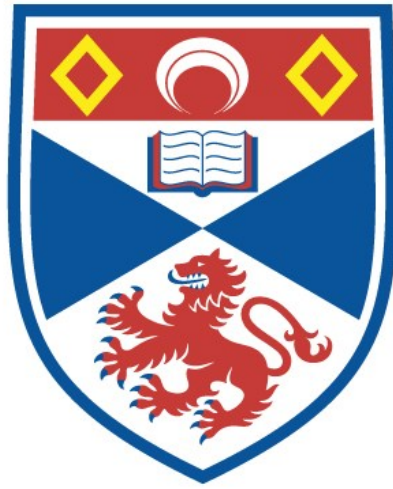


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**Behavioural and physiological aspects of the mid-year haul-out in southern elephant seals (*Mirounga leonina*) on Macquarie Island**



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Submitted in fulfilment of the degree of  
Master of Philosophy

Supervisor: Prof. M.A. Fedak  
Dr. P.P. Pomeroy

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E458

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I would sincerely like to thank Mike Fedak, Harry Burton, Clive McMahon and John van den Hoff (Snake) for giving me the opportunity to work on elephant seals and “experience” Macquarie Island. The Australian Antarctic Division provided logistic support. The Natural Environment Research Council (NERC) provided financial support for laboratory analysis. My sincere thanks to Iain Field, Corey Bradshaw, Julian Harrington, Martin Biuw and members of the 52<sup>nd</sup>, 53<sup>rd</sup> and 54<sup>th</sup> Australian National Research Expeditions (ANARE) on Macquarie Island, for assistance in the field. Special thanks to Robb Clifton, Cath Deacon and TASPAS personnel who continued resighting efforts on Macquarie Island during the winter of 2001, and for the hours they spent entering data into a database. Lex Hiby provided mathematical modelling, and Corey Bradshaw provided valuable statistical support. I would also like to thank Mike Fedak, Paddy Pomeroy, Corey Bradshaw, Martin Biuw and Martin Schultz for valuable comments on this thesis. Data were collected under approval from the Australian Antarctic Animal Ethics Committee (for ASAC project 2265) and with Tasmanian Parks and Wildlife Service access and handling permits.



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## Abstract

During the austral autumn and winter months, some adult and juvenile southern elephant seals (*Mirounga leonina*) travel thousands of kilometres to haul out on Macquarie Island for several days or weeks. This mid-year haul-out is not obligatory for the species, as some individuals do not participate while others haul out one or more times. Haul-out behaviour was examined for seven age and sex classes. The energetic costs associated with hauling out for underyearlings were also examined. There were significant differences in haul-out behaviour between the sexes, across all age classes. More males returned for the mid-year haul-out and arrived consistently earlier than females. As animals approached sexual maturity their attendance and residence time decreased. Residence time for females was significantly negatively correlated to arrival time, i.e. females that arrived later in the season remained ashore for a shorter period. However, there was no such correlation for males and younger males tended to haul out a second time, two to three months after the first haul-out. Underyearling females that returned to haul out were significantly smaller at weaning than females that did not haul out, but there were no differences in wean mass for males that hauled out versus those that did not. On average, mass loss was composed of 32.9% water, 56.9% fat and 9.0% protein. Mid-year haul-out arrival date, mass and duration influenced which animals returned for the moult. There were no significant differences at the time of the moult in mass gain, % fat or mass loss rate between animals that had returned for the mid-year haul-out and animals that had not. Inter-annual differences in survival rates could affect parameters of the mid-year haul-out. Monitoring haul-out behaviour over several years could provide valuable information about changes within a population.

## Chapter 1

### Introduction

The southern elephant seal (*Mirounga leonina* Linn.) has been described as one of the more abundant phocid species of the world (Laws 1994). They have a circumpolar distribution, with major breeding populations on islands around the Antarctic Convergence (Hindell and Burton 1987). The entire population has been divided into three main stocks, defined as the South Georgia stock, the Kerguelen stock and the Macquarie Island stock (Laws 1994).

The southern elephant seal population of Macquarie Island has been in decline since the 1960's (Hindell 1991; Hindell *et al.* 1994). This decline corresponds with similar declines on several other subantarctic islands in the Southern Indian Ocean (Hindell and Burton 1987, Guinet *et al.* 1992). There is no evidence to suggest that the declines are the result of factors influencing the seals while on land; thus, it has been hypothesised that they result from factors operating while the animals are at sea (Laws 1994). Valuable information about an individual's success at sea can be measured by their condition upon returning to land.

Southern elephant seals haul-out on Macquarie Island for the terrestrial phases of their life cycle (Fig. 1.1). In the austral spring (early September to November) adult males and females come ashore to breed (Carrick *et al.* 1962). Females wean and leave their pup 21-23 days after birth and pups depart on their first foraging trip three to nine weeks after weaning (Arnbom *et al.* 1993). Juveniles come ashore for the annual moult from mid-November to January, adult females return to moult in January and February, and adult males moult from February to April (Carrick *et al.* 1962; Hindell and Burton 1988). During

the austral autumn and winter months (March to August) a number of mostly underyearling and juvenile elephant seals return to Macquarie Island for a “mid-year haul-out” (Carrick *et al.* 1962). This is unique compared to the moult in that not all individuals’ return and of the ones that do return, some return again for a second haul-out.

Between juveniles and adults, there is a degree of synchronization in haul-out behaviour for the moult (Carrick *et al.* 1962; Hindell and Burton 1988). However, it is not known whether synchronization is apparent for the mid-year haul-out. Synchronicity of haul-out behaviour may develop as the result of one or more intrinsic or extrinsic factors. For example, interactions between individuals may promote temporal variation in haul-out behaviour, or body condition may influence when or how long an animal hauls out.

Temporal changes in population size can be assessed by monitoring haul-out periods (Hindell and Burton 1988). However, reliable population estimates require accurate information on seasonal haul-out patterns for different age and sex classes. Little is known about how many animals return for the mid-year haul-out, what determines which animals come ashore and what factors influence its timing. Therefore, examining factors that influence haul-out behaviour may provide clues as to its function, and have important implications for the assessment of the population. To date, no comprehensive study of the midyear haul-out exists.

The objective of this study was to describe several aspects of the mid-year haul-out on Macquarie Island. The first part employed the use of an existing long-term mark-recapture program of southern elephant seals on Macquarie Island (Australian Antarctic Division). Haul-out behaviour was examined for

seven known age classes. Specifically, how many animals hauled out, the timing of the haul-out, and the length of the haul-out for each cohort and sex. The second part of this study focused on underyearling elephant seals. This examined what factors influenced haul-out behaviour in underyearlings, and the consequences of the mid-year haul-out on future haul-outs and survival. Describing the timing and duration of haul-outs over several years could give insight into changes within the population. This information should expand our knowledge about the status of the population and aid in our understanding of its decline.

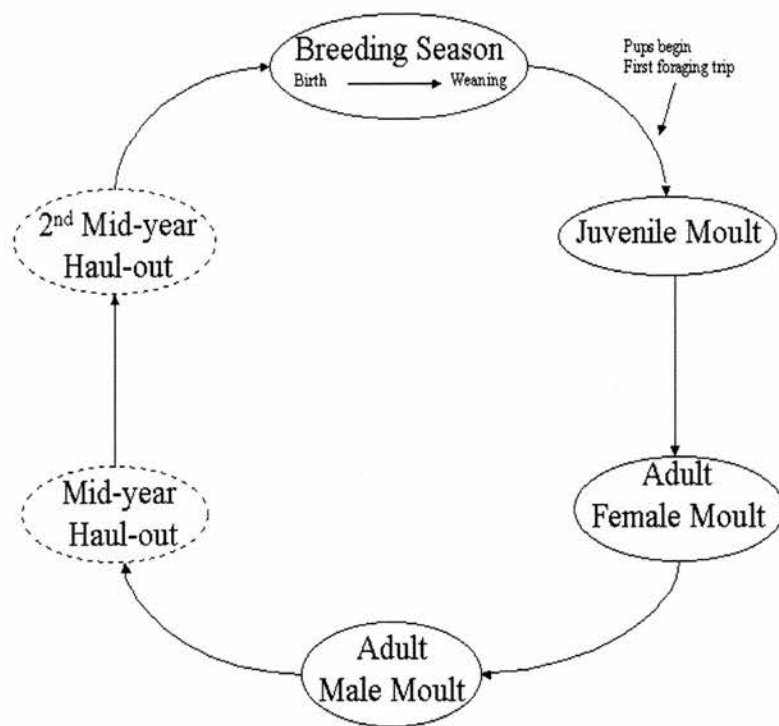


Fig. 1.1 *Flow chart of the annual haul-out cycle on Macquarie Island.*

## Chapter 2

### **The mid-year haul-out: temporal patterns of island haul-out use by different age and sex classes of southern elephant seals (*Mirounga leonina*) on Macquarie Island**

#### **Summary**

Between the end of February and October 2000 all beaches on Macquarie Island were searched for tagged or branded southern elephant seals returning for the mid-year haul-out. A model was created to provide maximum-likelihood estimates of arrival and residence times for seals of selected age and sex classes. Seals that were seen less than twice were eliminated from estimates to provide residence times of seals that visit the island for more than one day. Females above the age of three were rarely seen on more than one occasion; therefore, arrival and residence distributions could not be calculated for these cohorts. Males arrived consistently earlier than females across all age classes (underyearlings to three-years old). Residence times increased by age two, then dropped for females and remained relatively constant for males. For females between the ages of underyearling to two-years old, residence time was significantly negatively correlated to arrival time (i.e. individuals that arrived later did not remain ashore as long). However, this was not observed in males of any age class. Sighting probability decreased with older animals. In general, haul-out behaviour was significantly different between males and females of all age classes. These results have implications on the models used to estimate population size of southern elephant seals on Macquarie Island.

#### **Introduction**

Most phocid seals have two annual periods of terrestrial fasting within their lifecycles: one associated with breeding and the other with moulting (Baker 1978). Southern elephant seals (*Mirounga leonina*) spend virtually all of their time at sea (Hindell *et al.* 1991; McConnell and Fedak 1996, Hindell *et al.* 1999); however, these two periods of fasting are for the most part discrete and regular each year, with different age and sex classes hauling out at different times (Carrick *et al.* 1962; Condry 1979; Hindell and Burton 1988). They also have different characteristics in terms of animal behaviour and energetic requirements (see Condry 1979; Fedak and Anderson 1982; Slip *et al.* 1992; Worthy *et al.* 1992; Boyd *et al.* 1993; Fedak *et al.* 1996).



As adults, southern elephant seals come ashore during both haul-out periods, to breed and to moult. However, as juveniles, they are only required (physiologically) to come ashore to moult. In spite of this, some adults and many juveniles travel thousands of kilometres to return to Macquarie Island during the austral autumn and winter. This mid-year haul-out can span several days or weeks and therefore differs from the shorter (i.e., hours to several days) haul-outs of other species of seals. There is some evidence from another species (harbour seal, *Phoca vitulina*) that hauling out may be necessary for reasons other than reproduction and moulting (Brasseur *et al.* 1996). However, most adults and some juvenile elephant seals are not involved in the mid-year haul-out (Carrick *et al.* 1962; Hindell and Burton 1988; McMahon *et al.* 1999); consequently, coming ashore during the autumn and winter cannot be obligatory for this species. Since the mid-year haul-out appears to be optional, examining animals that “choose” to take part might provide an indication as to its function.

Numerous hypotheses have been proposed to explain the purpose of the mid-year haul-out. Carrick and Ingham (1962) suggested that increased radiation while ashore may help increase Vitamin D to a level that will enable columnar dentine to be deposited. Carrick *et al.* (1962) hypothesized that there might be some advantage in practicing and conditioning the organ-systems for the terrestrial functions important later in life such as locomotion, thermoregulation, fasting, and the utilization of stored reserves. In contrast, Condry (1979) suggested that animals returning were unable to withstand prolonged periods at sea. Similarly, Ling and Bryden (1981) have classified it as simply a “resting” haul-out. More generally, this haul-out may facilitate social interaction among animals of the same cohort, eliciting play behaviour that may allow juveniles to

develop necessary motor skills, learn the meaning and social context of these varying behaviours, and be able to perform them adequately in their true agonistic context as adults later in life (Neumann 1999).

In the 1950s and 1960s, an extensive branding program took place on Macquarie Island (Carrick *et al.* 1962; Hindell 1991). From initial analysis of mark-resight data, Carrick *et al.* (1962) provided a detailed description of haul-out patterns for different age and sex classes on the island. Records of sightings were principally from searches of the northern isthmus study area (Appendix Fig.1). Most other sightings around the island were opportunistic, except during two years (1952 and 1959) when there were structured resighting trips of the entire island (Appendix Fig.2). Unfortunately, in describing the mid-year haul-out Carrick *et al.* (1962) combined census records from 1955, 1957 and 1959. Therefore, any differences in haul-out pattern within and among years might be masked by the overlapping years.

In 1993, the Australian Antarctic Division (AAD) implemented a large-scale mark-recapture program on the southern elephant seal population of Macquarie Island. By classifying the age structure of a population, it enables an accurate determination of many important life-history parameters that can influence population numbers (Hindell 1991). This program offered a unique opportunity to study the temporal patterns of island haul-out use by examining all marked seals (of known age classes) that come ashore during the mid-year haul-out.

In this study I examined variation in haul-out behaviour of seven age classes of males and females during the entire duration of the mid-year haul-out (end of February to October). The main objectives were: (1) to determine the

probability of sighting an individual of each age cohort (by sex) ashore during the mid-year haul-out; (2) to describe and compare the mean arrival and residence times between age and sex; and (3) to examine the correlation between time of arrival and residence time ashore.

## **Methods**

### *Resighting effort*

From the end of February through October 2000 isthmus beaches on Macquarie Island (Appendix Fig. 1) were searched daily for tagged and branded animals. Adjacent beaches on the east and west coasts of the island (to Nuggets and Handspike Points, respectively) were searched approximately every three days (Appendix Fig. 2). Since a greater number of seals haul out on the northern third of the island (Carrick *et al.* 1962; Nicholls 1970; McMahon *et al.* 1999) and juveniles haul out more frequently on the east than the west coast (McMahon *et al.* 1999; K.E. Wheatley, unpubl. data), the entire east coast and to Bauer Bay on the west were searched every week to ten days. There were observed haul-out preferences for parts of the shoreline along the west coast; therefore, these were searched approximately every 2 weeks. The whole island was surveyed once a month.

The presence on shore of tagged and branded animals (aged underyearlings to age 6) was recorded as described in McMahon *et al.* (1999). Macquarie Island was sectioned into one-km grid squares (Appendix Fig. 2). During surveys around the island, the location of each animal was recorded based on the corresponding grid reference. The isthmus was divided into sections

according to natural landmarks (Appendix Fig. 1) and each animal's location was recorded according to these sections.

