THE ECOLOGY OF THE SOUTHERN ELEPHANT SEAL *MIROUNGA LEONINA* (LINNAEUS 1758), AT MARION ISLAND

by

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ABSTRACT

Southern elephant seals at Marion Island inhabit the leeward coasts, where the beaches have a flat profile and smooth surface. Bulls hauled out in August, pregnant cows hauled out in September reaching peak numbers in mid-October, and pups reached peak numbers in mid-November. The arrival and departure of the cows was well synchronized. The moulting season extended from November to April, different age and sex groups moulting at different times. Moulting adults and subadults moved inland, where they first caused and then maintained changes in the vegetation and topography of the moulting areas.

Tagging was carried out over four years, effort being concentrated on the pups. No long distance movement to other island groups was recorded, and no females tagged as pups matured during the three years of observations. Some tagged beachmasters maintained their status at the same sites for three consecutive seasons. Harems of 60 – 130 cows included an assistant beachmaster, and larger harems contained two assistant beachmasters.

The breeding population (including pups) declined from 1951 to 1975 ($r = -0{,}048$), and present population size is approximately 4 500 seals. Mortality in the first and second years of life was high with female recruitment to the third year being the apparent population limiting factor, and appeared to be the result of killer whale predation. Net reproductive rate was less than one (R_o = 0,69), and the mean generation interval (T) was 6,65 years.

Pup development was similar to that which occurs elsewhere, but age specific body mass and size from birth to 40 days of age were the smallest so far recorded for this species.

ACKNOWLEDGEMENTS

I wish to sincerely thank Dr. J.A.J. Nel and Prof. J.D. Skinner for their guidance and support throughout this study, which was made possible by the Department of Transport, who provided the financial and logistic support for which I am extremely grateful.

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I am grateful to the Captain and crew of the RSA who provided the means to visit Prince Edward Island, and to the members of the Public Works Department teams who built the mammal and bird laboratory on Marion Island, as well as various pieces of field and laboratory equipment for this study. I would also like to thank the Captain and crew of SAS Protea (South African Navy) and members of Flight 22 (South African Airforce) who's logistic support made erection of the field huts possible in November/December 1974.

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CHAPTER 1

GENERAL INTRODUCTION

Introduction

The Prince Edward Islands (Figure 1), consisting of Marion Island (46° 54'S, 37° 45'E) and Prince Edward Island (46° 38'S, 37° 57'E), lie approximately 2 300 km southeast of Cape Town. Both islands were annexed by South Africa from Britain in the summer of 1947/48, and a meteorological station (46° 53'S, 37° 52'E) was established on Marion Island in March 1948 (Marsh 1948, Van Zinderen Bakker Sr. 1971).

Southern elephant seals *Mirounga leonina* (Linn.) inhabiting these islands were exploited by man during the last and early part of the present centuries. According to Rand (1962) sealers were living on Marion Island at the turn of the century. Marsh (1948) stated that the firm Irvin and Johnson made an attempt in October 1930 to resume sealing, but their ship "Kildalkey" had to return without success, mainly because of bad weather. Rand (1962) believed this to be the last attempt at sealing on Marion Island, but noted that one account of the operation gives a catch of 151 bulls and 1 339 cows, indicating that it was not unsuccessful. These catch figures may however refer to fur seals *Arctocephalus tropicalis* (Gray 1872), which were slaughtered by the sealers for their pelts. Shaughnessy (1976), in discussing the exploitation of the Amsterdam Island fur seal *(A. tropicalis)* at Marion Island noted that, "unfortunately, the Cape Town based sealing company (Irvin and Johnson, Shaughnessy *pers. comm.*) that was most active in sealing on the Prince Edward Islands during the early years of this century recently informed the Cape Town Archives that they had long since destroyed their sealing records." It is therefore no longer possible to determine the number of elephant seals taken from Marion Island by this company, and since few sealers in any event kept reliable records, the general history of elephant seal exploitation on Marion Island remains somewhat obscure and confusing. All that remains today from the elephant sealing era are a few large three-legged iron "trypots" used to render the blubber, and scant remains of stone and wood huts.

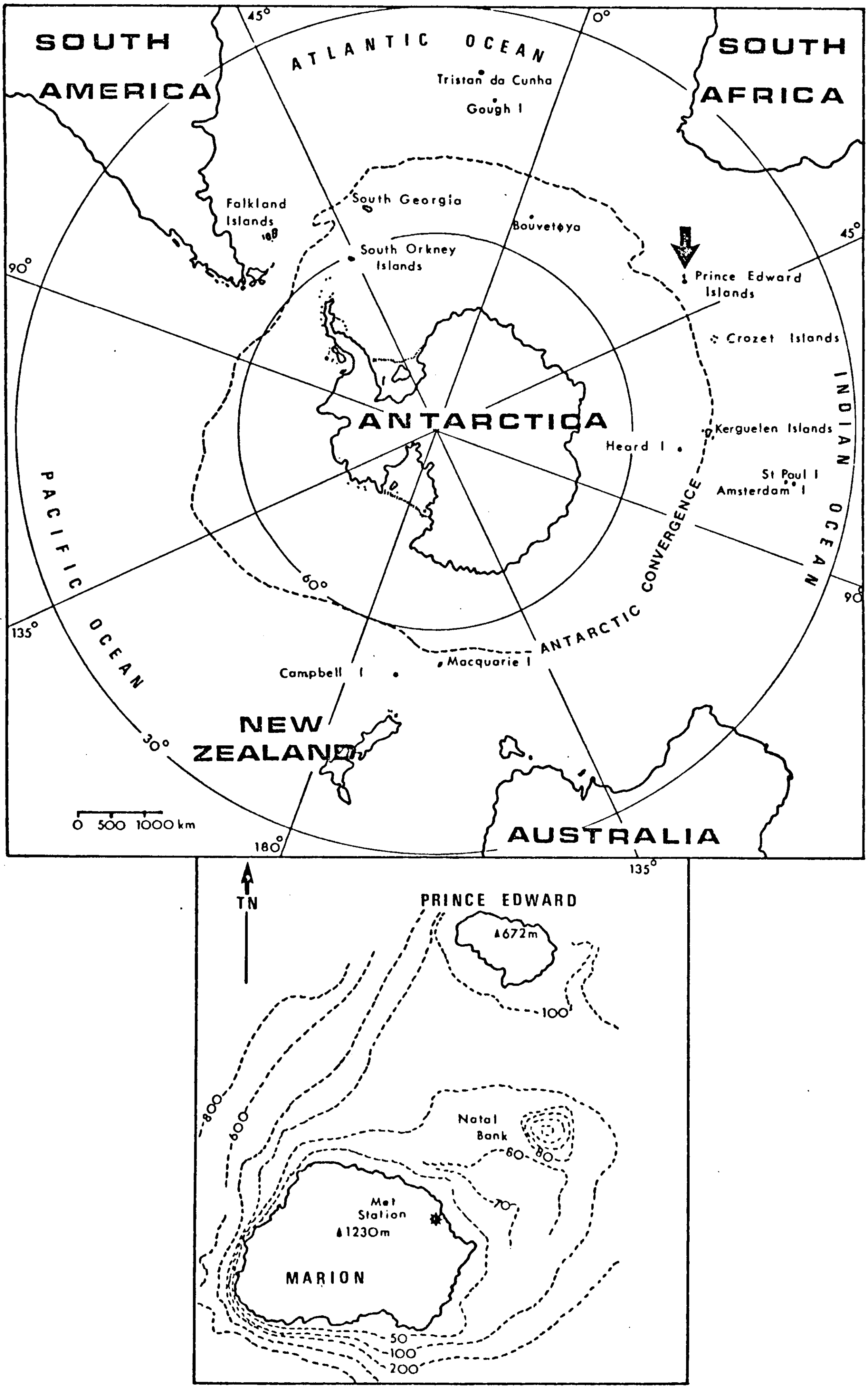


FIGURE 1

The Antarctic and Sub-Antarctic regions with the position of the Prince Edward Islands indicated. The relative sizes and positions of Marion and Prince Edward Islands are shown below (ocean depth in metres).

Assuming that the last sealing expedition did occur in October 1930, the elephant seal population can be considered to have remained undisturbed since then, and this date taken as the start of the population's recovery.

History of Research

Rand (1955, 1962) and La Grange (1962) were the first to study the elephant seals on Marion Island. Rand (1962) paid more attention to the population status, while La Grange provided limited data only on the seasonal pattern of occurrence. In 1952 Van Zinderen Bakker Sr. (1971) sought support for botanical and palaeobotanical research on the Prince Edward Islands, and at a later date the Zoological Society of Southern Africa proposed a project for zoological research on the islands. Professor J.M. Winterbottom, at that time Director of the Percy Fitzpatrick Institute for African Ornithology, drew up plans for ornithological research only, to co-ordinate with the botanical and geological proposals. In January 1965 a team of biologists comprising botanists, a palynologist, a geologist, a surveyor, a marine biologist, and an ornithologist landed on Marion Island to conduct the first detailed biological investigations. Logistically this programme was supported by the Department of Transport, and was officially recognized and co-ordinated by a biology subcommittee of the South African Scientific Committee for Antarctic Research (SASCAR). The results of this programme were published by Van Zinderen Bakker Sr., Winterbottom and Dyer (1971) and only brief mention is made of the mammals. Some data on mammals were collected and published separately (Van Zinderen Bakker Jr. 1967), but the zoological effort concentrated on ornithological and marine invertebrate aspects.

Following the initial 1965/66 biological programme, two others followed in the summers of 1971/72 and 1972/73, but with slightly increased interest in censusing the seals, particularly the Amsterdam Island fur seal *A. tropicalis* (De Villiers and Ross 1976). However the elephant seals remained relatively unstudied. In April 1973 Grindley (1973, unpublished) visited Prince Edward Island and made notes on the distribution and number of elephant seals there. Although his visit was made very late in the summer haul out season, Grindley's report contains the most useful information on elephant seals since the data published by La Grange and Rand.

To increase the amount of attention being given to the mammals of the islands, SASCAR appointed the Mammal Research Institute of the University of Pretoria to initiate and co-ordinate mammal studies on the island (Condy 1975a). The present study started in 1973 and has focussed mainly on the elephant seal population. Other studies undertaken concurrently by myself and others will be reported on elsewhere. The data contained in this thesis were collected between July 1973 and May 1975, but incorporates where pertinent that data on censusing and tagging obtained for the author from May 1975 to November 1976, by the other mammal programme's biologists studying the cats and mice.

CHAPTER 2

THE STUDY AREA

Climate of Marion Island

Systematic meteorological observations have been made at Marion Island since 1948, but at only one recording station namely the Meteorological Station on the leeward east coast (Figure 2). The climate is basically marine with modifications due to the topography of the island itself, and the main features are; predominantly strong westerly winds, high relative humidity, relatively low mean temperature showing little annual and diurnal variation, abundant precipitation in the form of rain, snow and groupel ("ice rain"), and a high degree of cloudiness (Schulze 1971).

The island lies in the West Wind Drift, the speed of this current being 0,4 to 0,8 knots. An important feature in the same oceanic region as the Prince Edward Islands is the Antarctic Convergence (Figure 1), the boundary between cold more dense antarctic surface water with a relatively low saline content and warmer, less dense subantarctic water with a higher salinity. This boundary, where the dense colder antarctic water sinks below the warmer subantarctic water, is therefore characterised by a sharp change in surface temperature, in addition to a change in salinity. Its mean position in this region is 50°S Latitude (Schulze 1971) some 290 km south of Marion Island, but according to Mackintosh (*In:* Taljaard 1957) an 80 km displacement north or south is not uncommon although maximum displacement does not exceed 160 km. Occasionally therefore it could approach fairly close to Marion Island, and lower local air and sea temperatures. A summary of climatic data for Marion Island, recorded at the Station, is given in Table 1.

Topography of Marion Island

The island is 290 km^2 in area, roughly oval shaped, and has a maximum altitude of 1 230 metres (State President Swart Peak). It measures 24 km from east to west and 17 km from north to south, and has a smooth circumference of 72 km although the length of the actual coastline itself has been estimated at 120 km or more. The nearest land is I'le aux Cochons in the Crozet archipelago, 925 km to the east, apart from Prince Edward Island only 22 km to the north and which is part of the same island group.

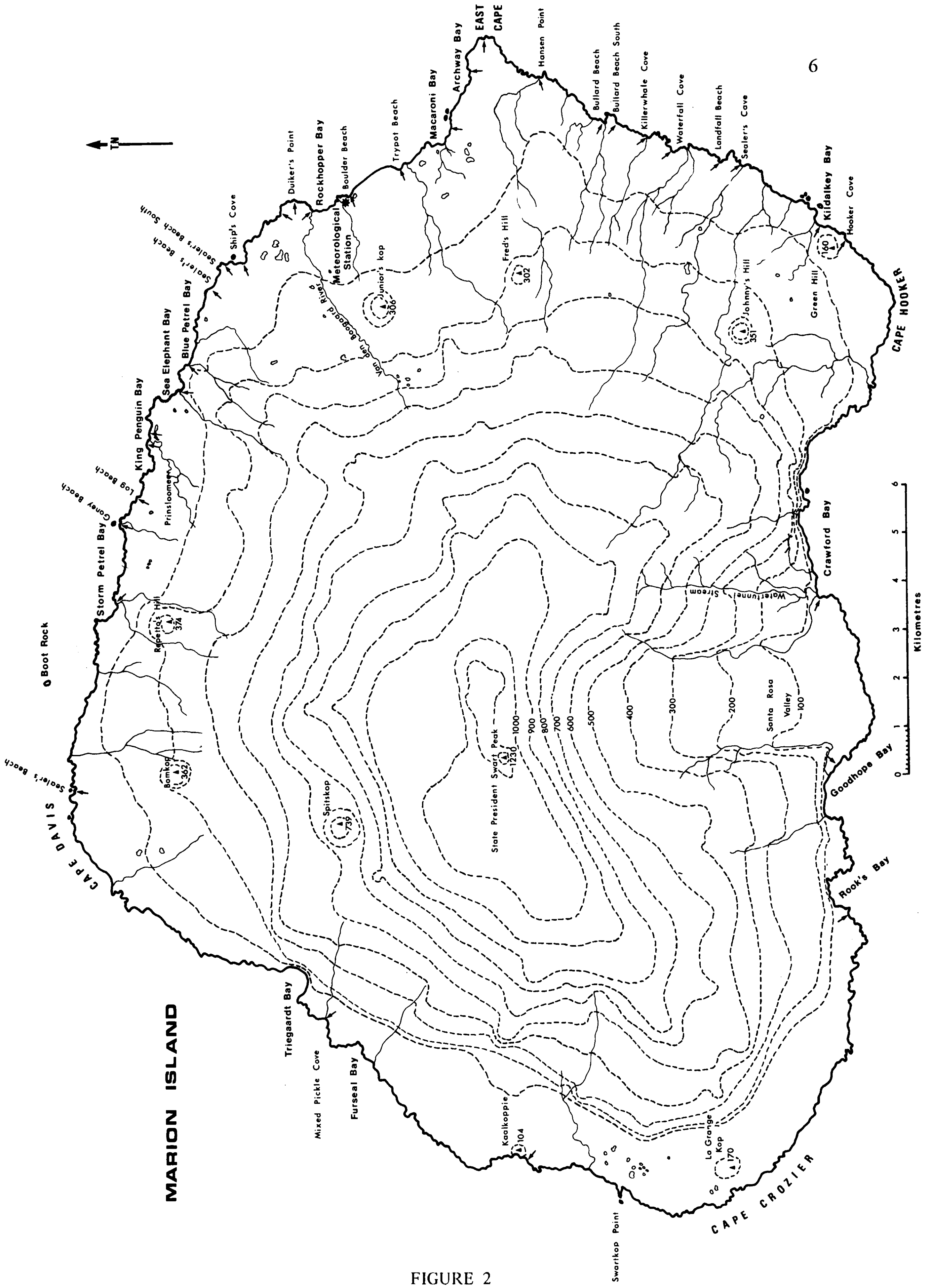


FIGURE 2

Marion Island (46°54'S, 37°45'E) showing the coastal features (↑ = beaches occupied by elephant seals) and topography (contours in metres). Drawn from a 1:50 000 map compiled by Verwoerd (Geological Survey, Pretoria), in 1968.

TABLE 1: Climatic data for Marion Island (from Schulze 1971)

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Year
Mean monthly sea surface temperature, °C. (1951–1965)	5,7	6,1	6,1	5,7	5,0	4,7	4,3	4,0	4,0	4,2	4,7	5,1	5,0
Mean monthly air temperature, °C. (1949–1960).	6,7	7,3	7,2	6,0	4,8	4,0	3,6	3,2	3,3	4,3	5,1	5,8	5,1
Mean monthly air temperature extremes, °C. (1961–1965). Maximum	16,6	16,8	16,6	14,1	12,2	11,2	10,8	11,0	11,1	13,8	15,2	14,8	
Minimum	0,7	0,8	0,5	–0,2	–1,4	–2,5	–3,5	–3,8	–3,7	–2,2	–0,9	0,0	
Mean monthly wind speed, km per hour. (over 10 years).	25,1	23,5	25,4	25,4	25,1	27,5	28,7	29,1	27,2	26,6	26,1	27,0	26,4
Frequency of days with gales (> 55 km per hour). (over 10 years)	8,7	6,2	6,5	8,0	8,6	9,5	10,7	10,3	11,4	8,4	8,4	10,1	106,8
Mean monthly precipitation, mm. (1951–1965)	222	207	225	238	249	232	231	185	201	165	196	225	2576
Mean monthly relative humdity, % (1949–1960)	81	83	83	84	83	83	84	83	83	81	81	81	83
Mean monthly cloud amount, Oktas. (1959–1963)	6,5	6,1	5,5	6,5	5,7	5,5	5,7	5,9	6,0	5,9	6,2	6,1	6,0
Mean daily radiation reaching the surface, cal. cm.$^{-2}$ day^{-1}. (over 5 years)	495	435	316	196	142	82	113	181	273	416	494	508	304
Mean daily amount of transmitted radiation reaching the surface, % (over 5 years)	49	51	49	46	53	40	49	52	51	55	52	49	50

According to Verwoerd (1971) the island has several distinct physiographic regions; a central highland, an island slope divided into relatively high and relatively low-lying areas, and a coastal plain separated in places from the island slope by an escarpment. The island slope comprises the greater part of the island, and includes the area between the coast and central highland on the east and north coasts. An escarpment, known as the Western Escarpment, and from 200 to 300 m high, runs parallel to the west coast between one and two kilometres inland. It coincides with the present coast at Goodhope Bay on the south coast and at Triegaardt Bay on the northwest coast. The coastal plain lies between the western coastline and the escarpment, and is generally 50 m above sea level. It originated by volcanic outbuilding upon a deeper wave cut platform, and is not simply a raised marine terrace.

The island is an extinct shield volcano, basaltic effusions alternating with explosive eruptions from numerous centres through its history (Verwoerd 1971). Two main volcanic stages have been distinguished, the first creating the island some 276 000 ± 30 000 years ago and the most recent stage, building on what existed and extending the coastline some 15 000 ± 8 000 years ago (McDougall 1971).

The coast formed by the more recent volcanic activity is extremely irregular with numerous small bays, smaller coves, off-shore rocks, arches and caves. Generally the land terminates in sea pounded cliffs up to 15 m high, and this type of coastline comprises the greater part of the island's coast. Where the older substrate meets the ocean the topography is very different, consisting of higher cliffs of up to 30 m in height and escarpments of hundreds of metres high. Initial irregularities have been smoothed out into wide, open bays with stony beaches along the bottom of the cliffs.

Prince Edward Island

This island lies 22 km NNE of Marion Island, is elongated in shape having a maximum diameter of 10 km, a smooth circumference of 29 km, and an area of 44 km^2. The altitude of its highest peak (Van Zinderen Bakker Peak) is 672 m (Figure 3). Little climatic data for this island are available, but it can be considered that the climate is essentially similar to that of Marion Island, although Verwoerd (1971) considered the weather to be considerably drier on Prince Edward Island despite orographic clouds being generally present.

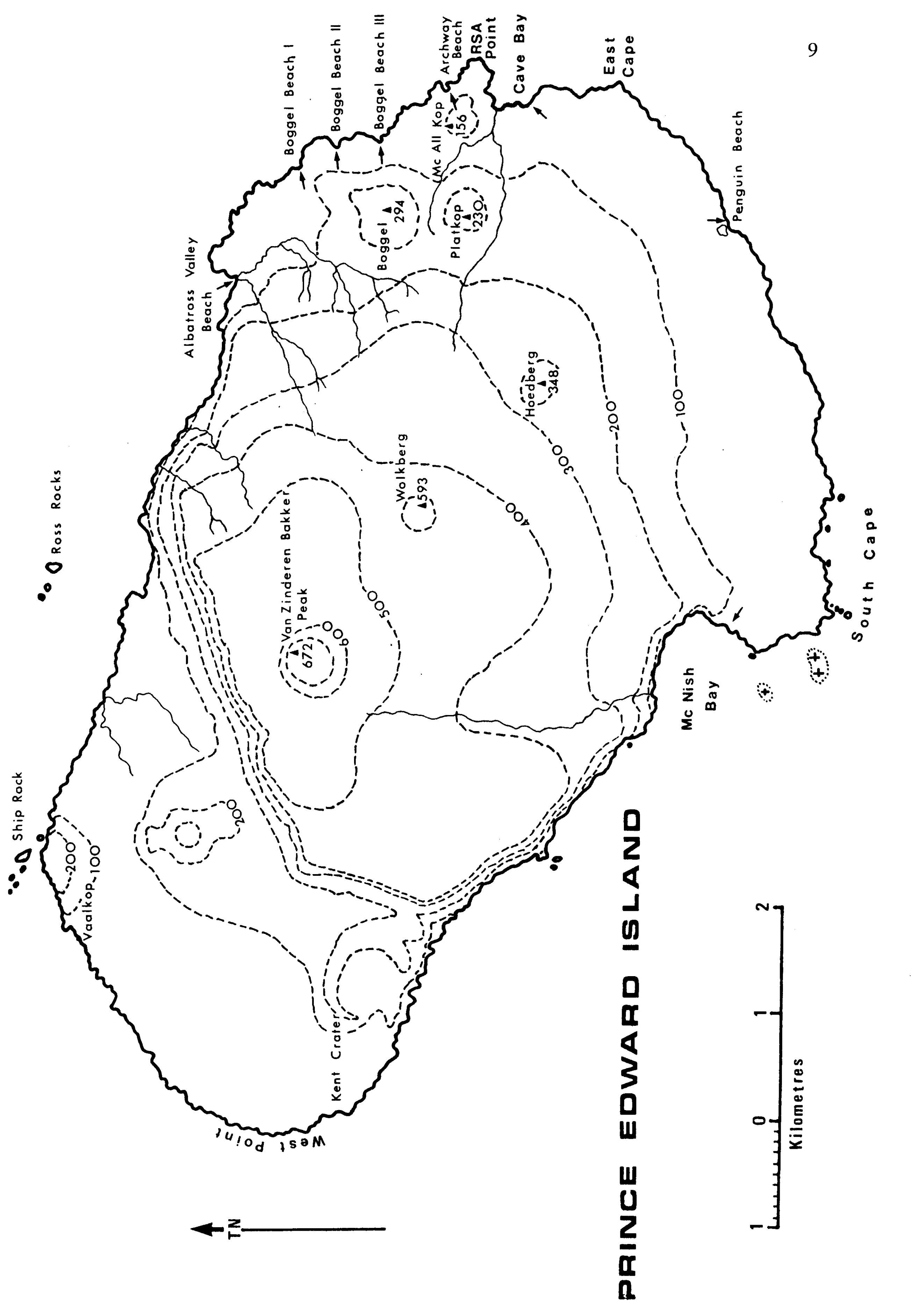


FIGURE 3

Prince Edward Island (46°38'S, 37°57'E) showing the coastal features (↑ = beaches occupied by elephant seals) and topography (contours in metres). Drawn from a 1:50 000 map compiled by Verwoerd (Geological Survey, Pretoria), in 1968.

Features that this island have in common with Marion Island are a western escarpment, a coastal plain on the west coast, an island slope on the east and northeast sides, and a central highland. According to Verwoerd (1971) this island has considerable vertical relief although its summit is only half the altitude of Marion Island.

Two main stages of volcanic activity, almost identical to those of Marion Island, are distinguishable and are of the same age as those on Marion Island (McDougall 1971, Verwoerd 1971). The two islands are described as closely related, coalescing shield volcanoes and not twin peaks of a single volcano (Verwoerd 1971). The coastline is essentially similar to Marion Island, although much more of it is formed from the younger volcanic stage and is therefore irregular and indented, more so on the leeward east coast than the windward west coast. The submarine shelf between Marion and Prince Edward islands lies at an average depth of 180 m (Verwoerd 1971), and appears to be fairly rich in marine benthic and planktonic life (Grindley 1976, unpublished).

Cartography of Marion and Prince Edward Islands

Langenegger and Verwoerd (1971) surveyed both islands and produced topographic maps of them. They retained names given by previous authors and surveyors, and added several new names. Their maps are the most recent, and were used throughout this study but some beaches unnamed by them were given unofficial names for the purpose of this study and are:

(a) **Marion Island** (see Figure 2)

Boulder Beach (46^o 52,6'S, 37^o 51,7'E), in Transvaal Cove.

Bullard Beach South (46^o 55,6'S, 37^o 52,8'E), south of Bullard Beach.

Waterfall Cove (46^o 56,4'S, 37^o 53,4'E), south of Killerwhale Cove and marked "W" on the original abovementioned map.

Landfall Beach (46^o 56,8'S, 37^o 52,2'E), north of Sealer's Cave and marked "L" on the original map.

Hooker Cove (46^o 58,6'S, 37^o 50,4'E), on Cape Hooker south of Kildalkey Bay.

Sealer's Beach, Cape Davis (46^o 49,4'S, 37^o 41,9'E).

Goney Beach (46^o 50,0'S, 37^o 46,5'E), west of Log Beach.

Sealer’s Beach South (46° 51,1’S, 37° 50,7’E), south of Sealer’s Beach on the northeast coast and north of Ship’s Cove.

Macaroni Bay South and North Beaches – the bay is centrally divided by a waterfall marked “W” on the original map, North Beach being that part of the coast north of the waterfall, and South Beach being that part of the coast southeast of the waterfall towards Archway Bay.

(b) **Prince Edward Island** (see Figure 3)

Albatross Valley Beach (46° 36,8’S, 37° 59,2’E) at the foot of Albatross Valley.

Boggel Beach I (46° 36,8’S, 38° 00’E), below Boggel.

Boggel Beach II (46° 37,4’S, 38° 00,2’E), below Boggel.

Boggel Beach III (46° 37,7’S, 38° 00,3’E), sandy beach below Boggel.

Boggel Beach I is the most northerly of the three, Boggel Beach III (sandy) the most southerly towards RSA Point.

Archway Beach (46° 37,9’S, 38° 00,7’E), below Mc All kop.

Beach Topography

The structure of the beaches on Marion Island varied considerably. On the exposed south and west coasts, which lie in the face of the prevailing wind and ocean swell, the beaches were comprised of large, sometimes massive, and often jagged boulders piled haphazardly on top of each other (Plate 1a). It appears that all but the biggest boulders on these beaches are washed away, so that with few exceptions the surface topography of the beaches was very rough and irregular. Small beaches situated in well protected coves such as Mixed Pickle Cove, at Kaalkoppie, and in Goodhope Bay (see Figure 2), had much less rugged surfaces even though they occurred on the exposed coastline. Their surfaces usually consisted of smooth rounded rocks less than half a metre in diameter (Plate 1b).

On the leeward east and north coasts which are protected by the island from the full oceanic onslaught, the majority of beaches were made up of small rounded rocks, stones, and pebbles (Plate 1c). Their surfaces were usually flat and regular, although the relief of any one beach was changed two to three times a year by heavy seas and/or the activities of elephant seals. Most beaches occurred at places where streams or rivers meet the coast (see Figure 2), and therefore they provided routes enabling the seals to move inland along the drainage lines. However some beaches occurred at the base of coastal cliffs, especially in areas where the older substrate meets the ocean, and although these beaches could be fairly wide (up to 40 m) and very long (nearly one kilometre in Macaroni Bay), they did not provide access inland (Plate 1d).

Only two sandy beaches occur on Marion Island, at Ship's Cove and Goodhope Bay. The reason why these beaches were sandy is not well understood, but since both beaches were very well protected from heavy seas the sand has remained. Occasionally following exceptionally heavy seas the sand was washed away, exposing a flat rocky substrate, but the sand was returned over a period of a few weeks following the storm. It appeared that at these two sites the ocean floor sloped much more gradually away from the coast than elsewhere.

The situation on the leeward east and south coasts of Prince Edward Island was very similar to that on the leeward coasts of Marion Island. No visit was made to the windward west coast of Prince Edward Island, but it was inspected from the sea aboard the RSA, and it appeared that although there were a few beaches, they had very rugged surfaces unsuitable to elephant seals. One small sandy beach occurs on the northeast coast (Boggel Beach III, see Figure 3).

PLATE 1

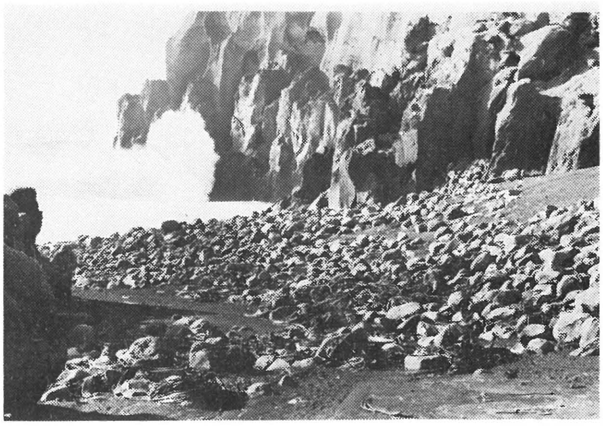
a. A typical west coast beach area (Fur Seal Bay) on Marion Island, showing a rugged and uneven profile.

b. A small atypical beach on the west coast (Kaalkoppie), occurring in a well protected cove.

c. A typical drainage line beach on the leeward east coast (Trypot Beach), showing a flat and even profile.

d. A typical leeward coast beach at the base of coastal cliffs (Macaroni Bay).

a



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CHAPTER 3

METHODS

Censuses on Marion Island

From August 1973 to December 1976 elephant seal censuses were carried out once each week at Trypot Beach and Boulder Beach. From August to January of 1974, 1975, and 1976 censuses were carried out once each week at an additional four beaches; Archway Bay, Macaroni Bay South, at the mouth of the Van den Boogaard river in Rockhopper Bay, and at Ship's Cove (Figure 4). In November 1973 and 1976 a census of the pup population was made round the entire coast, and in November 1974 and 1975 only partial counts were made. Censuses were conducted on foot and made by direct counting of all animals hauled out. All beaches and inland areas occupied by elephant seals were accessible on foot, but even when counts were made from cliff tops all adult seals were visible, largely due to their bulk. Closer approach was necessary during the pupping season to ensure accurate counting of the small pups and yearlings.

Since estimation of the number of elephant seals at any site was never necessary, no correction factors have been incorporated in the raw data to adjust for over or undercounting. Since the elephant seals remained ashore once they had hauled out to breed or moult, diurnal fluctuations in numbers hauled out did not occur, and therefore correction factors for time of counts were not necessary.

Censuses on Prince Edward Island

Two expeditions to this island were made during the study period, the first from 5 – 12 May, 1974 and the second from 19 – 29 April, 1976. Censuses were made along the eastern coastline from Albatross Valley Beach to Mc Nish Bay (see Figure 3). However bad weather prevented the census teams from crossing the Western Escarpment to census seals on the west coast.

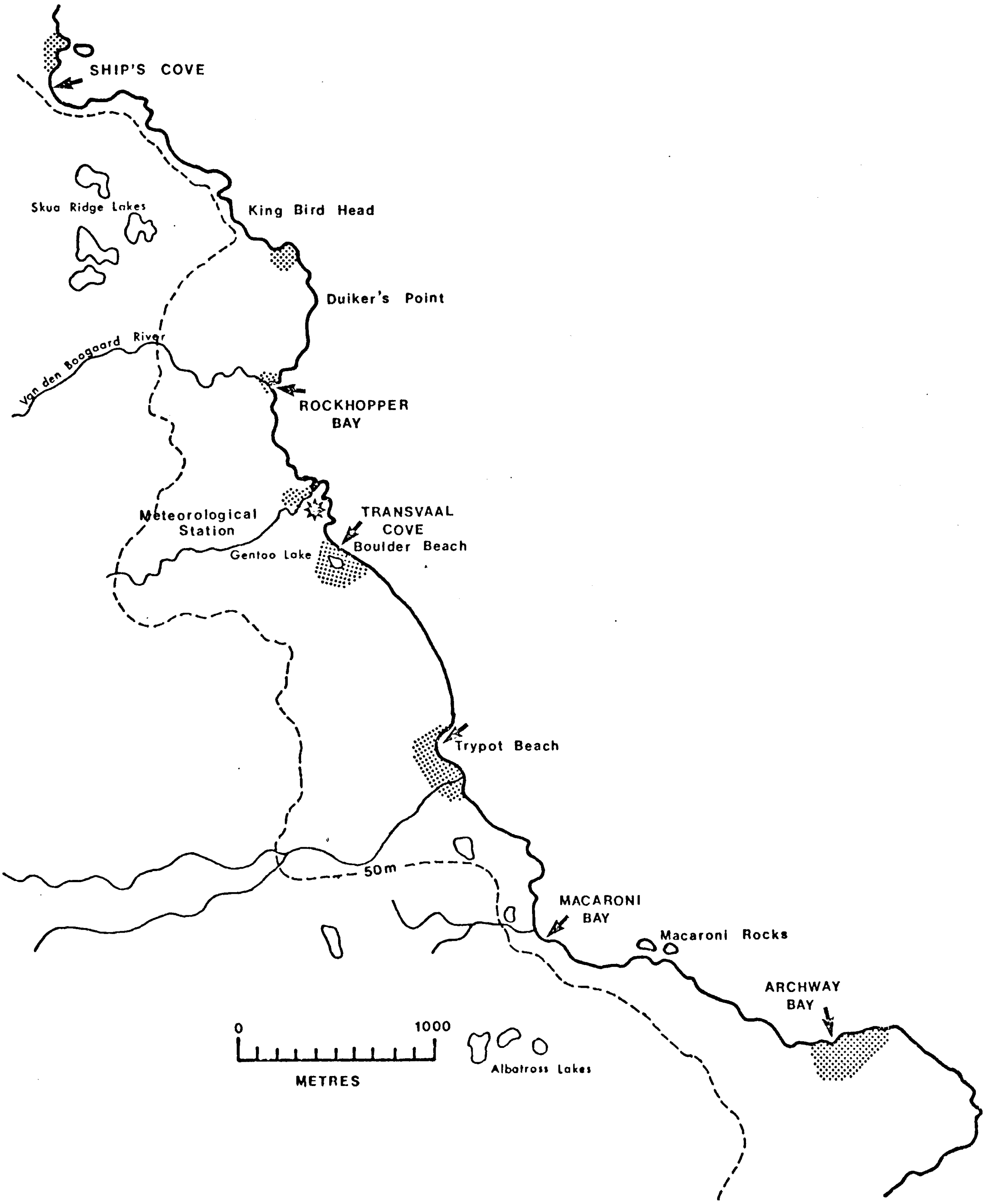


FIGURE 4

The main study area on Marion Island, showing the position of beaches (→) and moulting areas (⁙⁙⁙) censused during the once weekly counts.

