Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island

P.R. Condy

The annual cycle of southern elephant seals, *Mirounga leonina*, was studied at Marion Island (46° 54′ S, 37° 45′ E), between August 1973 and December 1976. Data on the breeding and moulting haul-out of different age and sex classes were obtained by conducting once weekly censuses in a selected study area. The haul-out sequence, characterized by a high degree of synchronization and annual regularity was similar to that occurring at other breeding grounds. Photoperiod, in particular the mean monthly increase in day length, appeared to act as an obligatory proximate factor initiating the haul-out to breed and onset of hair growth. Temperature and radiation appeared to act as obligatory ultimate factors initiating the haul-out to moult.
S. Afr. J. Zool. 14: 95-102 (1979)

Die jaarlikse siklus van die suidelike olifantrob, *Mirounga leonina* is bestudeer op Marioneiland (46° 54′ S 37° 45′ O) vanaf Augustus 1973 tot Desember 1976. Inligting aangaande die teel en verharing aankomstydperke van verskillende ouderdoms- en geslagsgroepe is verkry deur die uitvoer van een-weeklikse volktellings in 'n geselekteerde studiegebied. Die aankomsvolgorde, gekenmerk deur 'n hoë mate van sinkronisasie en jaarlikse gereeldheid, was soortgelyk aan dié van ander teelbevolkings. Photoperiodisiteit, veral die gemiddelde maandelikse toename in daglengte, tree waarskynlik op as 'n onmiddelike verpligtende faktor wat die aankoms om te teel en die aanvang van haargroei inlei. Temperatuur en radiasie blyk om op te tree as 'n fundamentele verpligtende faktor wat die aankoms vir verharing reguleer.
S.-Afr. Tydskr. Dierk. 14: 95-102 (1979)

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The Prince Edward Islands, consisting of Marion Island (46° 54′ S, 37° 45′ E) and Prince Edward Island (46° 38′ S, 37° 57′ E), lie 2 300 km South East of Cape Town in the South Indian Ocean. The climate is basically oceanic, with modifications due to the topography of the island itself (Schulze 1971), and the main climatic features are summarized in Table 1.

The southern elephant seals *(Mirounga leonina)* on Marion Island were first studied by Rand (1955; 1962) and La Grange (1962), the former providing data on the population size and distribution of *M. leonina*, and the latter limited data on the annual cycle. In 1973 a broad based biological research programme was initiated on the Prince Edward Islands by the South African Scientific Committee for Antarctic Research (SASCAR), who appointed the Mammal Research Institute to supervise studies on the mammalian fauna of the islands. The data presented in this paper comprised part of a larger study on the seals of the islands (Condy 1977; 1978 *in press*), and were obtained between August 1973 and December 1976.