### *Data analysis*

All recorded sightings of seals, including individuals only seen on one occasion, were used to calculate the total number of seals ashore for the mid-year haul-out. The raw data of the number of individuals ashore each day was standardized to 1 (based on the peak number that was ashore) and haul-out distribution was graphed for each cohort and sex. A local linear regression (LLR) smoother was applied to all graphed curves.

By establishing where animals were first seen, how often beaches were searched and the probability of seeing a particular animal (e.g., it would not be seen if it was in the surf), a model was developed to provide maximum-likelihood estimates (MLE) of arrival and residence times of each age cohort by sex. Juveniles do not often change location during the mid-year haul-out (Wilkinson and Bester 1990; K.E. Wheatley, unpubl. data). We assumed that if an animal did change location that movement would be no greater than two grid squares ( $\sim 2$  km) either side of the reference square where it was first sighted. Therefore, when the original beach was re-surveyed and an animal was not observed again, search effort on these adjacent beaches was used in the model to estimate mean residence times.

We created a resighting probability matrix by calculating preferences that each seal had for each location as the proportion of the total sightings [of that seal] that were on each site, divided by the relative frequency at which the site was surveyed. Those preferences were then combined with the matrix of survey effort for each date to provide the probability that the seal was at a particular

surveyed site on the date of survey. For seals that were only seen on the isthmus study area (which was surveyed daily) the probability matrix was “1” for every day because if the seal was ashore then it must have been at a surveyed site during its residency period.

When the data matrices were constructed, sightings of seals in each age and sex class were only included as long as they occurred within 14 days of the previous sighting. Otherwise, the individual was considered to have left the island within this period and subsequently returned for a second haul-out. This number was based on the fact that most beaches were searched at least twice within 14 days. Individuals having less than two sightings within this time period were excluded from the data matrices. The reason for this being, that when seals seen just once are included, the residence time distribution (assumed to be a gamma distribution) is always skewed to the right. It is also possible that some seals come ashore for just a day or two, so that the residence time distribution should be ideally bimodal. However, eliminating such seals leaves a unimodal distribution for residence times of seals that visit the island for more than a few days.

Four parameters were calculated for males and females of each age class: (1) mean arrival day ( $\pm$  s.d.), (2) mean residence time ( $\pm$  s.d.), (3) the correlation coefficient between arrival and residence time, and (4) sighting probability. Differences in haul-out behaviour between males and females were tested by calculating the maximum likelihood estimates for each sex separately and then by combining both sexes. To test the significance of the correlation parameter it was set to zero (i.e., no correlation), and the model rerun. Log-likelihood ratio

chi square tests were used to determine significance between the different MLE's (Lex Hiby, pers. communication).

## Results

### *Total number of animals ashore*

More underyearlings and yearlings came back to Macquarie Island for the mid-year haul-out, than any other age class (Table 1) in 2000, and the total number of animals ashore for the haul-out decreased with age (Fig. 2.1). For the first mid-year haul-out there is no obvious difference between the number of males and females ashore until the age of three, after which female attendance drops off noticeably.

A number of sexually mature females were recorded ashore during the mid-year haul-out. Of the ten six-year old females that came ashore (see Table 1), three had bred once before, and one was seen with a pup the following breeding season. Two of the five-year old females ( $n = 8$ ) that returned had bred once before, but none were seen in the following breeding season.

Table 1: *The observed total number of branded animals that came ashore during the mid-year haul-out (end of February to October) in 2000.*

	First Haul-out			Second Haul-out			Third Haul-out		
Age (yrs)	Male	Female	Total	Male	Female	Total	Male	Female	Total
6	78	10	88	0	0	0	0	0	0
5	104	8	112	3	0	3	0	0	0
4	196	18	214	4	0	4	1	0	1
3	216	74	290	19	1	20	1	0	1
2	372	356	728	49	12	61	3	0	3
1	483	522	1005	134	100	234	7	1	8
underyearlings	493	521	1014	57	48	105	1	1	2

Note. There was one 1 year old female that hauled out a total of 4 times, with a minimum time between consecutive sightings of 21 days.

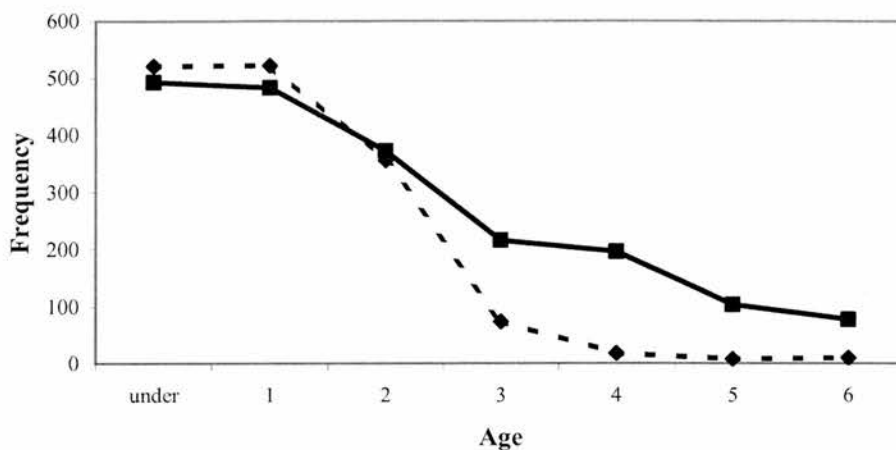


Fig. 2.1 Total number of male (solid) and female (dashed) southern elephant seals (underyearling to six-years old) that came ashore for the mid-year haul-out on Macquarie Island in the autumn/winter of 2000.

By standardizing (to one) the total number of seals ashore for each age and sex class, comparisons could be made between the profiles of each haul-out (Appendix Figs. 3 & 4). There was a steep incline in the number of yearling males ashore until a peak the second week in April, and then numbers dropped quickly. There was another slight increase in August as a number of individuals (19.9%) returned for a second haul-out. Underyearling male numbers peaked in the second week in May, and dropped gradually with a second, smaller peak at the beginning of July. Two-, three- and four-year old males all had similar peaks around the second week in May, and the total number ashore was extended over a longer period with increasing age. Finally, five- and six-year old males peaked in the first week of June while the number of five-year olds ashore decreased slowly and the number of six-year olds declined more abruptly.

One-year old female numbers reached a maximum earliest in the season. The haul-out profile of female underyearlings was similar to that of the males



although it peaked slightly later (9 days) than the males. It also had a similar, smaller peak at the end of June. At two-years old the peak for males and females was almost identical. At three-years old, haul-out pattern was much more variable because fewer females came ashore, and more females were only seen on one occasion. Therefore, 'peaks' were difficult to define.

The incidence of a second haul-out was a function of sex, age and timing of the first haul-out. A higher proportion of males than females returned for a second haul-out (Fig. 2.2). Yearlings (the first age group to arrive for the mid-year haul-out) had a greater number of animals returning for a second haul-out (27.7% males; 19.2% females) than any other age class. Even though underyearlings arrived much later in the winter for the first haul-out, they had a similar return rate as two-year old males. However, by the age of two there was a distinct decrease in the proportion of animals returning for a second haul-out. A third mid-year haul-out was uncommon, but it was again more prevalent in the younger age classes.

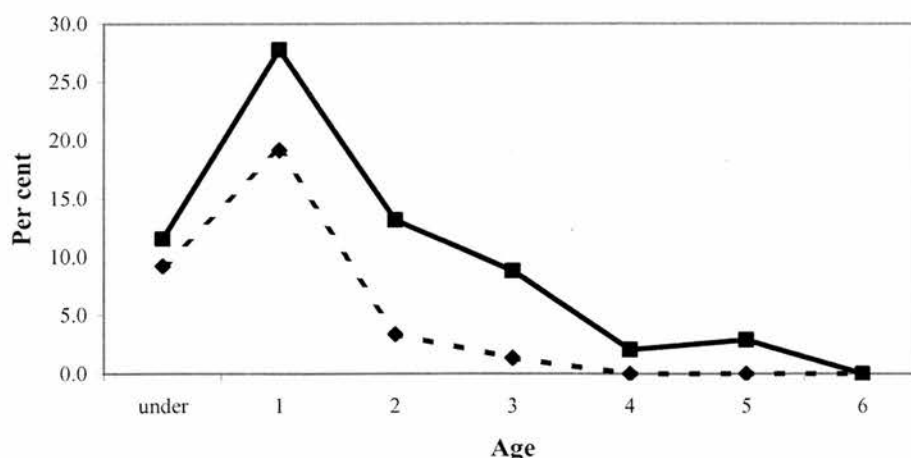


Fig. 2.2 *Per cent of male (solid) and female (dashed) elephant seals (underyearlings to six-years old) that returned for a second mid-year haul-out on Macquarie Island in the autumn/winter of 2000.*

### *Sighting probability*

After the age of one, sighting probability decreased with increasing age (Fig. 2.3), with no significant difference between males and females ( $P > 0.05$ ).

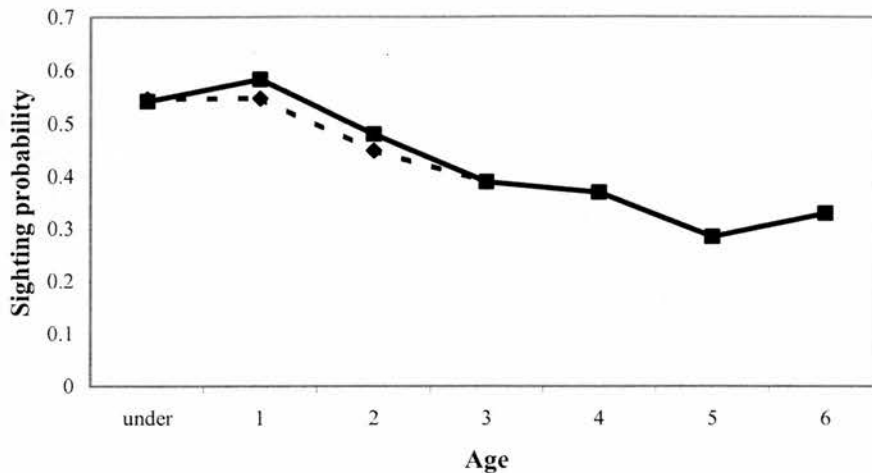


Fig. 2.3 The probability of sighting male (solid) or female (dashed) elephant seals of different age cohorts, if present on the surveyed site.

### *Arrival and Residence times*

The majority of females aged four- to six-years old were sighted on just one occasion. Since the model only used animals that were sighted more than once, there were not enough data to calculate average arrival and residence times for these age cohorts. For all other age cohorts, males arrived significantly earlier than females for the mid-year haul-out ( $P < 0.001$ ; range 9 – 26 days; Fig. 2.4). However, sample sizes were large so that these differences might not have any biological significance.

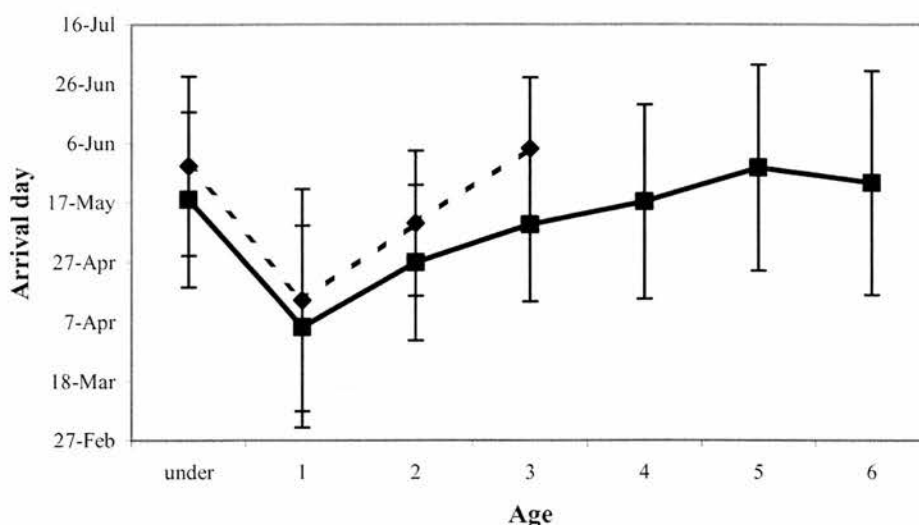


Fig. 2.4 The mean arrival day ( $\pm$  s.d.) for the mid-year haul-out on Macquarie Island of male (solid) and female (dashed) southern elephant seals.

Residence time ashore increased with age, except for three-year old females (Fig. 2.5). Underyearling and one-year old male and female southern elephant seals spent similar times hauled-out on Macquarie Island ( $P > 0.05$ ). By the age of two, time ashore started to decrease for females but continued to increase until the age of three for males, after which this value reached a plateau.