Age Classification of Census Data

No animals of known age existed in the elephant seal population at the start of the study, and no seals were culled during the study. Thus morphometric data were not available to define age classes for the Marion Island population.

Age classes were however defined, being subjective but based on those defined by Laws (1953). His class I animals corresponded to the Marion Island yearling class, Class II to the animals in their second year, Class III to all subadults (in their third year), Class IV to subadult females and subadult males (in their fourth year), Class V to adult females and subadult males (in their fifth year) and Classes VI to XII to all adults in their sixth year and older. Pups were defined as being up to one month old, since most had been weaned at that age, and yearlings from one to 12 months old.

Wherever a count of elephant seals was made, the animals present were recorded in the above categories as well as according to sex when possible. Sexing adults and subadults was generally easy because of the exaggerated sexual dimorphism which exists in this species, but in the case of pups, yearlings, and second year old animals sex was recorded only when positively verified. Identification was made by observing the presence or absence of a penis vent or nipples, but the animals were not handled or otherwise disturbed to note this. Therefore only those lying on their backs or sides could be sexed.

Tagging

Hasco 1005 monel metal tags (size 49, National Band and Tag Company, Newport, USA) were used, with the words "Marion Island" stamped on the outside face of one flange of each tag, and a number preceded by the letters RSA stamped on the outside face of the other flange (Plate 2a). Two tags were attached to each animal, both tags bearing the same identification number. The tags were attached to the posterior edge of the interdigital web, usually between the third and fourth digits, on each hind flipper (Plate 2b). Two people were required to tag the seals, one holding the flipper and the other applying the tag and recording the tag number and sex of the seal. Tagging of seals on Marion Island has already been discussed by Condy and Bester (1975). The immediate objective was to determine the local movements of yearlings during the winter season following their birth. The long term objectives were to provide a reservoir of known aged animals for life history studies, and to provide data on fidelity to breeding grounds and more specifically even to birthsites.

Tagging was started in November 1973 when adult females, yearlings, and subadults were concentrated on. From then effort was concentrated on the pups in the 1974, 1975, and 1976 pupping seasons, with a few older animals, mainly second year animals and adult males, being tagged when possible. Pups were tagged after weaning, when they tended to congregate away from the harems at the periphery of the breeding beaches (Plate 2c). There they could be tagged with minimum disturbance to the harems, and as the congregations often occurred in or near to the surf zone, drenching by sea water helped to heal the small tag wounds (Condy and Bester 1975). Unweaned animals lay close to or in the harems, where they were not only difficult to reach, but also they lay in the harem's detritus and tag wounds tended to become infected, sometimes fatally.

At the time of tagging the date, locality, sex, tag number and number of tags (i.e. one or two) successfully attached, age class, body measurements if any, territorial status (of bulls), and stage of moult (unmoulted, less than half moulted, more than half moulted, moulted) were recorded. This information was put on record cards, one card per seal, and the cards are now kept at the Mammal Research Institute. When tagged seals were resighted, the date, tag number and number of tags still attached, sex, age class, locality, territorial status, and stage of moult were noted and written on the reverse side of the individual's record card.

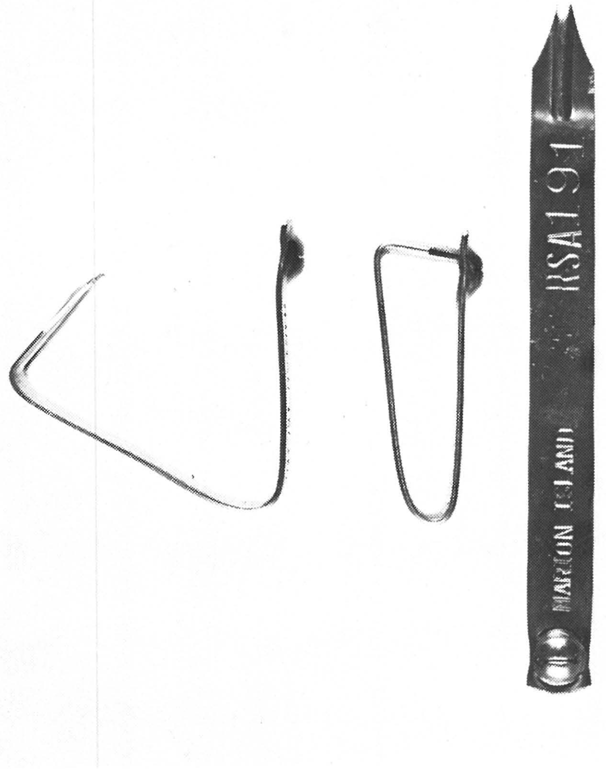
Seals were tagged on Prince Edward Island during 5 – 12 May, 1974 and 19 – 29 April, 1976. No particular age group was singled out for special attention, and attempts were made to tag any seal hauled out at these late stages of the summer haul out season.

PLATE 2

a. The Hasco monel metal tags used to tag elephant seals at Marion Island, before application (top), after application (middle), and the identification code (bottom).

b. The position of a tag, after application to the hind flipper of an elephant seal, is shown.

c. Pups were tagged after weaning when they tended to congregate away from the harems. Groups of weaned pups, such as shown, occurred towards the edge of the beaches.



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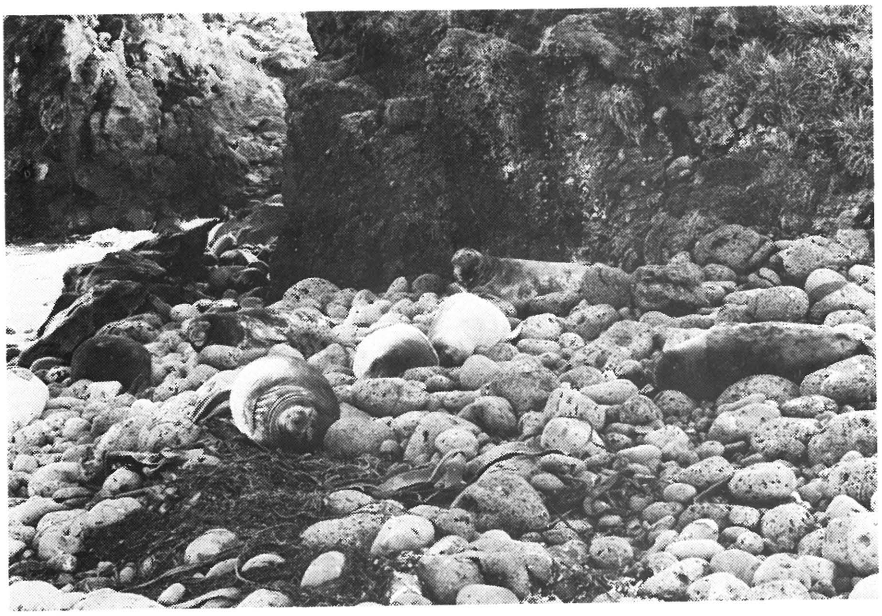

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Morphometric Data

Eighteen pups on Boulder Beach (10 males and 8 females) were measured and their mass determined, at two to four day intervals from birth up to 40 days of age during the 1974 pupping season. Measurements were made according to the recommendations of the Committee on Marine Mammals, American Society of Mammalogists (1967), for the standard measurement of seals. The measurements made were body mass, curvilinear body length from nose to tip of tail flesh over the dorsal curve of the body, while the seal was flat on its belly, and girth immediately posterior to the fore flippers (axillary girth).

White stercolite bands, punched with holes to identify them, were tied around the femur of each pup to identify it. An attempt was made to measure each pup within two hours following birth, at 10 hours and 24 hours after birth, and thereafter at two day intervals. However the schedule was often upset by windy conditions which made mass measurement impossible, and the aggression shown by some of the cows which made it sometimes difficult to retrieve their pups. Thus on every second day only those pups which could be retrieved were measured, and if weather conditions prevented the operation, it was not carried out but resumed two days later on the next scheduled day of measuring.

For the first 18 days after birth the pups could be handled quite easily, but thereafter became too strong and heavy to handle unless immobilized. Succinylcholine chloride (Scoline), manufactured by Glaxo-Allenburys (SA), Germiston, South Africa, was used to immobilize the pups, and was administered intramuscularly by hand using plastic disposable 10 ml syringes fitted with 20 gauge needles 38 mm long. The injection site was approximately 10 cm forward of the tail and slightly to one side of the dorsal midline, and the needle was inserted at an angle of approximately 45° to the body surface. The immobilized seal was measured and then lifted onto a small home-made stretcher on which it was mass measured. A portable aluminium tripod was erected over the stretcher, and the latter was linked to the scale hanging from the tripod by a small block-and-tackle system.

CHAPTER 4

DISTRIBUTION OF ELEPHANT SEALS

RESULTS

Distribution During the Pupping and Mating Season (September to November)

During the pupping and mating season the adult elephant seals stayed on the beaches (Plate 3a), but whether they hauled out or not on a particular beach depended upon its physical nature. They only hauled out on beaches with a flat even profile, where the surface consisted of smooth rounded rocks and boulders (< 0,5 m in diameter), or rocks, stones, and pebbles. The leeward east and north coasts had many suitable beaches, while on the exposed west and south coasts which lie in the face of the prevailing oceanic onslaught, the beaches were generally too rugged, although a few which occurred in well protected coves and had a more flat and even profile were utilized (see Plate 1b).

Negotiability seemed to be the critical factor in the selection of hauling out beaches. The most negotiable beaches were those where the surfaces were flat and even, and comprised of small stones and pebbles. Since most such beaches occurred on the leeward east and north coasts, the great majority of elephant seals occurred on those coasts. The present distribution of breeding beaches is shown in Figure 5, as well as the distribution of breeding colonies recorded by Rand (1962) in 1951/52. Throughout the study the two largest elephant seal breeding colonies were located at Kildalkey Bay and Archway Bay, where 24,1 per cent of the total island pup crop was born (see Table 6). Between Kildalkey Bay on the southeast corner of the island and Goney Beach on the central north coast, 84,4 per cent of the total pup crop was produced (Table 6).

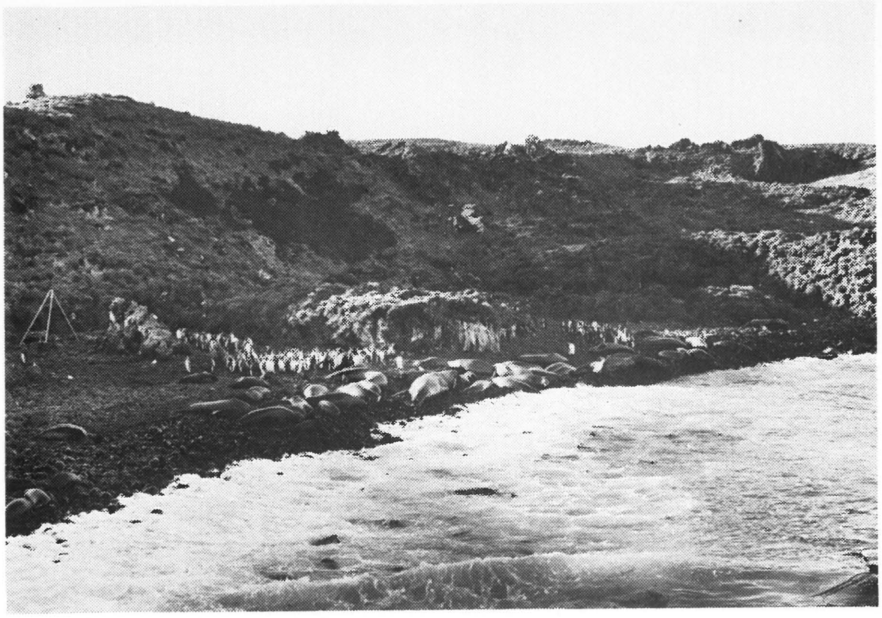
Since most drainage line beaches were small, varying from as little as 50 m^2 up to 5 000 m^2, each was generally occupied by one harem only (Plate 3a). However, on the few longer beaches (up to 1,0 km in length) located at the base of coastal cliffs (eg. Ship's Cove and Macaroni Bay), two separate harems were

PLATE 3

a. One elephant seal harem occupying the drainage line beach at Trypot Beach, on the leeward east coast of Marion Island.

b. Two separate elephant seal harems on the long beach (about 0,3 km) at the base of coastal cliffs in Ship's Cove.

c. Moulting subadult male elephant seals in a wallow at the Trypot Beach moulting area.



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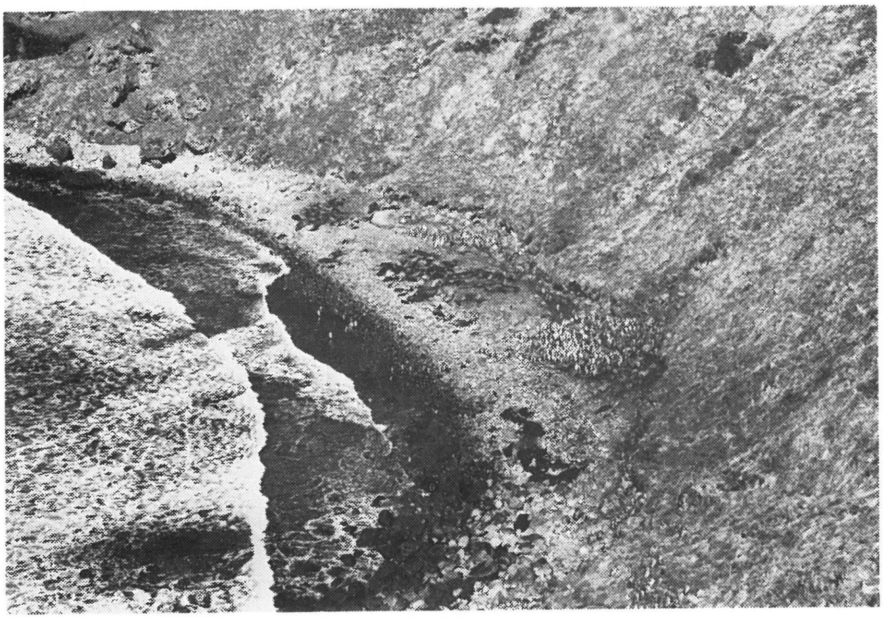

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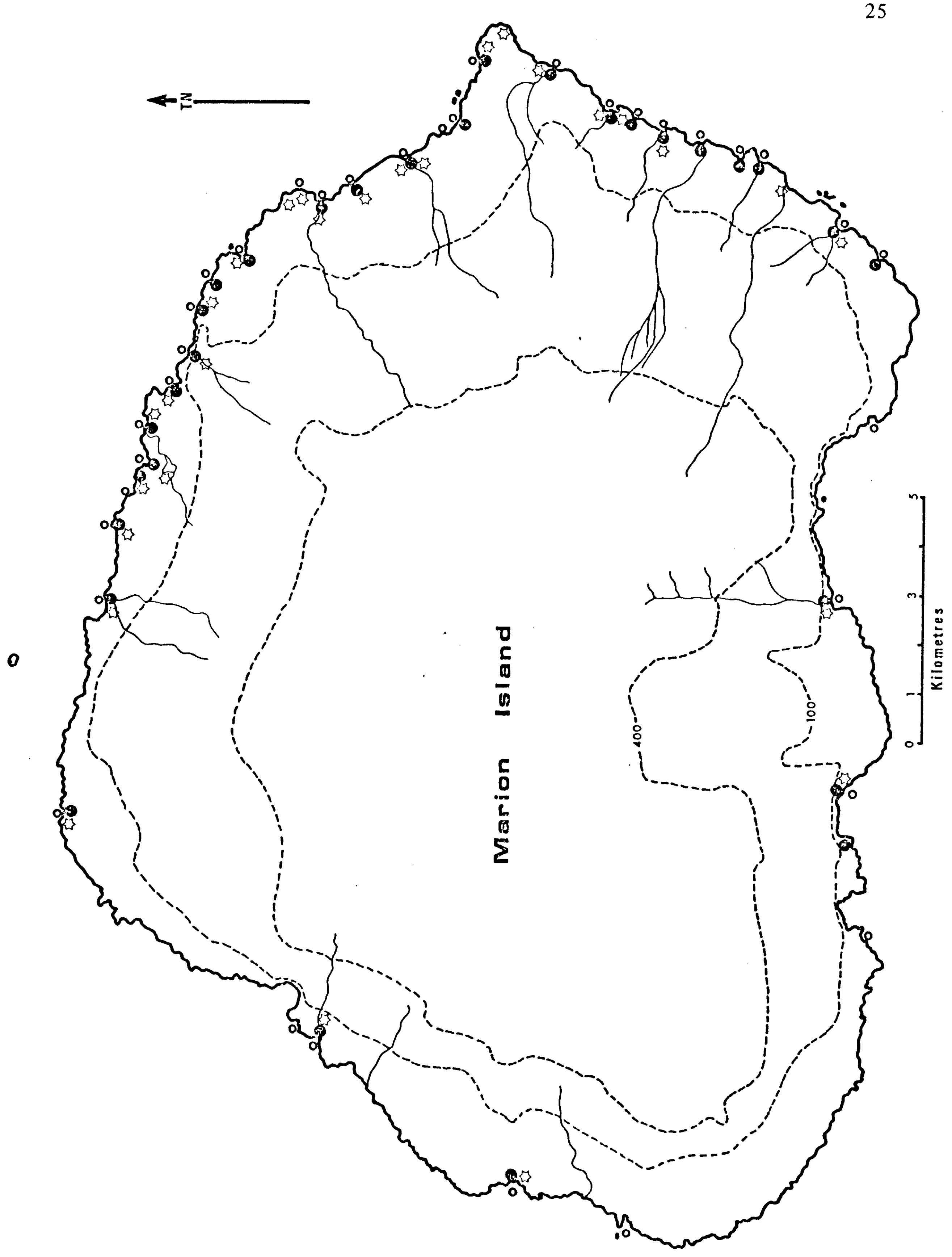


FIGURE 5

Present distribution of southern elephant seal pupping and mating (●) and moulting (☆) sites on Marion Island. The beaches occupied in 1951/52 (○) according to Rand (1956) are also shown.

sometimes formed, but never more than this (Plate 3b). As the substrate on these latter beaches was composed of slightly larger rocks and boulders than that of the drainage line beaches, the paucity of harems on them may have been due to a preference for the drainage line beaches, at which most available space at each site was occupied by a single harem.

At the west and south coast beaches, where the terrain was too rugged for elephant seals to negotiate it, large numbers of Amsterdam Island fur seals *(A. tropicalis)* occurred. It appeared that these fur seals, numbering some 6 000 – 8 000 in total (Condy 1975b, unpublished), favoured the more rugged beaches on the west and south coasts since very few occurred on the smoother flat east and north coast beaches. Small numbers (about 200, Condy 1975b, unpublished) of Kerguelen fur seals *(A. gazella)* also occurred on the west and south coast beaches, amongst the more numerous Amsterdam Island fur seals. Thus during this study the fur seals bred almost entirely on the exposed west coast, while the elephant seals bred mainly on the leeward east coast. While the latter are never likely to start pupping on the exposed portion of the island's coastline, the fur seals may in time become even more numerous and start pupping on the leeward coastline. However at the present time the breeding elephant seals and breeding fur seals on Marion Island are well separated.

Prince Edward Island was not visited during the breeding season, due to lack of transport. However all beaches on the leeward east and northeast coasts have a similar topography and profile to those on Marion Island, and are therefore believed to be occupied by elephant seals during the pupping and mating season (Figure 6).

Distribution During the Moulting Season (November to April)

At the beginning of their second year of life, individuals returned to moult towards the end of November, and tended to remain on the beaches while moulting. They occurred around the island on the same beaches occupied earlier in the season by the breeding animals, but the majority occurred on the east and north coasts.

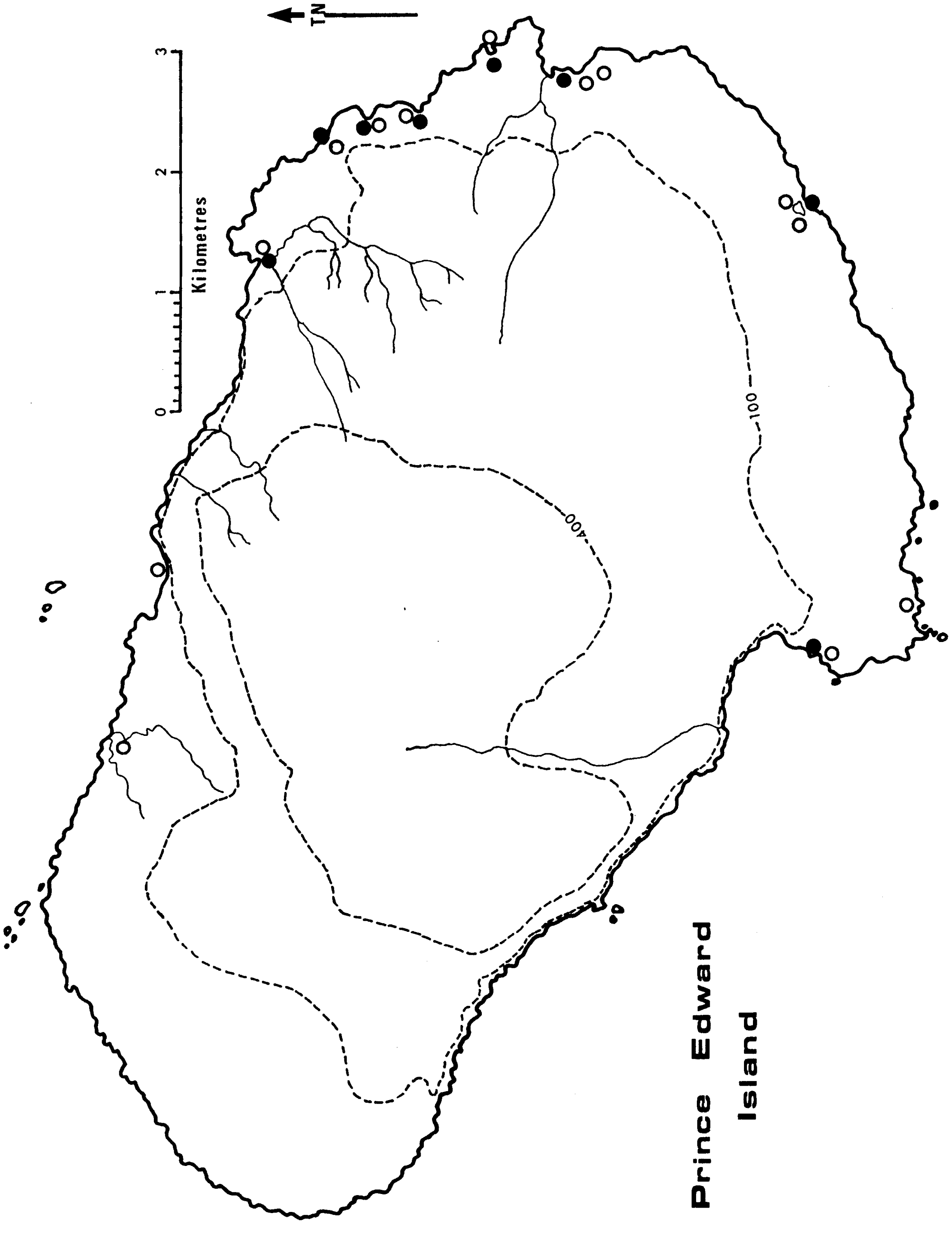


FIGURE 6

Present distribution of southern elephant seal pupping and mating (●) and moulting (○) beaches on Prince Edward Island.

All older animals hauled out onto the beaches but then moved up rivers and streams or any other negotiable route giving access to inland areas. There they lay (Plate 3c), in groups of up to 20 individuals, in either natural depressions or those artificially created by the mass and movement of the seals. Rainwater, together with earth, urine, and faecal matter tended to create a semi-liquid, foul smelling "ooze" partly filling these "wallows" within which the seals lie, although some were relatively dry if newly created, or occurred in well drained areas.

The availability of access routes to inland areas was the critical factor affecting distribution during the moulting season, although the extent of a suitable inland area also appeared to be of importance. The extent and accessibility of these moulting areas enforced a shift in distribution of elephant seals at this stage of the summer haul out season. The largest moulting areas occurred at Crawford Bay along the Watertunnel Stream and south of Kaalkoppie on the west coast, and at Sea Elephant Bay, Transvaal Cove, Trypot Beach, and Archway Bay on the east coast, although many smaller moulting areas occurred around the island (Figure 5).

Prince Edward Island was visited late in the moulting season on both occasions, at a time when most moulting seals had departed. However it appeared that the largest moulting areas occurred behind Penguin Beach and in the Cave Bay area, both on the eastern coast. The western coast was not visited but may contain a few major moulting areas on the northwest coast (Figure 6).

Distribution During the Winter Season (May to September)

From May to July only yearlings and animals in their second year occurred regularly on Marion Island. Occasionally very old or injured animals, of any age or sex older than two years, hauled out for periods of varying length. Overwintering animals regardless of age or sex generally remained on the beaches and did not move inland, but tended to select the most sheltered places there.

From July to September bulls started hauling out in advance of the forthcoming pupping and mating season to select territories, and there was much fighting. Most other seals present on the beaches started to depart as the bulls started competing with each other, but a few remained and tended to move either to the periphery of the beach, or the adjacent moulting area if one was present.

Influence of the Seals on the Environment

During the pupping and mating season when the seals remained on the beaches, their urine and faeces are washed into the sea, and placentae as well as carcasses (mainly of pups) provide food for giant petrels *(Macronectes* spp.) skuas *(Stercorarius skua),* gulls *(Larus dominicanus),* and sheathbills *(Chionis minor).* Yearlings and cows are preyed upon by killer whales *(Orcinus orca)* in October and November, their presence at the island apparently being a major attractant to killer whales, which also have an influence on other prey species such as the king penguins *(Aptenodytes patagonica),* and scavengers such as gulls and skuas (Condy, Van Aarde and Bester, in press, and Chapter 10).

Lavigne, Barchard, Innes and Øritsland (1976) estimated that for pinnepeds in general faecal energy loss was in the order of 9 – 10 per cent of Gross Energy, and urinary energy loss of the order 7 – 8 per cent of Digestible Energy. Taking an adult harp seal *(Pagophilus groenlandicus)* as an example, they estimated that faecal energy loss was 25,96 – 28,89 kJ kg^{-1} day^{-1}, and urinary energy loss 18,42 – 21,35 kJ kg^{-1} day^{-1}. While this loss in energy is not necessarily gained by marine invertebrates in the same form (i.e. joules), the organic and inorganic compounds and salts released in the faeces and urine are probably reincorporated at some lower level in the food chain. Thus while the elephant seals are in the vicinity of Marion Island, and assuming that they show similar if not greater faecal and urinary losses as the harp seal, their contribution to the organic and inorganic constituents of the local oceanic environment could be considerable, and important to the inshore invertebrate food chain.

During the moulting season, most metabolic waste is deposited further inland, where the physiological effect of manuring and the mechanical effect of trampling in the moulting areas have a significant influence on the vegetation. The presence of seals in these inland moulting areas on Marion Island has two major effects according to Huntley (1971); vegetation changes, and maintenance of the resulting coprophilous vegetation. The original plant species namely *Blechnum penna-marina, Azorella selago, Acena adscendens,* and *Tillaea moschata* are replaced by the coprophilous *Poa cookii, Poa annua, Cotula plumosa, Montia fontana, Callitriche antarctica, Stellaria media, Cerastium holosteoides,* and *Ranunculus biternatus* (Huntley 1971). Apart from the indicative vegetation, the physical nature of the ground surface becomes quite distinctive in the moulting areas (Plate 4a). A complex of hollows and mounds develops, some of the hollows being partially connected to other adjacent ones by smaller rounded and depressed ridges (Plate 4b).

Huntley (1971) has discussed in greater detail the successional stages in the vegetation of the Marion Island elephant seal moulting areas, and Grobbelaar (1974) and Smith (1976) have discussed the accompanying changes in soil and wallow chemistry. The most important chemical changes were the increased levels of N and P, while the levels of K, Na, and Fe also increased but to a lesser degree (Smith 1976).

The elephant seals therefore have an effect on the Marion Island environment in three main ways; contribution to the organic and inorganic nutrient status of the local oceanic and inshore ecosystems, contribution to the food supply of predatory and scavenging birds, and first causing then maintaining changes in the vegetation and surface nature of inland moulting areas.

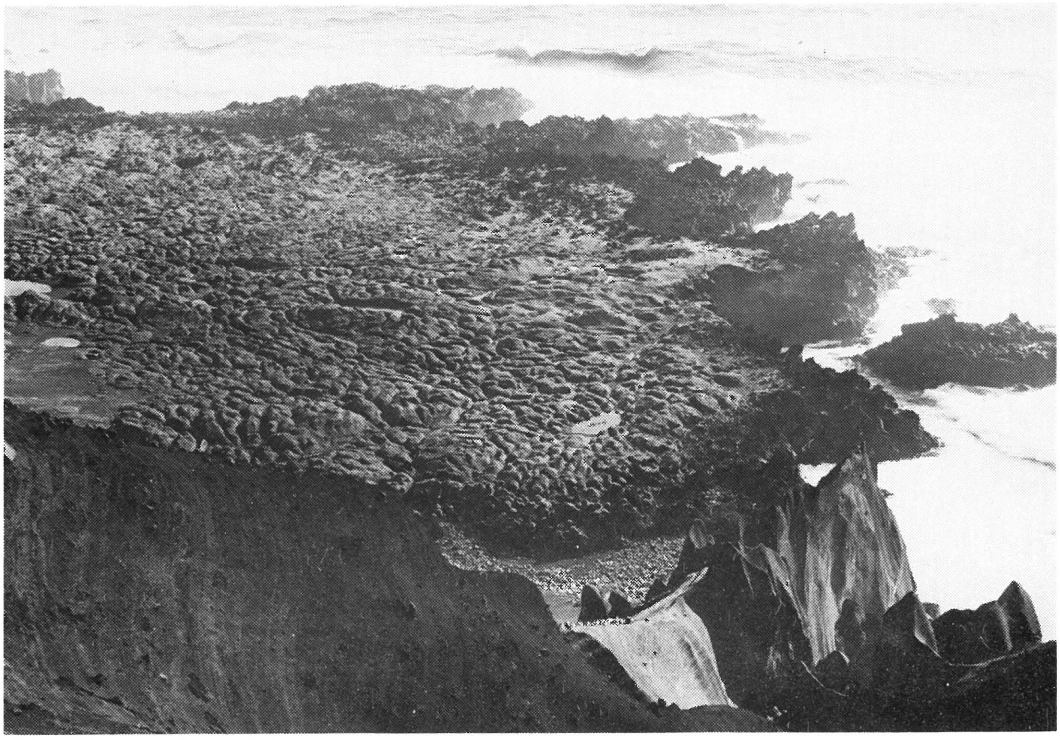
DISCUSSION

On Marion Island elephant seals remain on the beaches during the pupping and mating season. These beaches are generally small and sheltered, those on the leeward east and north coasts being better protected from the prevailing wind and sea swell than those on the exposed south and west coasts. The surface nature of the beaches dictates which of them are occupied during the pupping and mating season, and since most beaches with a suitably flat and even profile occur on the north and especially the east coasts, most breeding elephant seals occur on these leeward coasts. Carrick, Csordas, Ingham and Keith (1962c) believed that on

PLATE 4

a. An elephant seal moulting area at Kaalkoppie on the west coast of Marion Island. The complex of hollows (some waterlogged) and mounds gives the moulting areas a distinctive physical appearance.

b. The physical effect of trampling in the moulting areas is illustrated.



a

b

Macquarie Island ease of access to the beach for pregnant cows hauling out to pup determines the location of harems, rather than availability of preferred habitat. Many easily accessible beaches on Marion Island are not occupied by harems, but all these beaches have one factor in common – an uneven profile with a rough and broken surface of boulders piled so irregularly that the elephant seals would have some difficulty in traversing them. In some cases lone females haul out and pup on such beaches, but the pups invariably die within a few days of birth because they are apparently unable to reach and suckle from their mothers, or are crushed between the cows and the boulders.

