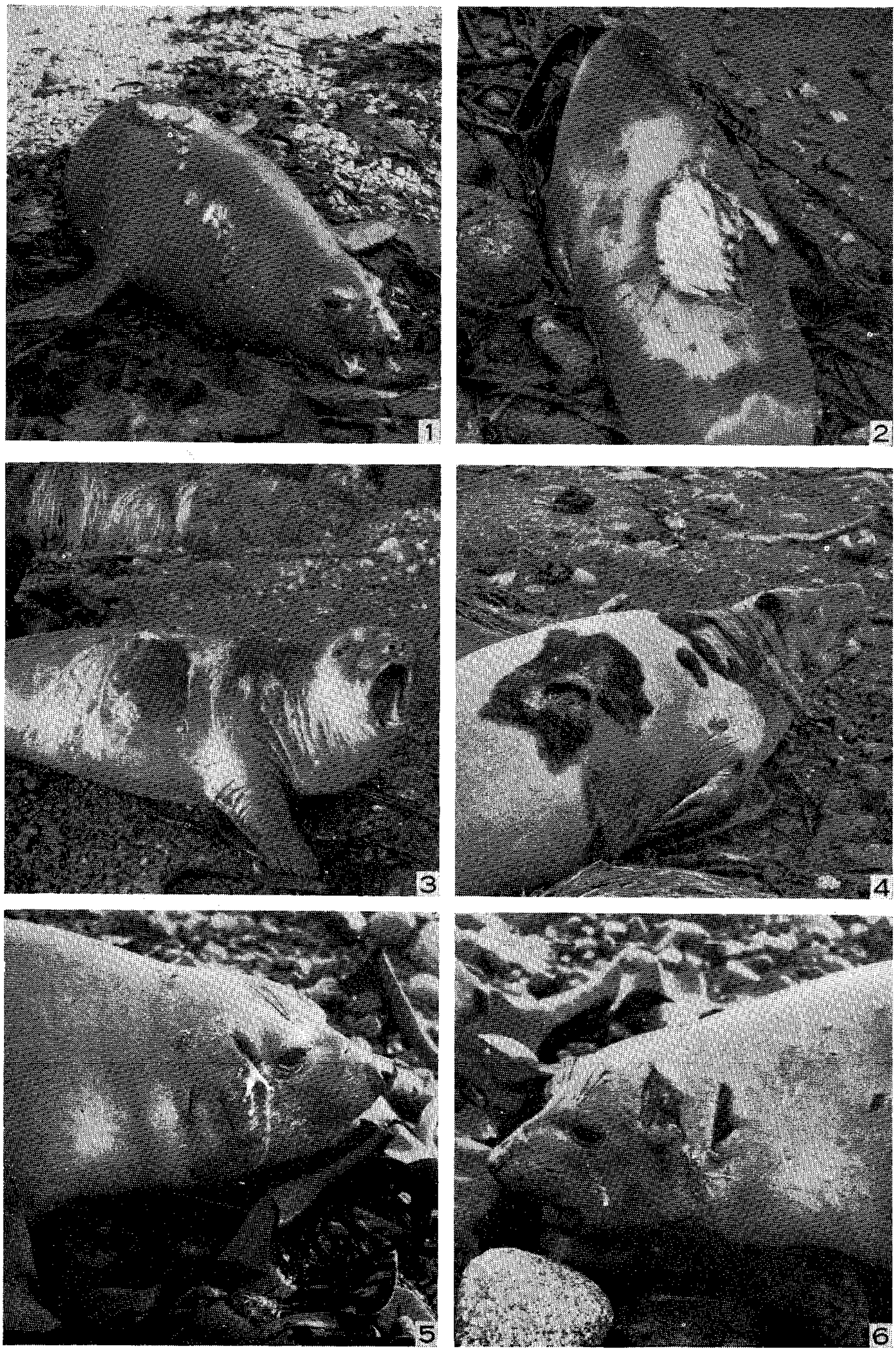

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