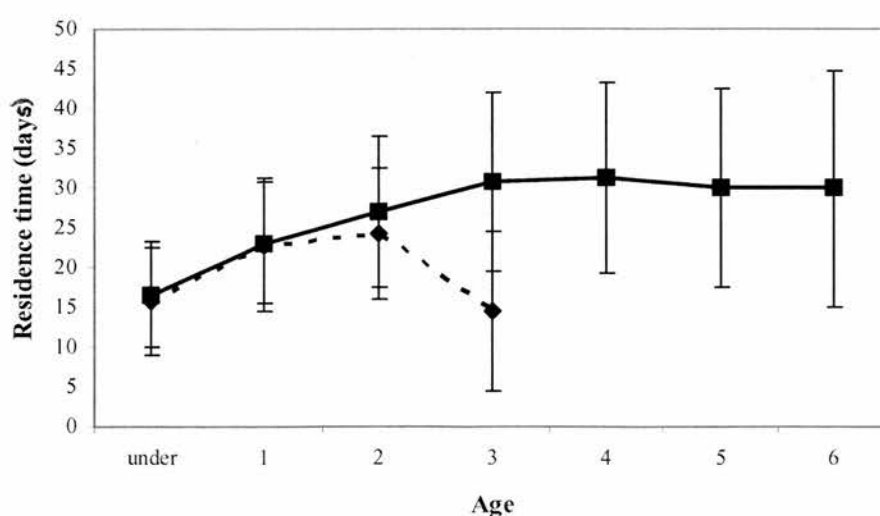
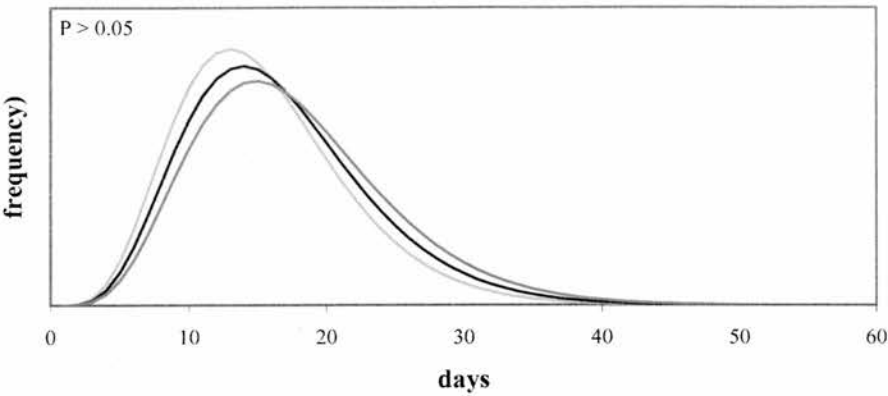


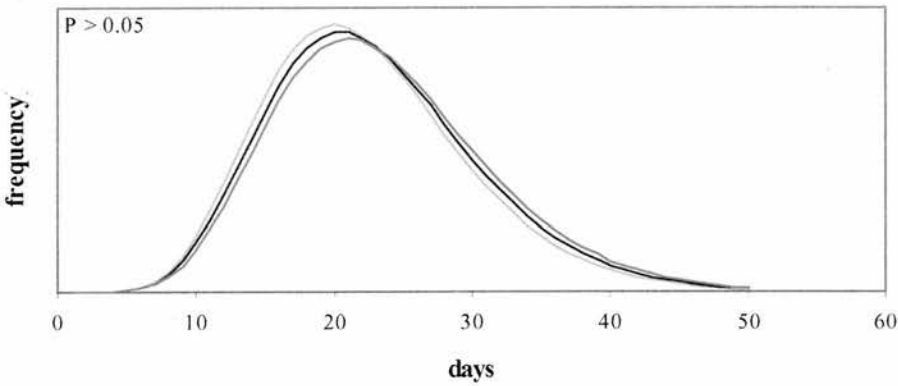
Fig. 2.5 The mean residence time ashore ( $\pm$  s.d.) for the mid-year haul-out on Macquarie Island of male (solid) and female (dashed) southern elephant seals.

For all males (underyearlings to age 6) there was no correlation between date of arrival and residence time ashore ( $P > 0.05$ ; Fig. 2.6 a-g). This lack of correlation means that no matter when males arrived for the mid-year haul-out (early or late), they remained ashore for a similar amount of time. This is illustrated graphically with residence distribution curves, where if there was no correlation the three curves (early, mean and late arrival) would be identical (Fig. 2.6 a-g). For females aged underyearling to two-years old, the correlation coefficient between arrival date and residence time was negative and significantly different from zero ( $P < 0.05$ ). Therefore, females that arrived earlier had longer residence times, and females that arrived later had shorter residence times (see residence distribution curves Fig. 2.7a-c). Although the correlation for three-year old females was not significant ( $P > 0.05$ ), the same trend appears in the residence distribution curves (Fig. 2.7d), indicating some synchronization in behaviour across all age classes of female southern elephant seals.

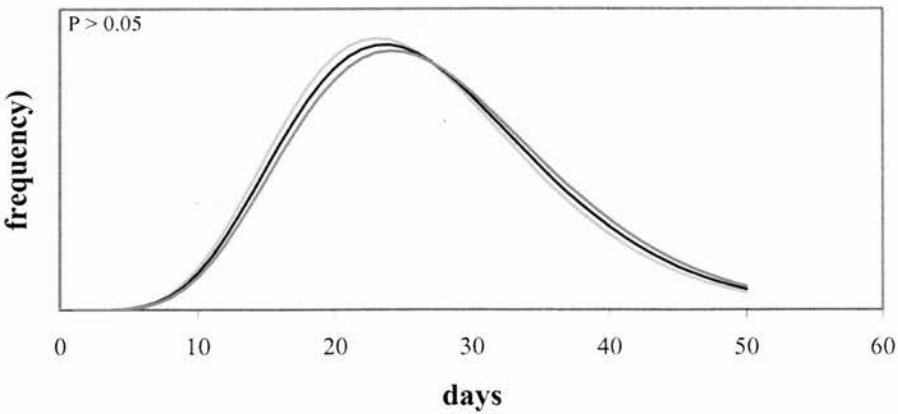
**(a) underyearling males**



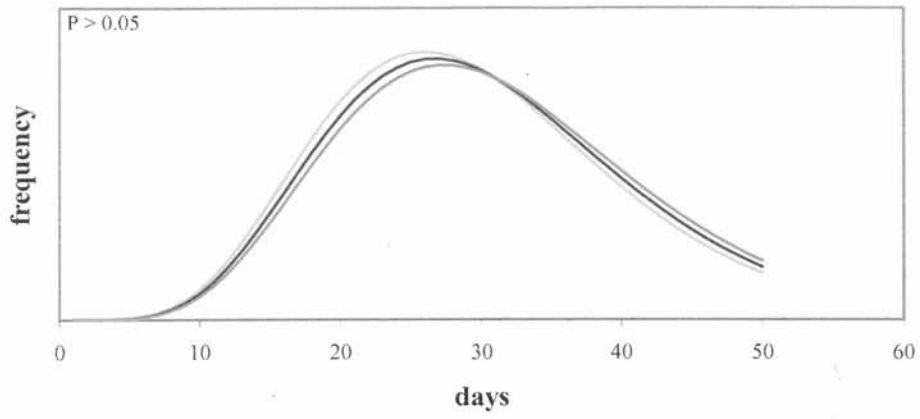
**(b) 1 year old males**



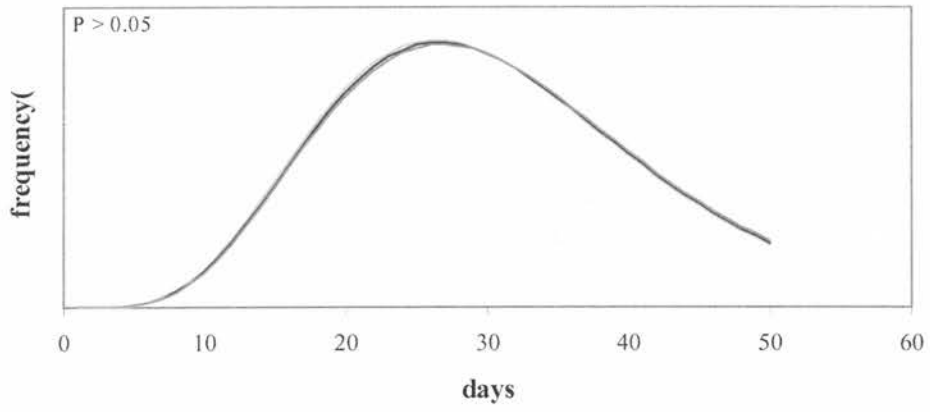
**(c) 2 year old males**



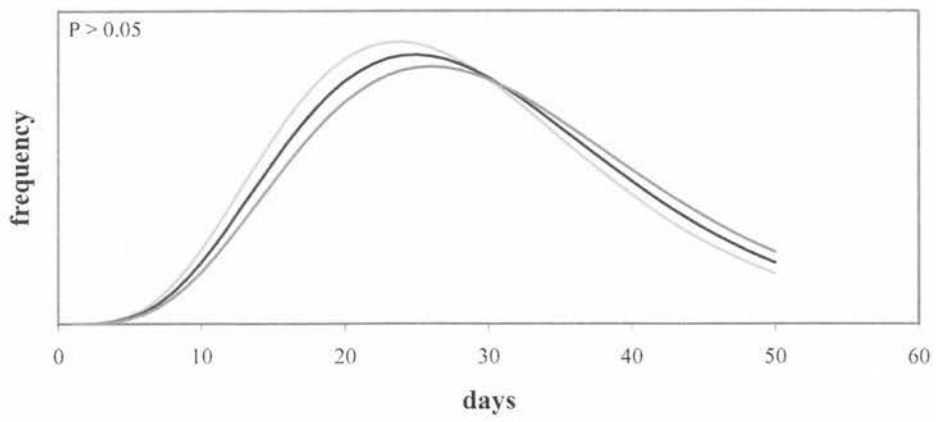
**(d) 3 year old males**



**(e) 4 year old males**



**(f) 5 year old males**



**(g) 6 year old males**

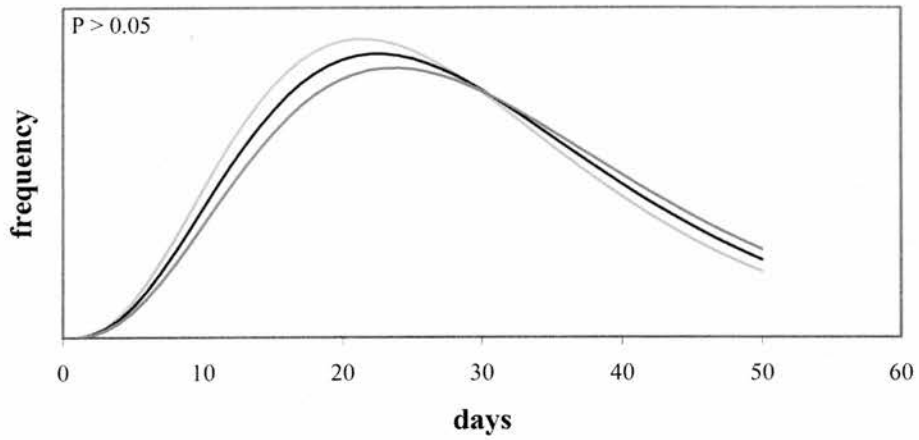
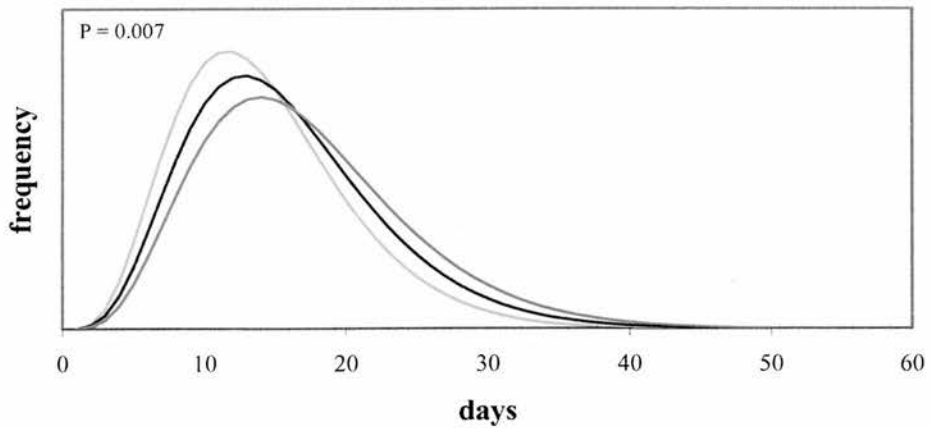


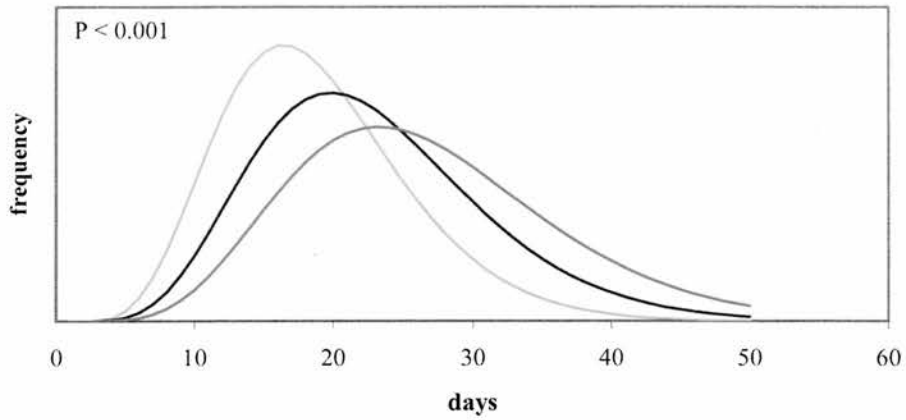
Fig. 2.6 Model estimated residence distribution curves of all males (aged underyearling to six-years old) for the mid-year haul-out. Frequency range is from 0-1. Black lines represent the mean arrival residence distributions; yellow lines represent late arrival and pink lines represent early arrival. Under the null hypothesis of resident time being independent of arrival time, all three distributions should be identical.

**(a) underyearling females**

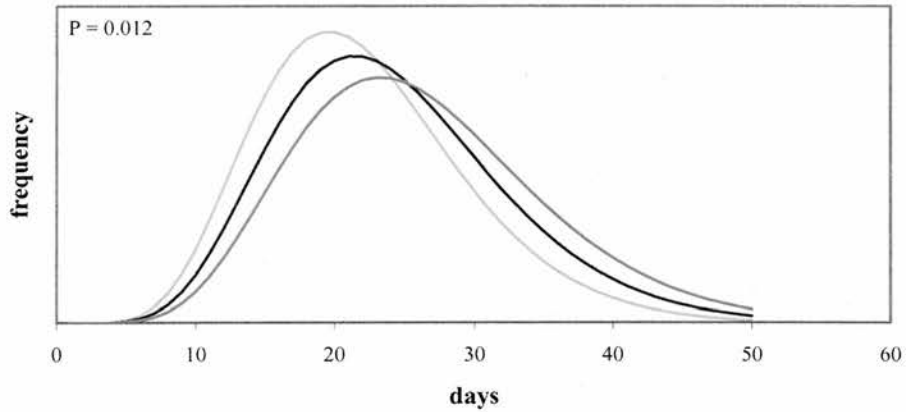




**(b) 1 year old females**



**(c) 2 year old females**



**(d) 3 year old females**

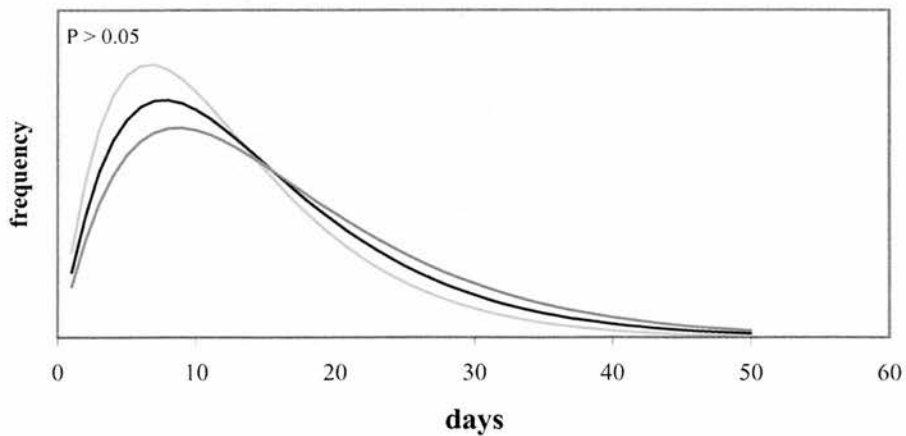


Fig. 2.7 Model estimated residence distribution curves of females (aged underyearling to six-years old) for the mid-year haul-out on Macquarie Island. Frequency range is from 0-1. Black represents the distribution for the mean arrival time, yellow for late arrival, and pink for early.