It appears that the size of the breeding beaches on Marion Island are generally much smaller than those on Macquarie and Heard Islands (Carrick and Ingham 1960), South Georgia and Signy Island (Laws 1956a), and Campbell Island (Sorensen 1950). Amsterdam and St. Paul Islands (Paulian 1957), and the Kerguelen Islands (Angot 1954) also seem to have much larger and longer stretches of suitable breeding habitat, while it appears that the situation on the Crozet Islands (Despin, Mougin and Segonzac 1972) is similar to that on Marion Island. On those islands with large expanses of suitable beach habitat many harems, all of varying sizes, occur scattered about the occupiable area. On Marion Island however the sizes of harems are physically limited by space, each suitable space being filled by a single harem, and the harems are separated from each other by intervening coastal cliffs. Thus it appears that on Marion Island the elephant seals during the pupping and mating season are more scattered along the coastline than they are on the major breeding grounds such as Macquarie and Heard Islands, South Georgia, and the Kerguelen Islands. The situation on Prince Edward Island is similar to Marion Island as most suitable habitat occurs on the east coast, but differs in that the great majority of seals probably occur on only two (i.e. Cave Bay and Penguin Beach) of the six likely pupping beaches. The distribution during the pupping and mating season is probably much more clumped than on Marion Island, tending towards the pattern at the major breeding grounds.

During the moulting season it appears that the movement of seals inland is a pattern common to most if not all breeding grounds. In some cases such as on

Gough Island (personal observation) movement inland is prevented by cliffs, and moulting seals remained on the beaches although tending to move into the vegetated areas immediately below the cliffs. As is the case on Marion Island, Carrick *et al.* (1962c) found that on Macquarie Island young immature seals moulted on the beaches, and subadult males and females as well as adult females moved inland to the wallow areas. However they noted that bulls moulted on the beaches, while on Marion Island they also tended to move inland to the wallows, although occasional individuals remained on the beaches.

During the summer of 1951/52 Rand (1962) studied the distribution of elephant seals on Marion Island (see Figure 5), and the pattern during both pupping and moulting seasons has remained essentially similar since then. He recorded 48 breeding beaches compared to only 28 found during this study. However since his study was carried out before the 1965 topographic survey (Langeneggar and Verwoerd 1971), after which there was a change in place names in some cases, it is difficult to reconstruct distribution according to his place names in some instances. It also appears that he refers to harems rather than to habitat sites, again making comparison difficult, although from the attempted reconstruction of the distribution of occupied sites in 1951/52 (Figure 5), it can be seen that the pattern is basically the same as it was during this study some 24 years later.

Gillham (1961) has discussed the modification of flora on Macquarie Island by elephant seals, and considered that the mechanical effects of trampling were of greater importance than the chemical effects of manuring. She believed that the effects of manuring are largely neutralized by high rainfall which washed nutrients from the soil, low evaporation which prevented excessive concentration of the soil solution, and the ability of the peat to retain water and thus act as a buffer to chemical changes. However she stated that where the effects of manuring can be dissociated from trampling, manuring may have a beneficial influence. Grobbelaar (1974) and Smith (1976) have in contrast shown that on Marion Island quite considerable soil, water, and plant chemical changes do occur as a result of manuring by elephant seals, and Huntley (1971) stated that despite the high rainfall on Marion Island, manuring exerted a profound influence on the vegetation.

He also noted that although the erosive effect of trampling varied, according to animal numbers and the length of occupation of an area, complete destruction of the vegetation was rare, and following the departure of the seals the change in chemical status of the wallows from eutrophic to oligotrophic was fairly rapid. In the case of elephant seals it is difficult to consider the effects of manuring divorced from the effects of trampling as Gillham (1961) suggested, since trampling to a greater or lesser extent must accompany manuring. It appears that in fact trampling is of major importance in altering the nature of the ground surface and possibly the water content of the soil, but manuring rather than trampling is of major importance on Marion Island in affecting vegetational changes. According to Smith (1976) the effects of manuring on Marion Island can last for some years in the absence of further visits to the area by the animals responsible. The effect of trampling on the other hand is probably much longer lasting, the local topography of certain areas indicating that they were at some stage in the past (before 1965) occupied by moulting elephant seals, even though the vegetation was no longer characteristic of moulting areas.

CHAPTER 5

ANNUAL CYCLE

RESULTS

The Pupping and Mating Season

Use of the word breeding to define a particular stage in the seasonal cycle of a species can be confusing, since in the literature it has been applied to either the period of mating or of parturition. In the case of seals, mating usually follows within a few days of parturition with no lactational anoestrus, and so the term breeding has also been frequently used to collectively describe the periods of pupping and mating as the breeding season. To avoid confusion, the term pupping and mating season has been used in this thesis to describe that period of the summer haul out season.

The mean annual numbers of bulls, cows, and pups counted each week in the study area, for the period August to January 1974, 1975, and 1976, are illustrated in Figure 7. Following the winter when most elephant seals were away from the island, the first to return were the bulls which started hauling out in early August. The first of the pregnant cows arrived a month later in the first week of September, and the first pups were born a few days later. In general cows gave birth three to seven days after hauling out, so that the increase in number of pups ran parallel to the increase in number of cows, but lagged about a week behind. From about the third week in September the number of cows hauled out increased rapidly reaching a peak in mid-October, and then declined rapidly. By mid-November all cows had departed, some 12 weeks after the first of them arrived. Each cow spent approximately 28 days ashore, and pups were weaned on average 22 days after birth. However since the number of pups continued to increase until only two weeks before the last of the cows had departed, the last pups born were weaned when only about 14 days old, approximately two thirds the normal age, so that the departure of the cows remained as well synchronized as their arrival.

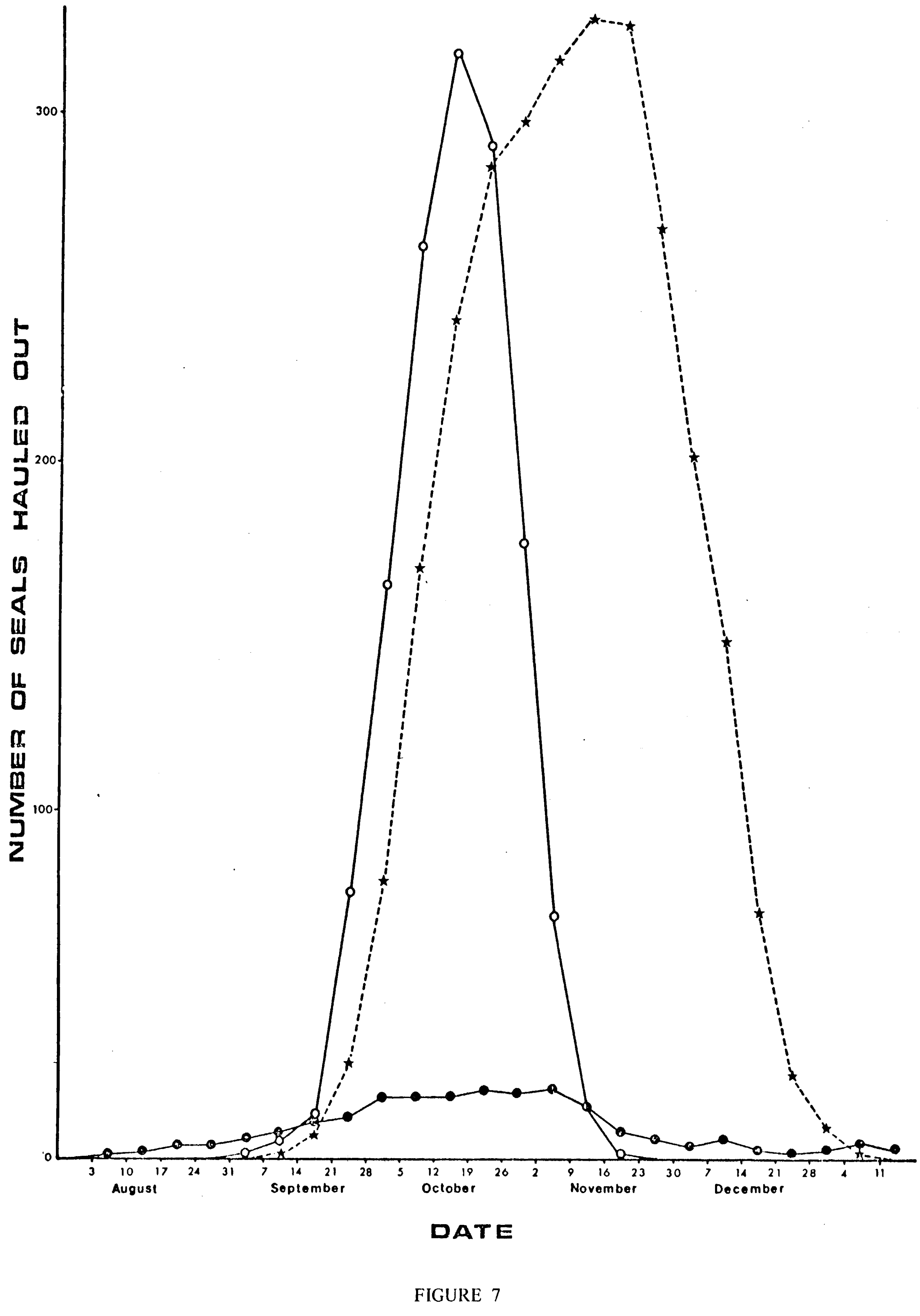


FIGURE 7

Mean annual number of breeding southern elephant seal cows (○) and bulls (●) counted each week in the main study area. Mean annual number of pups/yearlings (★) counted each week at the same beaches is shown.

After weaning the pups remained on the beaches for an average of a further eight to 10 days before they started feeding very close inshore, initially within the surf zone on days when the sea was calm. After 36 days post weaning they began to depart, and the last of them left the beaches in early January, some eight weeks after the last cows had departed. By this stage all pups were older than one month and had entered the "yearling" class.

The bulls started competing with each other as soon as they arrived, and by the time the cows arrived a month later territorial status and male hierarchy had been established. However changes in status could take place at any stage in the season, but in particular during the peak mating period. Cows were mated four to eight days post partum, so that the peak mating period lasted for some two weeks after the numbers of cows reached a peak. The numbers of bulls on the breeding beaches reached a maximum during this time, but most had already arrived at the island during August. Those defeated in territorial fights, as well as the recently matured young bulls, tended initially to stay away from the breeding beaches, hauling out in small and usually sheltered inlets, coves, and isolated beaches at the foot of cliffs. However during the peak mating period they returned to the breeding beaches where they usually managed to mate some of the cows, especially those on the periphery of the harems. Following the peak mating period in late October and early November, the number of bulls began to decline until only the occasional one was seen from mid-December. Generally these remaining bulls suffered from injuries sustained earlier in the season, and remained near the island taking frequent rest periods ashore, until they started to moult later in December.

The Moulting Season

Seals in all age classes older than the yearling class returned once every year to moult after the pupping and mating season. The mean annual number of moulting animals counted each week at Boulder and Trypot beaches for the period November to May 1973/74, 1974/75, and 1975/76 is illustrated in Figures 8, 9 and 10.

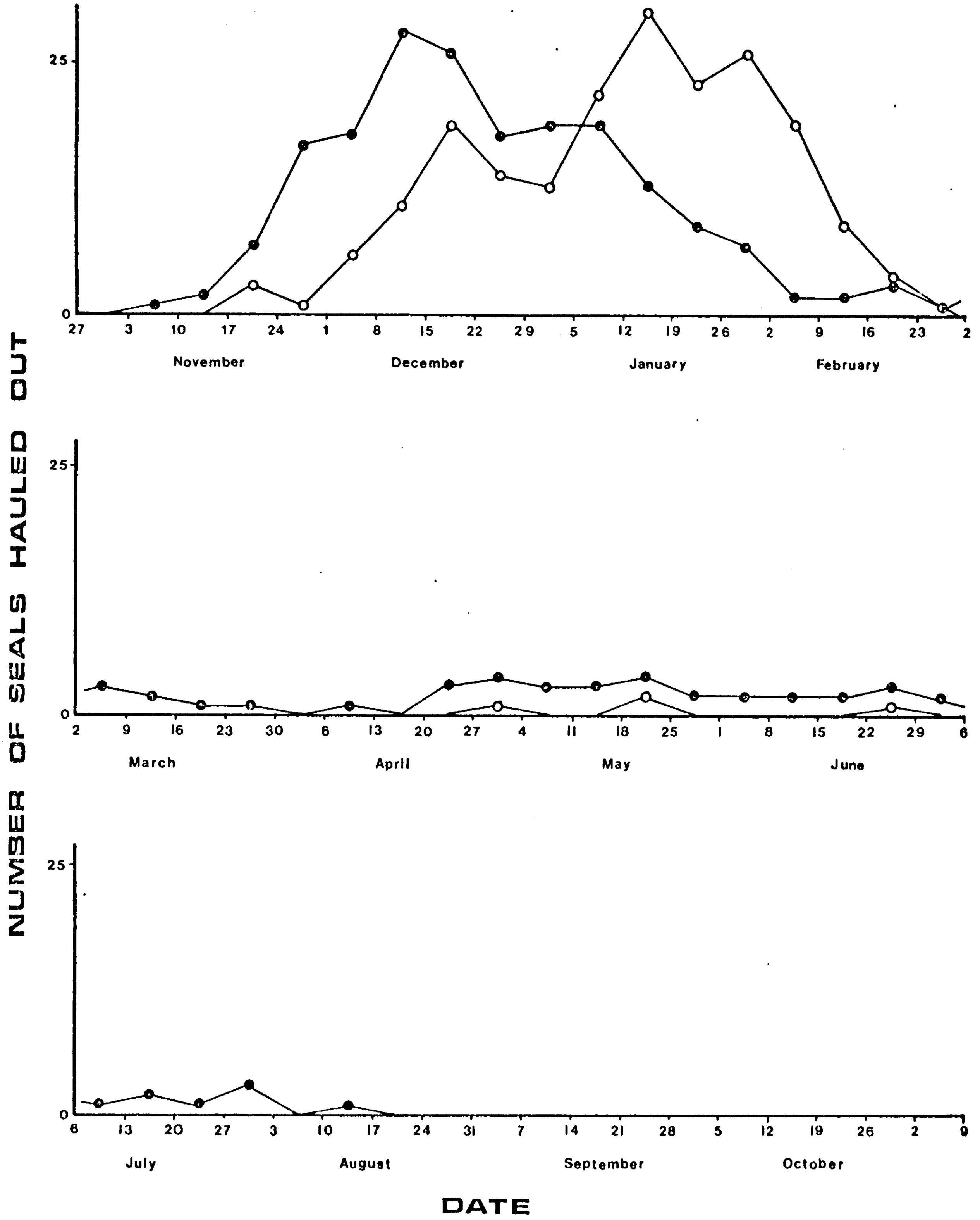


FIGURE 8

Mean annual number of moulting subadult southern elephant seals (○ = females, ● = males) counted each week at the Trypot and Boulder Beach moulting areas. The number present during the winter season is also illustrated.

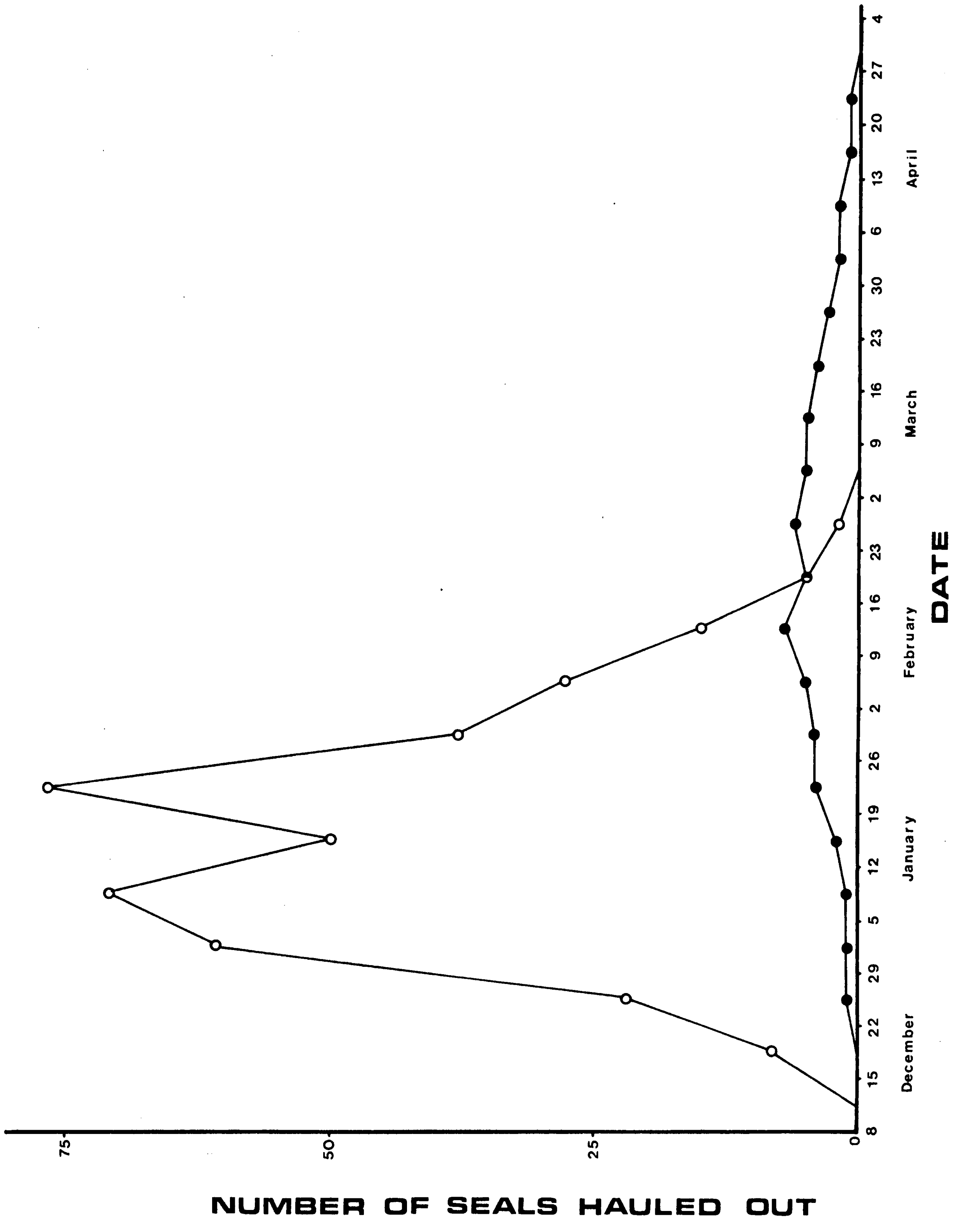


FIGURE 9

Mean annual number of moulting southern elephant seal cows (○) and bulls (●) counted each week at the Trypot and Boulder Beach moulting areas.

Subadult males and females started hauling out to moult before the adults (Figure 8). Although both sexes arrived simultaneously in early November, the numbers of males increased more rapidly than the females, so that the peaks in their numbers were separated by five weeks. The haul out of subadult males overlapped only slightly with the last of the breeding bulls, and as the number of moulting bulls reached a peak later in the season, the number of moulting subadult males was already declining. The subadult males appeared to have synchronized their haul out period to fall between the two haul out periods of the bulls. On the other hand the peak in numbers of moulting subadult females coincided with the peak in numbers of both the moulting cows and moulting bulls.

Cows started returning to moult in the second week of December (Figure 9), approximately three weeks after the last of them departed at the end of the breeding season. Numbers reached a peak in late January, and then declined to zero in early March, by which stage moulting cows had been present over a period of 12 weeks. Their haul out pattern was characterized by two distinct peaks some 14 days apart.

Although a few bulls remained on the island after the end of the pupping and mating season, the real return to moult started in mid-January (Figure 9) and only very few were present during the first peak of moulting cows. However as the second peak in numbers of cows got under way the numbers of bulls increased, reaching a peak in mid-February. Cows had generally completed their moult within 25 days of hauling out, so that most of those in the first peak had departed by the time the bulls reached peak numbers. The bulls took from 28 to 42 days to moult, with their moulting season lasting some 18–20 weeks, and by early May the last had departed.

Animals in their second year of life also started hauling out to moult in early November (Figure 10), about the same time that the subadults started arriving and before the last of the breeding cows departed. Numbers increased rapidly to a peak in mid-December and most had departed by early February, but some six to eight weeks later, in late March, there was another definite though less spectacular increase in the numbers hauled out. The reason for this second haul out period

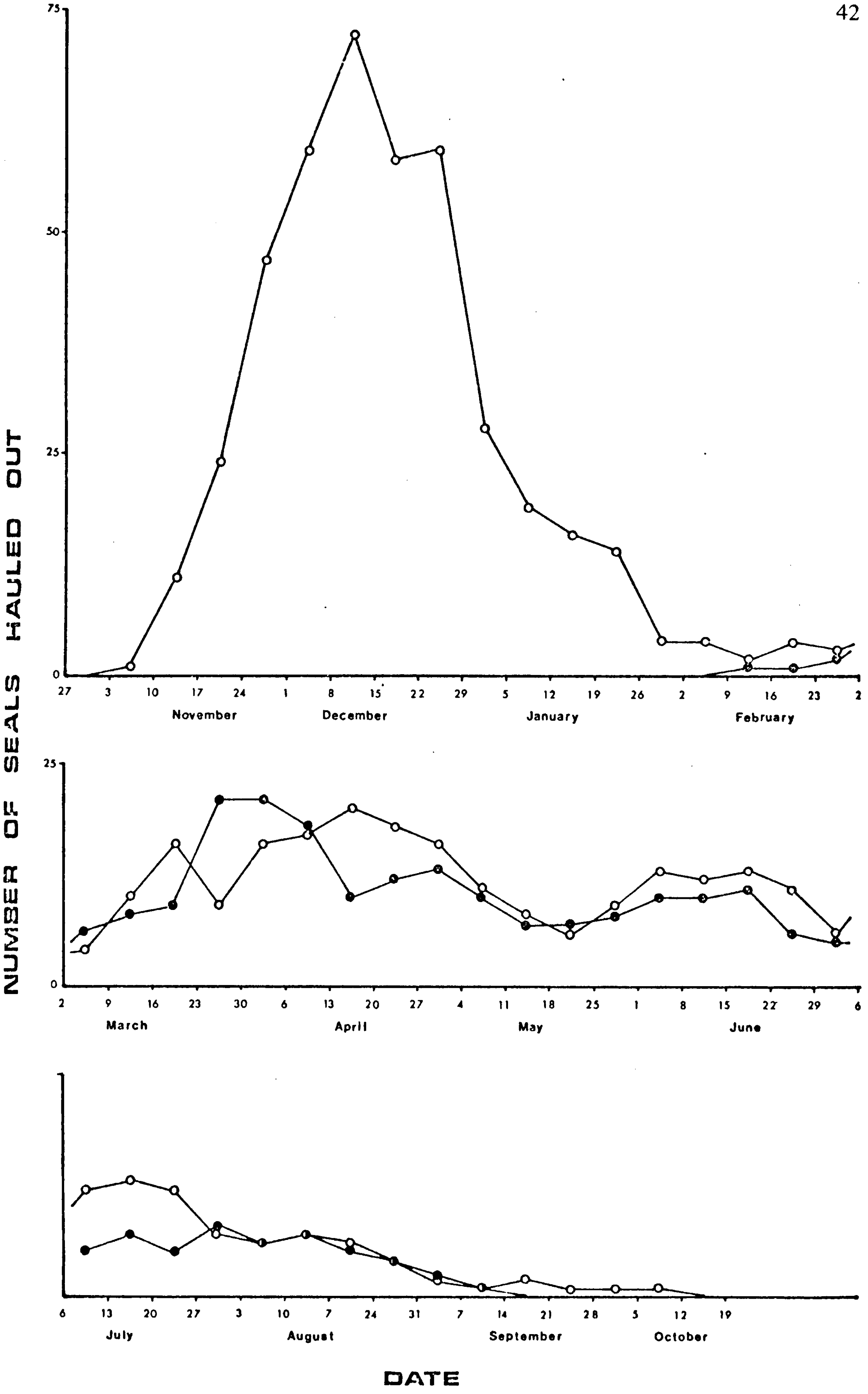


FIGURE 10

Mean annual number of moulting second year old (○) southern elephant seals counted each week at Trypot and Boulder Beaches. The mean annual numbers of second year old (○) and yearling (●) seals present during the winter season are also illustrated.

was not clear, but it is possible that the general exodus of moulted cows and subadults in January/February, which coincided with the end of the second year animal's first haul out period, either disturbed them or induced them to follow suite. Thus they too showed a rapid decrease at that time, and most may have followed the older animals on their migration. However, those whose departure was induced prematurely by the exodus of older seals, or which were not capable of following the older seals on the migration because of illness or injury, probably returned to cause the second haul out period. These animals tended to overwinter, eventually departing in early October (Figure 10).

Some of the yearlings, born during the pupping and mating season and which had departed by mid-January (Figure 7), returned a few weeks later in mid-February (Figure 10), after most moulted cows, subadults, and second year animals had departed. The reason for this autumn return was not clear, and the number of those returning was very much lower than the number of them weaned earlier in the season. It is possible that those which returned were those born late in the breeding season, and consequently weaned at an earlier age than normal so that the departure of their mothers could be synchronized with the general exodus of cows. They were therefore probably smaller and weaker than other yearlings, most of which may have joined the migration, and also overwintered, eventually departing in mid-September.

The Winter Season

Cows were absent from the island from early March (Figure 9) to early September (Figure 7), a period of some 26 weeks, while bulls were absent from early May (Figure 9) to early August (Figure 7), a period of only 12 weeks.

A few subadult males were hauled out right through the winter (Figure 8), but by mid-August when the bulls were returning for the next pupping and mating season, all had departed. Excluding these few overwintering animals, subadult males were absent from the island from the end of one moulting season in mid-February to the beginning of the next in early November (Figure 8), a period of some 38 weeks. Although occasional subadult females hauled out during the winter

(Figure 8), they were generally only present during the moulting season from late November to early March (Figure 8), also being absent for 38 weeks.

The second year old animals which returned in the second haul out period tended to overwinter (Figure 10), eventually departing in early October. The arrival of pregnant cows and the birth of their pups at this time precipitated their departure, probably as a result of aggression especially from the lactating cows. The decline in their numbers actually started earlier in late July, and was probably induced by the arrival of the bulls, some of which were seen to attempt to mate two year old animals regardless of the latters' sex. Excluding the overwintering animals, most of the members of this age class were absent from the island from the end of the moulting season in early February to the beginning of the next moulting season in early November (Figure 10), a period of some 40 weeks.

The yearlings which returned in February/March also overwintered, eventually departing in mid-September about a month before the last of the overwintering two year old animals (Figure 10). Their departure was probably also precipitated by the arrival of the cows, but since only few cows were present when they departed, aggression may not be an important factor. The arrival of breeding bulls also induced a steady decline in their numbers, and although no bulls were seen molesting the yearlings, the presence of the bulls appeared to have an effect. Generally yearlings were absent from the island from the end of the pupping and mating season in early January (Figure 7), to the onset of their next main haul out season to moult in early November (Figure 10) a period of some 44 weeks.

Duration of Haul Out Periods

Since the elephant seals have an influence on the island environment, especially on land during the moulting season, data on the amount of time spent on the island have been summarized in Table 2.

Bulls were present over a longer period than any other age class, being found on the island for 76,9 per cent of the year. The island was occupied by cows for just under half the year (46,1%), while yearlings occurred on the island over approximately one third (30,8%) of the year. For 26,9 per cent of the year second year animals were present, and subadult males and females were each present for 28,8 per cent of the year, but since the haul out period of the males and females was not exactly synchronized, subadults (sexes combined) occurred on the island over approximately 17 weeks (32,7% of the year).

TABLE 2: Duration of southern elephant seal haul out periods on Marion Island

Age Class	Main Haul Out Periods				Total Haul Out Time		Winter Presence
	Pupping and Mating Season		Moulting Season				
	Weeks	% of year	Weeks	% of year	Weeks	% of year	
Bulls	21	40,4	19	36,5	40	76,9	–
Cows	12	23,1	12	23,1	24	46,1	–
Subadult males	–	–	15	28,8	15	28,8	Occasional. seals only.
Subadult females	–	–	15	28,8	15	28,8	
Second year animals (both sexes)	–	–	14	26,9	14	26,9	Some only.
Yearlings	6	11,5	10	19,2	16	30,8	Some only.

Cows and subadult females together would appear to be the biggest contributors to the inland manuring which occurred during the moulting season. Bulls and subadult males together were fewer in numbers than cows and subadult females, but as the individual bulk of the males is considerably greater than that of the females, they probably contributed equally to the trampling effect but less to the manuring effect. Since the younger seals tended to stay on the beaches, they therefore contributed little if any to both the trampling and manuring effects on inland areas.

DISCUSSION

The annual cycle of southern elephant seals has been investigated at Heard and Macquarie Islands (Carrick *et al.* 1962b, 1962c), Signy Island and South Georgia

(Laws 1956a), Iles de Kerguelen (Angot 1954), and in less detail at Campbell Island (Sorensen 1950), Amsterdam and Saint-Paul Islands (Paulian 1957), and the Crozet Islands (Despin, Mougin and Segonzac 1972). Both La Grange (1962) and Rand (1962) gave some details on the seasonal pattern at Marion Island, and Van Zinderen Bakker Jr. (1967) and Grindley (1973, unpublished), have made brief comments on this pattern.

The results from the present study indicate that the annual cycle of elephant seals on Marion Island is essentially similar to that occurring on Signy Island and South Georgia (Laws 1956a), Kerguelen (Angot 1954), and Macquarie and Heard Island (Carrick *et al.* 1962b, 1962c). However the onset of the summer haul out season appears to be retarded or advanced according to the position of the breeding ground in relation to the Antarctic Convergence. The onset of the spring pupping and mating season on Marion Island (Table 3) coincides with that on Macquarie Island, both islands lying close to and north of the convergence although Macquarie Island is nearly eight degrees of latitude further south than Marion Island. On those islands lying in the colder regions south of the convergence (Table 3) the onset of the pupping and mating season occurs about two weeks later. Although this effect is carried through to the moulting season, it becomes less evident in the mid-summer period. However although the onset of the pupping and mating season may vary with latitude and in relation to the convergence, the peak cow haul out period remains fairly constant regardless of latitude, except at the extreme southern breeding range such as on Signy Island, where the peak haul out period occurs about a week later than the normal mid-range date. The constancy of a peak cow haul out period viewed in conjunction with the varying time of onset of the haul out implies that the pupping and mating period is shorter, and the haul out cycle more synchronized, towards the limits of the range than in the mid-range breeding grounds.

On Macquarie and Heard Islands (Carrick *et al.* 1962c) the haul out pattern during the cow moult showed a single peak, except in the case of fourth year females for which there is a second haul out phase some two weeks after the first and major one. On Marion Island there were however two distinct peaks

TABLE 3: The annual cycle of southern elephant seals at the main breeding grounds, with respect to the position of the breeding ground in relation to the Antarctic Convergence

Island and Position	Distance from Antarctic Convergence	Breeding Season			Moulting Season		References
		Haul out period of cows	Maximum cows hauled out	Maximum pups	Peak of cow moult	Peak of bull moult	
Signy Island (60°43'S, 45°36'W)	402 km south	Oct. 6 – Dec. 3	Oct. 22	Oct. 28	Jan. 26	early April	Laws (1956a)
Heard Island (53°00'S, 73°30'E)	320 km south	mid-Sept.– late Nov.	Oct. 18		end Jan.	Mar. 20	Carrick *et al.* (1962c)
South Georgia (54°17'S, 36°30'W)	240 km south	Sept. 26 – late Nov.	Oct. 22	Nov. 13			Laws (1956a)
Kerguelen Islands (49°21'S, 70°12'E)	on it		Oct. 15		Jan.	Mar.	Angot (1954)
Macquarie Island (54°29'S, 157°00'E)	160 km north	early Sept. late Nov.	Oct. 16	Oct. 25	Jan. 25	Mar. 19	Carrick *et al.* (1962d)
Marion Island (46°55'S, 37°45'E)	290 km north	Sept. 7– Nov. 26	Oct. 15	Nov. 10	Jan. 22	Feb. 11	Present study
Campbell Island (52°33'S, 169°09'E)	800 km north		Oct. 16				Sorensen (1950)

in the cow moult (Figure 9), and it is not quite clear why this occurs. It may be misleading, the second peak containing in fact only fourth year females but appearing in the overall pattern because some fourth year females may have been included as adults during the censuses. On the other hand Gibbney (1957) and Carrick *et al.* (1962c) state that on Heard and Macquarie Islands cows in their first pregnancy moult earlier with the immatures, while adult cows moult progressively later each year. Since the annual cycles on Macquarie and Marion Islands are so similar it appears reasonable to assume that the above trends also occur on Marion Island, thus suggesting that the second peak consists of adult cows while the first peak consists of cows in their first pregnancy and subadult cows in their fourth year.

Carrick *et al.* (1962c) also found a second haul out peak in autumn (April) of second year seals at Macquarie and Heard Islands, but gave no explanation. Since the number of seals hauled out during the second phase was considerably lower than the number which originally hauled out to moult during the first phase, it would appear that many had left the island by autumn. As already suggested those that remained may have done so because of an inability to withstand an extended period at sea. However, it is worth noting that there may not in fact be a movement away from the island over winter, and that the reduction in numbers from the summer haul out to the autumn haul out may be the result of predation by killer whales *(Orcinus orca).* In Chapter 10 it is indicated that elephant seals, especially the younger and smaller individuals, constitute a fair proportion of the diet of these predators at Marion Island.

At Macquarie Island most seals hauled out during the winter season were immatures, although a few cows, mainly those in their first pregnancy, also hauled out (Carrick *et al.* 1962c). At Heard Island (Gibbney 1957) and South Georgia (Laws 1956b) the situation was similar. On Marion Island the pattern was the same in so far as most seals present during winter were immatures, but differed in that over the three winters of observation no cows were observed in the study area. A few subadults (Figure 8) and numerous second year animals and yearlings (Figure 10) were present right through the winter. Of the few subadults most were males with only occasional observations of females. Since the age of first conception on Marion Island is not yet known, it is possible that these apparently "subadult" females were in fact in their first pregnancy and should therefore have been classed as adults, the situation on Marion Island then being similar to that on Macquarie and Heard Islands, and South Georgia.