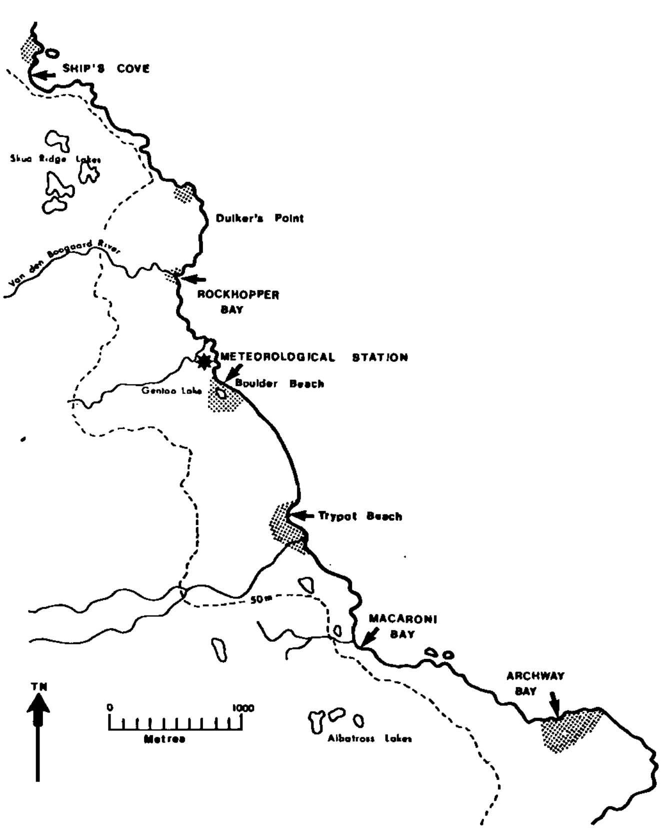
Materials and Methods

Two beaches, Trypot and Boulder beaches, were censused once weekly from August 1973 to December 1976. During the months August to January 1974-1976 an additional four beaches were also censused once weekly; Archway Bay, Macaroni Bay, Rockhopper Bay, and Ship's Cove. These beaches, including the former two, comprised the main elephant seal study area on Marion Island (Fig. 1). Censuses were conducted on foot, all sites occupied by elephant seals being accessible, and made by direct counting of all individuals hauled-out. At the time of counting individuals were allocated to broad age classes, which were based on the descriptions of body size and appearance given by Laws (1953). The classes were; bulls (>6 years old), cows (>5 years old), subadults (females 3-5 years old, males 3-6 years old), yearlings (13-24 months old), under-yearlings (1-12 months old) and pups (< one month old). Pups were defind as being < one month old as most had been weaned by that age, and animals in the pup to subadult classes were sexed whenever possible. At Boulder beach 18 cows were marked with paint such that

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 day length, hours	15,5	14,1	12,4	10,7	9,1	8,4	8,9	10,1	11,9	13,4	15,1	16,0	12,1
Monthly change in day length, % of previous month	-3,1	-9,0	-12,1	-13,7	-14,9	-7,7	+5,9	+13,5	+17,8	+12,6	+12,7	+5,9	-
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 amount of sunshine, hours	5,0	4,8	3,7	2,8	2,4	1,8	2,0	2,6	3,2	4,5	5,1	5,0	3,6
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 transmitted radiation reaching the surface, % (over 5 years)	49	51	49	46	53	40	49	52	51	55	52	49	50

*Data provided by Weather Bureau, Dept. of Transport, South Africa.



List of Figures

Fig. 1 The main study area on Marion Island, showing the positions of beaches (➡) and moulting areas (⁝⁝⁝) censused each week during the study.

they were individually identifiable. Within 24 hours post-partum each pup was marked with a numberd polyvynil covered nylon strap ("Sterkolite"), tied around the tibia-fibula portion of one hind flipper. Observations made on these individuals enabled determination of time elapsed between haul-out and parturition, parturition and mating, and parturition and weaning.

Results

The breeding season

The mean annual number of bulls, cows, and pups counted each week in the study area, for the periods August to January 1974-1976 are illustrated in Fig. 2. Following the winter when few elephant seals occurred on the island, the first to return were the bulls, in early August. The first of the pregnant cows arrived about a month later in early September. Cows gave birth approximately six days after hauling out (mean 6,1 ± 4,3 days, n = 18), so that the increase in number of pups paralleled the increase in number of cows, but lagged about a week behind. The cows returned to the sea 22-23 days after parturition (mean 22,5 ± 3,5 days, n = 18, when the pups were weaned.

After weaning, pups remained on the beaches fasting for 6 - 10 days, and then ventured into the sea on days when it was calm, remaining within a few metres of the shoreline. Approximately 60 days postpartum they became completely pelagic, with very few remaining on the island.

Bulls competed with each other as soon as they hauled out, and by the time the cows arrived the male hierarchy on each beach had been established. However, changes in bull status did occasionally occur, particularly during the peak mating period. Beachmasters (c.f. Carrick, Csordas and Ingham 1962b) were occasionally replaced, but most