When all four parameters were combined for statistical analysis, there was a significant difference ( $P < 0.001$ ) in haul-out behaviour between males and females from underyearlings to age three.

## **Discussion**

Although this study cannot eliminate any of the proposed hypotheses for the mid-year haul-out, it does offer general insight into the behaviour involved. Therefore, we only speculate reasons for the observed behaviour.

### *Sighting probability*

There are two possible explanations for a decrease in sighting probability with increasing age. The first is that brands became more difficult to read with age (Gales 2001). Secondly, while ashore older seals might move among coastal sections more often than younger seals. For example, as males aged they were increasingly more involved in social interactions with conspecifics (i.e., mock fighting), thereby causing movement along beaches and more frequent transitions to and from the water (K.E. Wheatley, unpubl. data).

### *Numbers of animals ashore and residence times*

The number of animals ashore for the mid-year haul-out differs between age classes. However, because older animals have experienced age-specific mortality for a greater period of time, these differences might represent the same proportion of the population (of each age class) returning. Unless survival probability differs temporally among cohorts, the proportion of animals (of each age class) returning could be compared by determining the number alive at the moult and the percentage of these that did not return for the mid-year haul-out.

Typically females first mate at three to six years of age, and bear their first pup the following year (Carrick *et al.* 1962a). However, most males reach sexual maturity at the age of six, but do not participate successfully in breeding activities until they are about ten years old (Ling and Bryden 1981). Female numbers and residence times decreased abruptly at age three, while the number of males gradually decreased until the age of six. This appears to indicate a change in behaviour due to the onset of sexual maturity. Since lactation is the most energetically demanding period faced by females (Fedak *et al.* 1994; Mellish *et al.* 1999), most females may conserve their energy (by not returning) and remain at sea to accumulate enough reserves to sustain themselves and their pup during lactation. As for males, five- and six-year old males came ashore for the mid-year haul-out noticeably later, and stayed longer than the younger age classes, sometimes overlapping with the beginning of the breeding season. Since size is an important factor for achieving dominance within the breeding hierarchy (Le Boeuf and Laws 1994) it may be more advantageous for these males to remain at sea to forage and grow. Similar findings were found in the harbour seal (*Phoca vitulina*) where haul-out behaviour of both sexes changed with sexual maturity (Härkönen *et al.* 1999) and in the northern elephant seal (*Mirounga angustirostris*) where sexual segregation developed during puberty (Stewart 1997).

Carrick *et al.* (1962) argued that storms and illness might affect the number of underyearling and one-year old elephant seals to haul-out. This was based on the fact that following a severe storm on April 30, 1959, a large number of juvenile seals were recorded on the isthmus. A similar storm occurred during the winter of 2000. However, given that adjacent beaches (south to Nuggets

Point and Handspike Point, Appendix Fig.2) were regularly searched for branded animals, this “new” influx of animals to the isthmus were individuals moving from these adjacent beaches, rather than new animals arriving to haul-out for the first time. From all animals captured during the 2000 season, few were noticeably unhealthy or injured. However, some animals that returned for a second haul-out had lost mass and condition during the short period at sea (see Chapter 3 Results).

#### *Arrival Times*

Compared to the breeding season and the moult, timing of the mid-year haul-out is slightly less co-ordinated, but there was still a noticeable degree of synchronization in arrival times between ages.

A number of studies have reported differences in foraging areas between male and female elephant seals (Hindell *et al.* 1991; McConnell and Fedak 1996; Stewart 1997; Campagna *et al.* 1999). Although most studies have concentrated on adults, consistent arrival of males earlier than females could reflect these differences across all age classes.

Arrival date was gradually later from one year of age onwards. However, underyearlings proved to be an exception with a later arrival date, possibly reflecting their need to remain at sea to obtain adequate food resources. Date of arrival for the older age classes could be correlated with arrival and departure from other haul-outs (moulting), but it would be necessary to study parameters of those haul-outs as well. Alternatively, the patterns of arrival for older age classes may be a gradual adaptation to the timing of these other haul-out periods (breeding and moulting). As our results suggest, the difference in arrival dates

between males and females diverges more as females mature and enter the breeding population earlier than males.

#### *Correlations between arrival and residence times*

Temporal variation in haul-out patterns by different age and sex classes affects opportunities for social interaction between those animals (Miller 1991). Therefore, temporal staggering during the mid-year haul-out may reduce crowding and intraspecific aggression on land as well as at sea (Ling 1969). On the other hand, it may arise due to differences in the physical and developmental status of the individuals (Härkönen *et al.* 1999).

It is not clear why correlation between arrival date and residence time exists for females, but not males and it would be worth determining if this correlation persists through the moult. Our results suggest that this correlation may be related to sexual maturity. Females enter the breeding population earlier than do males, and the correlation between arrival and residence time is displayed two to three years before maturity. This same pattern becomes evident in five-year old males as they begin to sexually mature.

An alternative hypothesis for this correlation is that there may be differences in mass and time of arrival. For example, if animals that arrive earlier are larger then they will be better equipped to endure a longer haul-out, while if smaller animals arrive later they will not be able to remain ashore as long. Here, differences in arrival mass would be related to foraging success, and this would only be true for females since that is where the correlation is present. However, Bell *et al.* (1997) described smaller females as returning earlier for the mid-year haul-out. Consequently, further investigation is required.

Time budgets of each cohort could reflect some measure of success at sea. Therefore, foraging success and condition could influence when and how many animals haul-out during the autumn and winter months. If this is the case, then inter-annual variation in haul-out patterns may reflect variations in prey availability, or changes in energy density of prey. For example, if a change in prey availability occurred and all cohorts reacted to this change in the same way, then the height, profile and distance between each peak would remain relatively constant. However, if one cohort reacted differently to environmental changes, then presumably there would be a shift of that curve in relation to the rest. This scenario would most likely be expected since younger seals are attempting to establish successful foraging patterns and therefore may be more susceptible to variation in prey availability. Because of the known variability in productivity of the southern ocean (Knox 1994), it would be necessary to model timing and duration of the mid-year haul-out among consecutive years, combined with condition measurements of a representative sample of each age cohort. It would also be ideal to determine relative foraging locations for all sex and age cohorts so that variations in haul-out behaviour and condition could be linked to these locations.

#### *Comparisons to the mid-year haul-out in 2001*

Resighting effort and collection of data was less structured on Macquarie Island during the winter of 2001. Therefore, detailed comparisons between years are problematic. Nevertheless, from preliminary observations, the timing of the mid-year haul-out changed between years for some age cohorts. The total number of underyearling seals ashore peaked mid- to late-June 2001, much later than it did in 2000 (mid-May). This was also substantiated by several

underyearlings who are equipped with satellite relay data loggers (SRDLs, Sea Mammal Research Unit), the majority of which did not return to the island until mid-July to mid-August (SMRU, unpubl. data). The number of one-year-old seals (underyearlings in 2000) ashore peaked earlier (April), however this was comparable to the one-year old seals in the previous winter. Two-year olds (i.e., one-year old in 2000), peaked in May, later than the previous year but again comparable to the two-year olds in 2000. This suggests that there appears to be some factor acting on each age cohort affecting the timing of the mid-year haul-out.

### *Conclusions and Future Research*

There were significant differences in haul-out behaviour between sexes and across ages in southern elephant seals. Further studies could involve investigating the effects of mass and condition on the timing and duration of the haul-out, as well as looking at the effects of one haul-out (i.e. timing and duration), on that of other haul-outs. If mass or condition affect haul-out behaviour, then monitoring a population over consecutive years may offer a different perspective into the status of the population.

The model that was developed to derive maximum likelihood estimates of arrival and residence times may have important implications on the assumptions involved in conventional mark-recapture models (Cormack 1979). Without equal sighting probability across ages (an assumption of the Cormack-Jolly-Seber model; Cormack 1972), the use of the mark-recapture model to estimate population size would underestimate survival in older age classes of southern elephant seals. In addition, our model accounted for site preferences by individual seals, which could also have implications on sighting histories.



## Chapter 3

### Significance of the mid-year haul-out for underyearling southern elephant seals (*Mirounga leonina*) on Macquarie Island.

#### Summary

Of first-year seals known to be alive at age one ( $n = 583$ ), the majority returned to Macquarie Island for the mid-year haul-out in 2000 ( $n = 509$ ). However, there were notable differences between the sexes. More males returned than females, and tended to arrive earlier. Females that did return were smaller at weaning than females that did not return, while no differences were detected for males. Smaller individuals were inclined to return to Macquarie Island a second time to haul out, the majority of these being males. Return for the moult was influenced by mid-year haul-out arrival date, mass and duration. Animals returning for the moult had proportionately more protein and less fat compared to animals that returned for the mid-year haul-out, indicating a growth in lean body tissue. This did not differ between individuals that had returned for the mid-year haul-out versus ones that had not. Fat and protein losses during the mid-year and moult haul-outs were dependent on the size of the animal and the body composition at the beginning of the haul-out i.e. smaller animals and animals with a relatively low fat content lost comparatively more protein than fat during the fast compared to larger and “fatter” animals. Although returning for the mid-year haul-out appears to offer no immediate advantage or disadvantage, inter-annual differences in the state of returning animals may be a useful indicator of changes in the condition of the population.

#### Introduction

For many species it is known that survival probability for all age classes is affected by body condition, particularly when there are seasonal and regional fluctuations in food supplies, and this effect is seen most clearly in neonates and juveniles of most large mammals (Clutton-Brock *et al.* 1997). In the life of the southern elephant seal, like most large mammals, the first year is one of high mortality (Hindell 1991; Australian Antarctic Division (AAD), unpubl. data). Previous studies have revealed that both weaning mass and condition have consequences for survival in the first year for some phocid seals (Hawaiian monk seal (*Monachus schauinslandi*), Craig and Ragen 1999; southern elephant seal, McMahon *et al.* 2000; grey seal (*Halichoerus grypus*), Hall *et al.* 2001), and that

in some mammals differences established early in life persist to adulthood (Bernstein 1978; Trillmich 1996). Given that southern elephant seals spend up to 85 % of their time foraging at sea (McConnell and Fedak 1996), valuable information about an individual's success at sea can be measured when they return to land. Body condition can indicate the nutritional state of animals and therefore reflect responses to changes of food availability in the environment over time (Virgl and Messier 1993; Arnould 1995). Therefore, changes in body condition can provide valuable information concerning future survival (Kirkpatrick 1980).

An individual's success at sea may also influence haul-out behaviour, such as whether or not an individual hauls out, and the timing and duration of a haul-out. Furthermore, changes in condition while ashore may also affect future condition and survival. Therefore, distinguishing factors that affect haul-out behaviour and measuring seasonal haul-out patterns may provide a predictable means of evaluating the condition of individuals within the population over time.

Breeding and moulting are necessary, but energetically expensive periods in the life of an elephant seal (Fedak *et al.* 1994), and they represent the only two periods that seals are required to haul-out on land. However, for many years there have been observations of an autumn-winter haul-out of juvenile southern elephant seals on several subantarctic islands in the Southern Indian Ocean (Carrick *et al.* 1962; Nicholls 1970; Condy 1979; Hindell and Burton 1988; Wilkinson and Bester 1990; McMahon *et al.* 1999). This "midyear" haul-out is different from other haul-outs in that only a percentage of the population return, while some animals remain at sea. Data related to the mid-year haul-out are

limited and there is considerable speculation as to the significance of the haul-out to both individuals and the population as a whole.

Assessing factors that might influence haul-out behaviour may reveal the significance of the mid-year haul-out. With mortality being the highest in the first year (AAD, unpubl. data), first year animals are most likely to show these features clearly. Understanding the causes and consequences of an animal interrupting foraging to haul out for days or weeks for no apparent reason may be a particularly useful indicator of the condition, status and survival of animals involved.

In this study, the aims were: (1) to determine factors that influence which underyearling southern elephant seals haul-out in the autumn or winter, (2) to quantify the energy expenditure required of underyearlings during the mid-year haul-out, and (3) to determine the consequences of returning for the mid-year haul-out on subsequent condition and survival.

## **Methods**

### *Study site and animals*

Data were collected on Macquarie Island (54° 37' S, 158° 53' E) between September 1999 and March 2001.

During the 1999 breeding season, as part of a large-scale mark-recapture program run by the Australian Antarctic Division, one thousand pups were weighed at birth and weaning (see McMahon *et al.* 1997). This represented approximately 5% of the total pup production on the island. At birth each pup was marked with two plastic flipper tags (Jumbo Rototags®, Dalton supplies Ltd, Henley-on-Thames, UK). Approximately three weeks after weaning, these

pups and an additional 1000 were marked permanently using hot iron brands on both flanks with an individual letter-number code (McMahon *et al.* 1997). In combination with another study investigating partitioning and utilisation of maternal resources (M. Biuw unpubl. data), 122 (similar numbers of males and females) of the 1000 weaners with known birth and weaning weights were selected for this study. Animals were selected to represent a complete size range.

### *Field procedures*

Isthmus beaches (Appendix Fig. 1) were searched daily for all newly weaned animals. Animals were considered to have weaned when first observed outside their natal harem. Pups were captured within 24 hours of weaning. They were weighed (to the nearest 1 kg) using a net sling, a rope pulley system and a 300 kg Salter® spring balance attached to an aluminium tripod. Body measurements were made to the nearest centimetre. The dorsal standard body length (McLaren 1993) was measured as a straight-line distance from the tip of the nose to the tip of the tail, and the axial girth was measured just behind the fore flippers. Weaners were restrained manually during all procedures.

Pups lose approximately 30% of their weaning mass before departing on their first foraging trip (Wilkinson and Bester 1990; Arnbohm *et al.* 1993, Carlini *et al.* 2001). Therefore, departure date was predicted using daily mass loss rates from the previous year (M. Biuw, unpubl. data) and pups were recaptured so that mass was measured again at that time.

Isthmus beaches were surveyed daily, and adjacent beaches (to Nuggets Point and Handspike Point; Appendix Fig. 2) were surveyed every 3 days, for the presence of all study animals. Beaches on the east coasts to Sandy Bay, and on the

west coast to Bauer Bay were searched approximately every two weeks. The end of the post-weaning fast was defined as the last day on which the pup was sighted. If this differed from the day captured then departure mass and body composition were estimated by linear extrapolation, using the average daily loss for that animal. Of the animals that remained ashore for >10 days from the last capture, most were recaptured, weighed and measured again.