Weir and Rowlands (1973) commented that in the wild state a non-pregnant female is either "juvenile, senile, or a failure, and mechanisms must operate to safeguard the species against any of these occurring too frequently." It is necessary in mammals that the male and female are brought together at a time when each can produce mature gametes. In mammals such as the elephant seal which rely on terrestrial breeding and moulting, but are dispersed in the marine environment for the rest of the annual cycle, synchronization of the time of arrival on land ensures optimum breeding success. However unless adjustment of the terrestrial phase occurs, with respect to the time of arrival of different age classes, crowding and intraspecific competition would occur on the small island haul out grounds (Ling 1969). Bartholomew (1970) suggested that polygyny has evolved not only because it is a highly efficient reproductive pattern, but also because "it allows the congruent organization of a large number of ecological, physiological, and behavioral elements which would otherwise be incompatible". The well synchronized and adjusted terrestrial phase of the annual cycle of southern elephant seals seems to have evolved to bring together the widely dispersed members of a population to breed, and thus ensure species survival. However terrestrial breeding alone does not necessarily ensure species survival, but the timing of the whole terrestrial phase has enabled elephant seals to fully exploit the most favourable climatic period of the year with respect to pup rearing, mating, survival of newly independent young, and moulting, without creating overcrowding. The evolution of terrestrial gregariousness is positively advantageous since it greatly improves the efficiency of synchronized breeding and moulting, provided it occurs on terrestrial environments free from predators, such as oceanic islands. There, the limited terrestrial mobility of elephant seals combined with their gregarious behaviour and synchronized haul out, results in the breeding process taking place under extraordinarily congested (Bartholomew 1970), but efficient and non-overcrowded circumstances.

The moult of cows and immatures (especially the second year animals) is well synchronized. According to Ling (1965) hair growth and follicle activity start in September, and a normal uninterrupted four month activity period enables the immatures to moult in December/January. Oestrogens and androgens have an inhibitory effect on hair growth and moulting (Mohn 1958, Davis 1963), so that in the case of mature elephant seals breeding and lactating probably delays the moult. Because parturition followed by copulation and pregnancy are so well synchronized in mature female elephant seals, the decline of the inhibitory oestrogens also occurs synchronously and the moult follows, being as equally well synchronized as parturition. Ling (1965) believed that androgens produced a less well defined inhibition of hair growth, so that breeding bulls had a more extended and less synchronized moult. The synchronized cow moult and less well synchronized bull moult observed on Marion Island appears to corroborate his suggestions.

Ling (1972) suggested that temperature may affect both the autonomous cyclic rythm of epidermal proliferation as well as the rate of moulting. On Marion Island mean monthly air temperature (Table 1) remains fairly constant, but increases to above the yearly average (5,1°C) from December through to April (5,8 – 5,7°C), being warmest in February (7,3°C) and March (7,2°C) which is the period when the majority of adult seals moult. Thus temperature, acting as both an ultimate and a proximate factor, appears to play an important part in the regulation of the annual haul out cycle at any one breeding ground, as well as causing slight modifications to the onset of the haul out season according to latitude.

CHAPTER 6

LOCAL MOVEMENT AND MIGRATION

RESULTS

The number of elephant seals tagged since the start of the marking programme in November 1973, and the number of resightings up to November 1976 are shown in Table 4. Although only 7,1 per cent of the tagged seals have been resighted, some having been seen more than once, the resightings do however provide some information on movement, mainly inter- and intra-seasonal local movement.

TABLE 4: The number of southern elephant seals tagged and resighted on Marion Island from November 1973 to November 1976

Age Class and Sex	Number Tagged	Number Resighted	Resightings (%)
Adults:			
males	71	11	15,5
females	18	7	38,9
Subadults:			
males	33	3	9,1
females	32	5	15,6
sex unknown	2	0	0
Second Year:			
males	46	1	2,2
females	50	5	10,0
sex unknown	6	0	0
Yearlings/Pups:			
males	550	30	5,5
females	578	37	6,4
sex unknown	23	1	4,3
Total	1 409	100	7,1

Local Movement of Cows

All of the resighted cows were tagged while moulting so that there is no information on fidelity to pupping sites, and there appeared to be little fidelity to moulting sites. Four of the 11 resighted cows were resighted during the pupping season, none being at the same beach where they were tagged. It appeared that there was a tendency to pup and moult at different sites. There also appeared to be a tendency to haul out at various sites on arrival at the island following a winter absence, before finally selecting one on which to pup. Although there was no evidence to indicate fidelity to pupping sites, it seems that this tendency could facilitate recognition of a previously used pupping site, and therefore influence site selection in favour of such beaches.

Local Movement of Bulls

Two tagged harem bulls were each resighted the following two breeding seasons at the beaches where they were tagged, both still possessing the same status. Thus there was some evidence suggesting that territorial status could be retained for at least three years, and that dominant bulls showed strong fidelity to the breeding sites on which they held superior status. Three bulls tagged while moulting were each resighted in the following two moulting seasons, but never at the same site, indicating that they too showed little fidelity to moulting sites.

Local Movement of Subadults

All subadults were tagged while moulting and those observed in subsequent moulting seasons were always at new sites, again indicating that there was change from year to year in choice of moulting sites. No tagged subadults were seen during subsequent pupping and mating seasons. This is surprising since it was expected that some females at least would have reached maturity during the study and reappeared during a breeding season, and thus given some idea of the age of first parturition. The first subadult females marked were tagged in December and January 1973/74, in their third to fourth years at that time. After two years, by which stage some would have been in their fifth and sixth years, none had been resighted. Very few were tagged however (see Table 4), and it is possible that tag loss and the low chances of resighting so few tagged animals masked the return of data, rather than there being a possibility that the age of first parturition is greater than six years.

Local Movement of Second Year Animals

Very few animals in their second year were resighted, although some were resighted more than once. Four tagged on Prince Edward Island in April/May were seen on Marion Island the following August, on average 23 km away from the site of tagging. Those which overwintered on Marion Island moved about considerably along the east and north coasts. They appeared to spend one to four days on land in one place, went to sea for a few days, then hauled out at a different site for a few days, and so on through the winter.

Local Movement of Yearlings

Large numbers of yearlings were tagged at the end of the pupping and mating seasons, but relatively few were resighted (see Table 4). Those which returned in April/May showed no positive fidelity to their birthsites, equal numbers being resighted at birthsites and away from birthsites. Those which overwintered also moved about considerably during winter, and three eight month old males crossed to Marion Island from Prince Edward Island for at least part of their first winter.

None of the yearling females tagged in 1973 and 1974 were resighted during subsequent breeding seasons falling within this study. This suggests that females do not produce their first pups until at least the end of their fourth year, but additional resightings are necessary to substantiate this.

Tag Survival and Tagging Effort

With few exceptions, yearlings were double-tagged as described by Condy and Bester (1975). Information from the resightings indicated that 8,0 per cent of tagged yearlings had lost one tag within six months, 14,9 per cent within 12 months, 23,9 per cent within 18 months, and 24,5 per cent within 24 months. No seals tagged as yearlings were resighted more than 24 months after being tagged. Too few adults and subadults were resighted to produce really meaningful data on their tag survival. However of those resighted 3,8 per cent had lost one tag within six months, 11,5 per cent within 12 months, 11,5 per cent within 18 months, 23,1 per cent within 24 months, and 26,9 per cent within 30 months.

Tagging effort was concentrated on pups and yearlings as indicated in Table 4. A summary of the tagging effort in the main study area (Archway Bay to Ship's Cove) is given in Table 5. Over the study period 87,4 per cent of the pups surviving to weaning were tagged, which represents considerable effort.

Long Distance Movement

No seals tagged on Marion or Prince Edward Islands were resighted elsewhere, and no seals marked elsewhere were resighted on Marion or Prince Edward Islands. However Carrick *et al.* (1962c) stated that two elephant seals branded on Heard Island (53° 00'S, 73° 30'E) were resighted on Marion Island in November 1953. One of the resighted animals was a female aged two years one month old when resighted, and the other a male of the same age.

DISCUSSION

Although no elephant seals had been marked on the Prince Edward Islands prior to this study, southern elephant seals have been marked on many of the other antarctic and subantarctic islands namely; hot branding on Campbell Island (Sorensen 1950), Heard and Macquarie Islands (Chittleborough and Ealey 1951, Carrick and Ingham 1960, 1962a, Nicholls 1970), and South Georgia (Matthews 1929); and tagging on South Georgia and Signy Islands (Laws 1953, 1960, Dickinson 1967), and Gough Island (Condy and Bester 1975, Shaughnessy 1975). Apart from hot branding and tagging, other marking methods such as paints and dyes (Carrick and Ingham 1962a, Laws 1956a), and caustic soda brands (Laws 1953) have also been tried on southern elephant seals but with little success, the marks lasting a short time only. Condy and Bester (1975) discussed the choice of a marking technique for the seals of Marion and Gough Islands, and came to the conclusion that in terms of the logistics and effort required to mark large

TABLE 5: The number of southern elephant seal pups tagged in the main study area on Marion Island, from October 1974 to November 1976

Beach		1974			1975			1976			Study Period		
		No. Tagged	*Max. Count	% Tagged	No. Tagged	*Max. Count	% Tagged	No. Tagged	*Max. Count	% Tagged	No. Tagged	*Max. Count	% Tagged
Ship's Cove	♂♂	36			27			29			92		
	♀♀	37			27			23			87		
	??	2			0			0			2		
Total		75	76	98,7	54	59	91,5	52	52	100,0	181	187	96,8
Boulder	♂♂	7			5			4			16		
Beach	♀♀	7			4			3			14		
	??	1			0			0			1		
Total		15	15	100,0	9	10	90,0	7	13	53,8	31	38	81,6
Trypot	♂♂	26			22			25			73		
Beach	♀♀	38			35			26			99		
	??	1			0			0			1		
Total		65	67	97,0	57	60	95,0	51	59	86,4	173	186	93,0
Macaroni	♂♂	41			36			26			103		
Bay	♀♀	41			31			25			97		
	??	0			0			0			0		
Total		82	87	94,2	67	68	98,5	51	55	92,7	200	210	95,2
Archway	♂♂	78			30			39			147		
Bay	♀♀	62			32			40			134		
	??	0			0			1			1		
Total		140	147	95,2	62	112	55,4	80	112	71,4	282	371	76,0
Study Period		377	392	96,2	249	309	80,6	241	291	82,8	867	992	87,4

*Maximum Count – excluding dead pups. The figures given therefore include only live taggable pups.

numbers of seals, tagging was the most suitable. The results indicate that even though 24,5 – 26,9 per cent of resighted seals had lost one tag within 24–30 months, valuable data are nevertheless being slowly obtained with respect to local movements and site fidelity. By November 1977 only four years will have elapsed since the first pups were tagged, but from then on information relating to fidelity to birthsite and age of first parturition should start accruing. The pup tagging programme was initiated knowing that such data would only start becoming available four to six years later, after the completion of this thesis.

The data given in Table 5 indicate a steady decline in the number of pups counted and marked on each beach in the study area from the 1974 to 1976 summer seasons. In 1974 a total of 392 pups was counted of which 377 (96,2%) were tagged, while in 1976 only 291 were counted of which 241 (82,8%) were tagged, indicating a decline in numbers counted of 25,8 per cent. The data in Table 6 (next chapter) indicate that between 1973 and 1976 there was very little change in the total island pup crop, suggesting that the decline of 25,8 per cent in the study area represented merely a shift in distribution out of the study area. This shift was probably due to disturbance of the remaining lactating cows when the weaned pups on each beach were tagged, even though the technique was designed to keep disturbance to a minimum. It is suggested that tagging in the study area be undertaken each alternate year only, between which effort can be concentrated on Kildalkey Bay, Bullard Beach, Hansen Point, Sealer's Beach, Sea Elephant Bay, King Penguin Bay, and Goney Beach. If tagging effort is as successful on these beaches as it was in the study area (ie 87,4 per cent of pups were tagged over the study period), then some 340 pups should be tagged each alternate year at these other sites, representing approximately 32,0 per cent of the present annual pup crop.

Carrick *et al.* (1962c) noted that pups and subadults at Macquarie Island moved about quite considerably during the summer season, as was the case on Marion Island. However Nicholls (1970) found that on Macquarie Island a greater proportion of marked seals were found in the study area where they were marked, than at more remote locations. According to Carrick *et al.* (1962c) immature seals were most widely dispersed on Macquarie Island during their second year of life. The resightings of second year seals at Marion Island support this, especially in view of the observed movements from Prince Edward Island to Marion Island, and in general the data from Marion Island do not support Nicholls' findings.

During the pupping and mating season on Macquarie Island most marked cows were resighted in the study area where they were originally marked (Carrick *et al.* 1962c), but there was no apparent constancy of location between pupping and moulting season, and the situation on Marion Island was similar. Nicholls (1970) stated that at Macquarie Island many mature females returned to their birthsites to breed, and that this preferential selection applied equally to all age classes of cows from four to 11 years old, and each year the same proportion of cows bred away from their birthsites. The tendency for pregnant cows on Marion Island to haul out at various sites before finally selecting one on which to breed suggests that there may be a preferential selection of sites, since this behavioural pattern might enable visual recognition of the birthsite. Bulls on Macquarie Island were usually resighted near to their birthsite during the breeding season (Nicholls 1970), and although no evidence for fidelity to birthsite was available for Marion Island, fidelity to at least breeding site was demonstrated.

During the moulting season Nicholls (1970) found that recently matured cows on Macquarie Island were found near to their birthsites while older cows were relatively more common away from their birthsites. Since no known aged cows with known birthsites occurred in the Marion Island population, the presence or absence of such a trend in this study population could not be confirmed. Nicholls (1970) also found that moulting bulls were evenly spread through the Macquarie Island population, and even occurred at other islands in the region such as Campbell Island. On Marion Island moulting bulls showed no fidelity to moulting sites and were similarly dispersed through the local population, but no movement to Prince Edward Island or other islands was recorded.

With regard to long distance movement, Carrick and Ingham (1960) and Carrick *et al.* (1962c) recorded movements between Heard and Macquarie Islands, as well as movements from Heard Island to Marion Island, Amsterdam Island, and the

Vestfold Hills (Antarctica), from Macquarie Island to Campbell Island and vice versa, and to the Chatham Islands. They believed that any large scale movement between breeding grounds should have been revealed by a much greater number of records, and they showed that most long distance movements were made by seals at any time during their immature years. Laws (1956a) recorded movements from Signy Island to McMurdo Sound, Scott Island, Cape Denison, and Terre Adélie all in the Antarctic, and Dickinson (1967) recorded movements from South Georgia to Signy Island, South Argentina, and Tierra del Fuego. It would appear that the long range movements so far recorded are not indicative of any form of general migratory tendencies, but rather of isolated instances, and that in general elephant seals show strong fidelity to the breeding grounds where they were born. This is to some extent supported by Dickinson's (1967) observations that of 15 204 animals tagged on South Georgia, only four were resighted elsewhere during the course of eight years. However, tag loss must be considered and may be masking the actual extent of movements, since Laws (1956a) stated that "perhaps 15,0 per cent of the South Georgia herd" hauled out during the summer months at the Falkland Islands, the South Orkney Islands, and the South Shetland Islands.

Ross (1969) and Best (1971) discussed the occurrence of elephant seals on the coast of southern Africa, and both considered that the seals observed originated from the Prince Edward Islands, despite the westward moving West Wind Drift current separating the Prince Edward Islands population from southern Africa. It seems more likely that they originated from the "South Georgia Stocks" (Laws 1960) of South Georgia, the South Sandwhich or South Orkney Islands. In fact Vaughan (1967) recorded the appearance of a 14 month old seal from South Georgia at Quoin Point near Bredasdorp on the Cape Coast. Warneke (1976) discussed the occurrence of elephant seals in the more northerly Australasian Region, away from the main Macquarie Island breeding ground, and considered that it suggested eventual recolonization in New Zealand waters and in Western Bass Strait by seals from the Macquarie Island stocks. The occurrence of elephant seals on the southern African coast, especially on the western and southwestern coasts may likewise suggest possible colonization or recolonization trends. The potential for a world wide trend in elephant seal range expansion probably exists as a result of the near to full recovery following the sealing era, of most major subantarctic stocks to former levels. It is also possible that the present world stock has surpassed (or may exceed) original levels as a result of an increased food supply following the decline in numbers of squid eating sperm whales *Physeter catodon* (Gulland 1974). Should this be the case the regular appearance of elephant seals on continental coasts and islands may indicate that a true range expansion is underway. On the other hand, if the increasing attention being paid to the commercial potential of fish, krill, and squid resources of the Southern Ocean results in large scale exploitation of these resources by man (El-Sayed 1976), a stabilization of elephant seal stocks, or even an eventual decrease could be expected.

CHAPTER 7

POPULATION DYNAMICS

RESULTS

Observed Size of the Breeding Population

The results of the ground counts for the whole island, carried out each November from 1973 to 1976 are given in Table 6. Approximately 115 bulls participated in territorial and/or mating activities. Although the mean number of pups at weaning was 1 049, the mean annual number of cows counted was only 741. However cows must have been present in at least equivalent numbers to the pups, the reason for the low number of cows being that the counts were conducted in mid-November at a stage in the season when many cows had weaned their pups and departed, but when the number of pups was at a maximum (see Figure 7). Apparent twinning was observed only twice, accounting for only 0,19 per cent of the total pup crop.

Theoretical Size of the Breeding Population

Data on total island pre-weaning mortality during the study period are given in Table 7. Pup carcasses were usually easy to observe on the beaches but each year some may have been washed away by heavy seas before being counted. The calculated figure for pre-weaning mortality (2,53%) therefore represents a minimum value. Taking the number of pups surviving to weaning as 1 050 and pre-weaning mortality as 2,53 per cent, then at least 1 077 births occurred.

Ignoring twinning there must then have been at least 1 077 cows present to produce these pups. Since no culling was done, no specific data on pregnancy rates were available for the Marion Island population. However Laws (1960) gave an estimated 82,0 per cent pregnancy rate for the population at South Georgia, at a time when that population was increasing and being exploited. As the number of pups counted in each year of this study remained fairly constant (Table 6), the pregnancy rate if not similar to that for South Georgia, was probably lower.

TABLE 6: Maximum number of southern elephant seals counted during the pupping and mating season (September to November), at Marion Island (A = adults, P = pups).

Beach	1973			1974			1975			1976			*Mean		
	A♂	A♀	P	A♂	A♀	P	A♂	A♀	P	A♂	A♀	P	A♂	A♀	P
Transvaal Cove (Boulder Beach)	3	16	11	2	18	15	2	11	10	2	12	13	2	14	12
Trypot Beach	6	72	72	4	62	67	1	67	60	5	52	59	4	63	65
Macaroni Bay (South Beach)	5	90	78	7	78	87	3	63	68	7	51	55	6	71	72
Archway Bay	3	120	93	9	155	147	5	116	112	13	109	112	8	125	116
Hansen Point	2	13	13				1	3	13	2	6	11	2	7	12
Bullard Beach	2	24	18							1	17	39	2	20	28
Bullard Beach South	3	20	21							3	13	20	3	16	20
Killerwhale Cove	2	8	14							2	11	13	2	9	13
Waterfall Beach	1	3	6										1	3	6
Landfall Beach	1	10	30							3	13	34	2	11	32
Sealer's Cave	4	20	24							3	15	23	3	17	23
Kildalkey Bay	14	50	151				5	34	101	12	65	163	10	50	138
Cape Hooker (Hooker Cove)	1	3	5							0	1	4	1	2	4
Crawford Bay	10	20	28	13	9	20				13	37	43	12	22	30
Goodhope Bay				7	17	60	3	1	67	10	48	65	7	22	64
Kaalkoppie	14	21	47	12	7	52				10	33	38	12	20	46
Mixed Pickle Cove										1	0	1	1	0	1
Cape Davis (Sealer's Beach)	2	8	13				1	12	4	1	7	10	1	9	9
Storm Petrel Bay	1	8	8							1	12	13	1	10	10
Goney Beach	9	70	63	6	5	58				6	45	60	7	40	60
Log Beach	1	9	10	0	1	6				0	6	4	1	5	7
King Penguin Bay	7	36	46	6	8	37	8	13	35	6	53	65	7	28	46
Sea Elephant Bay	2	29	41	3	11	58				4	30	39	2	18	35
Blue Petrel Bay	1	10	8	3	18	24	4	10	30	2	29	29	3	17	23
Sealer's Beach	3	50	84	3	44	96	2	17	53	3	44	60	3	39	73
Sealer's Beach South	3	20	25	3	18	34				2	20	13	3	19	24
Ship's Cove	7	119	104	6	72	76	5	55	59	6	48	52	6	74	73
Rockhopper Bay (mouth of the van den Boogaard River)	7	14	15	1	7	6	1	10	3	1	10	5	3	10	7
Total	111	863	1028	85	530	843	41	412	615	119	787	1043	115	741	1049

*Mean calculated to nearest whole number

Assuming that 82,0 per cent represents the maximum pregnancy rate for the Marion Island population, and that 1 077 cows gave birth each year of the study, then some 236 (18%) additional cows were not pregnant each year, giving a total of 1 313 cows.

TABLE 7: Pre-weaning mortality of southern elephant seals on Marion Island

Year	Number of Live Pups	Number of Dead Pups	Total Number of Births	Mortality (%)
1973	1 028	27	1 055	2,56
1974	843	15	858	1,75
*1975	321	12	333	3,60
1976	1 043	.30	1 073	2,80
Total	3 235	84	3 319	2,53

*The figures for 1975 refer only to the main study area of Archway Bay to Ship's Cove.

The present breeding population of elephant seals on Marion Island thus totals 1 428, with approximately 1 313 cows and 115 bulls. The total pup crop is approximately 1 077, but since pre-weaning mortality in the study area (see Table 11) indicates that it is greater than 2,53 per cent (Table 7), the total pup crop is probably closer to 1 100.

Population Trend

Prior to this study two counts of the elephant seal population were made, the first a total count by Rand (1962) in the 1951/52 summer season, and the second a partial count by Van Zinderen Bakker Jr. (1976, unpublished) in the 1965/66 summer season. Their data are summarized, and compared to those (mean values from Table 6) obtained during this study, in Table 8.

Assuming that the environment is non-limiting to population growth, the intrinsic rate of natural population increase under such favourable conditions is given as:

TABLE 8: Results of recent and previous counts of the southern elephant seal population on Marion Island

Beach	1975/76 (Present study)			1965/66 (Van Zinderen Bakker Jr. 1976, unpublished)			1951/52 (Rand 1962)		
	Bulls	Cows	Pups	Bulls	Cows	Pups	Bulls	Cows	Pups
Ship's Cove	6	74	73	3	143	175	–	–	–
Sealer's Beach	3	39	73	5	150	100	–	–	–
Mixed Pickle Cove	1	0	1	1	7	12	–	–	–
Van den Boogaard river mouth	3	10	7	2	40	33	–	–	–
Subtotal	13	123	154	11	340	320	–	–	–
Total breeding population	115	1 313	1 077	–	–	–	350	4 000	3 662

$$\frac{dN}{dt} = rN \qquad \text{(Birch 1970, Odum 1971, Wilson and Bossert 1971).}$$

where N = number of individuals in the population at a given moment, t = time, and r = instantaneous coefficient of population growth. By solving this differential equation a second more useful equation, which allows the rapid projection of N through as long a period of time into the future or past as required, can be obtained;

$$N_t = N_o e^{rt} \qquad \text{(Birch 1970, Odum 1971, Wilson and Bossert 1971).}$$

where N_o = the number of individuals in the population at the start of the observations, N_t = the number after elapsed time t, and e = the base of natural logarithms. By taking the natural logarithm of both sides of this equation it is converted into the form;

$$\log_e N_t = \log_e N_o + rt \qquad \text{(Odum 1971)}$$

and it follows that $r = \dfrac{\log_e N_t - \log_e N_o}{t}$ (Odum 1971)

which is the form used for calculating r.

The breeding population – according to the data in Table 8, the number of elephant seals present during the pupping and mating season (ie. bulls, cows, and pups) in 1951 was 8 012, and 2 505 in 1975, indicating a decline in the population since 1951/52. Using the above equation the instantaneous coefficient of population growth (r) is calculated as;

$$r = \frac{\log_e 2505 - \log_e 8012}{24} \qquad \text{where } N_t = 2505$$

$$= \frac{7{,}826 - 8{,}989}{24} \qquad N_o = 8012$$

$$= -0{,}048 \qquad t = 24$$

and indicates a decline of 4,8 per cent per year between 1951 and 1975.

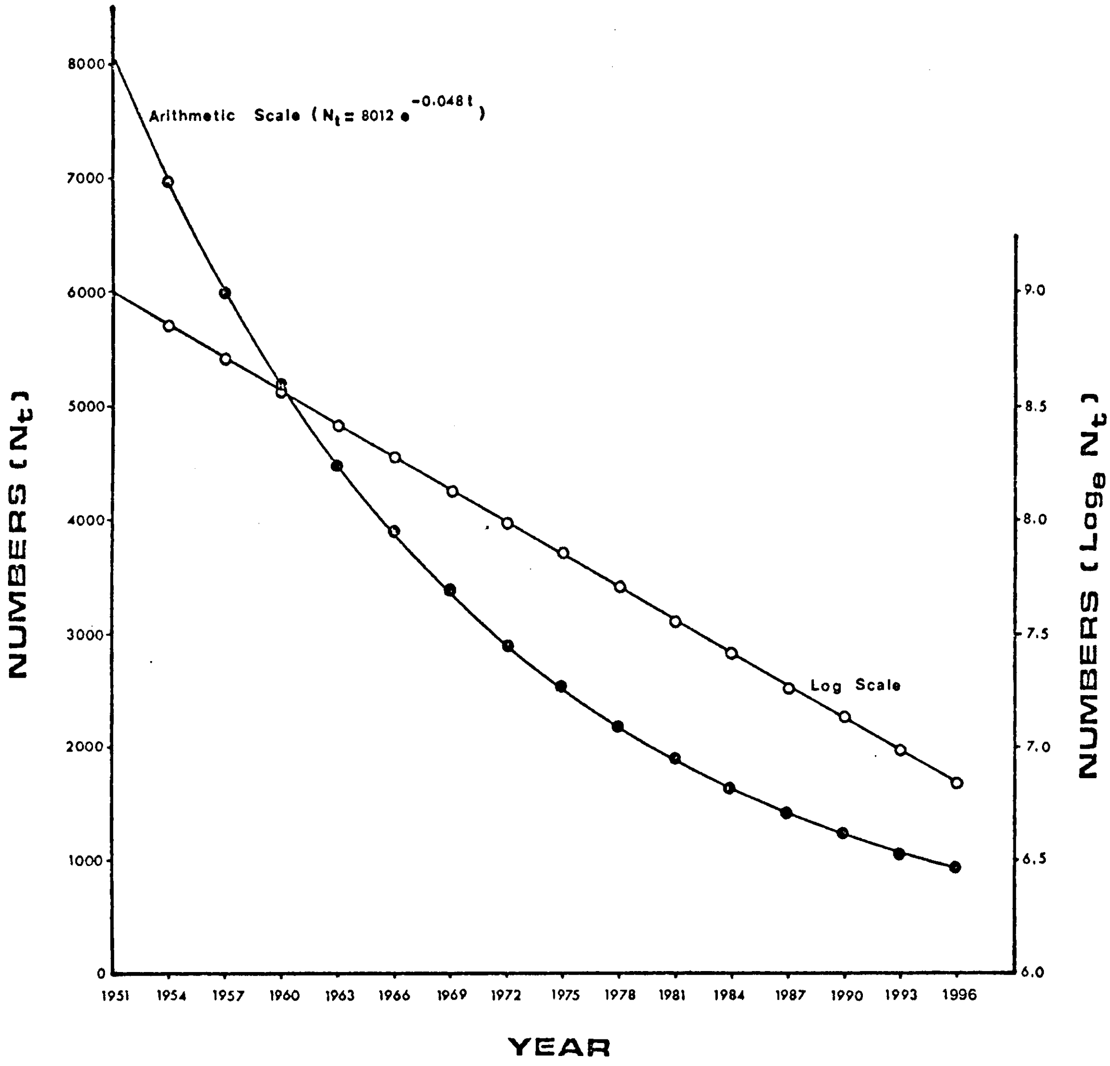


FIGURE 11

Population trend of southern elephant seals (breeding adults and pups) on Marion Island from 1951 to 1975, and projected through to 1996.

$r_{(\text{cows, } 1965-1975)} = -0{,}102$

$r_{(\text{bulls, } 1965-1975)} = -0{,}017$

$r_{(\text{pups, } 1965-1975)} = -0{,}073$

$r_{(\text{total in study area, } 1965-1975)} = -0{,}084$

These values indicate that there has been a more rapid decline at at least four breeding sites for which there is reliable data since 1965, compared to the decline for the period 1951 to 1975.

Using Rand's (1962) data as a baseline, the values of r for cows, bulls, and pups have been calculated on the same basis and are;

$r_{(\text{cows, } 1951-1975)} = -0{,}046$

$r_{(\text{bulls, } 1951-1975)} = -0{,}046$

$r_{(\text{pups, } 1951-1975)} = -0{,}051$

Survivorship

Since seal tagging on Marion Island was only recently initiated and no elephant seals were culled during the present study, there were no data on mortality or survival rates for each age class from yearlings upwards. However both Laws (1960) and Carrick and Ingham (1962e) gave some information on age specific mortality or survival for the South Georgia and Macquarie Island populations respectively. Although their data are not necessarily applicable to the Marion Island population *per se,* it is of interest to examine survivorship on Marion Island based on their data from South Georgia and Macquarie Island.

Each year during this study approximately 1 077 pups were born. However, pre-weaning mortality in the study area only was 5,99 per cent (Table 11) compared to 2,53 per cent for the whole island (Table 7), so that it is assumed that in fact approximately 1 100 pups were born, of which 51,2 per cent were males and 48,8 per cent females (i.e. 563 males and 537 females).

(a) **Female survival** – Both Laws (1960) and Carrick and Ingham (1962e) considered that 40 per cent die in their first year, but thereafter their opinions differed with respect to age specific mortality. Laws (1960) considered that on South Georgia age specific mortality was (age/% mortality); 1/20,0; 2–10/13,0; 11/22,0; 12/23,0; 13/25,0; 14/30,0; 15/42,0; 16/48,0; 17/52,0; 18/60,0; 19/80,0; 20/100,0; while on Macquarie Island Carrick and Ingham (1962e) considered that age specific survival was (age/% survival); 4/46,5; 6/39,5; 8/20,5; >8/ a steady decline "so that the average breeding female is unlikely to live more than 10 years".

Since it has already been shown that in many respects the elephant seal populations on Marion and Macquarie Islands are similar, computation of age specific survival on Marion Island has been based mainly on the pattern at Macquarie Island, which has been given above. Computation of age specific survival of females is shown below and has been based on the format used by Laws (1960).

SEALS ALIVE AT BEGINNING OF YEAR			SEALS DYING NATURALLY DURING THE YEAR	
Age. (in years)	Number	% Surviving	Number	% Mortality
0	537	100,00	215	*/** 40,0
1	322	59,96	26	8,0
2	296	55,12	24	8,0
3	272	50,65	22	8,0
4	250	*46,55	20	8,0
5	230	42,83	18	8,0
6	212	*39,48	59	28,0
7	153	28,49	43	28,0
8	110	*20,48	33	30,0
9	77	14,34	32	42,0
10	45	8,38	22	48,0
11	23	4,28	12	52,0
12	11	2,05	7	60,0
13	4	0,74	3	80,0
14	1	0,19	1	100,0

*Corresponds to age specific survival on Macquarie Island (Carrick and Ingham 1962e)

**Corresponds to age specific mortality at South Georgia (Laws 1960).

It has been assumed that mortality is constant from the age of 1 – 5 years, and from the age of 6 – 7 years. Laws (1960) also considered that mortality was constant during these periods, but was higher at South Georgia from age one to five (13,0%), and lower from age six to seven (13%). Mortality at South Georgia only exceeded 28,0 per cent per year from the 14 year of age when it was given as 30,0 per cent by Laws (1960). Applying the South Georgia mortality rates of from 30,0 per cent onwards to the above computation once mortality reaches 28,0 per cent, the population on Marion Island is seen to decline steadily so that by the time they are 10 years old only some 8,38 per cent of the females survive, and some of these survive to an age of 14 years. This approximates the situation believed to exist on Macquarie Island (few survive after age 10) by Carrick and Ingham (1962e).

(b) **Male survival** – Laws (1960) considered that at South Georgia mortality in the first year of life was 56,7 per cent, while Carrick and Ingham (1962e) considered it to be of the order 40,0 – 50,0 per cent at Macquarie Island. Observations at Marion Island during the yearling autumn haul out (see Figure 10) indicated that males and females were approximately equal in number, and since the pup sex ratio did not differ significantly from unity (see page 77) it has been assumed that male mortality in the first year of life on Marion Island is similar to that for the females (ie. 40,0%). Laws (1960) gave age specific mortality at South Georgia as (age/% mortality); 1/30,0; 2–10/17,0; 11/23,0; 12/24,0; 13/26,0; 14/30,0; 15/42,0; 16/50,0; 17/60,0; 18/80,0; 19/90,0; 20/100,0; while for Macquarie Island Carrick and Ingham (1962e) gave age specific survival as (age/% survival); 4/40,1; 6/26,5; 8/14,0; >8/ such that they appear to survive "with a much slower mortality rate to 20 or more years old". Computation of age specific survival of males is shown below, and has been based on the pattern at Macquarie Island and South Georgia.

SEALS ALIVE AT BEGINNING OF YEAR			SEALS DYING NATURALLY DURING THE YEAR	
Age (in years)	Number	% Surviving	Number	% Mortality
0	563	100,00	225	40,0
1	338	62,94	42	12,5
2	296	52,58	37	12,5
3	259	46,00	32	12,5
4	227	*40,32	43	19,0
5	184	32,68	35	19,0
6	149	*26,47	40	27,0
7	109	19,36	29	27,0
8	80	*14,21	14	**17,0
9	66	11,72	11	**17,0
10	55	9,77	9	**17,0
11	46	8,17	11	**23,0
12	35	6,22	8	**24,0
13	27	4,79	7	**26,0
14	20	3,55	6	**30,0
15	14	2,49	6	**42,0
16	8	1,42	4	**50,0
17	4	0,71	2	**60,0
18	2	0,35	1	**80,0
19	1	0,18	1	**100,0

*Corresponds to age specific survival on Macquarie Island (Carrick and Ingham 1962e)

**Corresponds to age specific mortality on South Georgia (Laws 1960).

It has been assumed that mortality for age groups 1 – 3 years old, 4 – 5 years old, 6 – 7 years old, and 8 – 10 years old is constant within each, but differs from group to group. From the age of eight years onwards Laws' (1960) mortality figures have been used, and approximates the situation believed to exist on Macquarie Island (mortality rate is slower and some individuals survive to an age of 20 years) by Carrick and Ingham (1962e).