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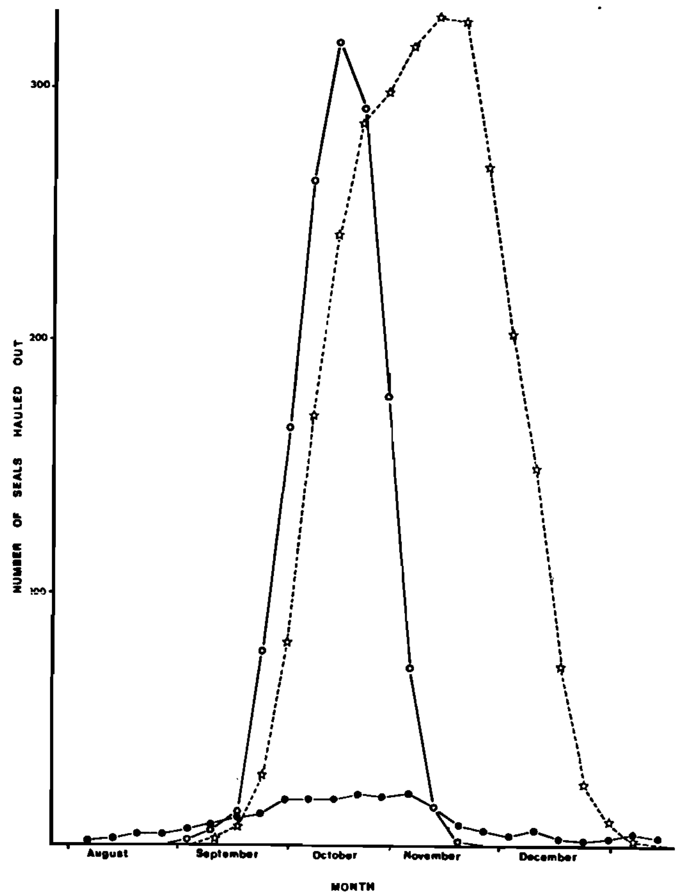

Fig. 2 Mean annual number of southern elephant seal cows (o), bulls (●) and pups (★) counted each week in the main study area.

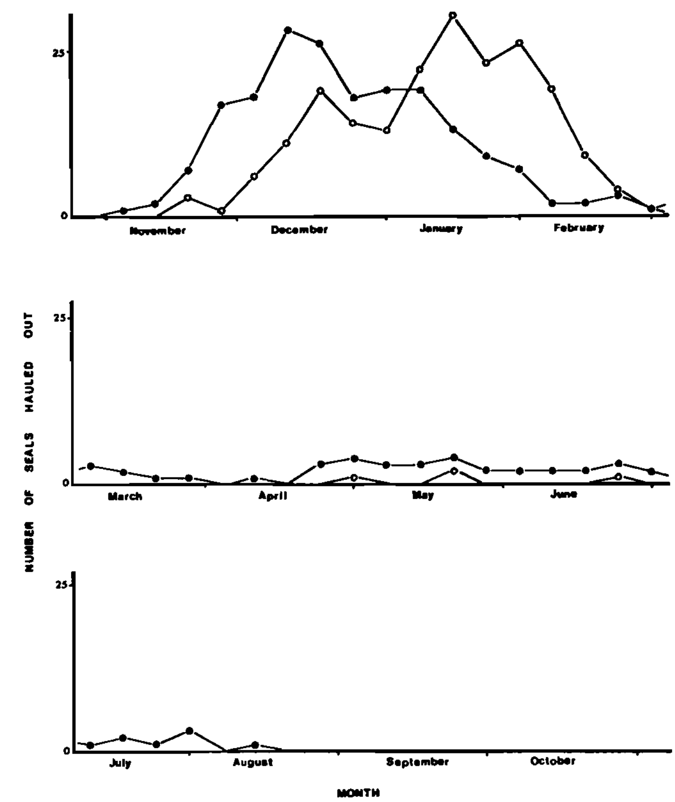

Fig. 3 Mean annual number of moulting subadult elephant seals (o = females, ● = males) counted each week at Trypot and Boulder beach moulting areas. Numbers present on the beaches overwinter are also shown.

changes were challengers being accepted by the beachmaster as assistant beachmaster, with an accompanying decrease but not disappearance of hostility between the two. Defeated challengers as well as bachelor bulls often stayed away from the breeding beaches once the cows arrived, and they hauled-out in small inlets, coves, and on small unoccupied beaches until the peak mating period. They then returned to the breeding beaches where they remained on the periphery of the harems, but usually managed to mate cows which moved away from the harems. Cows were mated about 18 days postpartum (mean 18,4 ± 3,5 days, n = 18), with the peak mating period falling in late October and early November. Following the peak mating period the number of bulls hauled out on breeding beaches declined, and by mid-December individuals were only occasionally seen. Most of these suffered from injuries sustained through fighting earlier in the season.

The moulting season

Seals in all age classes older than the under-yearlings returned once each year to moult, and the sequence of the moult haul-out is illustrated in Figs 3, 4, and 5.