During the mid-year haul-out (March through October 2000) and the moult (November 2000 to March 2001) the island was searched (as described in Chapter 2) for the return of study animals ( $n = 122$ ). Animals were captured within 3 days of first sighting. Once captured, seals were immobilized by an intravenous injection of Telazol® (combination of 1:1 teletamine:zolazepam), at an average dose rate of 0.6 mg/kg, into the extradural vein, or intramuscularly at an average dose rate of 1.0 mg/kg, in the rear flank. When animals were caught in more remote locations where nets, scales and tripods were inaccessible, then standard body length and 6 girth measurements were made. The first girth measurement (G1) was measured at the base of the skull, G3 (axial girth) was measured just behind the fore flippers and G6 was measured at the pelvic bones. Next, G2 was measured at the midpoint between G1 and G3, and G4 and G5 were measured at equal distances between G3 and G6 (see Fig. 3.1). Animals captured on the isthmus and places where scales were accessible, were weighed (to the nearest 1 kg) and length and 6 girth measurements were also recorded. These measurements were used to develop a multiple regression equation to estimate mass for animals with only length and girth measurements ( $n = 16$ ). If animals were not weighed within the first 24 hours of being sighted (always

weighed within 3 days), mass at the time of sighting was estimated by linear extrapolation using the average daily mass loss for that haul-out.

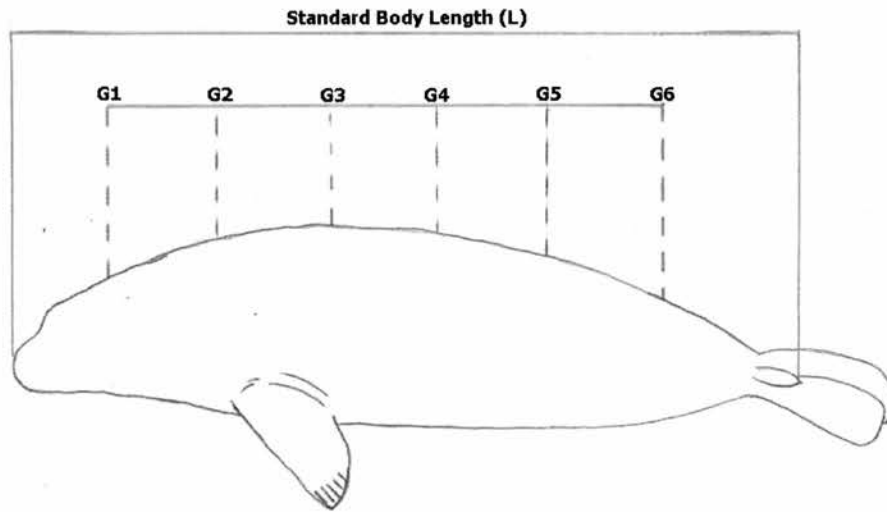


Fig. 3.1 *Locations for body measurements on underyearling and yearling southern elephant seals.*

For the mid-year haul-out body composition was measured using the hydrogen isotope dilution method. To measure total body water (TBW), a 20 mL blood sample was collected in heparinized vacutainers to measure background isotope levels. Immediately after this, a pre-weighed dose (to the nearest 0.1mg) of tritiated water (HTO; 0.5mCi/mL) was administered intravenously through the extradural vein. The syringe was flushed with blood twice to ensure complete HTO delivery. After complete equilibration with body water (2 hours post-injection; K.E. Wheatley, unpubl. data), a second blood sample (10 mL) was taken to determine the enrichment level.

To monitor changes in mass and body composition during haul-outs animals were recaptured at the end of the fast. The majority of our study animals did not return to the isthmus during the mid-year haul-out and moult. Since

maximum effort was spent searching for new animals as they arrived ashore, we were limited in our ability to recapture these animals before departure. For that reason, we captured every individual from the 1999 cohort (with birth and weaning weights) that was first sighted on the isthmus study area during the mid-year haul-out and moult. From previous years' data (1999), animals appeared to remain ashore for approximately 15-20 days. Therefore, all animals were recaptured a minimum of 15 days after the first sighting. If animals remained ashore longer than 15 days their departure mass and body composition was estimated by extrapolating the average daily loss for that animal over that fasting period. On average, animals remained ashore for 2.8 days (range 0-12 days) after the recapture. One animal that remained ashore >10 days after recapture, was reweighed a second time. During the moult, the same procedures were used to measure total body water (by HTO dilution) for all study animals returning to Macquarie Island. Beaches were searched daily and the stage of moult was recorded for each animal. When animals had completely moulted their old skin they were presumed to be ready for departure and were recaptured.

### *Sample analysis*

Within 24 hours of collection, blood samples were centrifuged at 3000 rpm for 8 minutes. For HTO analysis (5-16 months later), plasma aliquots were pipetted and transferred into plastic vials and stored at -20°C. The specific activity of HTO in plasma samples was determined by liquid scintillation spectrometry. Weighed plasma samples of 100 µl were added to 10 mL of Pico-Fluor™ MI scintillant and counted in triplicate, for 10 min, in a Tri-Carb® 2000 scintillation counter. Correction for quenching was made by external

standardization. Specific activity of plasma was corrected to specific activity of plasma water by determining the water content of the plasma. The proportion of water in plasma samples was measured by pipetting 100 µl of plasma onto pre-weighed glass microscope slides, in duplicate. Slides were then re-weighed and dried for 1 hour on both a hot plate and a cold plate. Per cent water content in each sample was determined by mass difference. To determine the specific activity of the tritium injected, samples of the injectant were diluted to concentrations similar to *in vivo* levels and measured simultaneously with the plasma samples. Samples had a coefficient of variation < 2%.

#### *Data analysis and calculations*

Isotope dilution space was calculated by the methodology described in Reilly and Fedak (1990). Measuring TBW by dilution space consistently overestimates water volume (Reilly and Fedak 1990; Lydersen *et al.* 1992; Arnould *et al.* 1996; Oftedal *et al.* 1996); therefore, a correction was made on all estimates of TBW (Reilly & Fedak 1990). Total body fat (%TBF), total body protein (%TBP) and total body gross energy (TBGE) were then estimated from body mass and total body water using equations derived for grey seals by Reilly and Fedak (1990):

$$\text{TBW (kg)} = (0.971 \times \text{H-space}) - 0.234$$

$$\% \text{TBF} = 105.1 - (1.47 \times \% \text{TBW})$$

$$\% \text{TBP} = (0.42 \times \% \text{TBW}) - 4.75$$

$$\text{TBGE (MJ)} = (40.8 \times \text{body mass in kg}) - (48.5 \times \text{TBW in kg}) - 0.4$$



Mass, length and 6 girth measurements were measured for 171 animals (of the 1999 cohort) returning for the mid-year haul-out and moult. A backward multiple regression model was used to create an equation to predict mass based on these body measurements.

For all animals known to be alive at age one (i.e. sighted at least once during the moult;  $n = 583$ ) a series of logistic regression models were tested to determine if sex, wean date, wean mass or an index of wean condition ( $\text{mass}/\text{length}^3$ ; Cone 1989; Read 1990) influenced whether or not an animal returned for the mid-year haul-out. These same variables were also used to distinguish between animals that returned for a second haul-out. A series of general linear models were constructed to test whether pup sex, wean mass, post-weaning fast duration or departure date (the last day the pup was seen) affected arrival date (ML estimate, Chapter 2) for the mid-year haul-out. Model selection was based on Akaike's information criterion (AIC; Lebreton *et al.* 1992; Buckland *et al.* 1997), with the best model having the highest model weight.

A total of 504 animals returned for the mid-year haul-out. A series of logistic regression models were tested to determine if mid-year haul-out arrival date, arrival mass, duration or sex influenced whether or not individuals returned for the moult. Of the animals that did return ( $n = 291$ ), a general linear model form of analysis of covariance (ANCOVA; Sokal and Rohlf 1981) was used to determine if the differences in mass gain between weaning and moult, and mass loss rate during the moult, differed between yearlings that returned for the mid-year haul-out, and those that did not. A general linear ANCOVA model was also used to determine if there was a significant difference in body composition at the

moult between animals that had returned for the mid-year haul-out, and animals that had not.

Animals are referred to as underyearlings for the mid-year haul-out and yearlings for the moult. Mid-year haul-out arrival dates and durations are taken from maximum likelihood estimates (see Chapter 2). Statistical analysis was done using SPSS V 10.0. Values are presented as mean  $\pm$  standard error (SE) unless otherwise stated.

## Results

### *Mass Estimation*

Mass was best estimated by length (L) and 4 girth measurements (G1, G3, G4 and G5;  $r^2 = 0.932$ ;  $F_{5,165} = 451.667$ ;  $P < 0.001$ ). G4 explained 87.1% of the  $r^2$ , length accounted for 4.7%, G5 for 0.9%, G3 for 0.4% and G1 for 0.2%. Mass was estimated from the following equation:

$$\text{Mass} = -216.177 + (0.638 \times L) + (0.306 \times G1) + (0.4 \times G3) + (0.864 \times G4) + (0.498 \times G5)$$

### *Post-weaning fast*

The average duration of the post-weaning fast was  $45.0 \pm 1.0$  days ( $n = 123$ ; range 19 – 71 days). Seventy-five weaners were recaptured prior to departure for their first foraging trip. Mass loss rate during the post-weaning fast averaged  $0.84 \pm 0.01 \text{ kg} \cdot \text{day}^{-1}$  (range 0.61 – 1.19  $\text{kg} \cdot \text{day}^{-1}$ ). There was a higher correlation between mass loss rate and weaning mass for females ( $r = 0.740$ ;  $P < 0.001$ ) than for males ( $r = 0.527$ ;  $P = 0.003$ ; Fig. 3.2a). The relationship between post-weaning fast duration and weaning mass was similar for females and males

( $r^2 = 0.434$ ;  $F_{1,63} = 48.253$ ;  $P < 0.001$  and  $r^2 = 0.466$ ;  $F_{1,52} = 45.319$ ;  $P < 0.001$ , respectively; Fig. 3.2b). Animals remained ashore until they had reached  $69.3 \pm 0.01\%$  ( $n = 75$ ; range 59 – 80%) of their weaning mass.

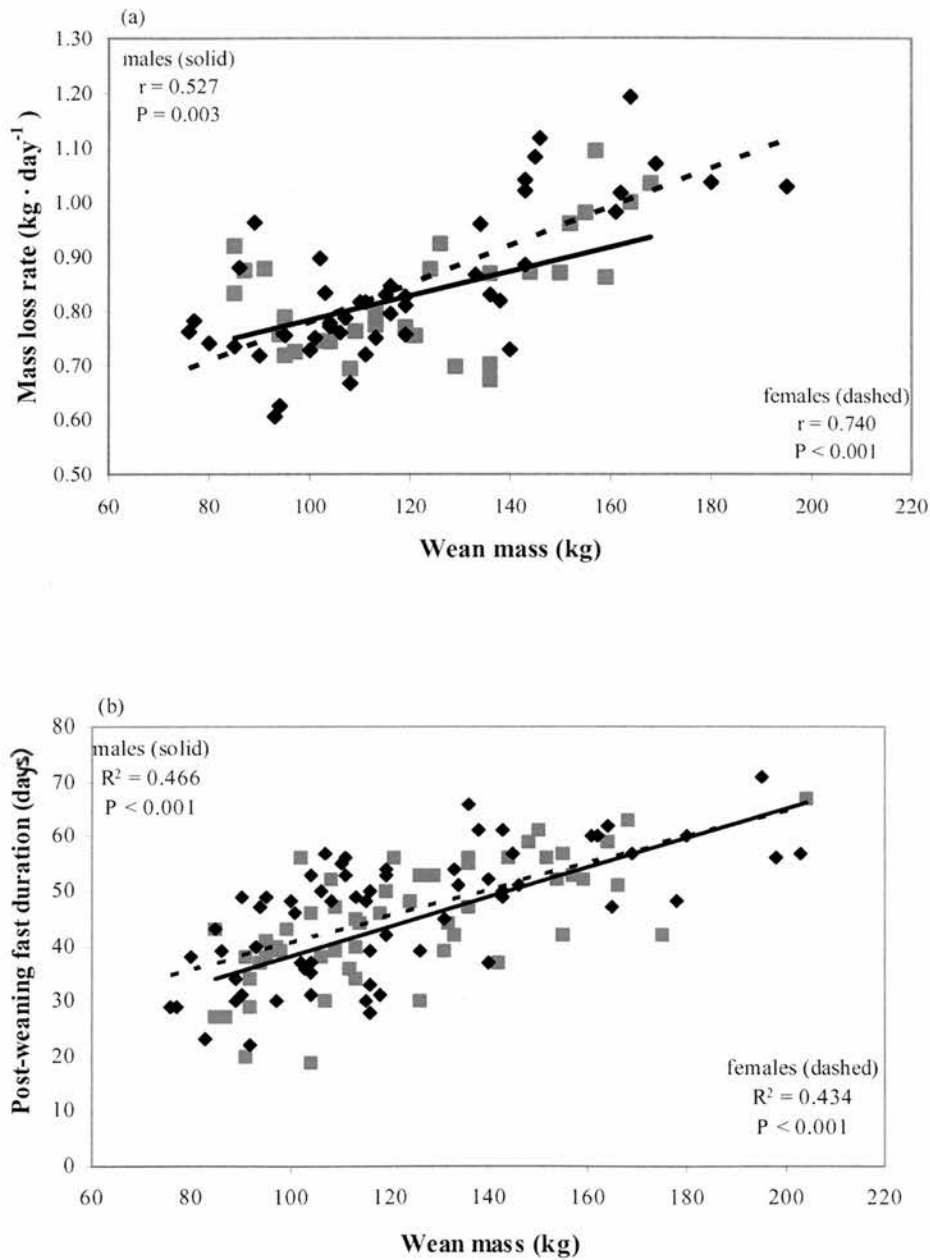


Fig. 3.2 Relationships between (a) mass loss rate ( $\text{kg} \cdot \text{day}^{-1}$ ) and weaning mass (kg) and (b) the post-weaning fast duration and weaning mass of male (squares) and female (diamonds) southern elephant seals in 1999. (a) males  $y = 0.002 + 0.560x$ ; females  $y = 0.004 + 0.425x$ ; (b) males  $y = 0.270 + 11.178x$ ; females  $y = 0.240 + 16.720x$ .