Observed Size of the Immature Population

Subadults and second year animals hauled out to moult each year from December to April (see Figures 8 and 10). The moulting period was somewhat extended and there were individuals arriving and departing throughout this period, although numbers reached peaks in mid-December (subadult males and second year old seals), and mid-January (subadult females).

The maximum number of moulting subadults and second year animals in the main study area at these times is given in Table 9. Over the study period the mean number of subadults observed was 267, and the mean number of second year old seals observed was 179.

TABLE 9: Maximum number of immature southern elephant seals in the study area during the moulting season (December to April) at Marion Island (S = subadults, 2Y = second year individuals).

Beach	1973/74		1974/75		*Mean	
	S	2Y	S	2Y	S	2Y
1. Transvaal Cove (Boulder Beach)	64	20	58	50	61	35
2. Trypot Beach	75	40	56	43	65	41
3. Macaroni Bay South	7	4	39	39	23	21
4. Archway Bay	45	3	52	82	48	42
5. Rockhopper Bay	50	15	9	18	29	16
6. Ship's Cove	47	17	35	31	41	24
Study Area	288	99	249	263	267	179

*Mean calculated to the nearest whole number.

Theoretical Size of the Immature Population

Since moulting subadults moved inland (see Chapter 4) and were widely dispersed, it was not possible to conduct an entire island count owing to the inherent logistic difficulties due to the dispersal of the seals, and the absence of one specific period during which all moulting immature seals were hauled out. This latter factor meant that if the total population of moulting immature seals was to be counted, at least three journeys round the island in quick succession were necessary. This was not possible since at the same time the once weekly counts in the main study area had to be maintained, as well as regular visits made to the main fur seal study colony at Cape Davis.

In order to obtain information on the size of the immature population, it was decided to monitor their numbers in the main study area by counting them once each week during their haul out periods, and then extrapolate from the known relationship between immatures (i.e. subadults and yearlings) and adults in the study area, to obtain the data for the entire population, of which only the number of adults was known. In addition it is also possible to obtain some idea of the total immature population by referring to the male and female survival rates (see page 75).

(a) **Relationship between immatures and adults in the main study area** – the mean numbers of cows, bulls, and pups in the main study area (Ship's Cove to Archway Bay) during the study are shown in Table 6, and the mean maximum numbers of subadults and second year individuals counted in the same area during their respective moulting seasons are shown in Table 9.

These data have been rearranged as follows so that multiple regressions relating (i) number of subadults (X_4) to number of bulls (X_1), cows (X_2), and pups (X_3), and (ii) number of second year individuals (X_5), to number of bulls (X_1), cows (X_2), and pups (X_3), could be computed;

*Beach		1	2	3	4	5	6
X_1	(bulls)	2	4	6	8	3	6
X_2	(cows)	14	63	71	125	10	74
X_3	(pups)	12	65	72	116	7	73
X_4	(subadults)	61	65	23	48	29	41
X_5	(second year)	35	41	21	42	16	24

*Beach numbers 1–6 correspond to those given in Table 9

The following two multiple regression equations (dependent variables X_4 and X_5) were determined using a statistical package for the social sciences (SP SSH – Release 6.02).

(1) $X_4 = (90{,}13 - 24{,}22\ X_1 + 1{,}79\ X_2 - 0{,}62\ X_3) \pm 14{,}38$; where the interval ($X_4 \pm 14{,}38$) will contain the real but unknown value for X_4 (ie. subadults) when predicted by X_1, X_2, and X_3 in 95 per cent of all cases.

(2) $X_5 = (49{,}91 - 14{,}36\ X_1 + 1{,}50\ X_2 - 0{,}69\ X_3) \pm 2{,}65$; where the interval ($X_5 \pm 2{,}65$) will contain the real but unknown value for X_5 (ie. second year animals) when predicted by X_1, X_2, and X_3 in 95 per cent of all cases.

These two equations have been used to predict the values of X_4 (subadults) and X_5 (second year individuals) for all beaches occupied by elephant seal colonies on Marion Island, and the results are shown in Table 10a. Clearly the regression equations are not satisfactory since the predicted total subadult and second year individual populations are only 414,01 ± 14,38 and 134,23 ± 2,65 respectively.

Examination of the data in Table 10a shows that the predicted values of X_4 and X_5 were usually negative when X_1 (ie. number of bulls) was large. In the actual computation of the regression coefficients the values of X_1 (see page 72) used in the calculations were generally small (mean 4,83 ± 2,23; range 2 – 8), and the equations predicted the known values for X_4 and X_5 with good accuracy (ie. the real value fell within the range of the predicted value ± S.D. in 95% of cases) as shown below;

Beach	Observed		Predicted	
	X_4	X_5	X_4	X_5
1	61	35	59,31 ± 14,38	33,91 ± 2,65
2	65	41	65,72 ± 14,38	42,12 ± 2,65
3	23	21	27,26 ± 14,38	20,57 ± 2,65
4	48	42	48,20 ± 14,38	42,49 ± 2,65
5	29	16	31,03 ± 14,38	17,00 ± 2,65
6	41	24	32,01 ± 14,38	24,38 ± 2,65

TABLE 10a: Number of subadults (X_4) and second year (X_5) southern elephant seals at Marion Island predicted from the equations; (1) $X_4 = (90,13 - 24,22\ X_1 + 1,79\ X_2 - 0,62\ X_3) \pm 14,38$, and (2) $X_5 = (49,91 - 14,36\ X_1 + 1,50\ X_2 - 0,69\ X_3) \pm 2,65$ (A = adults, S = subadults, 2Y = second year individuals).

Beach	Observed			Observed		Predicted	
	A♂ (X_1)	A♀ (X_2)	Pups (X_3)	S (X_4)	2Y (X_5)	S (X_4 ± S.D.)	2Y (X_5 ± S.D.)
Transvaal Cove (Boulder Beach)	2	14	12	61	35	+ 59,31 ± 14,38	+ 33,91 ± 2,65
Trypot Beach	4	63	65	65	41	+ 65,72 ± 14,38	+ 42,12 ± 2,65
Macaroni Bay (South Beach)	6	71	72	23	21	+ 27,26 ± 14,38	+ 20,57 ± 2,65
Archway Bay	8	125	116	48	42	+ 48,20 ± 14,38	+ 42,49 ± 2,65
Hansen Point	2	7	12	–	–	+ 46,78 ± 14,38	+ 23,41 ± 2,65
Bullard Beach	2	20	28	–	–	+ 60,13 ± 14,38	+ 31,87 ± 2,65
Bullard Beach South	3	16	20	–	–	+ 33,71 ± 14,38	+ 17,03 ± 2,65
Killerwhale Cove	2	9	13	–	–	+ 49,74 ± 14,38	+ 25,72 ± 2,65
Waterfall Beach	1	3	6	–	–	+ 67,56 ± 14,38	+ 35,91 ± 2,65
Landfall Beach	2	11	32	–	–	+ 41,54 ± 14,38	+ 15,61 ± 2,65
Sealer's Cave	3	17	23	–	–	+ 33,64 ± 14,38	+ 16,46 ± 2,65
Kildalkey Bay	10	50	138	–	–	– 148,13 ± 14,38	–113,41 ± 2,65
Cape Hooker (Hooker Cove)	1	2	4	–	–	+ 67,01 ± 14,38	+ 35,79 ± 2,65
Crawford Bay	12	22	30	–	–	– 179,73 ± 14,38	–110,11 ± 2,65
Goodhope Bay	7	22	64	–	–	– 79,71 ± 14,38	– 61,77 ± 2,65
Kaalkoppie	12	20	46	–	–	– 193,23 ± 14,38	–124,19 ± 2,65
Mixed Pickle Cove	1	0	1	–	–	+ 65,29 ± 14,38	+ 34,86 ± 2,65
Cape Davis (Sealer's Beach)	1	9	9	–	–	+ 76,44 ± 14,38	+ 42,84 ± 2,65
Storm Petrel Bay	1	10	10	–	–	+ 77,61 ± 14,38	+ 43,65 ± 2,65
Goney Beach	7	40	60	–	–	– 45,01 ± 14,38	– 32,01 ± 2,65
Log Beach	1	5	7	–	–	+ 70,52 ± 14,38	+ 38,22 ± 2,65
King Penguin Bay	7	28	46	–	–	– 57,81 ± 14,38	– 40,35 ± 2,65
Sea Elephant Bay	2	18	35	–	–	+ 52,21 ± 14,38	+ 24,04 ± 2,65
Blue Petrel Bay	3	17	23	–	–	+ 33,30 ± 14,38	+ 16,46 ± 2,65
Sealer's Beach	3	39	73	–	–	+ 42,02 ± 14,38	+ 14,96 ± 2,65
Sealer's Beach South	3	19	24	–	–	+ 36,60 ± 14,38	+ 18,77 ± 2,65
Ship's Cove	6	74	73	41	24	+ 32,01 ± 14,38	+ 24,38 ± 2,65
Rockhopper Bay (mouth of the Van den Boogaard River)	3	10	7	29	16	+ 31,03 ± 14,38	+ 17,00 ± 2,65
	115	741	1049			414,01 ± 14,38	134,23 ± 2,65

Thus when the value of X_1 was low (about four to five, mean 4,83) the regression equations predicted the real values of X_4 and X_5 with much greater accuracy than when the value of X_1 was high. It is of interest to re-examine the predictability of the equations by employing the same independent variable coefficients but substituting the value 4,83 for X_1 whenever its real value is greater than five. The results are shown in Table 10b, and appear to be more realistic following treatment in this manner. They indicate a subadult population of 1177,69 ± 14,38, and a second year seal population of 586,60 ± 2,65.

However, since the above treatment has been somewhat arbitrary from the arithmetical point of view, even if the results obtained appear to be more realistic, it is necessary to substantiate these results using a different technique.

(b) **From survivorship** – as mentioned earlier, it is possible to obtain some idea of numbers of subadults and second year individuals from the survival tables. According to the female survival table (page 68) there are 322 second year individuals, and from the male survival table (page 70) 338 second year individuals, giving a total of 660 second year elephant seals at Marion Island. In (a) above a total of 587 was calculated from the regression equations using the modified X_1 (= 4,83) value when real X_1 > 5. The two estimates differ by 73 animals (11,1%), and although it does not show close agreement, at least indicates that modification of X_1 as described has greatly improved the predictability of the regression equation for X_5 (ie. second year seals).

According to Chapter 3 (age classification), subadult females are those in their third and fourth years. From the female survival table (page 68) there are 296 seals in their third year, and 272 in their fourth year, giving a total of 568 subadult females. Similarly, their are 296 males in their third year, 259 in their fourth year, and 227 in their fifth year, thus giving a subadult male population of 782 animals. The total subadult population (males and females) is therefore 1 350. From the regression

TABLE 10b: Number of subadults (X_4) and second year (X_5) southern elephant seals at Marion Island predicted from the regression equations, but where observed $X_1 > 5$ it has been made $X_1 = 4{,}83$ (A = adults, S = subadults, 2Y = second year individuals).

Beach	Observed			Observed		Predicted	
	A♂ (X_1)	A♀ (X_2)	Pups (X_3)	S (X_4)	2Y (X_5)	S (X_4 ± S.D.)	2Y (X_5 ± S.D.)
Transvaal Cove (Boulder Beach)	2	14	12	61	35	+ 59,31 ± 14,38	+ 33,91 ± 2,65
Trypot Beach	4	63	65	65	41	+ 65,72 ± 14,38	+ 42,12 ± 2,65
Macaroni Bay (South Beach)	4,83	71	72	23	21	+ 55,60 ± 14,38	+ 37,71 ± 2,65
Archway Bay	4,83	125	116	48	42	+ 124,98 ± 14,38	+ 88,01 ± 2,65
Hansen Point	2	7	12	–	–	+ 46,78 ± 14,38	+ 23,41 ± 2,65
Bullard Beach	2	20	28	–	–	+ 60,13 ± 14,38	+ 31,87 ± 2,65
Bullard Beach South	3	16	20	–	–	+ 33,71 ± 14,38	+ 17,03 ± 2,65
Killerwhale Cove	2	9	13	–	–	+ 49,74 ± 14,38	+ 25,72 ± 2,65
Waterfall Beach	1	3	6	–	–	+ 67,56 ± 14,38	+ 35,91 ± 2,65
Landfall Beach	2	11	32	–	–	+ 41,54 ± 14,38	+ 15,61 ± 2,65
Sealer's Cave	3	17	23	–	–	+ 33,64 ± 14,38	+ 16,46 ± 2,65
Kildalkey Bay	4,83	50	138	–	–	– 22,91 ± 14,38	– 39,67 ± 2,65
Cape Hooker (Hooker Cove)	1	2	4	–	–	+ 67,01 ± 14,38	+ 35,79 ± 2,65
Crawford Bay	4,83	22	30	–	–	– 6,07 ± 14,38	– 7,15 ± 2,65
Goodhope Bay	4,83	22	64	–	–	– 27,15 ± 14,38	– 30,61 ± 2,65
Kaalkoppie	4,83	20	46	–	–	– 19,57 ± 14,38	– 21,19 ± 2,65
Mixed Pickle Cove	1	0	1	–	–	+ 65,29 ± 14,38	+ 34,86 ± 2,65
Cape Davis (Sealer's Beach)	1	9	9	–	–	+ 76,44 ± 14,38	+ 42,84 ± 2,65
Storm Petrel Bay	1	10	10	–	–	+ 77,61 ± 14,38	+ 43,65 ± 2,65
Goney Beach	4,83	40	60	–	–	+ 7,55 ± 14,38	– 0,85 ± 2,65
Log Beach	1	5	7	–	–	+ 70,52 ± 14,38	+ 38,22 ± 2,65
King Penguin Bay	4,83	28	46	–	–	– 5,25 ± 14,38	– 9,19 ± 2,65
Sea Elephant Bay	2	18	35	–	–	+ 52,21 ± 14,38	+ 24,04 ± 2,65
Blue Petrel Bay	3	17	23	–	–	+ 33,30 ± 14,38	+ 16,46 ± 2,65
Sealer's Beach	3	39	73	–	–	+ 42,02 ± 14,38	+ 14,96 ± 2,65
Sealer's Beach South	3	19	24	–	–	+ 36,60 ± 14,38	+ 18,77 ± 2,65
Ship's Cove	4,83	74	73	41	24	+ 60,35 ± 14,38	+ 41,18 ± 2,65
Rockhopper Bay (mouth of the Van den Boogaard River)	3	10	7	29	16	+ 31,03 ± 14,38	+ 17,00 ± 2,65
	(115)	741	1049			1177,69 ± 14,38	+586,60 ± 2,65

equation for X_4 (subadults) using modified X_1 values when necessary, a total of only 1 178 subadults were predicted. Clearly the regression equation of X_4 on X_1, X_2, and X_3 is not well tuned, less so than the regression equation of X_5 (second year seals) on X_1, X_2, and X_3. Nevertheless by modifying X_1 when applicable the predicted estimate has been considerably improved from initially 414 subadults (Table 10a) to 1 178 subadults (Table 10b), which differs by 172 animals (12,7%) from the number determined using the survival tables.

Sex Ratio

(a) **At birth** – the sex ratio is not known since it was not possible to get within the harems to determine the sex of each newborn pup by inspection, nor was it possible to do so by observation from a distance as newborn pups were invariably shielded from view by other members of the closely packed harems. However after weaning all surviving pups were tagged (Condy and Bester 1975), at which time they were also sexed.

Within the study area where 87,4 per cent of pups were tagged, the sex ratio at weaning was 1:1 (Table 5), but including pups tagged elsewhere the total number tagged was 578 males and 550 females, giving a sex ratio of 1:0,95. Using the formula;

$$\frac{\mathrm{fm}}{\mathrm{N}} \pm 1{,}96\sqrt{\frac{\frac{\mathrm{fm}}{\mathrm{N}}\left(1-\frac{\mathrm{fm}}{\mathrm{N}}\right)}{\mathrm{N}}} \qquad \text{(Simpson, Roe and Lewontin 1960)}$$

at the 95 per cent confidence interval for proportion of males, where fm = number of males, and N = number of males and females;

$$0{,}512 \pm 1{,}96\sqrt{\frac{0{,}512\ (1-0{,}512)}{1128}}$$

$$= 0{,}512 \pm 1{,}96\ (0{,}0149)$$

$$= 0{,}512 \pm 0{,}029$$

Thus since this interval includes the hypothetical value of 0,50 the sex ratio does not differ significantly from unity.

(b) **Second year** – during the 1973/74 moulting season, an attempt was made to sex as many of the animals counted during the weekly censuses as possible. Regular censusing was carried out in the study area (Ship's Cove to Archway Bay), as well as spot censuses at other sites. A total of 165 second year seals were counted in mid-December, the height of the second year moult, of which 40 were male, 54 female, and 71 (43,03%) were not sexed, giving a sex ratio of 1:1,35 which does not differ significantly from unity at the 95 per cent level of confidence.

(c) **Subadult** – in the same season that the second year individuals were counted to determine sex ratio, subadults were counted on the same basis and at the same sites, though the counting was carried out in early December for males and mid-January for females. A total of 506 animals were counted of which 157 were male, 240 female, and 109 (21,54%) unsexed, giving a sex ratio of 1:1,53 which differs significantly from unity at the 95 per cent level of confidence.

(d) **Adult** – according to previous calculations the adult population consists of 115 bulls and 1 313 cows, giving a sex ratio of 1:11,42, which differs significantly from unity at the 95 per cent level of confidence.

Population Structure

The age structure of the population is shown in Figure 12, and to obtain the necessary data for construction of this figure the following assumptions were made;

(a) Number of pups surviving to weaning is 1 050 (see page 60), and the sex ratio is 1:0,95 (see page 77).

(b) Number of adults is 1 428 (see page 62), and sex ratio is 1:11,42 (see above).

(c) Number of second year individuals, as determined from the survival tables (see page 75) is 660, and sex ratio is 1:1,35 (see above).

(d) Number of subadults, as determined from the survival tables (see page 75) is 1 350, and the sex ratio is 1:1,53 (see page 78).

The four age classes presented above are alone not sufficient to provide a meaningfull illustration of population structure. Thus an attempt has been made below to reduce the lumped "adult" and "subadult" age classes to the proportionate representation in numbers for each age (in years).

From the male and female survival tables it is possible to calculate the per cent subadults and per cent adults surviving for each actual age in the respective subadult and adult age brackets, assuming that subadult females are those in their third and fourth years and adult females are those in their fifth year onwards, while subadult males are those in their third to fifth years and adult males are those in their sixth year onwards (see Chapter 3). The computations are shown below;

Subadults – total number 1 350, sex ratio 1:1,53, therefore there are 534 males and 816 females.

Adults – total number 1 428, sex ratio 1:11,42, therefore there are 115 males and 1 313 females.

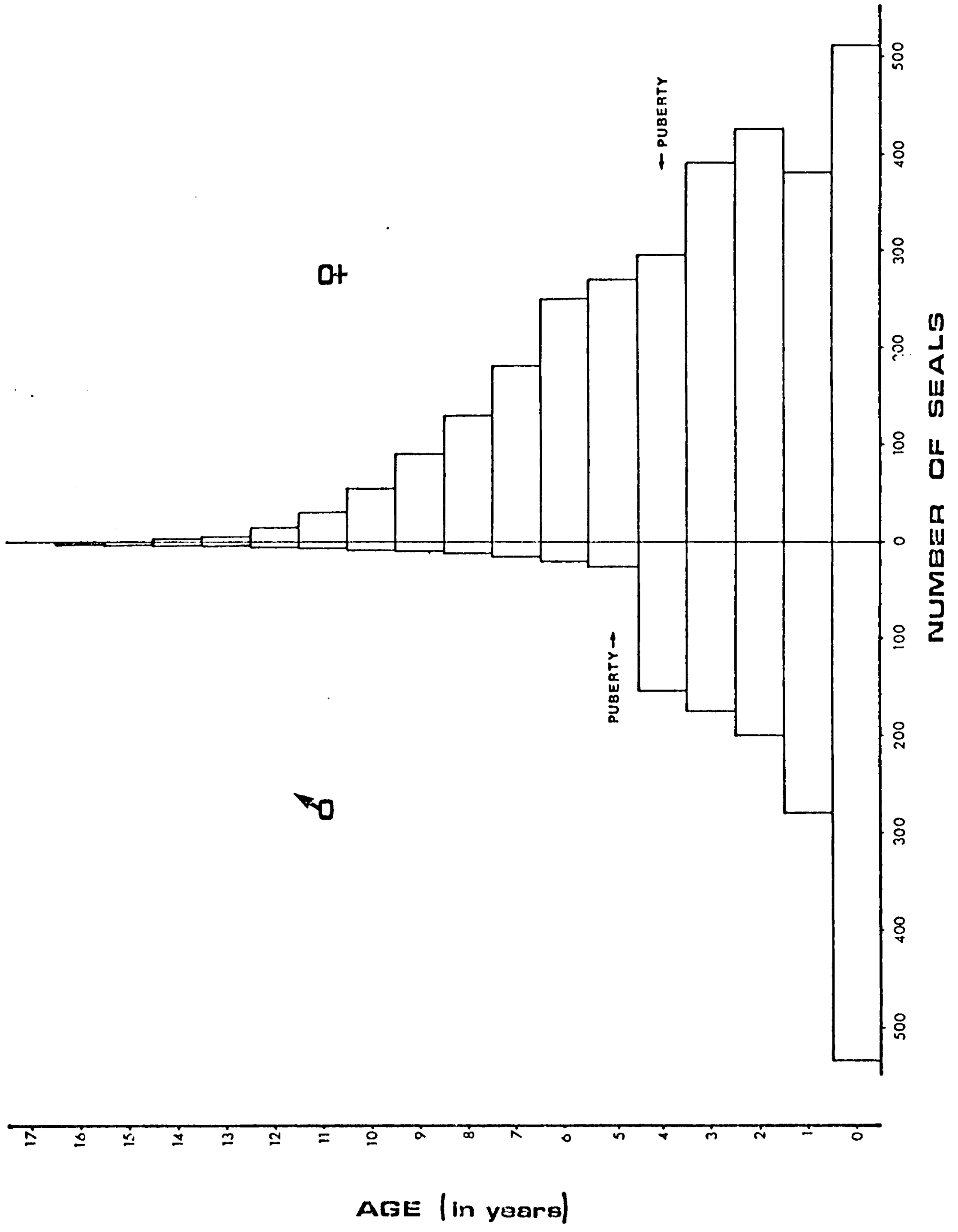


FIGURE 12

Population age pyramid for the southern elephant seals at Marion Island.

Females – age specific population structure;

Age Class	Total number in these classes	*Age in years	% Surviving in each year (from survival tables)	*Number of seals in each year
1st Year	512	0		512
2nd Year	379	1		379
Subadult	?	2	52,11	425
”	?	3	47,89	391
Subtotal (subadults)	816		100,00	816
Adult	?	4	22,40	294
”	?	5	20,61	271
”	?	6	19,00	249
”	?	7	13,71	180
”	?	8	9,86	129
”	?	9	6,90	91
”	?	10	4,03	53
”	?	11	2,06	27
”	?	12	0,98	13
”	?	13	0,36	5
”	?	14	0,09	1
Subtotal (adults)	1313		100,00	1313

*The data in the columns marked with asterics have been used to construct Figure 12

Males – age specific population structure;

Age Class	Total number in these classes	*Age in years	% Surviving in each year (from survival tables)	*Number of seals in each year
1st Year	533	0		533
2nd Year	281	1		281
Subadult	?	2	37,85	202
”	?	3	33,12	177
”	?	4	29,03	155
Subtotal (subadults)	534		100,00	534
Adult	?	5	23,00	26
”	?	6	18,62	21
”	?	7	13,62	16
”	?	8	10,00	12
”	?	9	8,25	9
”	?	10	6,87	8
”	?	11	5,75	7
”	?	12	4,38	6
”	?	13	3,38	4
”	?	14	2,50	3
”	?	15	1,75	2
”	?	16	1,00	1
”	?	17	0,50	0
”	?	18	0,25	0
”	?	19	0,13	0
Subtotal (adults)	115		100,00	115

*The data in the columns marked with asterics have been used to construct Figure 12

DISCUSSION

All the instantaneous coefficients of population growth (*r*) calculated in this Chapter indicate that the elephant seal breeding population (including pups surviving to weaning) has been declining, no matter whether Rand's (1962) or Van Zinderen Bakker's (1976, unpublished) data are used as a baseline with which to compare the data obtained during this study. Census results for the Ship's Cove to Archway Bay study area (Table 5) indicate a slow decline in the number of pups born, as well as in the number surviving to weaning, from 1973 to 1976. As was suggested in Chapter 6, the declining numbers in the study area are thought to be due to disturbance resulting from regular censusing and tagging.

Since the total island pup crop appears not to have changed much throughout the present study (Table 6), it is believed that the decline in the study area represented merely a shift in distribution away from the disturbed area. Rand (*pers. comm.*) has confirmed that his data are reliable, so that the decline in the elephant seal population since 1951 is real.

The apparent stability in the total pup crop and the number of breeding bulls from 1973 to 1976 (see Table 6), raises the question of whether the population is still declining as indicated in Figure 11. It would seem that the data from this study indicate a static trend, if not a very slight increase from 1 028 pups in 1973 to 1 043 in 1976 (Table 6). Although at this stage there is no supporting data other than the slight increase in the number of pups as indicated above, and which may be the result of improved census technique, it is suggested that the elephant seal population is fluctuating about some level as yet unknown, and has in at least the last decade prior to 1973 been in a downward phase of such fluctuations, from 1973 to 1976 been apparently static, and if the latter is true could therefore be expected to start on an upward phase of these fluctuations in the future, provided human disturbance is minimized.

According to Laws (1956a) the southern elephant seal feeds almost exclusively on cephalopods and fish, the latter being more important in inshore waters. Since there is no commercial fishing close to Marion, a reduction of inshore fish abundance should not have occurred and would not be the cause of the decline in elephant seal numbers, unless competition for the same fish species is being created by the increasing fur seal *(A. tropicalis)* population (Condy 1975b, unpublished). Such competition probably exists but at this stage seems unlikely to be severe enough to cause a decline in numbers of elephant seals, and in the past few decades when fur seal numbers were low (Rand 1956), little if any competition would have existed. In any event the majority of elephant seals when present at an island are usually hauled out and fasting, so that inshore food resources are not a critical factor. When away from land during the autumn and winter seasons pelagic food resources, especially cephalopods, are critical. However with the decline in numbers of sperm whales *Physeter catodon* (Gulland 1974), which feed on cephalopods, the availability of the pelagic food resources of elephant seals should if anything have increased, and would not therefore be the cause of the decline in elephant seal numbers. Thus it appears that the decline in elephant seal numbers at Marion Island is not related to food shortages.

The survivorship tables indicate a high mortality in the first year of life, with a much lower mortality in the next few years. However since these tables are based upon information on mortality at Macquarie Island and South Georgia, they do not necessarily represent the actual situation at Marion Island. Nevertheless it is clear from Figure 12 that the size of the female second year population is disproportionately small in comparison to the older population.

It appears that the regression equations for subadults (X_4) and second year animals (X_5) are not yet satisfactorily tuned, and therefore unfortunately of limited predictive value at present. However their accuracy can be improved by using a larger data sample, from for instance a further six beaches, including some on which the number of breeding bulls is high (>5). This should allow replacement of the modified X_1 value with the actual observed value, and thus remove the arbitrary element from the equations.

CHAPTER 8

POPULATION ECOLOGY

RESULTS

Life Tables

Life tables for male and female elephant seals have been constructed according to the methods used by Deevey (1970) and Odum (1971), where X = age in years, l_x = number of seals out of a 1 000 that survive after each year, d_x = number of seals dying at each age X, 1 000 q_x = mortality rate per 1 000 alive at the beginning of each age interval, L_x = the number of seals alive between ages X and X + 1, T_x = the total number of animal years, and e_x = life expectancy at the end of each age interval.

(a) **Females** – calculation of d_x in the computation below has been based on the age specific mortality rates as determined in Chapter 7.

X	l_x	d_x	$1000q_x$	L_x	T_x	e_x	$\log_e l_x$
0	1000	400	400,00	800,0	4243,0	4,24	6,908
1	600	48	80,00	567,0	3443,0	5,74	6,397
2	552	44	79,71	530,0	2867,0	5,19	6,314
3	508	41	80,71	487,5	2337,0	4,60	6,230
4	467	37	79,23	448,5	1849,5	3,96	6,146
5	430	34	79,07	413,0	1401,0	3,26	6,064
6	396	111	280,30	340,5	988,0	2,49	5,981
7	285	80	280,70	245,0	647,5	2,27	5,652
8	205	62	302,44	174,0	402,5	1,96	5,323
9	143	60	419,58	113,0	228,5	1,60	4,963
10	83	40	481,93	63,0	115,5	1,39	4,419
11	43	22	511,63	32,0	52,5	1,22	3,761
12	21	13	619,05	14,5	20,5	0,98	3,045
13	8	6	750,00	5,0	6,0	0,75	2,079
14	2	2	1000,00	1,0	1,0	0,50	0,693

(b) **Males** – calculation of d_x in the computation below has been based on the age specific mortality rates as determined in Chapter 7.

X	l_x	d_x	$1000q_x$	L_x	T_x	e_x	$\text{Log}_e\ l_x$
0	1000	400	400,00	800,0	3898,5	3,90	6,908
1	600	75	125,00	562,5	3098,5	5,16	6,397
2	525	66	125,71	492,0	2536,0	4,83	6,263
3	459	57	124,18	430,5	2044,0	4,45	6,129
4	402	76	189,05	364,0	1613,5	4,01	5,996
5	326	62	190,18	295,0	1249,5	3,83	5,787
6	264	71	268,94	228,5	954,5	3,62	5,576
7	193	52	269,43	167,0	726,0	3,76	5,263
8	141	24	170,21	129,0	559,0	3,96	4,949
9	117	20	170,94	107,0	430,0	3,67	4,762
10	97	16	164,95	89,0	323,0	3,33	4,575
11	81	19	234,57	71,5	234,0	2,89	4,394
12	62	15	241,93	54,5	162,5	2,62	4,127
13	47	12	255,32	41,0	108,0	2,30	3,850
14	35	11	314,28	29,5	67,0	1,91	3,555
15	24	10	416,67	19,0	37,5	1,56	3,178
16	14	7	500,00	10,5	18,5	1,32	2,639
17	7	4	571,43	5,0	8,0	1,14	1,946
18	3	2	666,67	2,0	3,0	1,00	1,099
19	1	1	1000,00	1,0	1,0	1,00	0

(c) **Survivorship curves** – logarithmic curves have been plotted for males and females using the l_x values determined in the life tables above. The curves (Figure 13) are of the "stair step" type (Odum 1971), indicating that survival rate undergoes changes in transition from one age interval to another, and thus age specific survival does not remain constant throughout life.

Net Reproductive Rate

In order to calculate the net reproductive rate (R*o*) for the female elephant seal population, certain assumptions have been made;

(1) Age specific mortality rates are as indicated in Chapter 7 (page 68) and the number of female seals out of 1 000 that survive each year (l_x) are as determined earlier in this Chapter.

(2) The attainment of reproductive maturity is similar to that on Macquarie Island, for which Carrick *et al.* (1962d) stated that first parturition occurred in one third (33,3%) of the females at the age

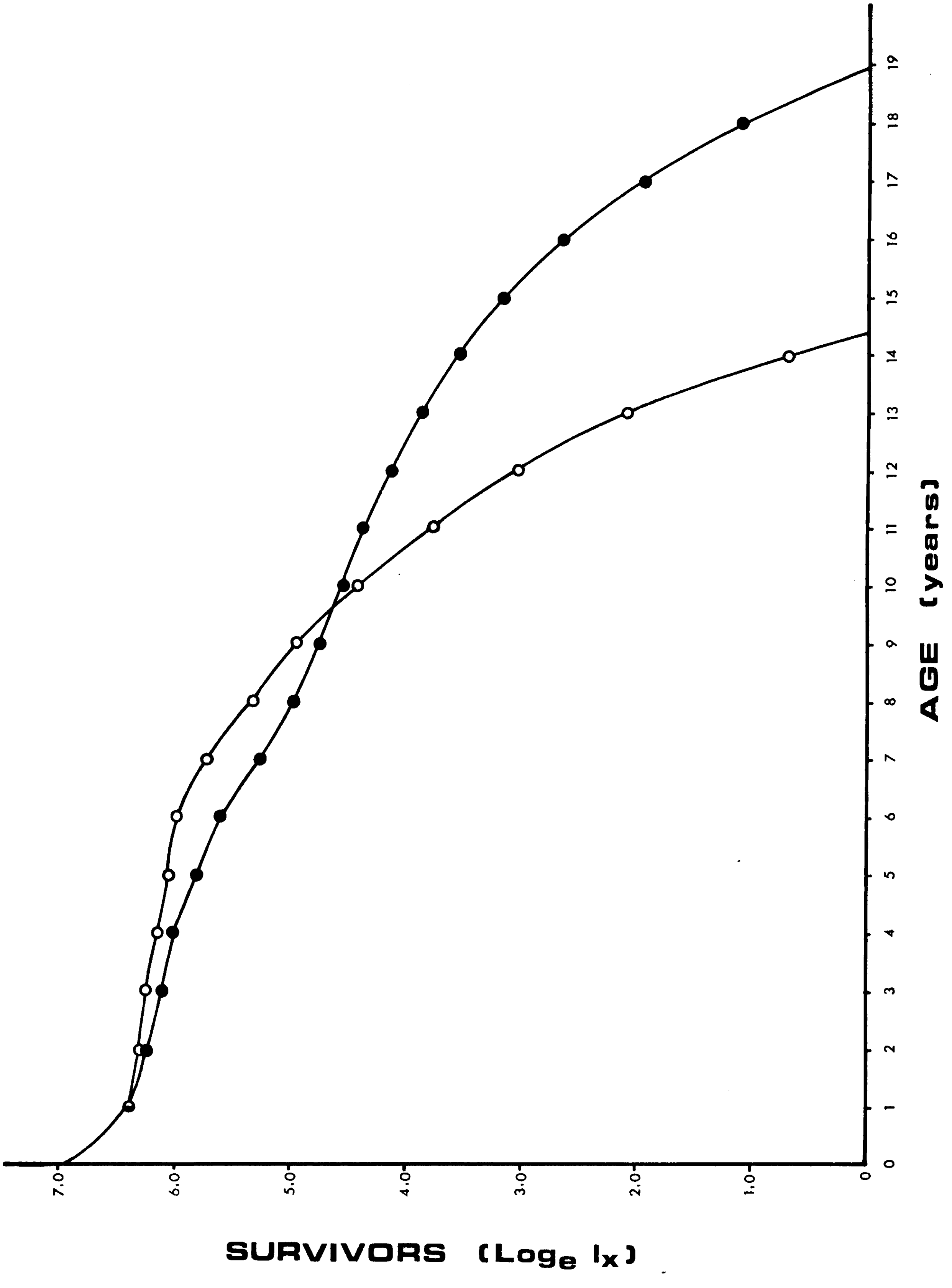


FIGURE 13

Survivorship curves for male (●) and female (○) southern elephant seals at Marion Island.

of four years, and maximum reproductive rate was attained at the age of six years. It has thus been assumed that at the age of five years two thirds (66,7%) of the females are mature, and at the age of six years all females are mature.