Subadult males and females hauled out to moult when the adults were departing at the end of the breeding season (Figs 2 and 3). Although both sexes arrived in early November, the number of males increased more rapidly than the females, so that the respective peaks were separated by approximately five weeks (Fig. 3). The subadult male haul-out overlaped slightly with the presence of the last of the breeding bulls, and as the number of moulting bulls reached a peak later in the season (Fig. 4), the number of moulting subadult males was declining.

It appeared that the subadult male moult was timed to fall between the breeding and moulting haul-out periods of the bulls. On the other hand, the peak in numbers of moulting subadult females (Fig. 3) coincided with the peak in numbers of moulting cows and bulls (Fig. 4). Cows and subadult females completed their moult within 25 days (mean 31,2 ± 10,6 days, n = 8), and subadult males within 28 days (mean 28,5 ± 9,3 days, n = 10).

Yearlings hauled out to moult in early November (Fig. 5), when the subadults arrived (Fig. 3) and before the last of the breeding cows had departed (Fig. 2). Their numbers increased rapidly reaching a peak in mid-December when subadult males reached peak numbers (Fig. 3). However, while all moulting adults and subadults moved inland to moulting areas (Condy 1977), yearlings remained on the beaches and, therefore, experienced little disturbance from older animals. The under-yearlings also occupied the beaches, but during December their numbers declined (Fig. 1). Most yearlings had moulted and departed by late January, but about six weeks later, in late March, they were involved in another definite though less spectacular haul-out, and many of these individuals overwintered at the island (Fig. 5). Some of the under-yearlings returned in late February, most of whom also overwintered (Fig. 5).

The winter season

A few subadults were hauled-out during the winter (Fig. 3), as were a few yearlings and under-yearlings (Fig. 5). However, during August when breeding bulls returned for the next breeding season (Fig. 2), the decline in their numbers was accelerated and by September when the cows

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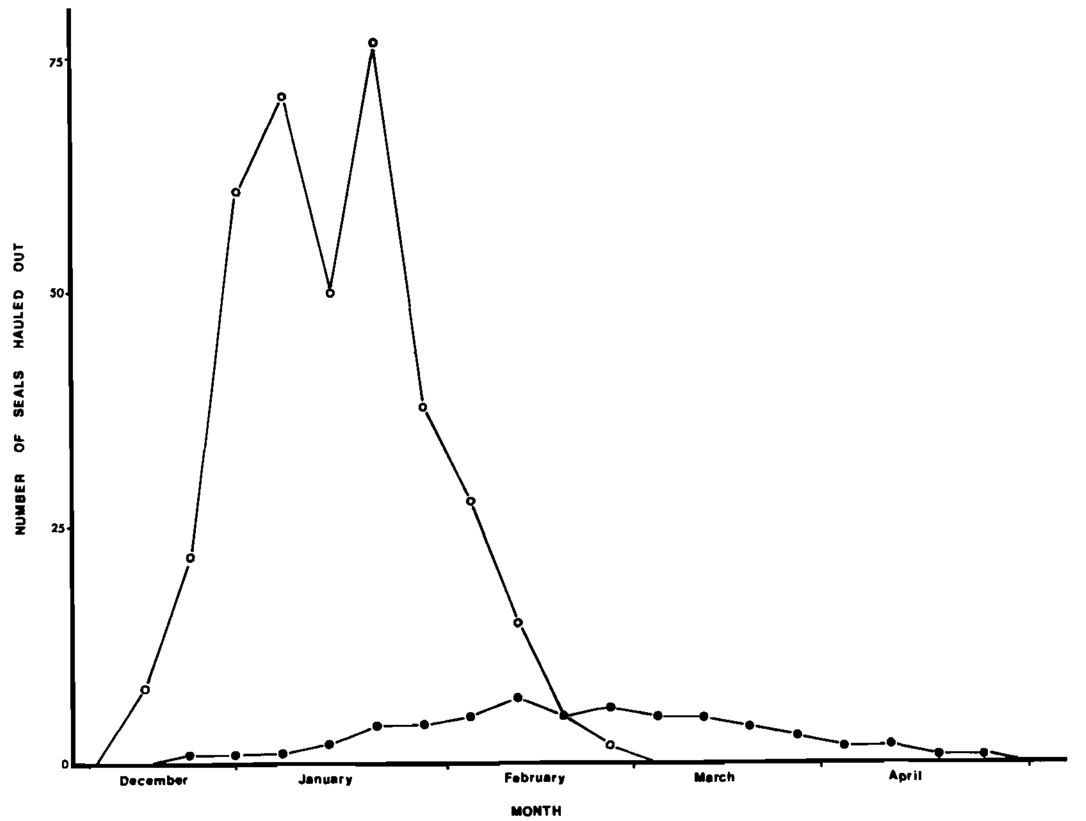

Fig. 4 Mean annual number of moulting southern elephant seal cows (o) and bulls (●) counted each week at Trypot and Boulder beach moulting areas.