### *Mid-year haul-out*

The mean arrival date for all male and female underyearling elephant seals for the mid-year haul-out in 2000 was 18 May and 29 May, respectively (see Chapter 2 Results). The best general linear model testing for the effect of sex, wean mass, post-weaning fast duration (PWF) and departure date on the date of arrival for the mid-year haul-out only included the departure date term (model weight = 0.0933;  $r^2 = 0.224$ ;  $F_{1,39} = 11.288$ ;  $P = 0.002$ ; Fig. 3.3). There were two other models that had higher AIC weights (model weights = 0.1916 and 0.1215). The first included the wean mass and departure date variables and the second included all terms and a sex-by-PWF interaction. Using log-likelihood ratio tests to examine significance in specific terms, all terms except departure date were not significant. Therefore, these alternative models were disregarded.

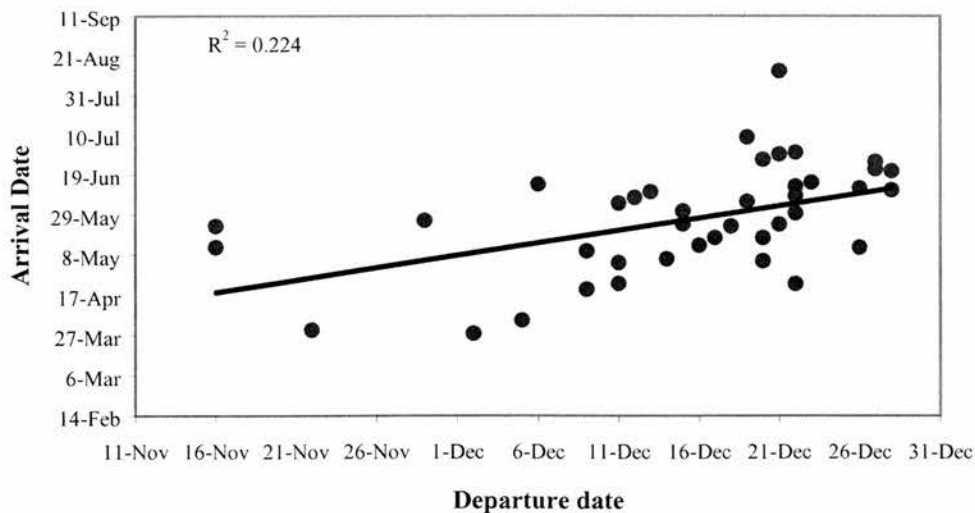


Fig. 3.3 Relationship between departure date from the post-weaning fast (last day sighted) and arrival date for the mid-year haul-out (ML estimate).

The average mass gain for individuals during the first foraging trip was  $58.4 \pm 2.8$  kg, or  $77.1 \pm 0.04\%$  ( $n = 28$ ) of their mass at the end of the post-

weaning fast. The rate of mass increase while at sea was  $0.35 \pm 0.02 \text{ kg} \cdot \text{day}^{-1}$  ( $n = 28$ ), and this was not related to departure mass for males ( $F_{1,12} = 6.48\text{E-}05$ ;  $P > 0.05$ ) or females ( $F_{1,12} = 1.413$ ;  $P > 0.05$ ). While all animals gained mass during the first foraging trip, some increased their mass by as little as 30%, while others more than doubled their departure body mass.

Mass changes during the mid-year haul-out were measured for 33 individuals (20 males, 13 females). The average total mass loss was  $26.8 \pm 1.10 \text{ kg}$  (almost half of what they had gained at sea), or  $1.40 \pm 0.05 \text{ kg} \cdot \text{day}^{-1}$ . There was a positive relationship between arrival mass and mass loss rate for females ( $r^2 = 0.500$ ;  $F_{1,11} = 11.011$ ;  $P = 0.007$ ) but not for males ( $r^2 = 0.098$ ;  $F_{1,18} = 1.968$ ;  $P > 0.05$ ; Fig. 3.4).

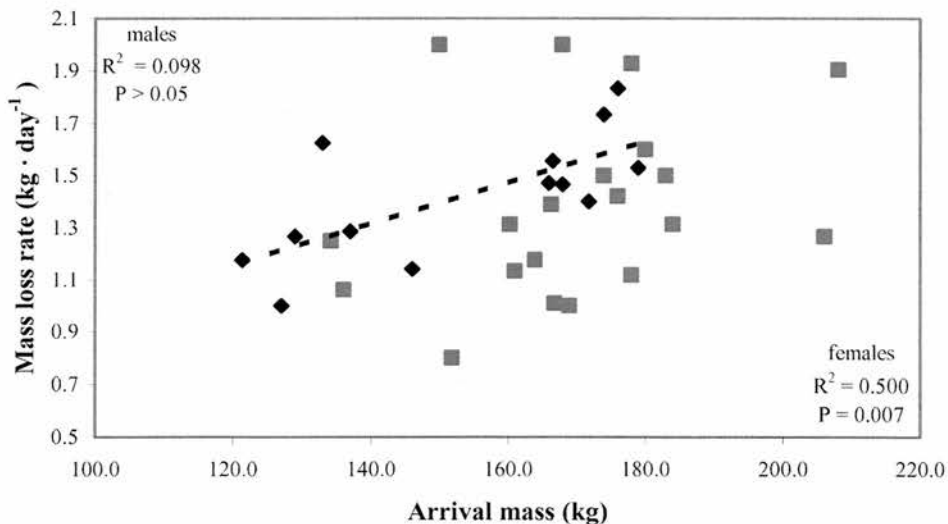


Fig. 3.4 The relationship between arrival mass and mass loss rate for male (squares) and female (diamonds) underyearling southern elephant seals during the mid-year haul-out. females  $y = 0.008 + 0.201x$ ;

For all yearlings (with birth and weaning weights) known to be alive during the winter ( $n = 583$ ), 79 did not return for the mid-year haul-out (i.e., 13.6 %). For models examining which animals came ashore for the mid-year haul-out,

several had similar AIC weights. Therefore, log-ratio tests were used to examine the significance of each term in these models. The variables important in the best model were sex, wean mass and the sex-by-wean mass interaction. Mass was the only term not significant in the model ( $P > 0.05$ ; Table 3.1). Proportionately, more males than females came back for the mid-year haul-out. There was negligible difference in average wean mass between males that did return for the mid-year haul-out ( $126.8 \pm 1.6$  kg;  $n = 242$ ) to males that did not ( $126.1 \pm 4.3$  kg;  $n = 32$ ; see Fig. 3.5). However, returning females were smaller at weaning ( $117.6 \pm 1.6$  kg;  $n = 262$ ), than females that did not return ( $133.8 \pm 3.8$  kg;  $n = 47$ ; Fig. 3.4).

Table 3.1 *Best logistic regression model indicating the effect of sex and wean mass for distinguishing which underyearling elephant seals come ashore for the mid-year haul-out on Macquarie Island. Significant terms in bold ( $P < 0.05$ ).*

Variable	B	S.E.	Wald	d.f.	P	Exp (B)
Mass	0.001	0.008	0.024	1	0.876	1.001
Sex	<b>2.935</b>	<b>1.299</b>	<b>5.102</b>	<b>1</b>	<b>0.024</b>	<b>18.819</b>
Mass * Sex	<b>-0.026</b>	<b>0.010</b>	<b>6.771</b>	<b>1</b>	<b>0.010</b>	<b>0.975</b>
Constant	1.874	0.976	3.690	1	0.055	

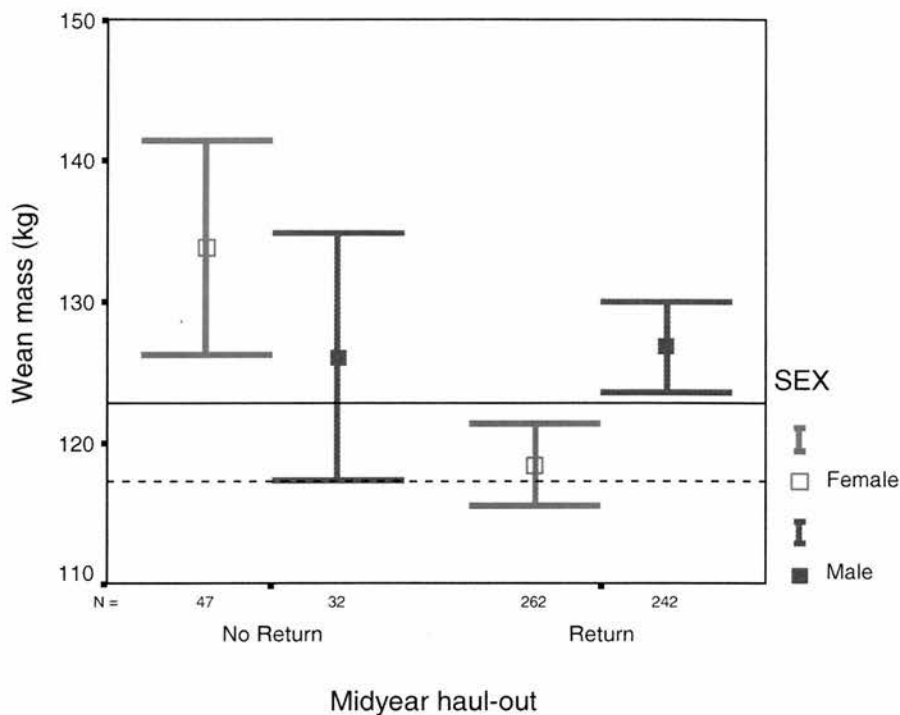


Fig. 3.5 Average wean mass of male and female underyearling elephant seals that did and did not return for the mid-year haul-out. The solid line represents the average wean mass of all males at weaning ( $122.82 \pm 27.18$  kg), and the dashed line represents the average wean mass of all females at weaning ( $117.22 \pm 26.46$  kg) in 1999 (Clive McMahon, pers. communication).

There was a significant logarithmic relationship between arrival mass and duration of the mid-year haul-out for females ( $r^2 = 0.086$ ;  $F_{1,48} = 4.510$ ;  $P = 0.039$ ), and males ( $r^2 = 0.080$ ,  $F_{1,52} = 4.366$ ;  $P = 0.042$ ; Fig. 3.6).

At the beginning of the mid-year haul-out, mass was composed of 42.4% water, 42.9% fat and 13.1% protein for females ( $n = 35$ ) and 42.5% water, 42.8% fat and 13.1% protein for males ( $n = 36$ ). At arrival and departure, larger underyearlings possessed absolutely more fat and protein than their lighter counterparts (Fig 3.7), but did not have relatively more fat or protein (Fig 3.8).

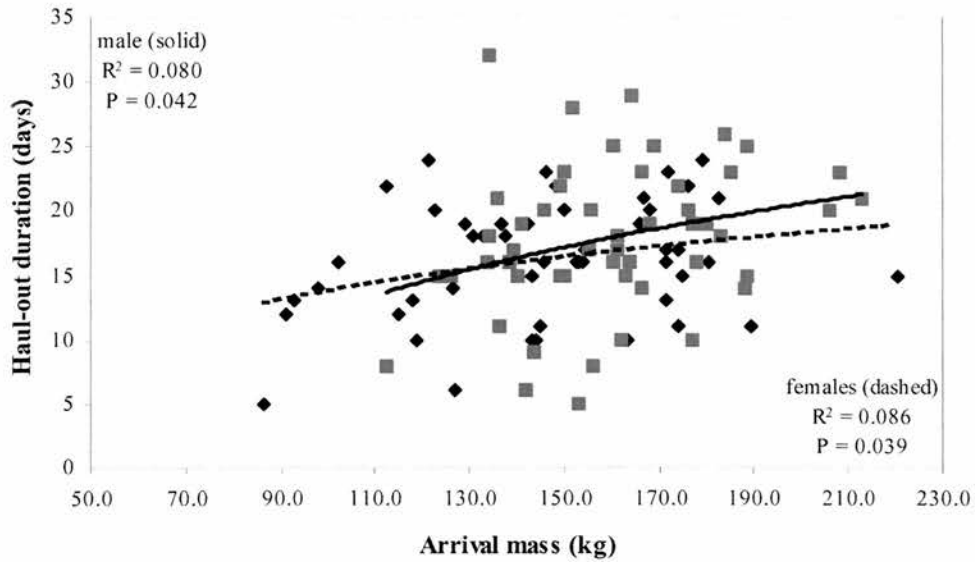
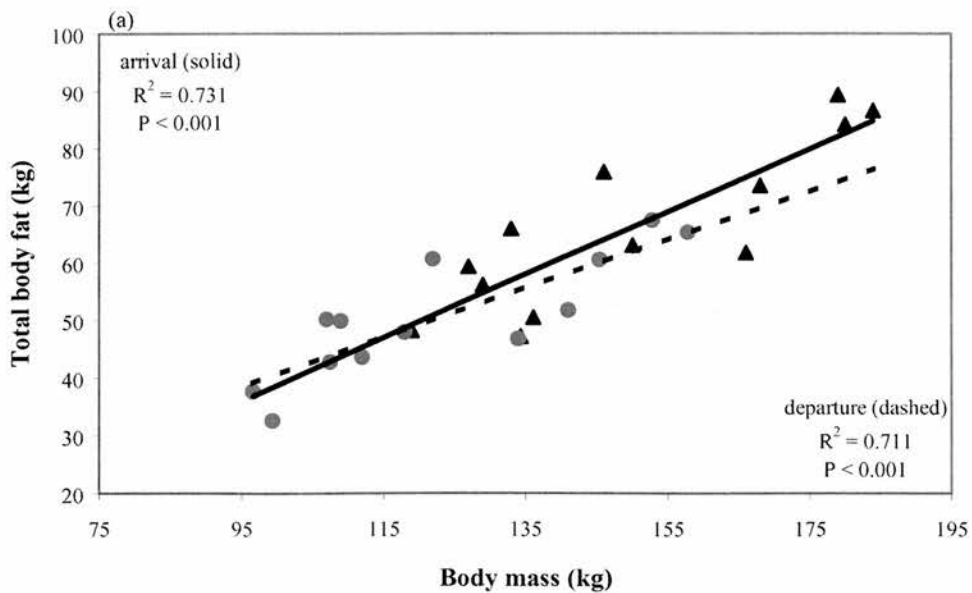


Fig. 3.6 Relationship between total days ashore (ML estimate) and arrival mass for male (squares) and female (diamonds) underyearling elephant seals during the mid-year haul-out. Males  $y = -42.381 + 11.881\ln(x)$ ; females  $y = -16.002 + 6.4768\ln(x)$