(3) Pregnancy rate is 82,0 per cent in mature females as Laws (1960) recorded for South Georgia, so that maximum pregnancy rate from the age of six years is 82,0 per cent.

(4) Each pregnant cow gives birth to one pup only.

(5) Cows continue breeding (82,0% pregnancy rate) from the age of six years to death.

(6) Female longevity is 14 years (from Chapter 7).

(7) Of the pups born 48,8 per cent are female (from Chapter 7), so that the probability of a pup being a female is 0,488 (or 0,49 for the purpose of the computations).

Calculation of R_o has been based on the methods illustrated by Birch (1970), Odum (1971), and Wilson and Bossert (1971).

(a) **Computation of age specific natality rates** – giving the mean number of female offspring per year per female (m_x);

See next page

Age (X) in years	l_x (♀♀)	Pregnancy Rate (%)	*Number of pups born	Probability of pups being♀♀	**Number of pups born(♀♀)	***m_x
0	1000	0	0	0	0	0
1	600	0	0	0	0	0
2	552	0	0	0	0	0
3	508	0	0	0	0	0
4	467	33,3	155,51	0,49	76,20	0,163
5	430	66,7	286,81	0,49	140,54	0,327
6	396	82,0	324,72	0,49	159,11	0,402
7	285	82,0	233,70	0,49	114,51	0,402
8	205	82,0	168,10	0,49	82,37	0,402
9	143	82,0	117,26	0,49	57,46	0,402
10	83	82,0	68,06	0,49	33,35	0,402
11	43	82,0	35,26	0,49	17,28	0,402
12	21	82,0	17,22	0,49	8,44	0,402
13	8	82,0	6,56	0,49	3,21	0,402
14	2	82,0	1,64	0,49	0,80	0,402

*Number of pups born = l_x x pregnancy rate.

**Number of female pups born = number of pups born x probability of pup being a female.

***m_x = number of female pups born ÷ l_x.

(b) Computation of the net reproductive rate (R_o);

Age (X) in years	l_x	m_x	$l_x m_x$	$Xl_x m_x$
0	1,000	0	0	0
1	0,600	0	0	0
2	0,552	0	0	0
3	0,508	0	0	0
4	0,467	0,163	0,076	0,304
5	0,430	0,327	0,141	0,705
6	0,396	0,402	0,159	0,954
7	0,285	0,402	0,115	0,805
8	0,205	0,402	0,082	0,656
9	0,143	0,402	0,057	0,513
10	0,083	0,402	0,033	0,330
11	0,043	0,402	0,017	0,187
12	0,021	0,402	0,008	0,096
13	0,008	0,402	0,003	0,039
14	0,002	0,400	0,001	0,014
			$\Sigma l_x m_x$ = 0,692	$\Sigma X l_x m_x$ = 4,603

$R_o = \Sigma l_x m_x = 0{,}692$ (Birch 1970)

This means that for every one female in the starting population 0,692 offspring are produced, and that the population multiplies by 0,692 times in each generation. It is clear from this alone that the population is declining, accepting that the assumptions made at the beginning of this section are relevant. Since it has already been shown that the population is declining (Chapter 7), it appears that these assumptions are therefore reasonably accurate. It is possible to calculate a value for r once R_o has been determined, and since this would serve as a useful cross check on the r value (–0,048) calculated in Chapter 7, it has been done as follows;

R_o has little value unless seen in conjunction with the mean length of the generation of the population concerned, and the relationship between numbers and time in a population growing exponentially is given by the equation;

$$N_T = N_o e^{rT} \quad \text{(Birch 1970)}$$

When T = the mean length of a generation, then from the definition of net reproductive rate;

$$\frac{N_T}{N_o} = R_o \quad \text{(Birch 1970)}$$

hence $$R_o = e^{rT} \quad \text{(Birch 1970)}$$

and $$T = \frac{\log_e R_o}{r} \quad \text{(Birch 1970)}$$

From this last equation it can be seen that an accurate estimate of T cannot be obtained unless the value of r is known, but an approximate estimate of T can be calculated independently of r using the form;

$$T = \frac{\Sigma X l_x m_x}{\Sigma l_x m_x} \quad \text{(Birch 1970)}$$

by which parturition is considered as being concentrated at one point in time with successive generations being spaced T units apart. The two values required in this equation ($\Sigma X l_x m_x$ and $\Sigma l_x m_x$) have already been computed (see page 89).

Thus $$T = \frac{4,603}{0,692} = 6,652 \text{ (= mean length of a generation)}$$

and from the equation $$T = \frac{\log_e R_o}{r};$$

thus $$r = \frac{\log_e R_o}{T}$$

$$r = \frac{\log_e 0,692}{6,652}$$

$$= \frac{\log_e 6,92 + \log_e 10^{-1}}{6,652}$$

$$= \frac{1,9344 + \bar{3},6974}{6,652}$$

$$= \frac{1,9344 + (0,6974 - 3,000)}{6,652} = -0,055$$

The value of *r* above (–0,055), although being slightly different to the previously calculated value (–0,048), is only an approximate value since the value of T was only an estimate, and falls within the range of all the *r* values calculated in the previous Chapter (mean = –0,058 ± 0,023; n = 8). It differs only slightly from the more accurate value, but nevertheless indicates that the assumptions made to determine the net reproductive rate (R_o) were reasonably accurate, and confirms the negative population trend discussed in the previous chapter. The value for the mean length of a generation (T = 6,653) indicates that first parturition occurs in the seventh year and not at age four as suggested earlier in this and the previous chapters.

Mortality

Figures for pre-weaning mortality in the entire population were given previously (Table 7), since they provided information on the total number of births, and hence the number of breeding cows. Data on pre-weaning mortality in the study area only are given in Table 11, and the causes of this mortality are discussed below;

(a) **Starvation** – pup deaths in the large harems were most frequently caused by starvation after separation from the cow. This was the major cause of mortality at breeding sites composed of large boulders (eg. Boulder Beach and Rockhopper Bay), where the newborn pups became wedged between the boulders and were too weak to extricate themselves. Under these circumstances mortality was density independent, whereas on the smooth surfaced beaches separation from the cow was to some extent related to the harem size, and therefore to density.

(b) **Trampling by bulls** – harem bulls sometimes crushed pups while moving from cow to cow during the peak mating period. When bachelor or challenger bulls approached the harems, the harem bulls tended to charge the intruders, trampling any cows and pups lying in their path, and sometimes pups were crushed to death as a result. Crushing occurred less frequently on the rough surfaced beaches where pups were often protected between rocks and boulders. Since death by crushing increased in frequency with increasing harem size, this mortality factor was also density dependent.

(c) **Drowning** – heavy seas, which usually occurred at least once during a breeding season, tended to wash away the younger and weaker pups. The impact these storms had depended upon their severity and the time at which they occurred. The most vulnerable period was the first half of the pupping season when most pups were young and still weak. In the second half of the pupping season when the pups were being weaned and were therefore heavier and stronger, they were less likely to be washed away.

TABLE 11: Pre-weaning mortality of southern elephant seals at the six beaches in the study area on Marion Island

Beach	1973			1974			1975			1976			Total		
	Total births	Total deaths	% mortality	Total births	Total deaths	% mortality	Total births	Total deaths	% mortality	Total births	Total deaths	% mortality	Births	Deaths	% mortality
Ship's Cove	108	4	3,70	79	3	3,80	59	0	–	54	2	3,70	300	9	3,00
Rockhopper Bay (mouth of the Van den Boogaard River)	20	5	25,00	8	2	25,00	5	2	40,00	13	8	61,54	46	17	36,96
Boulder Beach (Transvaal Cove)	18	7	38,89	23	8	34,78	14	4	28,57	15	2	13,33	70	21	30,00
Trypot Beach	76	4	5,26	72	5	6,94	63	3	4,76	62	3	4,84	273	15	5,49
Macaroni Bay (South Beach)	82	4	4,88	94	7	7,45	70	2	2,86	56	1	1,79	302	14	4,64
Archway Bay	96	3	3,13	153	6	3,92	113	1	0,88	114	2	1,75	476	12	2,52
Study Area	400	27	6,75	429	31	7,23	324	12	3,70	314	18	5,73	1467	88	5,99

(d) **Cow aggression** – generally the pups stayed near their mothers, but disturbances such as fights between bulls, and human interference, caused the cows to move. The pups being much less mobile tended to move to the nearest cow to suckle, which was normally the pups mother, but if the cows had moved and the pups approached the wrong mothers they were sometimes snapped at. Occasionally this led to the immediate death of the pup, but more commonly wounds caused in this way tended to become infected and death sometimes followed as a result of the infection.

(e) **Other** – numerous other less important factors caused pre-weaning mortality, such as rockfalls onto the beaches, stillbirth which was rare, and predation on the newborn (the bleeding umbilical cord, foetal sack remains, and afterbirth, being the main attractant) by giant petrels (*Macronectes* spp.), skuas *(Stercorarius skua),* sheathbills *(Chionis minor),* and gulls *(Larus dominicanus).*

The overall pre-weaning mortality rate in the study area during this study was 5,99 per cent (Table 11), which falls within the range of 5–10 per cent recorded at Macquarie Island by Carrick and Ingham (1962e).

From weaning to maturity the single most important cause of mortality appeared to be predation by killer whales (see Chapter 10), although other factors such as molesting by breeding bulls, malnutrition in inefficient or inexperienced food finders (Carrick and Ingham 1962e), battering by heavy seas, and disease all probably contributed to mortality.

During the present study one dead bull (killed in a territorial fight) and two dead cows (causes of death unknown) were found in the study area. A large rockfall in the study area (at Macaroni Bay) on the 18 December 1974 killed a further three cows, with possibly others being completely buried. It was the only rockfall known to have killed adult elephant seals during the study period. Two dead bulls and three dead cows were found elsewhere, the causes of the deaths being unkown.

Only two cows, one bull, and four subadult seals carried old scars attributable to attacks by killer whales. No wounded or scarred yearling and second year seals were seen, which according to Carrick and Ingham (1962e) is indicative of their inability to escape from killer whales. The causes of mortality in adults are therefore likely to be mainly fighting, disease, and possibly battering by heavy seas. Predation by killer whales seemed to be of less importance in the adult age classes than in the immature classes. (see Chapter 10).

Total Population Size

From the computations in the previous chapter it is possible to estimate the present total population size of the elephant seals at Marion Island.

According to the data in Chapter 7 there are approximately 1 313 cows, 115 breeding bulls, and a pup crop of approximately 1 100. Although the regression equations for estimating immature population size were not well tuned, figures from the survivorship tables and the regression equations indicated 1 178–1 350 subadults (mean = 1 264), and 587–660 second year old seals (mean = 624).

The population is therefore theoretically comprised of;

Bulls	–	115
Cows	–	1 313
Subadults	–	1 264
Second year old seals	–	624
Yearlings (ex pups)	–	1 100
Total	–	4 416

and in actual fact probably lies between 4 000 – 5 000 in total.

Harem Sizes

Harem size on Marion Island varied enormously from place to place, being controlled largely by beach size and surface nature (see Chapter 4), and thus the bull to harem cow ratio also varied.

Bulls were categorized according to the definitions of Carrick *et al.* (1962d), as follows;

(a) **Breeding Bulls** – fully developed proboscis, body heavily scarred.

(b) **Beachmaster** – a breeding bull in sole possession of a harem, or the dominant bull if more than one bull was associated with the harem.

(c) **Assistant Beachmaster** – a breeding bull in charge of part of a large harem, or participating freely in mating activities within a large harem, but always subordinate to the beachmaster.

(d) **Challenger** – a breeding bull without a harem, but intermittently fighting a beachmaster for possession of a harem.

(e) **Bachelor** – A breeding bull, usually smaller and younger than those in the above categories, which does not fight for possession of a harem, but during the peak mating period usually approaches the harem and may mate with peripheral cows if not chased off by the beachmaster or assistant beachmaster.

Harem sizes and the occurrence of the above categories of breeding bulls are shown in Table 12. Inspections to obtain this data were timed to coincide with the period when numbers of cows hauled out was at a maximum. The data indicate that harems consisting of more than 60 cows included an assistant beachmaster, and those containing 130–150 cows included two assistant beachmasters per harem. The mean harem structure (beachmasters : assistant beachmasters : cows) was 1:0,53 ± 0,72 : 45,35 ± 43,77. Since the number of challengers and bachelors varied because they were not restricted to the harems, it was not possible to determine mean numbers per harem.

TABLE 12: Maximum number of harems and breeding southern elephant seals observed on Marion Island in mid-October 1973, 1974, and 1975

Beach	Harem Number	Number of Cows in the Harem	Number of Breeding Bulls			
			Beachmasters	Assistant Beachmasters	Bachelors	Challengers
Ship's Cove	1	65	1	1	2	0
	2	7	1	0	0	0
Van den Boogaard River mouth	3	10	1	0	0	0
Boulder Beach	4	18	1	0	0	1
Trypot Beach	5	70	1	1	2	0
Macaroni Bay (South Beach)	6	70	1	1	3	0
	7	10	1	0	1	1
Archway Bay	8	152	1	2	5	0
Hansen Point	9	13	1	0	0	1
Kildalkey Bay	10	130	1	2	10	0
	11	40	1	0	4	0
King Penguin Bay	12	18	1	0	1	0
	13	27	1	0	1	0
Sea Elephant Bay	14	38	1	1	1	0
Blue Petrel Bay	15	18	1	0	0	0
Sealer's Beach	16	80	1	1	4	0
	17	5	1	0	0	0
Total	17	771	17	9	34	3

DISCUSSION

The life tables indicate that life expectancy (e_x) is greatest at the end of the second year of life for both males and females. Thereafter it remains greater for females up to the age of nine years than for males, the age at which the two survival curves in Figure 13 crossed each other.

From the age of nine years onwards life expectancy for males is greater than for females. Up to the age of two years life expectancy is similar for both sexes, but from then until the age of nine years males, having a shorter life expectancy, suffer a greater mortality rate than the females. The population age pyramid (Figure 12) indicates clearly that males are subjected to a higher mortality rate, especially from the age of two years to puberty which is believed to occur at five years of age (ie. in the sixth year of life). Most deaths in males from puberty onwards were attributable to fighting, although the scarcity of carcasses on the island was surprising. As most of the fights observed took place in the surf it is possible that the carcasses were washed out to sea, or alternately the injured animals swam into deeper water before dying.

Regardless of the causes of mortality, the survivorship curves indicate clearly that mortality changes from one year to the next for both sexes, and overall is such that the net reproductive rate is less than one. This indicates that the population is not maintaining itself, and confirms the negative population trend determined in the previous chapter. The rate of decline (r = –0,048) established in the previous chapter was based on Rand's (1962) results which are considered to be reliable, while the mean of all the r values was –0,058 ± 0,023 (n = 8). However the rate of decline established in this Chapter (r = –0,055) is in reasonably close agreement, even though it is an approximate value only.

The calculations of life expectancy, age specific natality rates, and generation interval have been based largely on assumptions concerning age specific mortality. To determine age specific mortality much use has been made of published data concerning the elephant seal populations at Macquarie Island and South Georgia. However as was shown in earlier chapters, the biology of the elephant seals on

Marion Island is similar to that of the elephant seals at Macquarie Island, and the assumptions mentioned above have been shown to be at least reasonably accurate by the close agreement between the *r* values calculated in this and the previous chapters.

Harem sizes on Marion Island are much smaller than those on Macquarie Island (Carrick *et al.* 1962d), due largely to the fact that the total population on Marion Island is very much smaller than that on Macquarie Island, where the population numbers some 110 000 individuals during the breeding season (Carrick and Ingham 1962e). However, even there harems containing less than 50 cows had only one breeding bull in control at a time (Carrick *et al.* 1962d), a pattern which is very similar to that on Marion Island where assistant beachmasters started occurring in harems containing more than about 60 cows. It seems that regardless of population size or density, a bull is capable of maintaining exclusive control of 50 to 60 cows, but thereafter is unable to prevent the intrusion of at least one other bull, which however remains subordinate.

In 1951 (Rand 1955) considered that the elephant seal population on Marion Island numbered some 10 000 seals in total, and Laws (1960) estimated approximately the same number by multiplying Rand's (1955) pup count by a factor of 3,2 (total population size at South Georgia was 3,2 to 3,8 times the number of pups). At the present time the population numbers 4 000 to 5 000 only (3 850 if the pup crop of 1 100 is multiplied by 3,5).

CHAPTER 9

PUP DEVELOPMENT AND GROWTH

RESULTS AND DISCUSSION

Moult and Weaning

At birth elephant seal pups were covered in a furry black natal coat, and no cases of prenatal moult were recorded. The pups began to shed their black natal coats at approximately 13 days (mean 13,21 ± 4,81; n = 28), and the sequence of the moult was fairly constant, although there was individual variation. The first signs of moult appeared on the fore and hind flippers, then on the head, neck, and remainder of the body, in that order. The first area to show complete moult was the ventral body surface, followed in order by the flippers, head, neck, sides, and finally the dorsal body surface. In general the moult was completed at 28 days of age (mean 28,34 ± 5,68; n = 28), but in five instances in the study area there appeared to be a precocious moult completed at 18 days old. There was no significant difference between the sexes in the ages of the onset of moult and its completion.

Weaning occurred at 22–23 days after birth (mean 22,47 ± 3,52) in the 18 pups on Boulder Beach which were measured at approximately two day intervals. Elsewhere it appeared to occur at approximately 25 days old (mean 25,18 ± 2,67; n = 12), according to the data obtained from some pups marked at birth by hair clipping (six at Trypot Beach, four at Archway Bay, and two at Ship's Cove). This suggests that the regular measuring of the 18 pups on Boulder Beach disturbed the cows, eventually causing them to depart earlier than normal. At the larger breeding colonies in the study area the age of weaning appeared to decrease as the pupping season progressed, so that the last pups born were being weaned as early as 14 days after birth. The departure of the cows at the end of the pupping and mating season has been shown to be well synchronized (Chapter 5), and it appeared that the last cows to give birth weaned their pups early so that their departure could coincide with the rest of the cows. This pattern was not evident on Boulder Beach, mainly because all the pups studied were born during the first half of the season. Weaning appeared to be sudden, since six of the 18 cows on Boulder Beach were seen feeding their pups only two hours before they departed. The departure of all the remaining cows was known to within 12 hours, prior to which all had been seen allowing their pups to suckle.

After weaning, the pups at Boulder Beach remained on the beach fasting for eight to 10 days before they ventured into the water on days when the sea was calm, and started feeding very close inshore. Eighteen days after weaning (40 days after birth) they were venturing further offshore and spending up to at least four hours at a time at sea, and then returning to the same beach. It was not known how far the pups swam during this period at sea, nor was it known whether they swam close inshore parallel to the coast, or straight out to sea to the kelp *(Macrocystis spp.)* beds 100–200 m directly offshore. The period of absence appeared to remain fairly constant for a further 10 days, after which they started spending much more time away from the beach, and within a further 10 days (60 days after birth) they were not returning to the beach and appeared to have departed.

Immobilization of Pups

Newborn pups and those up to 10 days old were carried away from their mothers and measured. During the first six days most were too weak to struggle and could be measured easily without requiring restraint. From six to 10 days of age, mannual restraint became increasingly necessary, and after 10 days most were too strong to satisfactorily restrain by hand. From 10–18 days of age they were dragged by their hind flippers a short distance away from their mothers, and a sack pulled over the head, neck, and up to the fore flippers such that the fore flippers were pinned to the animal's side. They were then placed on a stretcher and carried further away from their mothers for measuring.

From 18–40 days of age most of the pups were too heavy and strong to handle using the sack technique, and were therefore immobilized with succinylcholine chloride (Scoline). The immobilizing technique has been described in Chapter 3, and the results are summarized in Table 13. There was no significant difference in dose rate and reaction to the drug between male and female pups. The mean dose rate (approximately 1,90 mg/kg) was very economical, and the reaction to its administration was quick enough and long enough to allow for an efficient system of drug administration to a number of seals followed by their measurement one by one.

TABLE 13: The effect of succinylcholine chloride (Scoline) on southern elephant seal pups, aged from 18 to 40 days old, at Boulder Beach, Marion Island

Sex	Drug level (mg/kg body mass)		*Time to first effects (minutes)		*Time to immobilization (minutes)		*Time to full recovery (minutes)	
	Mean ± S.D.	n	Mean ± S.D.	n	Mean ± S.D.	n	Mean ± S.D.	n
Male	1,91 ± 0,39	30	2,26 ± 0,47	30	3,07 ± 0,57	30	12,24 ±4,87	30
Female	1,84 ± 0,32	45	2,25 ± 0,57	45	3,05 ± 0,68	45	11,65 ±3,04	45
Combined	1,87± 0,35	75	2,25 ± 0,52	75	3,06 ± 0,63	75	11,92 ±3,86	75

*Time taken from time of injection

No pups died from overdosing although on six occasions a prolonged period of apnoea occurred. In each case the drug level administered was in excess of 3,0 mg/kg, and apnoea lasted for two to five minutes. Apnoea was characterised by cyanosis of the mouth and tongue, which were normally a bright pink colour. It was found that if the head of the animal was repeatedly lifted high and then lowered again by someone straddling but not sitting on the prone pup, breathing was induced. The pups appeared to suffer no ill effects from administration of the drug every second to sixth day. If no reaction was obtained from one administration, a second dose was administered after a minimum of six hours had elapsed since the first injection.

Growth in Body Mass

Data from the Boulder Beach pup measuring operation are given in Table 14. Although an attempt was made to measure each pup every two days, the operation was hampered on occasions by strong winds which made accurate measurement impossible. In addition about half the pups could not be reached on each occasion due to the aggressiveness of the cows, some of the cows preventing approach not only to their own pups, but also to weaned pups lying nearby. On any one occasion about half the weaned pups were either being protected by other cows, swimming in a nearby lake (Gentoo Lake, see Figure 4), or lying in the surf zone, and therefore not accessible. Usually eight (44,4%) of the 18 pups were measured on each occasion, and each pup was measured at least once every six days. There was no significant difference in mass at birth between the sexes, nor up to weaning. However, from 32 days post partum males were heavier than females.

TABLE 14: Age specific body mass (kg) of male and female southern elephant seal pups at Boulder Beach, Marion Island

Age (days)	Total body mass of males (kg)		Total body mass of females (kg)		Total body mass of sexes combined (kg)	
	Mean ± S.D.	n	Mean ± S.D.	n	Mean ± S.D.	n
<2 hours	38,20 ± 1,96	5	37,00 ± 0,87	3	37,75 ± 1,67	8
± 10 hours	36,83 ± 3,25	3	29,25 ± 4,63	4	32,50 ± 5,54	7
1	30,00 ± 4,71	4	31,00 ± 5,84	5	30,56 ± 5,06	9
2	29,25 ± 5,27	4	28,00 ±11,31	3	28,83 ± 6,53	7
4	32,00 ± 3,00	3	32,17 ± 1,44	3	32,08 ± 2,11	6
6	31,29 ± 4,97	7	37,60 ± 8,53	5	33,92 ± 7,11	12
8	41,40 ± 0,55	5	42,83 ± 4,83	6	42,23 ± 3,59	11
10	42,75 ± 4,33	6	46,75 ±10,74	5	44,35 ± 7,29	11
12	49,50 ± 6,99	6	55,33 ±18,15	3	51,69 ± 11,45	9
14	64,67 ± 5,75	3	64,17 ± 6,03	5	64,42 ± 5,28	8
16	74,13 ± 11,10	5	68,00 ± 3,91	5	71,50 ± 8,80	10
18	*80,00	1	83,17 ± 9,70	3	82,38 ± 8,08	4
20	86,13 ± 27,37	4	*90,03	1	86,91 ± 23,77	5
22	97,25 ± 8,35	4	97,13 ± 8,41	4	97,19 ± 7,76	8
24	93,13 ± 6,16	4	*96,80	1	93,86 ± 5,58	5
26	90,38 ± 21,57	4	96,50 ± 1,00	5	93,00 ± 15,61	9
28	78,38 ± 21,64	4	95,88 ± 3,66	4	87,13 ± 17,14	8
30	80,50 ± 8,03	5	*85,05	1	81,41 ± 7,24	6
32	*85,50	1	74,67 ±11,75	3	77,38 ± 11,02	4
34	97,70 ± 12,87	6	77,63 ±11,07	4	88,78 ± 15,52	10
36	109,00 ± 8,72	6	85,38 ± 7,19	5	98,50 ± 14,58	11
38	*109,75	1	92,50	1	101,13 ± 12,20	2
40	110,64 ± 10,96	7	90,63 ± 3,64	6	103,27 ± 13,29	13

*Total body mass from growth curves in Figure 14.

The change in body mass from birth to 40 days is illustrated in Figure 14. A drop in mass from birth (mass at < 2h of age) to two days is shown clearly, as is a

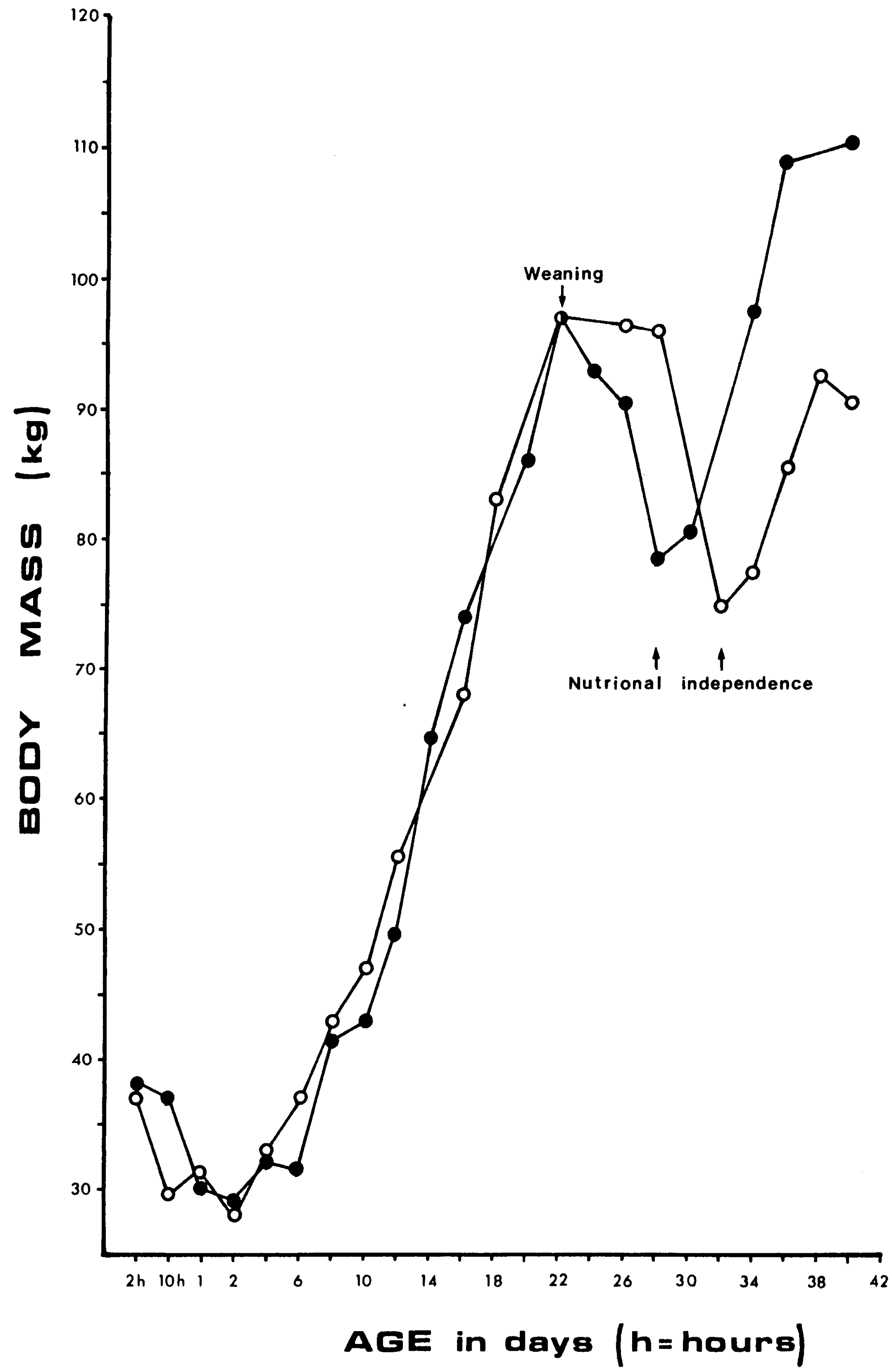


FIGURE 14

Growth in body mass (kg) of southern elephant seal pups (○ = females, ● = males) on Boulder Beach, Marion Island.

decrease in mass following weaning. Males lost mass faster than females following weaning, but did not ultimately lose as much mass, and started to recover it only six days after weaning, while the females continued losing mass for 10 days after weaning before showing a recovery. Observations on Boulder Beach indicated that male pups started feeding sooner after weaning than female pups. The curves in Figure 14 support these observations, and indicate that from the stage of nutritional independence onwards their increase in mass was more rapid than that in the females. As was mentioned earlier, the pups on Boulder Beach were weaned on average about three days earlier than appeared to be the case elsewhere. This indicates that a disturbance factor was present which may have influenced not only the age of weaning, but the growth rate of the pups over the entire 40 day study. Caution has therefore been excercised in interpreting these results, and when comparing males to females.

Nevertheless, it is interesting to compare the daily increase in mass of southern elephant seal pups at Macquarie Island and Signy Island, with the results from the present study. Bryden (1969) gave the mean mass (sexes combined) for pups on Macquarie Island at birth, and at seven, 14, and 21 days, and in a later paper (Bryden 1972) the mean mass (sexes combined) at 28, 35, and 42 days. Laws (1953) gave the mean daily mass of pups on Signy Island from birth to 19 days for males, and to 24 days for females. He also gave growth curves from birth to 34 days for males and females. From all of Laws' (1953) data it has been possible to calculate mean mass (sexes combined) from birth to 27 days, and at 30 and 34 days for elephant seals at Signy Island. Although the Marion Island data seems to have been modified to an unknown degree by the disturbance factor, it is likely that the same factor was present at Macquarie Island and Signy Island, affecting those results similarly and therefore making the data comparable. The comparative growth curves are illustrated in Figure 15.

Neither Laws' (1953) nor Bryden's (1969, 1972) results indicate a decline in mass following birth, but the growth curves are nevertheless distinctly different. Body mass at birth for male and female southern elephant seal pups at different breeding grounds are given in Table 15. Mean birth mass (sexes combined) at Marion

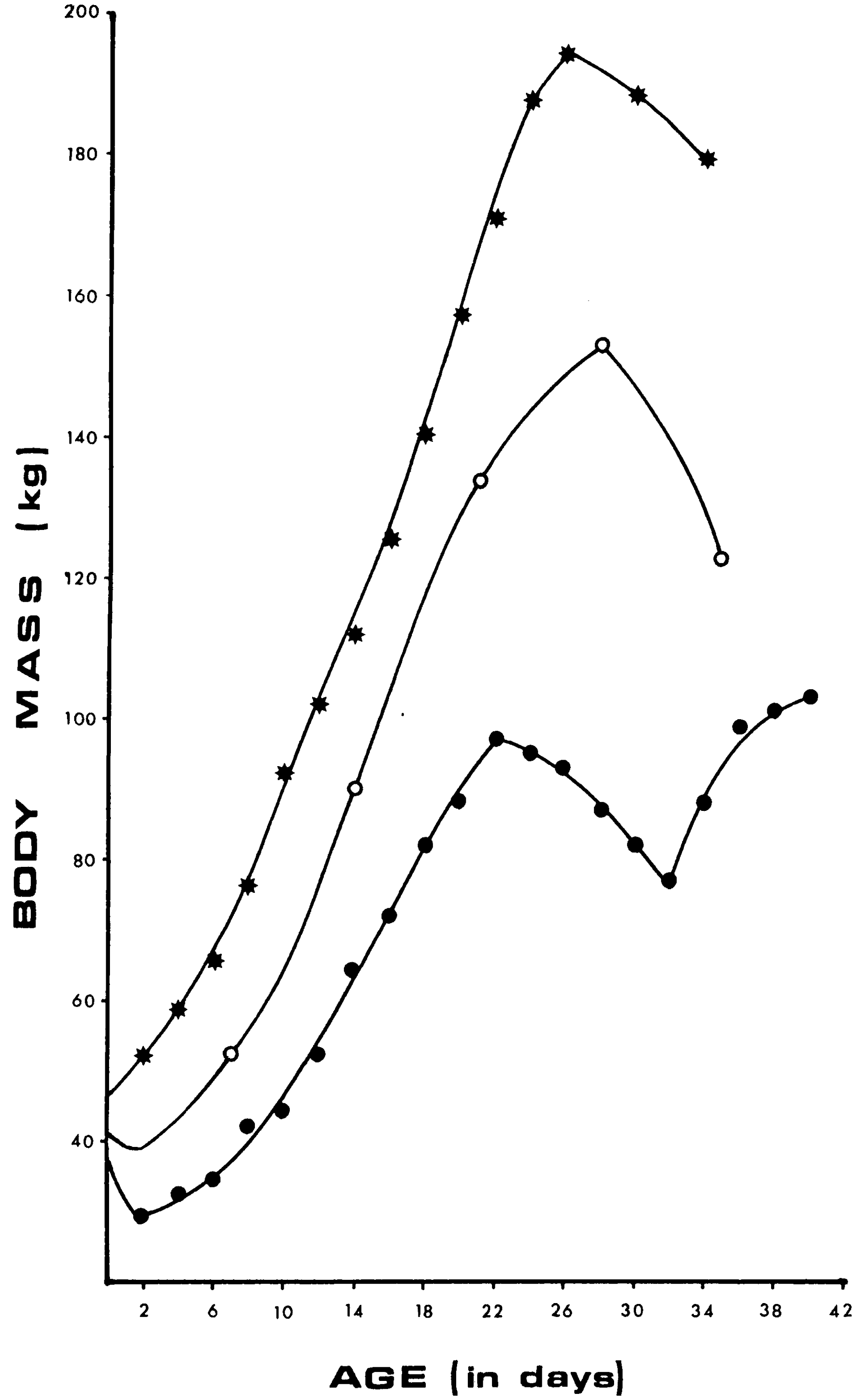


FIGURE 15

Growth in body mass (kg) of southern elephant seal pups at Signy Island (*, from Laws 1953), Macquarie Island (○, from Bryden 1969, 1972), and Marion Island (●, from the present study).