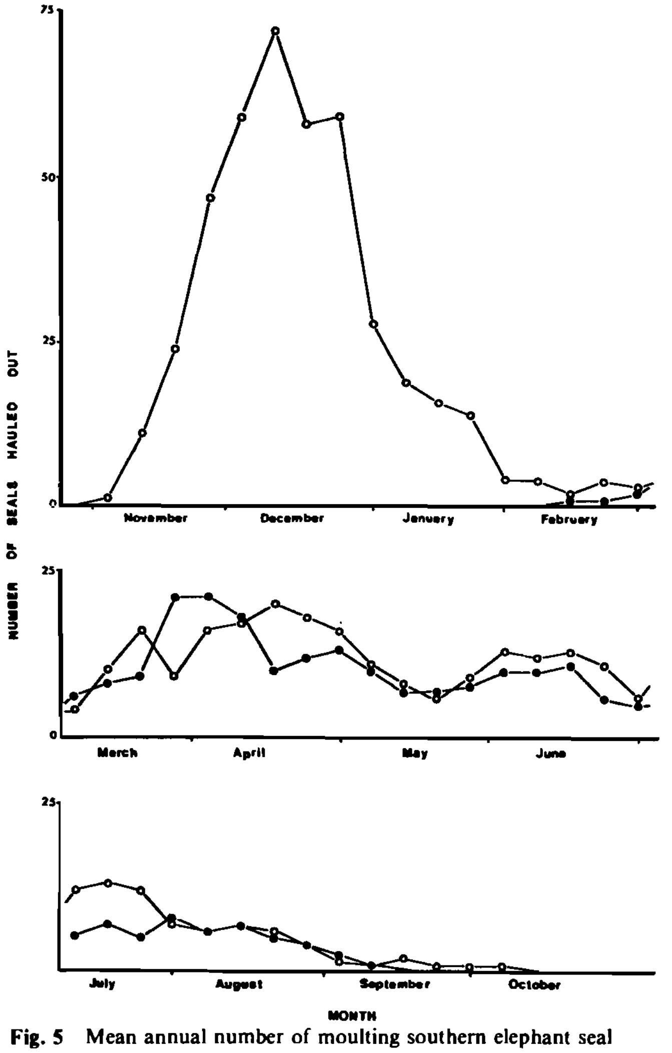

Fig. 5 Mean annual number of moulting southern elephant seal yearlings (o = sexes combined) counted each week at Trypot and Boulder beaches. Numbers of overwintering yearlings and under-yearlings (● = sexes combined) are also shown.

started hauling-out, very few immature seals remained on the island.

Duration of haul-out season

The mean amount of time spent by individuals in different sex and age classes on Marion Island is given in Table 2. Bulls were present over a longer period than any other class, while yearlings were present for the shortest period. period.

Table 2 Mean amount of time spent by individual southern elephant seals on Marion Island

Age class	Main haul-out periods						
	Breeding season		Moulting season		Total haul-out time		
	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	Some only
Subadult females	-	-	15	28,8	15	28,8	Some only
Yearlings	-	-	14	26,9	14	26,9	Some only
Under-yearlings	6	11,5	10	19,2	16	30,8	Some only

Biomass of seals hauled-out

Condy (1977) estimated that the elephant seal population on Marion Island consisted of 1 428 breeding adults (115 bulls and 1 313 cows), and 3 110 immatures (1 100 under-yearlings, 660 yearlings, 534 subadult males, and 816 subadult females). Bryden (1972) gave body mass data for elephant seals at Macquarie Island, and from his data the mean body mass of bulls has been taken as 2 300 kg, for cows 390 kg, for subadult males 400 kg, for subadult females 200 kg, and for yearlings and under-yearlings (sexes combined) 180 kg and 135 kg respectively.