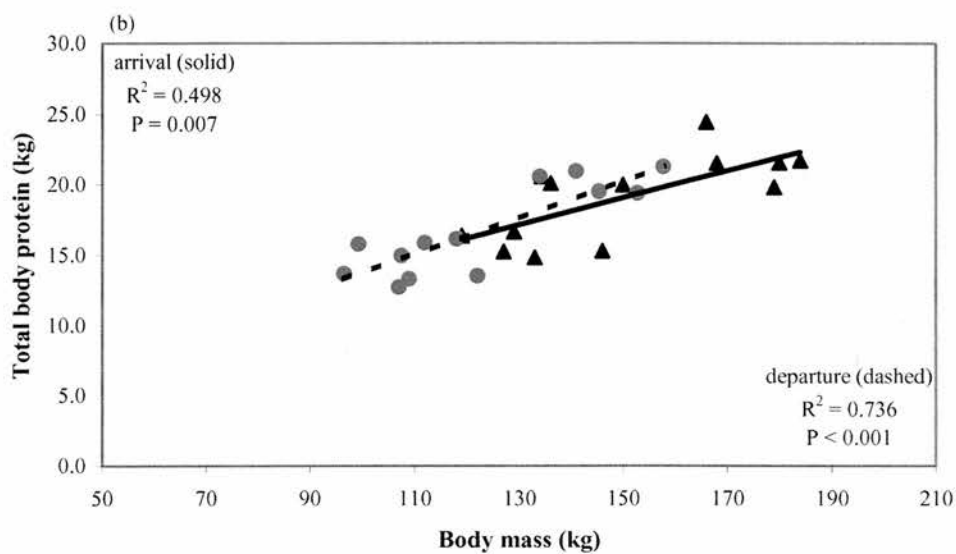
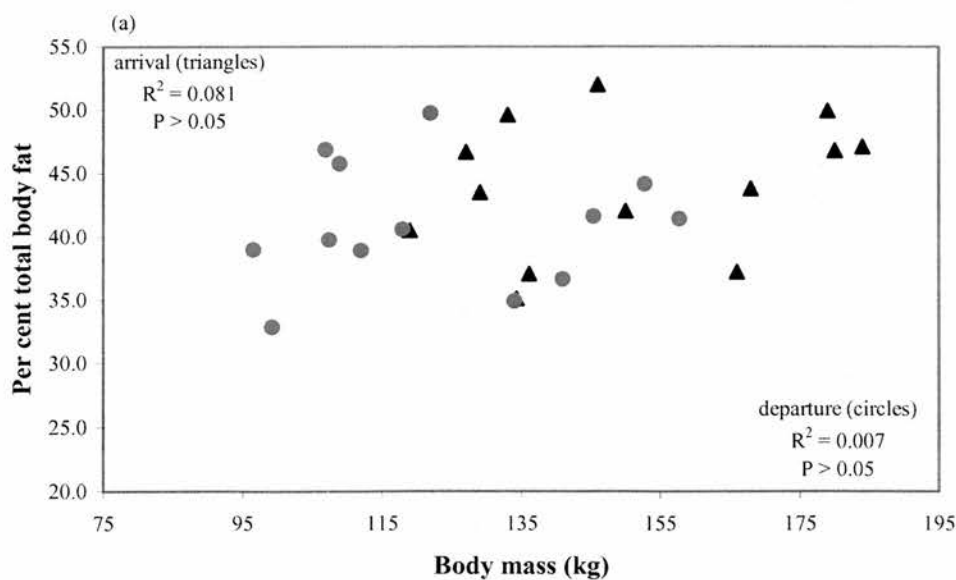


Fig. 3.7 Relationships of (a) total body fat (kg) to body mass (kg) and (b) total body protein (kg) to body mass (kg) at arrival and departure for the mid-year haul-out.



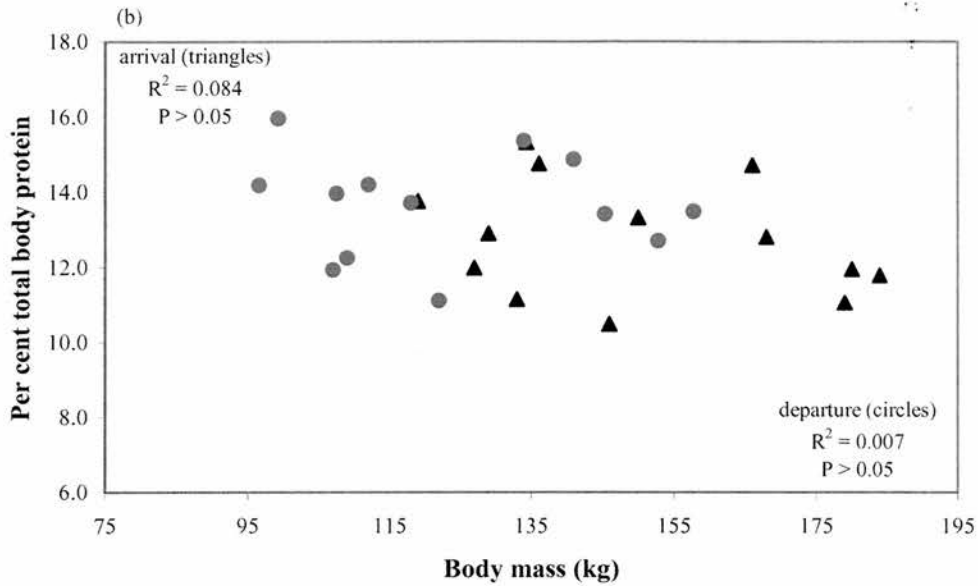


Fig. 3.8 Relationships of (a) per cent total body fat to body mass and (b) per cent total body protein to body mass at arrival and departure for underyearling elephant seals.

Body composition changes between the beginning and the end of the haul-out were measured for 13 underyearlings (6 males and 7 females; Table 3.2; Fig. 3.9 & 3.10). The average composition of the mass lost during the mid-year haul-out was  $32.9 \pm 0.04$  % water,  $56.9 \pm 0.05$  % fat and  $9.0 \pm 0.02$  % protein ( $N = 13$ ), indicating that fat was the primary source of energy. The energetic expenditure during the mid-year haul-out was  $682.1 \pm 74.4$  MJ on average (range 192 – 1156 MJ), with an average loss rate of  $35.5 \pm 3.9$  MJ  $\cdot$  day $^{-1}$  (11.3 – 64.2 MJ  $\cdot$  day $^{-1}$ ).

Table 3.2 Changes in mass and body composition of underyearling elephant seals during the mid-year haul-out.

Mid-year arrival composition							Mid-year departure composition							Total time ashore	
Seal	Sex	Mass (kg)	%TBW	%TBF	%TBP	TBGE(MJ)	Mass (kg)	%TBW	%TBF	%TBP	TBGE(MJ)	(days)	Loss (kg·day <sup>-1</sup> )		
T 814	M	185.1	39.40	47.37	11.80	4027	155.1	43.85	40.86	13.67	2953	23	1.31		
T 842	M	180	39.80	46.80	11.97	3869	149.6	41.80	43.86	12.81	2972	18	1.60		
T 893	M	135.5	47.73	35.17	15.30	2443	95.5	49.47	32.62	16.03	1225	32	1.25		
T 755	M	150	43.05	42.03	13.33	2988	108	45.38	38.62	14.31	1763	23	2.00		
T 012	M	168	41.84	43.80	12.82	3445	130	48.63	33.86	15.67	2167	19	2.00		
T 869*	M	137.1	46.58	36.85	14.82	2561	114.8	43.59	41.25	13.56	2164	21	1.06		
T 138	F	166	46.35	37.20	14.72	3041	138.1	46.77	36.58	14.89	2439	21	1.47		
T 839	F	121.4	44.00	40.65	13.73	2408	96.6	45.13	38.99	14.20	1779	19	1.18		
T 687	F	179	37.66	49.93	11.07	4033	142.3	43.84	40.88	13.66	2686	24	1.53		
T 476	F	133	37.87	49.62	11.16	2983	103.8	39.97	46.54	12.04	2172	18	1.62		
T 216	F	146	36.26	51.99	10.48	3389	119.7	37.92	49.55	11.18	2648	23	1.14		
T 705	F	129	42.06	43.48	12.91	2631	104.9	44.89	39.33	14.11	1916	19	1.27		
T 269	F	127	39.88	46.68	12.00	2725	109	40.50	45.77	12.26	2270	18	1.00		
Mean		150.6	41.73	43.97	12.78	3119	120.6	43.98	40.67	13.72	2376	21.54	1.42		
SE		6.22	1.02	1.49	0.43	162.3	5.64	0.92	1.36	0.39	147.2	1.05	0.09		

Note: Boldface indicates where animals were ashore for a period of time before or after captures. Mass and body composition were calculated based on average loss · day<sup>-1</sup> for each animal  
 \* appeared to be the only animal that lost proportionally more protein than fat compared to other seals.

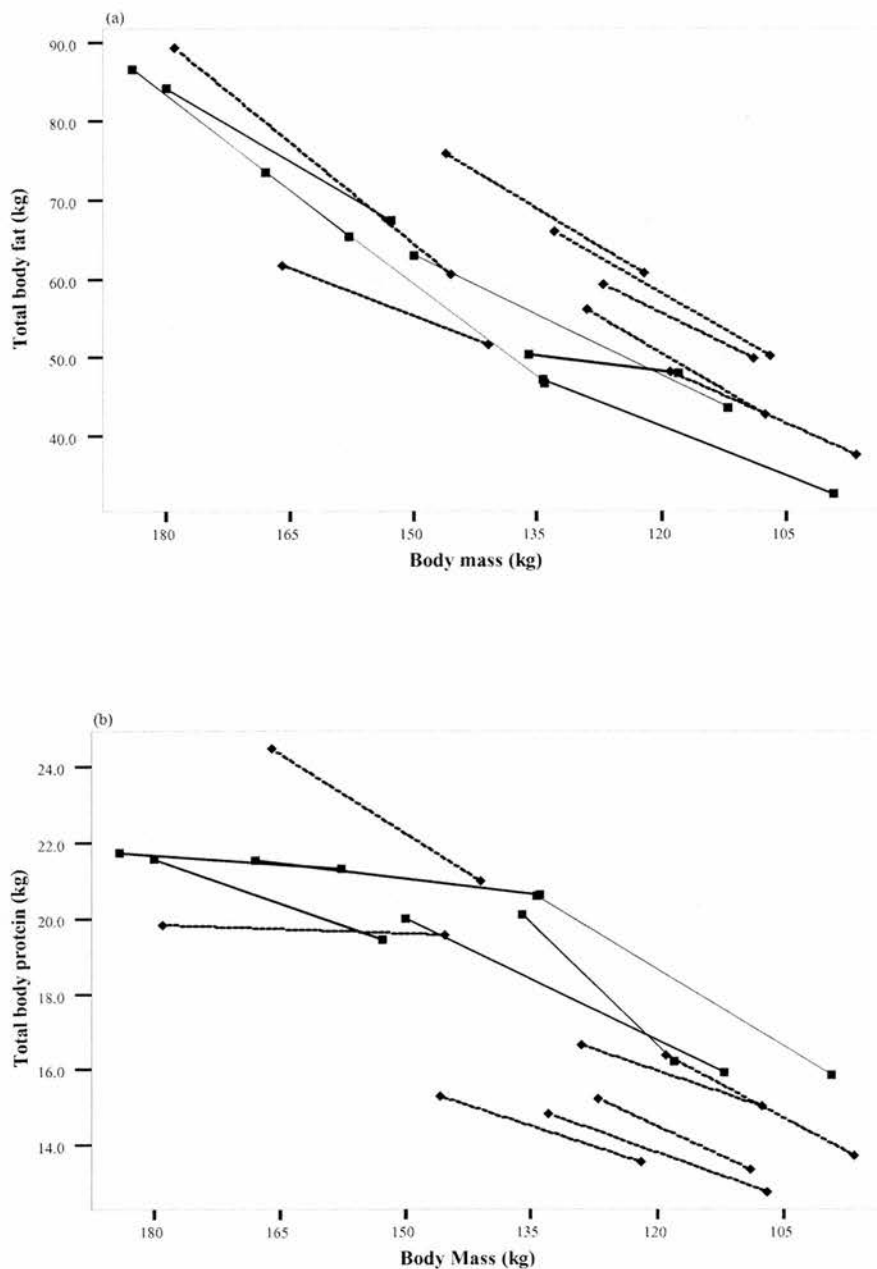


Fig. 3.9 Changes in (a) total body fat (kg) and (b) total body protein (kg) during the mid-year haul-out for male (solid) and females (dashed) elephant seals. Note: x-axis scale reversed.

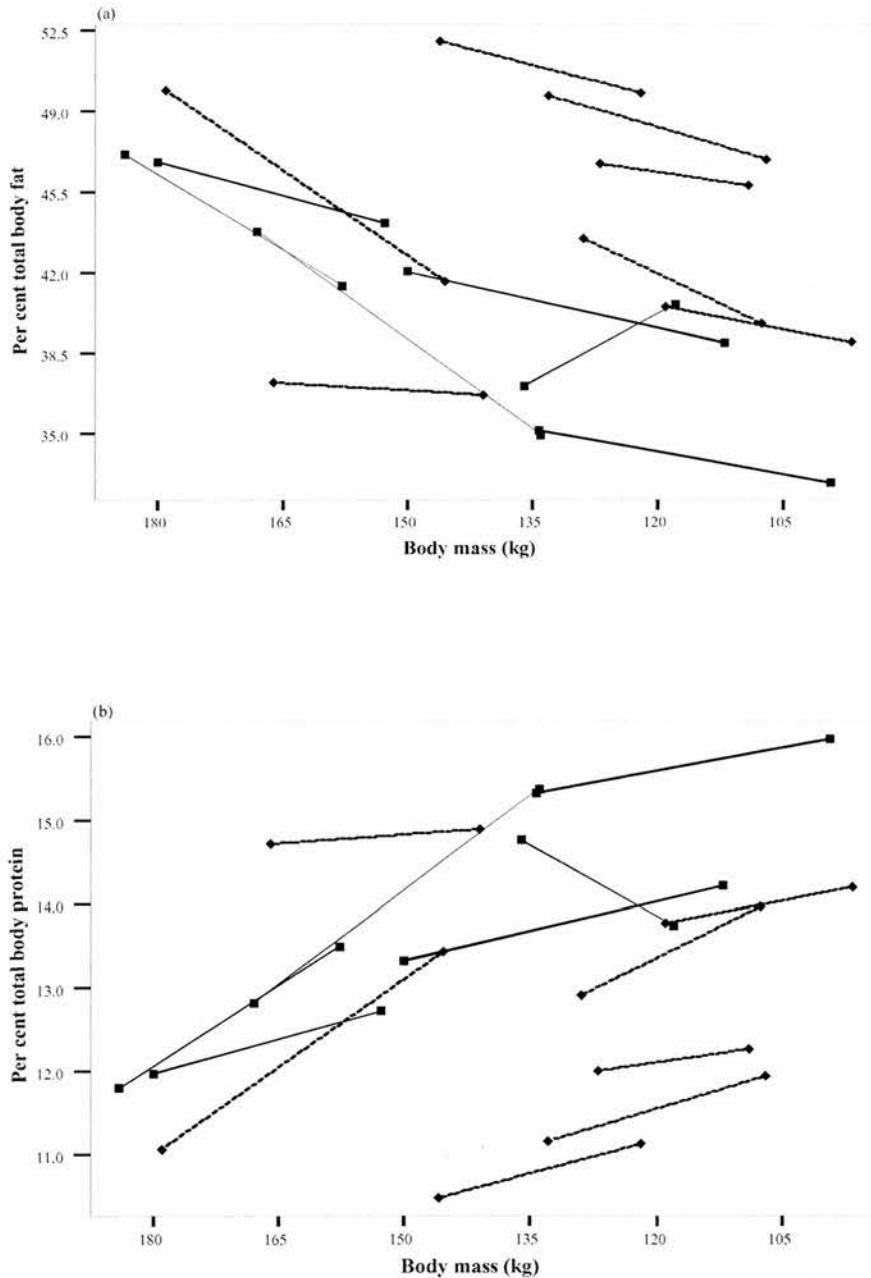


Fig. 3.10 Changes in (a) per cent total body fat and (b) per cent total body protein during the mid-year haul-out for male (solid) and female (dashed) underyearling elephant seals. Note: x-axis scale reversed

#### Second mid-year haul-out

Out of the 504 underyearlings that returned to Macquarie Island for the mid-year haul-out, 49 of these returned again for a second haul-out (i.e., 9.7 %).