TABLE 15: Birth mass (kg) of southern elephant seals at various breeding grounds

Breeding Ground	Birth mass (kg)						Reference
	Males		Females		Sexes combined		
	Mean ± S.D.	n	Mean ± S.D.	n	Mean ± S.D.	n	
Signy Island	49,05 ± 4,58	7	45,87 ± 4,23	8	47,36 ± 4,54	15	Laws (1953)
Heard Island	–	–	–	–	31,60 ± 2,74	3	Carrick *et al.* (1962d)
Macquarie Island	39,01	27	34,93	19	36,97	46	Carrick *et al.* (1962d)
	–	–	–	–	41,00	6	Bryden (1969)
	43,00	3	39,00	3	–	–	Bryden (1972)
Marion Island	38,20 ± 1,96	5	37,00 ± 0,87	3	37,75 ± 1,67	8	Present study

Island and Macquarie Island are similar, although the females at Marion Island appear to be slightly heavier at birth than those at Macquarie Island. Birth mass at Signy Island is considerably higher. However the results from this study show that unless the pups are measured within two hours of birth, any mass measured from then to six days post partum will not be a true reflection of birth mass. Since the actual age in hours of the newborn pups measured at Macquarie and Signy Islands are not precisely known, comparisons are not entirely valid in the light of this observation. From the sixth day following birth onwards, the growth of pups at Marion, Macquarie, and Signy Islands is different, and this may be a reflection of different growth potentials for these different southern elephant seal stocks.

Growth in Body Length and Girth

Age specific curvilinear body length measurements are given in Table 16. Of all the measurements made on the pups, curvilinear length was the most difficult one to make, and therefore was recorded on fewer occasions than the others. The two main difficulties encountered while recording this measurement were keeping the pups still and lying on their bellies, and finding a flat surface on which to lay them for measurement. It was found useful to place the pups facing directly at their mothers, which reduced the amount of turning and neck bending by them. Straight line length was even more difficult to measure and was done a few times only, but accuracy was less reliable than curvilinear length and this measurement was therefore discontinued early in the study.

There was no significant difference in curvilinear length at birth between the sexes, but at an age of 40 days males were about 10 cm longer than females. However, since curvilinear length is not only a function of body length, but of corpulence as well, and since at 40 days males have been shown to be about 20 kg heavier than females (Table 14), curvilinear length alone is not a reliable indicator of size differences.

TABLE 16: Age specific curvilinear body length (cm) of male and female southern elephant seal pups at Boulder Beach, Marion Island

Age (days)	Curvilinear length of males (cm)				Curvilinear length of females (cm)				Curvilinear length of sexes combined (cm)			
	Mean	±	S.D.	n	Mean	±	S.D.	n	Mean	±	S.D.	n
< 2 hours	116,00	±	9,72	6	116,00	±	2,58	4	116,05	±	7,40	10
± 10 hours	116,75	±	4,79	4	115,00	±	21,21	2	116,17	±	10,23	6
1	107,00			1		—		0				
2	116,00			1		—		0				
4	119,00	±	2,65	3	119,63	±	3,09	4	119,36	±	2,69	7
6	119,00			1		—		0				
8	126,64	±	7,17	5	125,00	±	9,90	2	126,17	±	7,16	7
10	115,50	±	4,95	2		—		0				
12		—		0		—		0				
14		—		0		—		0				
16		—		0		—		0				
18	122,57	±	8,25	3	130,00			1	124,00	±	4,08	4
20		—		0		—		0				
22	125,37	±	4,77	2	142,00			1	130,67	±	9,87	3
24	124,00	±	4,24	2		—		0				
26	137,42	±	10,09	6	133,67	±	11,15	3	136,17	±	10,03	9
28		—		0	140,00	±	0,00	2				
30		—		0	139,80	±	2,86	5				
32	131,00			1	135,50	±	12,02	2	134,00	±	8,89	3
34	129,00	±	21,21	2		—		0				
36	155,00			1	141,40	±	4,17	7	143,10	±	6,16	8
38		—		0		—		0				
40	152,50	±	11,13	5	143,50	±	3,55	7	147,34	±	8,53	12

Age specific axillary girth measurements are given in Table 17. There was no significant difference in axillary girth at birth between the sexes, but from about 12 days after birth females had in general a slightly larger axillary girth.

At Signy Island (Laws 1953) curvilinear body length at birth (sexes combined) was 127,00 cm (n = 14), and at weaning 172,72 cm (n = 14). At Macquarie Island curvilinear length at birth (sexes combined) was 125,73 cm (n = 34), according to Carrick *et al.* (1962d). At both islands curvilinear length at birth was approximately 7,9 per cent greater than at Marion Island, and at weaning (23 days) the pups at Signy Island had a 14,7 per cent greater curvilinear length than those on Marion Island at 40 days old. At Signy Island (Laws 1953) axillary girth (sexes combined) at birth was 93,47 cm and at weaning 161,29 cm, being greater than the girth of pups at Marion Island by 13,1 per cent and 27,8 per cent respectively. Both these length and girth measurements are influenced by body mass, and since the elephant seal pups at Signy and Macquarie Islands are heavier than those at Marion Island, a larger curvilinear length and axillary girth are to be expected.

Condition Index

Smirnov (1924) introduced the term, "degree of fatness", while working with the harp seal *(Pagophilus groenlandicus),* and defined it as;

$$\text{degree of fatness} = \frac{\text{maximum girth} \times 100}{\text{total length}}$$

Bryden (1969) considered that the term "condition index" was preferable to "degree of fatness", because the above expression was dependent not only on the amount of fat in the body, but also on the amount of muscle. His term is preferred and has been used in this study.

In calculating the condition index of elephant seals at Macquarie Island, Bryden (1969) used the straight line nose to tail length and axillary girth, but Laws (1953) used the curvilinear length and axillary girth to calculate the condition index for elephant seals at Signy Island. However although Laws (1953) used the

TABLE 17: Age specific axillary girth (cm) of male and female southern elephant seal pups at Boulder Beach, Marion Island

Age (days)	Axillary girth of males (cm)				Axillary girth of females (cm)				Axillary girth of sexes combined (cm)			
	Mean	±	S.D.	n	Mean	±	S.D.	n	Mean	±	S.D.	n
< 2 hours	80,50	±	0,71	2	81,67	±	3,55	3	81,20	±	2,61	5
± 10 hours	83,75	±	1,06	2	75,63	±	2,56	4	78,33	±	4,67	6
1	79,33	±	6,01	3	77,80	±	7,59	5	78,38	±	6,62	8
2	82,00			1	81,00			1	81,50	±	0,71	2
4	78,00	±		1	83,25	±	1,77	2	81,50	±	3,28	3
6	74,50	±	5,45	4	84,00	±	6,56	3	78,57	±	7,41	7
8	88,40	±±	6,77	5	85,30	±	5,55	5	86,85	±	6,06	10
10	87,75	±	13,08	2	86,83	±	3,33	3	87,20	±	6,97	5
12	85,00	±	11,31	2	91,88	±	10,54	5	89,91	±	10,33	7
14	90,33	±	6,66	3	107,50	±	3,54	2	97,20	±	10,66	5
16	100,00	±		1	100,00			1	100,00	±	0,00	2
18	94,50	±	7,78	2	100,25	±	14,50	2	97,38	±	10,06	4
20	105,67	±	1,15	3		—		0		—		
22	137,00			1	123,00			1	130,00	±	9,90	2
24	120,00	±	21,21	2		—		0		—		
26	114,33	±	17,39	3	123,50	±	9,34	3	118,83	±	13,50	6
28		—		0	121,00			1		—		
30		—		0	125,50	±	2,12	2		—		
32	109,67	±	13,61	3	115,50	±	3,54	2	112,00	±	10,30	5
34		—		0		—		0		—		
36	122,00	±		1	116,50			1	119,25	±	3,89	2
38		—		0	125,00			1		—		
40	111,67	±	12,74	3	121,33	±	3,21	3	116,50	±	9,85	6

same measurements as in the present study, it is difficult to compare the data because, (a) he gave a growth curve (sexes combined) for pup axillary girth from which it is difficult to extrapolate actual girth at any given age, (b) he gave a curve for condition index in which the age axis is graduated in years, so it is not possible to obtain the condition index per day for the first 40 days of life only, and (c) he did not indicate curvilinear lengths, except indirectly by way of the condition index curves. It is therefore not possible to compare the condition indices of pups at Macquarie and Signy Islands with those from Marion Island.

The change in condition index for the Marion Island elephant seal pups from birth to 40 days of age is illustrated in Figure 16. The formula given above was used to calculate condition index, the values of curvilinear length and axillary girth being taken from Tables 16 and 17.

There was a dramatic decrease in condition index following weaning, which was brought about by a big decrease in axillary girth combined with an increasing curvilinear length. Although the pups started to feed themselves at approximately 30 days after birth, and therefore showed an increase in body weight from this age onwards (see Figure 14), axillary girth increased only very slightly from 30 to 40 days after birth (See Table 17), while curvilinear length showed a much greater increase during this period (see Table 16). Since the increase in girth did not keep pace with the increase in length, the condition index continued to decline from the stage of nutritional independence to 40 days of age. Clearly these pups are able to withstand a considerable decline in body fat reserves without any apparent ill effect.

GENERAL DISCUSSION

Laws (1953) found on Signy Island that about 3,0 per cent of the pups underwent a complete prenatal moult, but did not see any cases of prenatal moult at South Georgia. At Macquarie Island Carrick *et al.* (1962d) noted a less than 0,5 per cent occurrence of prenatal moult. Laws (1953) noted that in the normal pup moult the ventral surface was the last area to show complete moult. On Marion Island this was the first part of the body to show complete moult, due

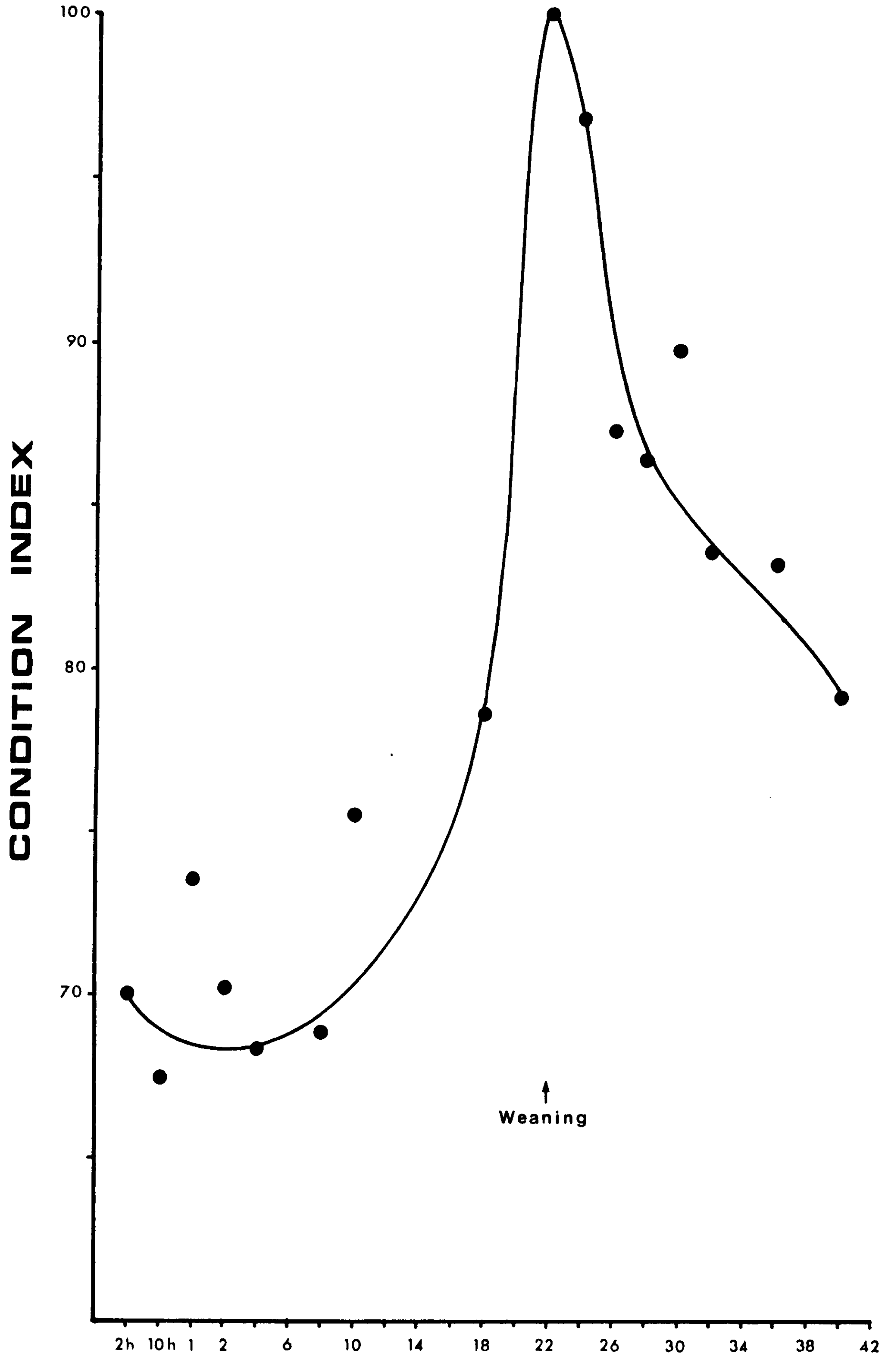


FIGURE 16

Change in condition index (sexes combined) for southern elephant seal pups on Boulder Beach, Marion Island.

probably to the abrasive nature of the beach surfaces. At Signy Island the moult was completed at 30–38 days (Laws 1953), and at Macquarie Island at or soon after weaning which occurred at 22–23 days (Carrick *et al.* 1962d). On Marion Island the pup moult was complete on average by 28 days after birth, which was later than at Macquarie Island but earlier than at Signy Island. However considerable variability was recorded at all three islands, and Carrick *et al.* (1962d) also recorded a few cases of exceptionally early or precocious moult.

The age at weaning at Macquarie Island (Carrick *et al.* 1962d) and Marion Island are almost the same (ie. 22,6 and 22,5 days respectively), and at Signy Island (Laws 1953) it occurred at 23 days. However as noted earlier in this chapter it appeared that weaning occurred a little later (about 25 days) at beaches on Marion Island which were not disturbed. Carrick *et al.* (1962d) noted the opposite, stating that the late weaning of the measured pups may have been due to the disturbance having slowed down growth. On Marion Island the disturbance appeared to cause a premature departure of the cows thus causing weaning to occur earlier than normal. At all three islands there was however considerable variability in the age of weaning, so that it appears that in general southern elephant seal pups are weaned at approximately 23 days after birth.

At Signy Island (Laws 1953) pups were first seen to enter the water at an average age of 34 days, and at Marion Island at 28–33 days. Laws (1953) noted that this corresponded to the age at which moulting was completed, and the results from the present study confirm his observation. The pups at Marion Island started swimming three to five days after the completion of their moult.

Although the age of weaning on Marion Island, Macquarie Island, and Signy Island is very similar, body mass at weaning is very different, as is increase in mass from birth (see Figure 15). The disturbance factor during the programme of regular measurement may have influenced the results such that they were not typical, but it is presumed that this factor was present at Macquarie and Signy Islands as well. Thus the growth patterns of pups should be comparable, and the difference is considered to reflect a real difference between the respective populations. Although birth mass does not appear to differ much, from then onwards mass for age does differ, and it seems that growth potential is greatest at Signy Island and least at Marion Island, with the growth potential of pups on Macquarie Island being intermediate.

Although Bryden (1969, 1972) did not illustrate a decline in body mass from birth to about 4–8 days old for elephant seal pups at Macquarie Island, Carrick *et al.* (1962d) showed that while most pups they measured at Macquarie Island did not gain mass for the first 5–6 days after birth, some even lost mass slightly during this period. At Signy Island (Laws 1953) the pups gained mass from the first day, and Carrick *et al.* (1962d) considered that this was due to the less crowded conditions there. The results from this study show that even under low density conditions elephant seal pups lost mass from birth to two days of age, and until the sixth day after birth body mass did not exceed birth mass. The significance of this is that unless body mass is recorded within a few hours of birth (< 2h at Marion Island), the mass obtained is not equivalent to birth mass. This means that the published birth masses for southern elephant seals are difficult to compare except for those published by Carrick *et al.* (1962d), and those from the present study.

At Marion Island the pups began to gain mass as soon as they became nutritionally independent. Initially they did not appear to spend much time at sea, so feeding during the period at sea is probably intensive, and since the pups are probably deficient in food-gathering experience, inshore food resources must be reasonably abundant to provide for the rapid gain in body mass. At the same time the pups are likely to be susceptible to killer whale predation (see Chapter 10).

Body size of the elephant seal pups at Marion Island is smaller than pups at Macquarie Island (Bryden 1969, 1972, Carrick *et al.* 1962d) and Signy Island (Laws 1953), and this corresponds to the lower body mass of pups at Marion Island compared to these other islands. Following weaning there was a dramatic decrease in condition index, indicating not only a change in body proportion (ie. length vs girth), but a decrease in body bulk. As stated before it appears that the pups are able to withstand a fairly large decline in body fat reserves, and this occurs at a time when the pups are becoming of necessity increasingly active. They are also having to endure the colder temperature of the sea for an increasing amount of time. It is interesting to note that the decline in fat reserves occurs in most pups during the first half of December and may continue into January. During these two months air and sea temperatures are above the yearly mean, although not at their warmest. Mean daily radiation is however highest in December and January, being 40,2 per cent higher than the yearly mean in December, and 38,6 per cent higher in January (see Table 1). This high radiation suggests that the pups are able to warm up fastest in December and January following prolonged exposure to the cold sea, and this facility occurs at a time when the natural insulating blubber layer is being rapidly depleted to carry the pups through the critical period of independent nutritional status.

CHAPTER 10

PREDATION

During the first summer of the present study the prominence of killer whales *(Orcinus orca)* was noticed. Without at that time realizing how important they were, an investigation into their seasonal occurrence and abundance was initiated, and observations of killer whales in the study area (Figure 4) were recorded from October 1973 to November 1976. Because of their unpredictable and erratic occurrence no set periods were assigned for observing killer whales. Instead sightings were logged as and when they occurred, taking care not to include repetitive sightings of the same individuals or the same groups. At each sighting the date, time, number of individuals, and distance offshore were recorded. To facilitate the latter four zones were alocated, namely Zone 1 – from 0–5 m offshore, Zone 2 – from 5–100 m offshore, extending up to the first belt of kelp (*Macrocystis* spp.), Zone 3 – from 100–500 m offshore, extending up to a second belt of kelp present in only parts of the study area, and Zone 4 – beyond 500 m offshore. Observations on killer whale behaviour, group size, and sex and age structure were also recorded, and have been reported on elsewhere by Condy, Van Aarde and Bester (in press).

RESULTS

Seasonal Occurrence and Abundance

The mean number of days per month on which killer whales were observed during three years of observation is illustrated in Figure 17, and the mean number of killer whales counted per month in the study area over the same period is illustrated in Figure 18. Observations indicated that elephant seal cows and young of the year were the main age/sex classes preyed on by the killer whales. In order to compare the seasonal occurrence of killer whales with the seasonal occurrence of elephant seal cows and young of the year (ie. pups and yearlings), the mean monthly number of cows and young of the year at Trypot and Boulder Beaches combined were included in Figure 18.

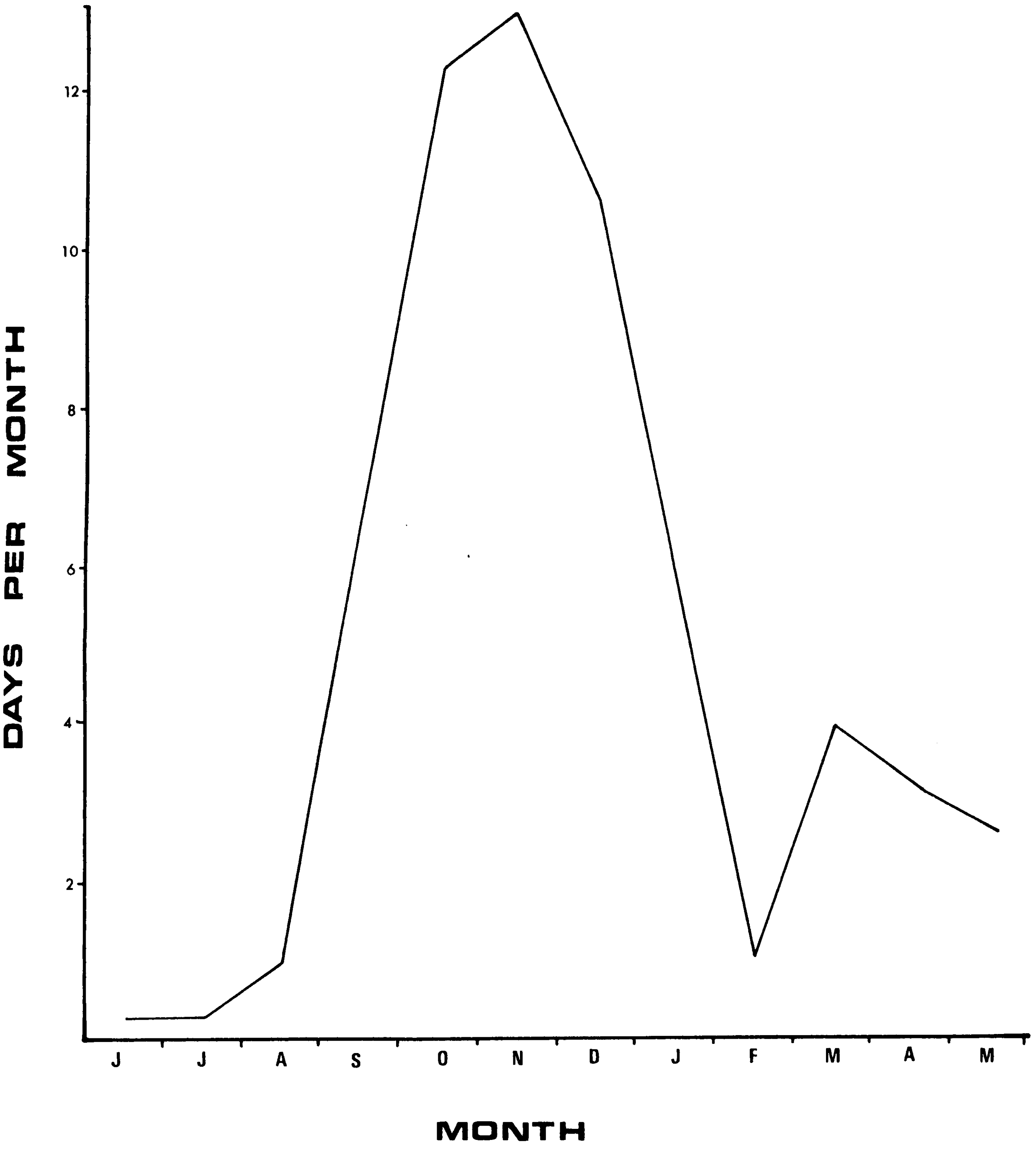


FIGURE 17

Mean number of days per month on which killer whales were observed at Marion Island, between October 1973 and November 1976.

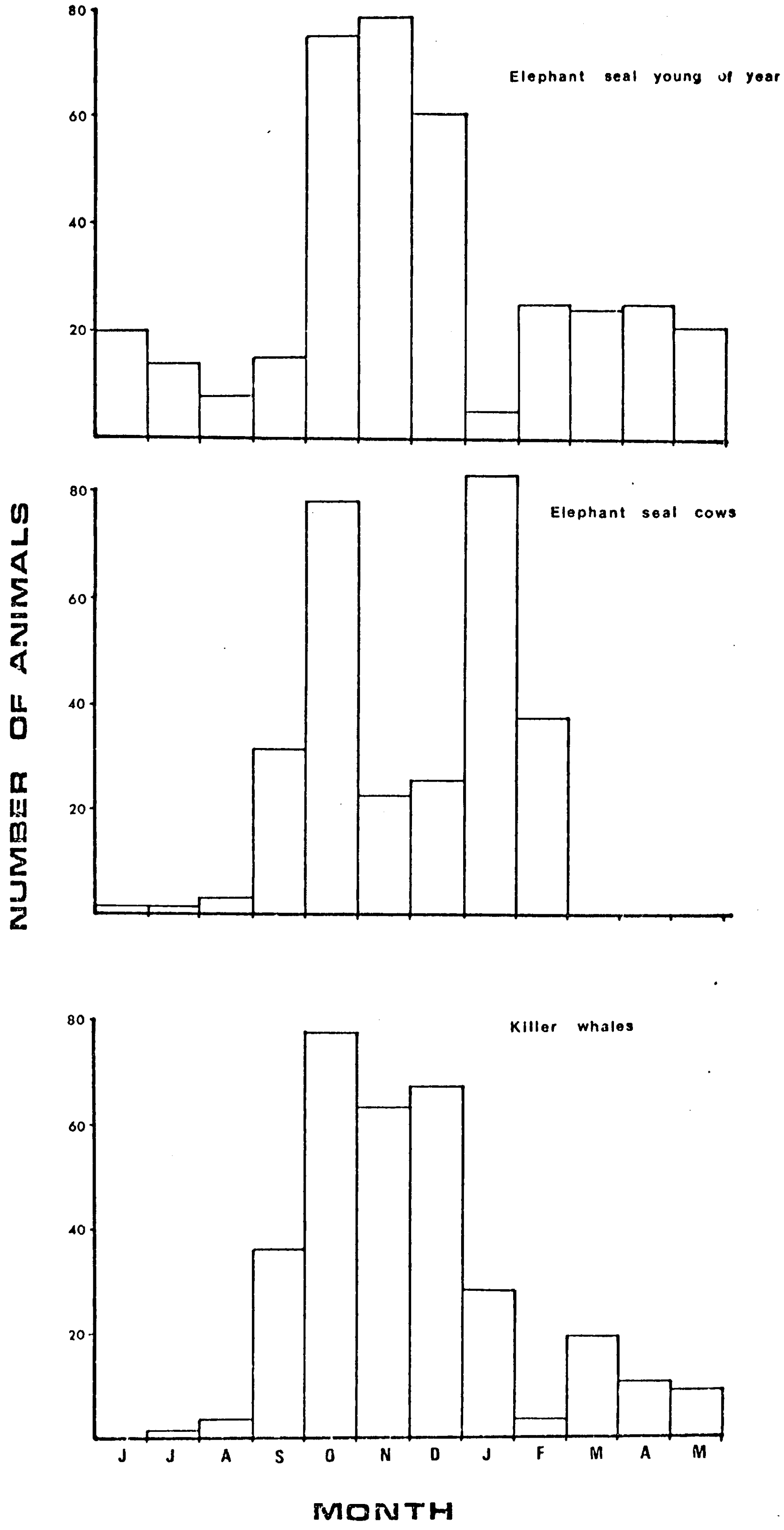


FIGURE 18

Mean number of killer whales counted per month in the study area at Marion Island, compared to the mean number of elephant seal cows and young of the year counted per month at Trypot and Boulder Beaches combined, between October 1973 and November 1976.

In an attempt to determine whether a meaningful relationship existed between the number of elephant seal cows and young of the year, and killer whales, the former two were separately related to the latter using standard regression equations of the form $Y = A_y + B_{yx}X$, where A_y and B_{yx} are the Y intercept and slope respectively of the straight line relating Y to X, Y being the dependent and X the independent variables. Once the regression coefficients A and B had been determined, the number of killer whales predicted from the equations were compared to the observed number and correlation coefficients were computed and tested. The results are shown below.

(a) $Y = 7{,}53 + 0{,}599X$ $\quad r_{yx} = 0{,}568$ $(P < 0{,}05)$

(b) $Y = 10{,}81 + 0{,}756Z$ $\quad r_{yx} = 0{,}849$ $(P < 0{,}01)$

where Y = mean number of killer whales observed per month in the study area, X = mean number of elephant seal cows counted per month on Trypot and Boulder Beaches combined, and Z = mean number of elephant seals less than one year old counted per month on Trypot and Boulder Beaches combined.

Diurnal Pattern

Killer whales were only visible between dawn and dusk, and data on the diurnal distribution of sightings are given in Table 18.

Since sightings of killer whales were largely incidental, it was thought that the diurnal spread of observations would reflect trends in human activity along the study area and at the Base Station. However, since meteorological observations were conducted throughout the 24 hours, except from 03h00 – 05h00, and those people involved with the meteorological observations were responsible for 40,0 per cent of all killer whale sightings, trend in human activity did not have much, if any influence on the data. During the summer fieldwork was conducted for all or part of the time between sunrise (02h30 – 03h30) and sunset (20h00 – 21h00), weather conditions dictating how much of this time was spent in the field. Thus in the case of observations made in the study area away from the Base Station (47,0% of all observations), weather conditions and not human activity had the greatest influence on the data.

TABLE 18: Diurnal distribution of killer whale observations between October 1973 and September 1976 at Marion Island

Period	Observations		Period	Observations	
	n	*% of total		n	*% of total
08h00 – 09h00	19	5,5	13h00 – 14h00	32	9,3
09h00 – 10h00	12	3,4	14h00 – 15h00	33	9,6
10h00 – 11h00	15	4,3	15h00 – 16h00	51	14,8
11h00 – 12h00	32	9,3	16h00 – 17h00	48	13,9
12h00 – 13h00	21	6,1	17h00 – 18h00	34	9,9

*% of total calculated from 345 observations, 48 of which occurred between 18h00 and 08h00.

Distance Offshore

Over the study period 34,0 per cent of the killer whales observed were in Zone 1; 27,6 per cent in Zone 2; 24,5 per cent in Zone 3; and 13,9 per cent in Zone 4. On many occasions (18,7% of all observations) killer whales were seen surfacing and then remaining on the surface in the first or second belts of offshore kelp. They never remained there for long (< 20 minutes), and it is believed that they were attracted to it by sheltering seals or penguins.

Feeding

Killer whales were actually seen feeding on elephant seals on two occasions, their prey in the first instance being a four month old yearling, and on the second occasion a cow. On another two occasions one group of five and another of 10 killer whales were seen to have cornered bull elephant seals against the coastal cliffs, in deep water and where retreat onto land was not possible. Although the seals were on both occasions almost surrounded, the killer whales never approached closer than a metre. After about 40 minutes, on both occasions, they moved on without ever having been in visible contact with the seals.

A group of three killer whales was seen to completely dispose of a flock of approximately 20 king penguins, and other fieldworkers often reported observations of killer whales eating king penguins. It appeared that king penguins were an important item in the diet of the killer whales at Marion Island.

Although almost six months in total were spent on the west and northwest coasts of Marion Island studying the fur seals, no killer whales were ever observed on that side of the island. Had they occurred there even half as frequently as they occurred on the east coast, at least a few sightings would have been recorded on the west and northwest coasts. Thus it appeared that during the present study elephant seals were the preferred prey, even though fur seals were more numerous than the elephant seals (Condy 1975b, unpublished).

DISCUSSION

Figures 17 and 18 show clearly that the occurrence of killer whales at Marion Island is seasonal, and both figures as well as the regression equations and correlation coefficients indicate a strong relationship between seasonal abundance of killer whales and elephant seal cows and young of the year (ie. pups and yearlings). This latter relationship, however, is related more to seal movement than to actual numbers hauled out, since any number of hauled out seals are of no immediate importance to killer whales although they are of potential importance. The critical factor is seal movement across the land/ocean interface, the point at which large numbers of initially well dispersed seals first become more and more concentrated as this interface is approached from the oceanic side, and then suddenly become non-available to killer whales as they haul out having crossed the interface. Thus for the killer whales, those seals moving straight through the inshore area from ocean to land and back again, and those moving about within the inshore area from beach to beach, are the important segments of the prey population. In terms of success per hunting effort the prime hunting area is therefore close inshore, and significantly most killer whales (34,0%) were observed within five metres (Zone 1) of the coast, and 61,6 per cent of all sightings occurred between the coast and 100 m offshore (Zones 1 and 2). Of the remainder 24,5 per cent fell between 100 – 500 m offshore (Zone 3), so that overall 86,1 per cent of all the killer whales observed were seen within 500 m of the coast (Zones 1, 2, and 3).