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Table 3 Estimated number of southern elephant seals hauled-out each month on Marion Island

Class	Number of seals hauled-out											
	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Cows	0	0	0	502	1 313	512	318	1 313	360	5	0	0
Bulls	0	0	16	70	115	89	28	46	115	83	23	0
Subadult ♂♂	53	32	11	5	0	144	534	304	43	37	32	75
Subadult ♀♀	0	0	0	0	0	46	424	816	250	7	0	0
Yearlings	131	111	68	20	5	209	660	169	33	118	179	106
Pups/ Under-yearlings	143	83	92	186	736	1 100	421	4	11	200	204	135

Based on the known percentage of the population occurring in the main study area, and their haul-out sequence, the total number of elephant seals, by age and sex class, hauled out each month on the island was estimated (Table 3), and using Bryden's (1972) data on body mass, it was possible to calculate the biomass of elephant seals hauled-out each month (Fig. 6).

Regularity of haul-out

The dates of first arrivals, peak numbers, and last departures of various age and sex classes at Trypot Beach (Fig. 1), between August 1973 and April 1977, are given in Table 4. Comparative data on the annual cycle of southern elephant seals at various breeding grounds are summarized in Table 5.

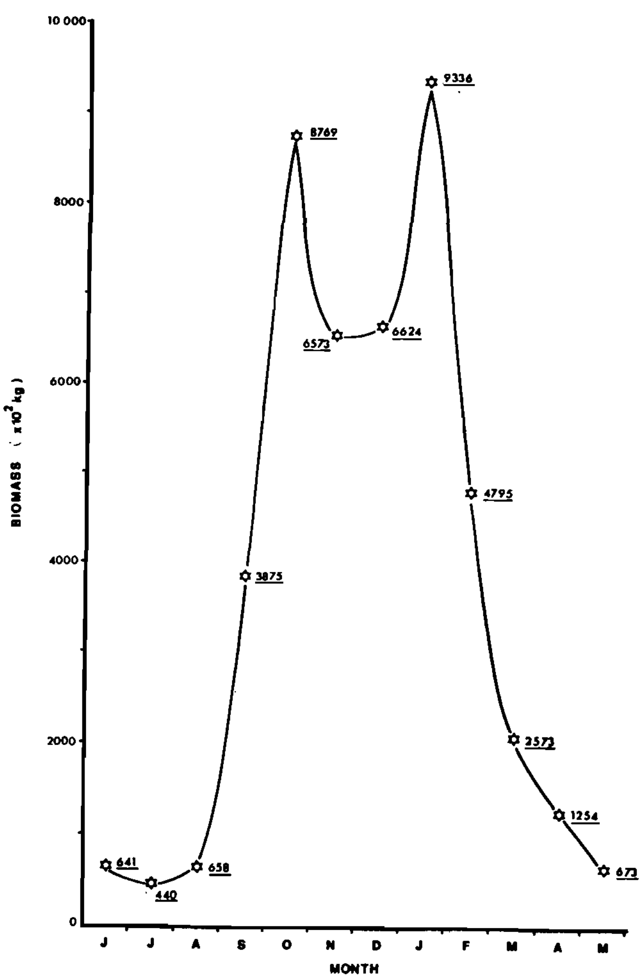

Fig. 6 Monthly biomass (x10²kg) of southern elephant seals hauled out on Marion Island. Numbers underlined are the actual monthly biomass values (x10² kg).

Discussion

The annual cycle of southern elephant seals has been investigated at Campbell Island (Sorensen 1950), Kerguelen (Angot 1954; Pascal *in press*), Signy Island and South Georgia (Laws 1956), Amsterdam and Saint Paul Islands (Paulian 1957), Heard and Macquarie Islands (Carrick *et al.* 1962a), and the Crozet Islands (Despin, Mougin and Segonzac 1972; Barrat and Mougin 1978). There appears to be a slight variation in timing of the spring haul-out according to position of the breeding ground (Table 5), with peak cow haul-out occurring in mid-October at, and north of, the Antarctic Convergence, but about a week later at breeding grounds far south of the Convergence. Presence of sea ice at southerly breeding grounds (e.g. Signy Island) may in part cause this delay in onset of the haul-out (Laws 1956), but by mid-summer when the sea ice has normally broken out and dispersed, there is little variation in timing of the summer moulting season (Table 5).

Gibbney (1957) and Carrick *et al.* (1962a) noted that primiparous cows moulted earlier than older cows, the latter moulting progressively later each year. The twin-peak cow haul-out in the moulting season at Marion Island (Fig. 4) may, therefore, reflect this differential haul-out pattern. Since primiparous cows would have spent much less time ashore during the breeding season, and departed sooner than lactating cows, it seems reasonable to assume that they would be able to moult earlier than the latter.

Carrick *et al.* (1962a) also observed a second autumn haul-out peak of yearlings (Fig. 5) but gave no explanation, and it is still not clear why this second haul-out occurred. It would seem that yearlings which returned at this time were unable to withstand the prolonged period at sea during winter, and appeared to be smaller than usual, although none were weighed or measured.

Generally, the annual haul-out cycle at Marion Island was similar to that of southern elephant seals at other breeding grounds. The two most remarkable aspects of this cycle, illustrated well by the data from this study, are the high degree of organization, with different age and sex classes hauling out at different times (Figs. 2-5), and the regularity of the cycle (Table 4). With regard to the degree of organization, Ling (1969) commented that unless adjustment of the terrestrial phase of southern elephant seals occurred with respect to the time of arrival of different age and sex classes, crowding would occur with an increase in intraspecific aggression. Weir and Rowlands (1973) commented that in the wild state, a non-pregnant female was either "juvenile, senile, or a failure, and mechanisms must operate to safeguard the species against

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Table 4 Dates of first arrival, peak number, and last departure of southern elephant seals at Trypot Beach, Marion Island

Annual haul-out pattern	Sample period	Date
Breeding season (first arrival)		
bulls	1973 - * 1977, n = 5	Aug 24 $\pm$ 6 days
cows	1973 - * 1977, n = 5	Sep 18 $\pm$ 5 days
pups	1973 - * 1977, n = 5	Sep 24 $\pm$ 4 days
Breeding season (peak number)		
bulls	1973 - 1976, n = 4	Oct 24 $\pm$ 3 days
cows	1973 - 1976, n = 4	Oct 17 $\pm$ 5 days
pups	1973 - 1976, n = 4	Nov 16 $\pm$ 3 days
Breeding season (last departure)		
bulls	1973 - 1976, n = 4	Nov 22 $\pm$ 7 days
cows	1973 - 1976, n = 4	Nov 11 $\pm$ 3 days
under-yearlings (ex pups)	1973 - 1976, n = 4	Dec 23 $\pm$ 3 days
Moulting season (first arrival)		
bulls	1974 - * 1977, n = 4	Jan 16 $\pm$ 8 days
cows	1973 - 1976, n = 4	Dec 19 $\pm$ 4 days
subadults ♂♂	1973 - 1976, n = 4	Nov 18 $\pm$ 9 days
subadults ♀♀	1973 - 1976, n = 4	Nov 19 $\pm$ 9 days
yearlings	1973 - 1976, n = 4	Nov 11 $\pm$ 3 days
Moulting season (peak number)		
bulls	1974 - * 1977, n = 4	Feb 18 $\pm$ 7 days
cows	1974 - * 1977, n = 4	Jan 20 $\pm$ 2 days
subadults ♂♂	1973 - 1976, n = 4	Dec 16 $\pm$ 9 days
subadults ♀♀	1974 - 1976, n = 3	Jan 18 $\pm$ 11 days
yearlings	1973 - 1976, n = 4	Dec 12 $\pm$ 4 days
**Moulting season (last departure)		
bulls	1974 - * 1977, n = 4	Mar 21 $\pm$ 8 days
cows	1974 - * 1977, n = 4	Feb 13 $\pm$ 10 days
subadults ♂♂	1974 - 1976, n = 3	Jan 30 $\pm$ 9 days
subadults ♀♀	1974 - 1976, n = 3	Feb 14 $\pm$ 7 days
yearlings	1974 - * 1977, n = 4	Jan 22 $\pm$ 3 days

*Data for 1977 from Erasmus (1978).
**Excluding overwintering animals.