Although seasonal abundance and occurrence of the killer whales has only been compared to the seasonal abundance and occurrence of elephant seal cows and young of the year, it is worth considering the other age/sex classes of the elephant seal population with respect to their movement across and within the land/ocean interface. Cows, bulls, and subadults tend just to arrive and depart, spending little time in the inshore area as they go through the land/ocean interface. On the other hand elephant seals in their first two years of life not only frequently go through the interface, but spend a considerable amount of time in the inshore area as well, and are therefore much more vulnerable to killer whales. In addition they are less experienced, probably slower with less endurance, and smaller than the older and bigger adults and subadults, all of which increase their vulnerability not only to adult killer whales, but to juveniles as well. Therefore it may be assumed that the elephant seals in their first two years of life are inherently the most vulnerable to the entire killer whale population, and consequently suffer the greatest predatory pressure.

Observations of killer whales increased rapidly in September when the elephant seal cows started arriving (Figures 7 and 18), and their numbers reached a maximum in October when elephant seal cows were both arriving and departing (Figure 7). From November to December killer whales remained abundant, and during this period elephant seal cows departed after weaning their pups (Figure 7) and returned to moult (Figure 9), subadults of both sexes arrived to moult and then departed after moulting (Figure 8), second year seals arrived to moult and then departed (Figure 10), and yearlings became nutritionally independent (Figure 7), spending a good deal of time feeding apparently close inshore (Chapter 9). Thus from September to December the amount of elephant seal movement through and within the inshore area was considerable, and was not surprisingly therefore the period when killer whales were most abundant.

The decline in the elephant seal population appeared to result mainly from a below population maintenance level of recruitment into the female third year age class (Figure 12). Since elephant seals in their first two years were the most vulnerable and were therefore subjected to the heaviest predatory pressure, it appears that killer whale predation is the cause of the below maintenance recruitment of third year female elephant seals. At the same time it appeared that elephant seal cows were also preyed upon when they arrived for and departed after the pupping and mating season. This alone would at the very least have had a detrimental influence on the population, but more likely is acting in combination with the low female recruitment to bring about the decline in the population. The high mortality of male elephant seals from birth to adulthood (Figure 12) might also be the result of predation by killer whales, but since the male:female harem ratio is no greater than at other breeding grounds, predation on males has not yet had a detrimental effect on the population. Carrick and Ingham (1962e) considered predation by killer whales an important mortality factor in immature, cow, and young bull elephant seal age classes at Macquarie Island. The paucity of immature seals bearing scars attributable to killer whales on Macquarie Island was believed to indicate an inability to escape from the predators, while scarred adult seals indicated that they did have an ability to escape (Carrick and Ingham 1962e). The situation on Marion Island was similar, and the observations of elephant seal bulls escaping untouched from killer whales reinforces Carrick and Ingham's (1962e) suggestion.

Since the elephant seal population on Marion Island has been undisturbed since at least 1951 when Rand's (1955, 1962) counts were made, the decline from then to 1975 has been naturally induced. As predation by killer whales appears to be responsible for this decline, it is of interest to examine what might have induced the killer whale presence. Penguins, especially king penguins, appeared to be an important food resource of the killer whales at Marion Island, although Voisin (1972, 1976) stated that at the Crozet Islands they did not appear to eat penguins. King penguins occur on Marion Island throughout the year but there is no data on their seasonal abundance. Their numbers at Heard Island have increased (Budd 1968, 1970; Budd and Downes 1965), and although the population trend on Marion Island is not known, it is possible that their numbers have also been increasing, especially in view of the increased availability of cephalopods following the decline in sperm whale stocks (Gulland 1974, El-Sayed 1975). The large number of king penguins at Marion Island may have attracted the killer whales there. They may then have turned their attention to the elephant seals, ignoring the fur seals which have only reached appreciable numbers (6 000 – 8 000, Condy 1975b unpublished) since the late 1960's. The impact the killer whales seem to have had on the elephant seals infers that from the time they initially started preying upon the seals until the present study, either their numbers increased, or their occurrence at Marion Island has become more regular and better synchronized with the elephant seal's seasonal occurrence. Unfortunately there are no data about their numbers, but there is historical evidence suggesting that at least their occurrence has become more regular. Both Rand (1955, 1956, 1962) and La Grange (1962) mention their occurrence, whereas Van Zinderen Bakker Sr. (1971) mentions not only their occurrence, but also comments on their prominence – "killer whales were regularly seen at close quarters when they patrolled the area near the meteorological station during the seal pupping season and the female seal moult period". These observations were made between January and March 1965, and Van Zinderen Bakker Jr. *(pers. comm.)*, who was on Marion Island during the 1965/66 and 1975/76 summer seasons, was of the opinion that he saw killer whales more frequently during the latter season than he could remember sighting during the former one. Results from the present study suggest that their occurrence has become more regular than that in 1965 (Van Zinderen Bakker Sr. *et al.* 1971). If their impact on the elephant seal population continues, then at some stage in the future when elephant seals become even less numerous, they will be forced to either turn most of their attention to other resources at the same island (eg. fur seals and penguins), or move elsewhere. In any event it is unlikely that the local elephant seal population will be reduced to extinction.

Voisin (1972, 1976) noted that the seasonal occurrence of killer whales at Possession Island (46° 25' S, 51° 45' E) and at Ile aux Cochons (40° 06' S, 50° 14' E) in the Crozet Archipelago also coincided with that of the elephant seals. At Possession Island killer whales were common from September to November and again from March to May, with a decline in numbers between these periods (ie. December to April) according to Voisin (1972). Figure 18 shows that at Marion Island a similar trend occurred, with very few observations in February. The decline in January and February is difficult to understand, since moulted cows and subadults (Figures 8 and 9) departed then so that there was still considerable seal movement through the inshore area. From March to May yearlings and second year seals returned (Figure 10) and moved about quite considerably in the inshore area, and killer whale observations increased again (Figures 17 and 18). It appears that either the decline in killer whale numbers through January and February was not prey related, or it indicates a preference for the younger seals returning and moving about from March to May, as opposed to the larger moulted cows and subadults departing in January and February. It would be necessary to investigate killer whale movement to determine whether there is an emigration in January and February, or whether they remain at the island but do not feed much on at least elephant seals, if at all. Most work on the fur seals inhabiting the west coast of Marion Island was conducted in January and February, and no killer whales were seen on that coast, indicating that there was not simply a shift in predation from the elephant seals to the fur seals. Since killer whale surveilance was maintained on the east coast while the fur seal studies were being conducted, and as Voisin (1972) also noted a decline in killer whale numbers at Possession Island during January and February, the decline observed on Marion Island was not simply related to reduced surveilance.

The diurnal spread of killer whale observations (Table 18) indicates that they hunted, or at least patrolled the coast, throughout most of the day. There was a slight increase in activity between 15h00 and 17h00, indicated by an increase in observations between these times.

CHAPTER 11

CONCLUSIONS

On Marion Island the availability of suitable beaches determines the distribution of the elephant seals. They prefer beaches which have a flat and smooth topography, and where the substrate consists of small rounded stones and pebbles. They cannot negotiate the rough and uneven beaches of the exposed windward coast, and since most of the suitable beaches occur on the leeward east and northeast coasts, the elephant seals are concentrated along them. The more numerous fur seals *(A. tropicalis* and *A. gazella)* occur mainly on the windward coast beaches, so that the distribution of elephant seals and fur seals overlaps only slightly. During the pupping and mating season the adult elephant seals remain on the beaches, but during the moulting season the majority move inland, where they have a considerable influence on the vegetation and topography of the moulting areas. The topographical changes which occur in these areas are caused by the tendency of the moulting seals to lie together, thus creating depressions in the soft ground. The vegetational changes which occur are the result largely of the manuring effect, although trampling and waterlogging of the hollows are important. The effects of trampling are long lasting, while the effects of manuring last for some years (Smith 1976) in the absence of further visits to the area by the seals. The presence of the elephant seals influences the island environment in two other important ways, namely contribution to the inshore organic and inorganic nutrient status during the pupping and mating season, and contribution to the food supply of scavenging bird species, especially during the pupping season.

The seasonal haul out pattern of the elephant seals at Marion Island is essentially similar to that which occurs at other breeding grounds. The onset of the cow haul out after the winter absence occurs slightly earlier than it does on islands south of the Antarctic Convergence, but coincides with the onset of the summer haul out on islands close to and approximately the same distance north or south of the convergence. Arrival and departure of the various age and sex groups in the population is well synchronized, and the haul out sequence enables large numbers of seals to occupy a small area without causing overcrowding.

Results from the tagging programme are limited, largely because the programme is still relatively young. However tag survival up to 24 months has been reasonably good although resightings have been low, but it is hoped that data on age of first parturition and fidelity to birthsite will start accruing over the next few years. Results indicate that animals in their second year have the greatest tendency to wander from their birthsites, and confirms similar observations made by Carrick *et al.* (1962c) at Macquarie Island. The increasing occurrence of elephant seals on the southern African coast may indicate that range expansion is taking place, and it is thought that the majority of elephant seals which occur on these coasts originate from the South Georgia stocks and not from Marion Island.

The adult and pup population has declined since 1951, and present total size is approximately 4 500 seals. The reason for the decline appears to be a below population maintenance level recruitment to the female third year age class, and the cause of this reduced recruitment is believed to be the result of predation by killer whales. Since sealing ended in 1930 the population has remained undisturbed, and in the summer of 1951/52 numbered some 10 000 seals (Rand 1955). The decline since then has been brought about naturally and is not thought to be the result of competition with the fur seals for space on the island or local food resources, and pelagic food resources, mainly cephalopods, are not thought to be limiting. The killer whales, which may have initially been attracted to the island by the abundance of king penguins, have synchronized their seasonal occurrence with that of the elephant seals. Their numbers reach a peak in the elephant seal pupping season and at the time when the weaned pups start feeding themselves, and it appears that yearlings and animals in their second year are the main age groups preyed upon. Although there is no evidence indicating that the number of killer whales has increased, there is historical evidence indicating that since 1951/52 their occurrence at the island has become more regular and better synchronized with the summer haul out pattern of the elephant seals.

Life expectancy for both males and females is greatest at the end of the second year of life, while survival rate undergoes changes in transition from one year to the next so that age specific survival is not constant through life. The net reproductive rate is less than one, confirming the negative population trend, and interestingly the mean length of a generation indicates that first parturition occurs in the seventh year only. However this is only an estimate requiring confirmation from the tagging programme. Pre-weaning mortality is between 5 – 10 per cent being similar to that on Macquarie Island, and starvation and trampling are the main causes of pup mortality. In adults fighting, disease, and battering by heavy seas are probably the main causes of mortality. Killer whale predation appears to be concentrated mainly on the immature seals, and of little importance in the older and stronger adult seals.

Harem size varies considerably, and is dependent largely on the size of the occupied beach as well as its surface structure. Beachmasters are able to maintain exclusive control of up to 60 cows, but beyond that they are unable to prevent the participation of at least one assistant beachmaster.

The development of pups from birth to weaning is essentially similar to that occurring on Macquarie and Signy Islands. However the increase in body mass and size is distinctly different, pups on Marion Island being smaller than those at Macquarie and Signy Islands. It is thought that the difference in pup growth between these islands may be indicative of stock specific body growth potentials, and if so then the growth pattern throughout life may also be different between the various stocks.

SUMMARY

During the pupping and mating season (September to November) the southern elephant seals at Marion Island inhabited the beaches. Their occurrence on a beach depended on its physical nature, and they preferred those beaches which had a flat and smooth profile, and where the substrate consisted of small rounded stones and pebbles. Beaches of this nature occurred mainly on the sheltered leeward east and northeast coasts of the island, and so the majority of breeding elephant seals occurred along these coasts. The Amsterdam Island *(Arctocephalus tropicalis)* and Kerguelen *(A. gazella)* fur seals inhabited the rugged and uneven beaches on the exposed windward west and south coasts of the island. Elephant seals are unable to negotiate such beaches, with the result that their distribution on the island overlapped only slightly with the fur seals.

During the moulting season (November to April) adults and subadults moved inland to moulting areas. The drainage line beaches provided access to these areas, and the distribution of these age classes depended upon the availability and accessibility of suitable inland areas. The distribution of moulting areas differed from the distribution of breeding beaches, so that during this stage of the season there was a change in the distribution of elephant seals. Elephant seals in their second year moulted on the breeding beaches, so that their distribution was the same as that of the adults during the pupping and mating season. The presence of elephant seals influenced the island environment in three main ways, namely contribution to the inshore organic and inorganic nutrient status especially during the pupping and mating season, when urine and faeces deposited on the beaches are washed into the ocean, contribution to the food supply of scavenging birds especially during the pupping and mating season, when afterbirth and pup carcasses are plentiful, and first causing and then maintaining changes in the topography and vegetation of the moulting areas through the effects of trampling and manuring.

Following a winter absence bulls hauled out in early August and fought each other for territorial dominance. Pregnant cows hauled out in early September, gave birth three to seven days after hauling out, weaned their pups approximately 22 – 23

days after birth, and then departed. The last cows departed by mid-November, and their arrival and departure was well synchronized. Pups reached peak numbers in mid-November, and by mid-January all had departed. Cows returned to moult in mid-December, reached peak numbers in late January, and had all departed by early March. Bulls moulted from mid-December to late April, and had the longest moulting season of all age and sex classes. Subadults moulted from early November to late February, males reaching peak numbers in mid-December and females in mid-January. Subadult males appeared to have synchronized their haul out to fall between the breeding and moulting haul out of the bulls, while the haul out of subadult females coincided with the moulting haul out of cows. Seals in their second year hauled out to moult from early November to late January, reaching peak numbers in early December. Some hauled out again in March and April and tended to overwinter, departing in August and September when the bulls and pregnant cows started returning at the beginning of the next summer haul out season. Some yearlings also hauled out in March and April and tended to overwinter, eventually departing in August when the bulls returned. The onset of the summer haul out at Marion Island occurred slightly earlier than it does on more southerly breeding grounds, but coincided with the haul out of elephant seals at breeding grounds equally close to, whether north or south of, the Antarctic Convergence.

Tagging was initiated in November 1973, using Hasco monel metal tags (size 49, National Band and Tag Company, USA). Seals were double tagged, one tag on each hind flipper. Effort was concentrated on weaned pups, and 87,4 per cent of pups surviving to weaning in the study area were tagged from the 1974 to 1976 seasons. Including all age and sex classes 1 409 seals were tagged, of which only 7,1 per cent were resighted, some being resighted more than once. Seals tagged after weaning were resighted up to 24 months after tagging, and 24,5 per cent of those resighted had lost one tag after 24 months. No information on fidelity to birthsite shown by pregnant cows was obtained, but a few cows tagged when mature showed no fidelity to pupping or moulting sites. However since the sample was small and since cows tended to haul out at various sites before selecting one on which to pup, indicating that beach recognition may occur, fidelity to birth and/or pupping sites may in fact occur. Two tagged beachmasters retained their status at the same sites for three consecutive seasons, indicating that mature bulls showed strong fidelity to breeding sites. Seals in their second year displayed the greatest tendency to wander, and some crossed to Marion Island from Prince Edward Island. No seals tagged on Marion Island were resighted at other breeding grounds.

Between the summers of 1951/52 and 1975/76 the elephant seal population on Marion Island declined, the rate of decline for breeding adults and pups combined being approximately 4,8 per cent per year ($r = -0{,}048$). The breeding population in 1975/76 consisted of approximately 1 313 cows and 115 bulls, with a pup crop of approximately 1 100. It is not known when the decline in the population commenced, since the population was not subjected to human interference from the end of 1930 as far as could be determined. An attempt to develop predictive equations to determine total population size of subadults and second year seals was made with partial success only. The equations given underestimated the total number of subadults and second year seals with a mean error of 11,9 per cent when compared to the total numbers obtained from the survivorship tables. The equations accurately predicted the number of subadults and second year seals when the number of bulls (X_1) was low, but when $X_1 > 5$ they were not reliable due to the fact that the regression coefficients were computed from only a few samples of known numbers of bulls, cows (X_2), pups (X_3), subadults (X_4), and second year seals (X_5), and in these samples X_1 was low (mean 4,83). Further samples in which all five variables are known are necessary to improve the predictiveness of the equations. The sex ratio at weaning and for second year seals did not differ significantly from unity (1:0,95 and 1:1,35 respectively), but subadult (1:1,53) and adult (1:11,42) sex ratio's differed significantly from unity. The population structure and age pyramid indicated that female recruitment to the third year was below maintenance and appeared to be the reason for the decline in population size. The cause of this poor recruitment is believed to be the result of killer whale *(Orcinus orca)* predation, since it was shown that at Marion Island abundance and seasonal occurrence of killer whales is closely related to the abundance and seasonal occurrence of the elephant seals, especially of those seals in their first and second years of life. There was no evidence for an increase in killer whale numbers, but there was historical evidence suggesting that since 1965 at least their occurrence had become more regular, and better synchronized with the elephant seal summer haul out pattern.

The life tables showed that life expectancy was greatest at the end of the second year of life for both sexes, females surviving to 14 years old and males to 19 years old. Net reproductive rate was less than one (R_0 = 0,69), confirming the negative population trend, and the mean length of a generation (T = 6,65), although being only an estimate, indicated that first parturition does not occur until six years old on average. Mortality from birth to weaning in the study area was 5,99 per cent, separation from the cow resulting in starvation, and trampling being the main causes of death. Other causes such as drowning by high seas and cow aggression also contributed. For yearlings and second year seals predation by killer whales was the main cause of death, and in adults fighting, battering by heavy seas, and possibly disease were the main causes of death, although cows were also preyed on to some extent by killer whales.

Harem sizes varied, their size being controlled mainly by beach size and surface nature. Beachmasters were able to maintain sole possession of up to 60 cows, accepted a subordinate assistant beachmaster when 60 – 130 cows were present, and a second assistant beachmaster when harem size exceeded 130 cows. Mean harem ratio (beachmasters:assistant beachmasters:cows) was 1:0,53 ± 0,72 : 45,35 ± 43,77 (n = 17).

Pups started moulting at 13 days old (mean 13,21 ± 4,81; n = 28), had completed their moult at 28 days old (mean 28,34 ± 5,68; n = 28), and were weaned at 22 days old (mean 22,47 ± 3,52; n = 18) on the beach where their growth was monitored. Elsewhere they were weaned at 25 days old (mean 25,18 ± 2,67; n = 12), and it is thought that the disturbance to the seals on the growth study beach caused the cows to depart prematurely. After weaning pups remained on the study beach fasting for 8 – 10 days before entering the water, 18 days after weaning they ventured further offshore and spent at least four hours at sea at a time, and then returned to the same beach. The period of absence remained fairly constant for a further 10 days, after which they spent an increasing amount of time at sea, so that within a further 10 days (60 days after birth) they were not returning to the study beach. Mean birth mass (sexes combined) was 37,75 ± 1,67 kg (n = 8), measured within two hours of birth, and there was no significant difference between the sexes. At weaning mean body mass (sexes combined) was 97,19 ± 7,76 kg (n = 8) and there was no significant difference between the sexes. From birth to two days old body mass declined, and only exceeded birth mass from the fifth day after birth. Increase in mass from then until weaning was similar for both sexes, but following weaning males lost mass faster than females although did not ultimately lose as much mass as the females. Males showed a recovery in mass six days after weaning, and females 10 days after weaning. From the stage of nutritional independence onwards, males were heavier than females. The age specific mass of pups at Marion Island was less than that at Macquarie and Signy Islands. Curvilinear length at birth (sexes combined) was 116,05 ± 7,40 cm (n = 10), and at weaning (sexes combined) 130,67 ± 9,87 cm (n = 3). Axillary girth at birth (sexes combined) was 81,20 ± 2,61 cm (n = 5), and at weaning (sexes combined) 130,00 ± 9,90 cm (n = 2). At birth and weaning pups at Marion Island had a smaller curvilinear length and axillary girth than those on Macquarie and Signy Islands.

Following weaning the decline in pup condition index occurred at a time when air and sea temperatures were above the yearly mean, but not at their warmest. However the amount of solar radiation reaching the surface was greatest at this time, and may be of importance in enabling the pups to recover after prolonged exercise and exposure to the cold sea water.

OPSOMMING

Gedurende die geboorte- en paarseisoen (September tot November) het die suidelike olifantrob op Marioneiland die strande beset. Hulle voorkoms op 'n strand hang af van die strand se fisiese geaardheid en hulle verleen voorkeur aan die strande met 'n plat en egalige profiel waarvan die onderlaag uit klein, ronde klippe en spoelklippies bestaan. Strande van hierdie aard kom hoofsaaklik op die beskutte oostelike en noord-oostelike kuste aan die lykant van die eiland voor en dus het die meerderheid van telende olifantrobbe langs hierdie kuste voorgekom. Die Amsterdameiland pelsrobbe *(Arctocephalus tropicalis)* en die Kerguelen pelsrobbe *(A. gazella)* het die ruwe en onegalige strande op die blootgestelde westelike en suidelike kuste aan die windkant van die eiland beset. Olifantrobbe is nie in staat om op sulke strande te woon nie en die resultaat is dat hulle verspreiding op die eiland dié van die pelsrobbe slegs effens oorvleuel.

Gedurende die verharingseisoen (November tot April) het volwassenes en onvolwassenes na die binnelandse verharingsgebiede beweeg. Die dreineringslynstrande het toegang tot hierdie gebiede verleen en die verspreiding van die ouderdomsklasse het afgehang van die beskikbaarheid en toeganklikheid van geskikte binnelandse gebiede. Die verspreiding van die verharingsgebiede het van dié van die teelstrande verskil sodat daar gedurende hierdie stadium van die seisoen 'n verandering in die verspreiding van olifantrobbe was. Olifantrobbe in hulle tweede jaar het op die teelstrande verhaar – hulle verspreiding was dus dieselfde as dié van die volwassenes gedurende die geboorte- en paarseisoen. Die teenwoordigheid van olifantrobbe het die eiland se omgewing op drie maniere beïnvloed, naamlik deur 'n bydrae tot die organiese en anorganiese voedingstoftoestand digby die kus, veral gedurende die geboorte- en paarseisoen wanneer uriene en uitwerpsels wat op die strand gelaat is, in die see ingewas word; 'n bydrae tot voedselvoorsiening aan aasvretende voëls, veral gedurende die geboorte- en paarseisoen wanneer nageboortes en welpiekarkasse volop was; en deur veroorsaking en instandhouding van die topografie en plantegroei van die verharingsgebiede as gevolg van vertrapping en bemesting.

Na die winterafwesigheid het die bulle vroeg in Augustus op Marioneiland aangekom en om heerskappy vir grondbesit begin veg. Dragtige koeie het vroeg in September op Marioneiland aangekom, het van drie tot sewe dae na aankoms geboorte gegee, hulle welpies ongeveer 22 tot 23 dae ná geboorte gespeen en dan weer vertrek. Die laaste koeie het teen middel-November vertrek en hulle aankoms en vertrek was goed gereguleerd. Welpiegetalle het 'n hoogtepunt in middel-November bereik en by middel-Januarie het almal reeds vanaf Marioneiland vertrek. . Koeie het teen middel-Desember weer teruggekeer om te verhaar, 'n getalshoogtepunt in laat-Januarie bereik en teen vroeg-Maart weer almal vertrek. Bulle het vanaf middel-Desember tot laat-April verhaar en hulle het ook die langste verharingseisoen van al die ouderdoms- en geslagsgroepe vertoon. Onvolwassenes het vanaf vroeg-November tot laat-Februarie verhaar; mannetjies bereik 'n getalshoogtepunt in middel-Desember en wyfies in middel-Januarie. Onvolwasse mannetjies het skynbaar hulle aankoms gereguleer om met die teel- en verharingseisoen van die bulle saam te val terwyl die aankoms van die onvolwasse wyfies met die verharingsaankoms van die koeie saamgeval het. Robbe in hulle tweede jaar het tussen vroeg-November en laat-Januarie vir die verharingseisoen aangekom met 'n getalshoogtepunt in vroeg-Desember. Sommige het weer in Maart en April gearriveer en het dan geneig om te oorwinter en in Augustus en September weer te vertrek wanneer die bulle en dragtige koeie begin terugkeer aan die begin van die volgende somerseisoen. Sommige jaarlinge het ook in Maart en April op die eiland aangekom, het geneig om daar te oorwinter en het uiteindelik in Augustus vertrek wanneer die bulle na Marioneiland terugkeer. Die begin van die someraankoms op Marioneiland het effens vroeër plaasgevind as wat dit gewoonlik gebeur op meer suidelike teelgronde, maar het saamgeval met die aankoms van olifantrobbe by teelgronde ewe naby, hetsy noord of suid van die Antarktiese Konvergensie.

Gedurende November 1973 is daar met die merk van robbe begin deur die aanhegting van genommerde Hasco monelmetaalplaatjies (grootte 49, 'National Band and Tag Company', VSA). Robbe is dubbeld gemerk met een plaatjie aan elke agterste vin. Die merkpoging was veral gerig op gespeende welpies en 87,4 persent van die welpies wat speenouderdom in die studie-area bereik het, is in die 1974 tot 1976 seisoene gemerk. Alle ouderdoms- en geslagsgroepe ingesluit, is daar

1 409 robbe gemerk, waarvan slegs 7,1 persent weer waargeneem is, sommige daarvan meer as een keer. Robbe wat na spening gemerk was, is weer tot meer as 24 maande na merking waargeneem. Daarvan het 24,5 persent een plaatjie na 24 maande verloor. Geen gegewens oor die verbondenheid van dragtige koeie tot hulle geboorteplek is verkry nie, maar 'n paar koeie wat as volwassenes gemerk was, het geen verbondenheid aan kraam-, welpings of verharingsgebiede vertoon nie. Aangesien die steekproef te klein was en omdat koeie geneig is om by verskillende lokaliteite aan te doen voordat een daarvan as kraamplek verkies word, mag verbondenheid tot geboorte- en/of welpingsgebiede wel voorkom. Twee gemerkte strandmeesters het hulle rang vir drie agtereenvolgende seisoene by dieselfde strande behou wat daarop dui dat volwasse bulle 'n sterk verbondenheid ten opsigte van teelgebiede toon. Robbe in hulle tweede jaar het die meeste neiging tot rondswerwing getoon en sommige het vanaf Prince Edwardeiland na Marioneiland geswerf. Geen robbe wat op Marioneiland gemerk is, is weer op ander teelgronde waargeneem nie.

Tussen die somers van 1951/52 en 1975/76 het die olifantrob bevolkingsgetal op Marioneiland afgeneem. Die tempo van afname vir telende volwassenes en welpies gekombineerd was ongeveer 4,8 persent per jaar ($r = -0{,}048$). Die telende bevolking in 1975/76 het uit ongeveer 1 313 koeie en 115 bulle bestaan met 'n welpie-oes van ongeveer 1 100. Dit is nie bekend wanneer die afname in bevolkingsgetal begin het nie aangesien die bevolkingsgetal, sover bekend, nie onderworpe was aan menslike versteuring sedert die einde van 1930 nie. 'n Poging om voorspelbare vergelykings te ontwikkel om sodoende totale bevolkingsgetal van onvolwassenes en tweede-jaar robbe te bepaal, was slegs gedeeltelik suksesvol. Die vergelykings aangetoon, het die totale getal onvolwassenes en tweede-jaar robbe met 'n gemiddelde fout van 11,9 persent onderskat wanneer dit met die totale getalle, soos verkry vanaf die oorlewingstabelle, vergelyk word. Die vergelykings het die getalle onvolwassenes en tweede-jaar robbe akkuraat voorspel wanneer die getal bulle (X_1) laag was, maar wanneer $X_1 > 5$ was, was die getalle nie betroubaar nie weens die feit dat die regressie-koëffisiënt verkry was van slegs enkele steekproewe van bekende getalle van bulle, koeie (X_2), welpies (X_3), onvolwassenes (X_4) en tweede-jaar robbe (X_5),en in hierdie steekproewe was X_1 laag (gemiddeld 4,83).

Verdere steekproewe waarin al die vyf veranderlikes bekend is, is nodig om die voorspelbaarheid van die vergelykings te verbeter. Die geslagsverhouding by spening en vir tweede-jaar robbe het nie betekenisvol verskil van gelykheid (1:0,95 en 1:1,35 onderskeidelik) nie, maar onvolwassenes (1:1,53) en volwassenes (1:11,42) se geslagsverhoudings het betekenisvol van gelykheid verskil. Die bevolkingstruktuur en ouderdomspiramide het aangetoon dat aanvulling van wyfies tot die derde jaar benede instandhoudingsvlak was en dit het voorgekom dat dit die rede is vir die afname in algehele bevolkingsgetal. Die oorsaak van hierdie swak aanvulling word aan die moordwalvis *(Orcinus orca)* se predasie toegeskryf aangesien dit aangetoon is dat die getalle en seisoenale voorkoms van die moordwalvisse by Marioneiland nou-verwant is aan die getalsterkte en seisoenale voorkoms van veral olifantrobbe in hulle eerste- en tweede lewensjare. Daar was geen bewys vir die toename in moordwalvisgetalle nie, maar daar was besliste aanduidings dat hulle voorkoms vanaf 1965 meer gereeld was tydens, en beter gesinkroniseerd was met die olifantrobbe se someraankomspatroon.

Die lewenstabelle het aangetoon dat lewensverwagting aan die einde van die tweede lewensjaar, vir beide geslagte, die grootste was; wyfies oorlewe tot 14 jaar en mannetjies tot 19 jaar. Netto voortplantingstempo was minder as een (R_0 = 0,69) wat die negatiewe bevolkingsneiging bevestig. Die gemiddelde geskatte generasietydperk (T = 6,65) het aangedui dat die eerste welping nie voorkom voor 'n gemiddelde ouderdom van ses jaar nie. Die sterftesyfer vanaf geboorte tot spening in die studie-area was 5,99 persent. Skeiding van die koei gevolg deur uithongering en vertrapping is die hoofoorsake vir sterftes. Ander oorsake soos verdrinking tydens ruwe see en aggressiwiteit van koeie het ook hiertoe bygedra. Predasie van moordwalvisse was die hoofoorsaak vir sterftes onder jaarlinge en tweede-jaar robbe, terwyl gevegte, beserings in seestorms en 'n moontlike siekte, die hoofoorsake vir sterftes onder die volwassenes was.

Haremgroottes het gevarieer; groottes was hoofsaaklik deur die strandgrootte en oppervlakgeaardheid beheer. Strandmeesters was in staat om alleen-besitreg van tot 60 koeie te behou. Hulle het 'n ondergeskikte hulp-strandmeester aanvaar wanneer 60 tot 130 koeie aanwesig was en 'n tweede assistent-strandmeester wanneer die haremgrootte meer as 130 koeie was. Gemiddelde haremverhouding (strandmeesters: assistent-strandmeesters:koeie) was 1:0,53 ± 0,72 : 45,35 ± 43,77 (n = 17).

Welpies het op 'n ouderdom van 13 dae begin verhaar (gemiddeld 13,21 ± 4,81; n = 28), verharing op 28 dae ouderdom voltooi (gemiddeld 28,34 ± 5,68; n = 28) en het op 22 dae ouderdom gespeen (gemiddeld 22,47 ± 3,52; n = 18) op die strand waar hulle nagevolg was. Elders was hulle op 25 dae ouderdom gespeen (gemiddeld 25,18 ± 2,67; n = 12) en dit word vermoed dat die versteuring van die robbe op die groeistudiestrand veroorsaak het dat die koeie vroeër vertrek het. Na spening het die welpies vir 8 tot 10 dae op die studiestrand agtergebly voordat hulle in die water ingegaan het. Agtien dae na spening het hulle verder vanaf die kus gegaan en tenminste vier ure op 'n slag in die see gespandeer om dan terug te keer na dieselfde strand. Die tydsduur van afwesigheid het vir 'n verdere 10 dae redelik konstant gebly waarna hulle vir 'n toenemende tydperk in die see vertoef het sodat hulle binne 'n verdere 10 dae (60 dae ná geboorte) nie meer na die studiestrand teruggekeer het nie. Die gemiddelde geboortemassa (geslagte gekombineerd), binne twee ure na geboorte vasgestel, was 37,75 ± 1,67 kg (n = 8) en daar was geen merkbare verskil tussen die geslagte nie. Tydens spening was die gemiddelde liggaamsmassa (geslagte gekombineerd) 97,19 ± 7,76 kg (n = 8) en daar was geen sigbare verskil tussen die geslagte nie. Vanaf geboorte tot op twee dae ouderdom het die liggaamsmassa afgeneem en die geboortemassa is eers vanaf die vyfde dag na geboorte oorskry. Toename in massa vanaf dan tot spening was vir beide geslagte eenders, maar na spening het mannetjies hulle massa vinniger verloor as die wyfies maar het nie uiteindelik sovéél verloor as die wyfies nie. Mannetjies het 'n herstel in massa ses dae ná spening en wyfies 10 dae ná spening getoon. Vanaf die tydstip van voedingsonafhanklikheid en daarna, was mannetjies swaarder as wyfies. Die ouderdomspesifieke massa van welpies by Marioneiland was minder as dié van Macquarie- en Signeyeiland. Die kromlynige lengte by geboorte (geslagte gekombineerd) was 116,05 ± 7,40 cm (n = 10) en by spening (geslagte gekombineerd) 130,67 ± 9,87 cm (n = 3). Spilomvang by geboorte (geslagte gekombineerd) was 81,20 ± 2,61 cm (n = 5) en by spening (geslagte gekombineerd) 130,00 ± 9,90 cm (n = 2). By geboorte en spening het welpies by Marioneiland 'n kleiner kromlynige lengte en spilomvang as dié van Macquarie- en Signeyeiland.

Na spening het die afname in welpies se toestandsindeks plaasgevind op 'n tydstip toe lug- en seetemperature bokant die jaarlikse gemiddelde was, maar nie op hulle warmste nie. Die hoeveelheid lugstraling wat die oppervlakte bereik het, was egter die meeste gedurende hierdie tydperk en mag van belang wees om die welpies in staat te stel om te herstel na langdurige oefening en blootstelling aan die koue seewater.

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