Table 5 The annual cycle of southern elephant seals at the main breeding grounds

Island and position	Breeding season				Moulting season		
	Distance from Distance from Antarctic Convergence	Haul-out period of cows	Maximum cows hauled out	Maximum pups	Peak of cow moult	Peak of bull moult	References
Signy Island (60°43′S, 45°36′W)	402 km south	Oct 6 - Dec 3	Oct 22	Oct 28	Jan 26	early April	Laws (1956)
Heard Island (53°00′S, 73°30′E)	320 km south	mid-Sep - late Nov	Oct 18		end Jan	Mar 20	Carrick *et al.* (1962a)
South Georgia (54°17′S, 36°30′W)	240 km south	Sep 26 - late Nov	Oct 22	Nov 13			Laws (1956)
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 Sep late Nov	Oct 16	Oct 25	Jan 25	Mar 19	Carrick *et al.* (1962b)
Marion Island (46°55′S, 37°45′E)	290 km north	Sep 7 - Nov 26	Oct 17	Nov 16	Jan 20	Feb 18	Present study
Campbell Island (52°33′S, 169°09′E)	800 km north		Oct 16				Sorensen (1950)

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any of these occurring too frequently". In mammals such as elephant seals, which rely on terrestrial breeding and moulting, but are dispersed in the ocean for the rest of the year, a highly organized and well synchronized terrestrial phase would be of paramount importance for their survival. If, however, the type of adjustment discussed by Ling (1969) did not occur, then the resulting overcrowded conditions would act against survival of the population. Bartholomew (1970) suggested that polygyny evolved not only because it was an efficient reproductive system, but also because it allowed the congruent organization of numerous ecological, physiological, and behavioural factors which would otherwise be incompatible. Terrestrial gregariousness would seem to be positively advantageous to southern elephant seals, particularly since the oceanic-island terrestrial environment is predator free. At the same time however, the limited terrestrial mobility of southern elephant seals, combined with their gregariousness, often leads to extraordinarily congested conditions (Bartholomew 1970), but because of the adjustment of haul-out periods, non-overcrowded circumstances prevail.

The regularity of the haul-out cycle (Table 4) is worthy of discussion. It would seem that photoperiod, the most constant environmental variable throughout the life span of an individual, must be a proximate obligatory control factor in the annual cycle of southern elephant seals. The small variation, if in fact any, in view of the influence of sea ice, in the haul-out cycle at different latitudes (Table 5) further implicates photoperiod, more specifically the monthly change in photoperiod which occurs synchronously at different latitudes. Parturition and mating, most of which occurs in October, do not coincide with longest day length, maximum daily sunshine, or maximum monthly change in day length (Table 1). However, the onset of the haul-out season, which occurs in August and mainly September, coincides with maximum monthly increase in day length (Table 1). Once hauled-out, it would seem that normal physiological reproductive mechanisms, combined with behavioural modifications arising from the presence of the opposite sex, act synchronously in all seals hauled out to maintain the degree of synchronization of parturition, mating, lactation, weaning, and finally departure of the adults. (Fig. 2).

Ling (1972) suggested that temperature affected the autonomous cyclic rythm of epidermal proliferation as well as the rate of moulting. From December to April mean monthly temperatures on Marion Island are above the yearly average, and mean daily radiation reaching the surface is highest from November to January, remaining above the yearly average from October to March (Table 1). Since most moulting occurred from December to February (Figs 3, 4, 5), with maximum biomass hauled out in January (Fig. 6) when daily radiation was only slightly less than the December peak, it would seem that temperature, and in particular radiation, act as obligatory ultimate factors regulating the moult cycle. According to Ling (1965) hair growth and follicle activity start in September, and a normal uninterrupted four-month activity period enables immatures to moult in December/January. Breeding and lactation appear to delay moult, due to the apparently inhibitory effect of oestrogens and androgens on hair growth (Davis 1963). However, because parturition followed by copulation and pregnancy are so well synchronized in the breeding female (Fig. 2), decline of inhibitory oestrogens occurs synchronously and the moult follows, being as equally well synchronized as was breeding (Fig. 4). Ling (1965) believed that androgens had a less well-defined inhibitory effect on hair growth, so that breeding bulls had a more extended, less synchronized moult (Fig. 4). Thus it would seem that photoperiod acts as an obligatory proximate factor for both breeding and moulting, causing adults to return to the breeding ground in August/September, and initiating hair growth and follicle activity in all seals during September. Photoperiod, temperature, and radiation appear to act as ultimate obligatory factors, initiating the moult haul-out. Behavioural and reproductive physiological factors then appear to act as ultimate factors initiating parturition and copulation in mature seals, with the latter factor also acting as an ultimate factor influencing the moult in breeding animals.

Acknowledgements

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