The best model (with the highest AIC weight) to describe the effect of sex, wean mass and wean date on the occurrence of a second haul-out included all main effects (model weight = 0.273). Several other models had similar, but lower AIC weights. These models differed only by the addition of interaction terms. However, these interaction terms were not significant. Therefore, the best model only included main effects. All terms (sex, wean mass and wean date) were significant in our model ( $P < 0.05$ ; Table 3.3). Proportionally, more males than females came back for a second haul-out (12.4 % males; 7.3 % females), and individuals that returned again were significantly smaller at weaning (males =  $115.8 \pm 3.95$  kg; females =  $101.0 \pm 3.96$  kg) than ones that did not return (males =  $128.4 \pm 1.73$  kg; females =  $119.7 \pm 1.53$  kg; Fig. 3.11). Although wean date was significant, the variation was high among animals that returned versus animals that did not. The mean difference in weaning date between females that did return for a second haul-out, and ones that did not was 0.58 days, while for males the difference was 1.65 days.

Table 3.3 *The best-fit logistic regression model describing the effect of sex, wean mass and wean date on which underyearling elephant seals return for a second mid-year haul-out on Macquarie Island. Significant terms in bold ( $P < 0.05$ ).*

Variable	B	S.E.	Wald	d.f.	P	Exp (B)
Mass	<b>-0.035</b>	<b>0.008</b>	<b>19.680</b>	<b>1</b>	<b>0.000</b>	<b>0.966</b>
Sex	<b>-0.953</b>	<b>0.327</b>	<b>8.477</b>	<b>1</b>	<b>0.004</b>	<b>0.386</b>
Date	<b>-0.075</b>	<b>0.029</b>	<b>6.797</b>	<b>1</b>	<b>0.009</b>	<b>0.928</b>
Constant	3.974	1.283	9.595	1	0.002	53.205

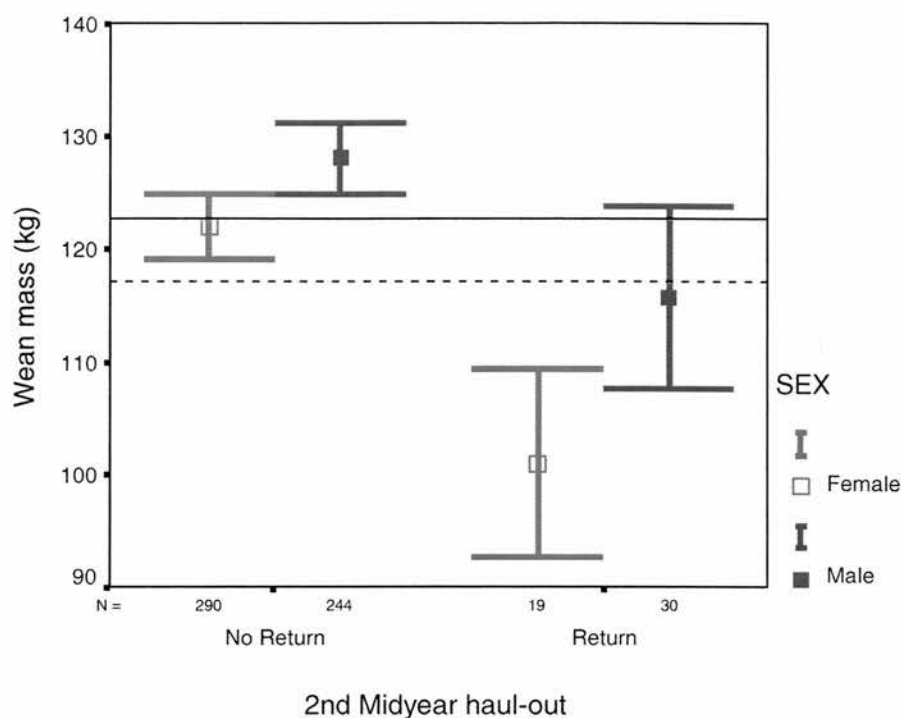


Fig. 3.11 Average wean mass (kg) of male and female underyearling elephant seals returning to Macquarie Island for a second mid-year haul-out. The solid line represents the average wean mass of all males at weaning ( $122.82 \pm 27.18$  kg), and the dashed line represents the average wean mass of all females at weaning ( $117.22 \pm 26.46$  kg) in 1999 (Clive McMahon, pers. communication).

Sixteen underyearlings were weighed on return to the island for a second mid-year haul-out (Table 3.4). Six had been weighed previously on the first haul-out. For these six, the time between the first and second midyear haul-out ranged from 71 - 147 days. All six animals lost mass between the two haul-outs (range 3 – 29 kg). I was able to measure body composition changes between the first and second haul-out for only one underyearling. T 878 remained ashore for 28 days during the first mid-year haul-out and his estimated departure mass was 130.2 kg. While at sea, there was an approximate mass gain of 16 kg. However, return mass for the second mid-year haul-out was still ~6 kg less than the first. Between the first haul-out and the second there was a gain in total body water of

20.3 kg, and in total body protein of 8.9 kg, but an overall loss in fat of 33.5 kg.

This represented a loss in energy of 1235 MJ.

Table 3.4 *Change in total mass of underyearling southern elephant seals between weaning, first mid-year haul-out and the second midyear haul-out.*

Seal	Sex	Wean mass (kg)	Mass at 1st haul-out (kg)	Time at sea (days)	Mass at 2nd haul-out (kg)	Total $\Delta$ Mass b/w weaning & 2nd haul-out	Present during moult
T 835	F	104	<b>90.8</b>	116	72	-32	N
T 839	F	101	<b>121.8</b>	83	92	-9	N
T 859	F	119	104	120	101	-18	N
T 219	F	76	91	83	65	-11	N
T 305	M	85	-	98	91	6	N
T 722	M	97	-	84	105	8	N
T 948	M	115	-	109	124	9	N
T 242	M	83	-	71	115	32	N
T 878	M	106	<b>152.6*</b>	114	146	40	Y
T 428	F	111	150	118	<b>122.8</b>	12.8	Y
T 782	M	104	-	72	147	43	Y
T 586	M	131	-	71	151	20	Y
T 316	M	96	-	100	118	22	Y
T 730	F	145	-	78	108	-37	Y
T 016	F	84	-	147	95	11	Y
T 780	F	76	-	125	108	32	Y

Note: Bold script indicates where capture was not on the first day ashore therefore the number of days of mass loss (1.40 kg·day<sup>-1</sup>) was added to the capture mass.

\* departure mass = 130.2 kg

### *Moult*

From the 504 animals that were ashore for the mid-year haul-out, 291 returned for the moult (i.e., 57.7 %). Four models competed for highest parsimony to describe which of the mid-year haul-out animals returned for the moult (Table 3.5). Log-likelihood ratio tests were used to examine each term for significance in the models. Midyear haul-out arrival date was not significant ( $P = 0.07$ ) and haul-out duration and arrival mass were significant terms ( $P = 0.05$ ;  $P = 0.04$ , respectively). It was difficult to choose the “best” model because each



variable described some of the variation between animals that returned for the moult versus animals that did not. The mid-year haul-out arrival mass was higher for animals that did return for the moult ( $159.36 \pm 3.02$  kg) than those that did not ( $147.33 \pm 4.05$  kg). Underyearling elephant seals that arrived later (12.93 days) and stayed longer (1.01 days) for the mid-year haul-out returned to Macquarie Island for the moult.

Table 3.5 *Top four AIC models describing the effect of mid-year arrival date, mass and duration on the likelihood of underyearlings returning to Macquarie Island for the moult.*

Model	-2logl	d.f.	AIC	$\Delta$ AIC	AIC wt
date + mass	133.684	2	139.684	0.000	0.098
date + duration	133.860	2	139.860	0.176	0.089
date + mass + duration	131.971	3	139.971	0.287	0.085
mass	136.994	1	140.994	1.310	0.051

There was no detectable difference in mass gain (between weaning and moult) between animals that returned and animals that did not return for the mid-year haul-out ( $F_{1,25} = 0.313$ ;  $P > 0.05$ ;  $n = 27$ ), i.e., animals that remained at sea did not gain proportionally more mass between weaning and the moult than those that had returned for the midyear haul-out.

Mass changes during the moult were measured for twelve one-year old seals. The average total mass loss was  $46.3 \pm 3.7$  kg or 27.3% of arrival mass, with an average loss rate of  $1.71 \pm 0.11$  kg  $\cdot$  day<sup>-1</sup>. For females, mass loss rate appears to be highly correlated with arrival mass ( $r^2 = 0.728$ ; Fig. 3.12a), but this was not significant ( $F_{1,3} = 8.033$ ;  $P = 0.06$ ). There was more variation in mass loss rate for males and no correlation was apparent ( $r^2 = 0.003$ ;  $F_{1,5} = 0.018$ ;  $P > 0.05$ ; Fig. 3.12a). There was no difference in mass loss rate during the moult

between animals that had returned for the mid-year haul-out ( $n = 9$ ;  $1.71 \pm 0.14$   $\text{kg} \cdot \text{day}^{-1}$ ) versus animals that had not ( $n = 3$ ;  $1.70 \pm 0.24$   $\text{kg} \cdot \text{day}^{-1}$ ;  $F_{1,10} = 0.146$ ;  $P > 0.05$ ). Although not significant, there was a slight correlation between duration of the moult and arrival mass for females ( $r^2 = 0.367$ ) and males ( $r^2 = 0.154$ ; Fig. 3.12b).

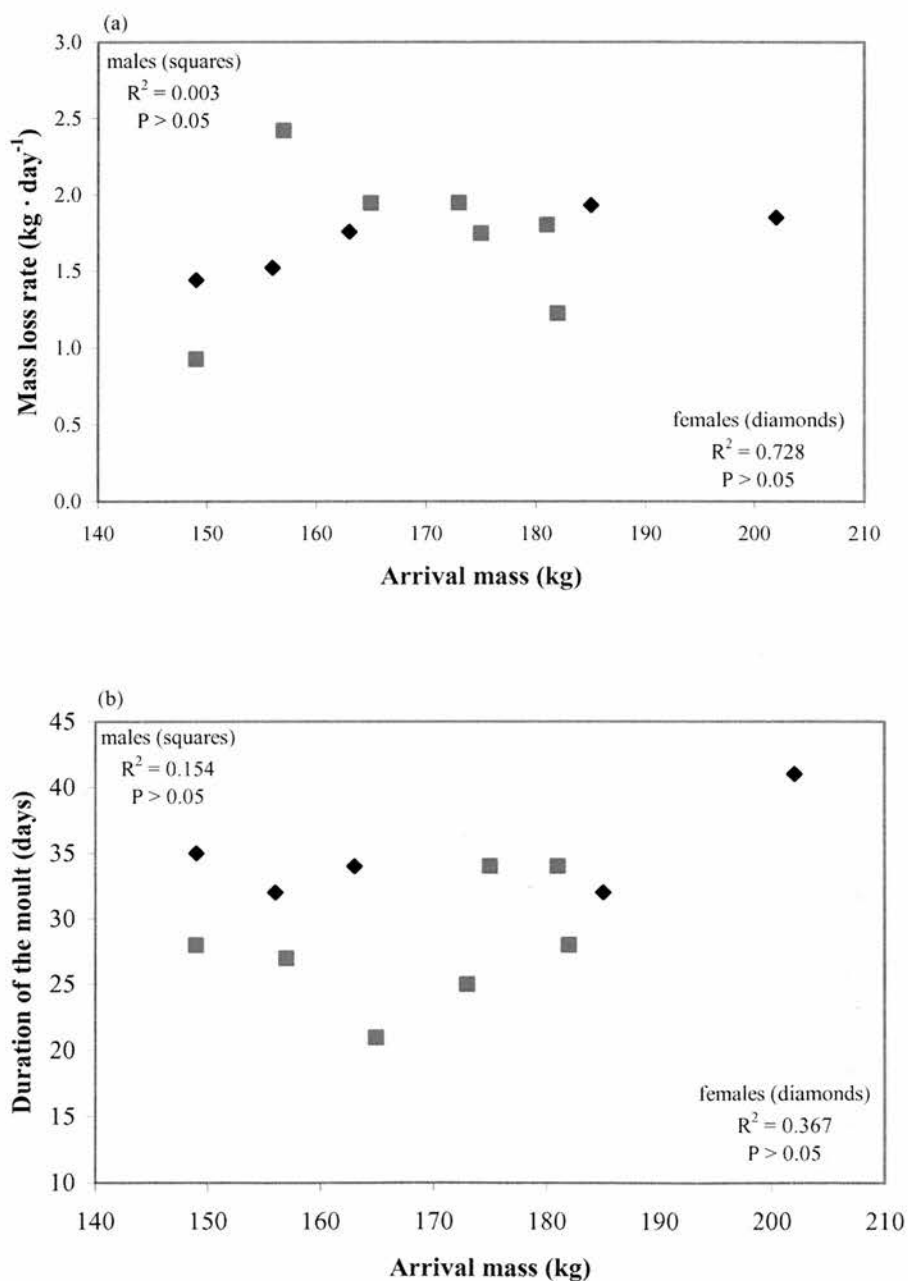
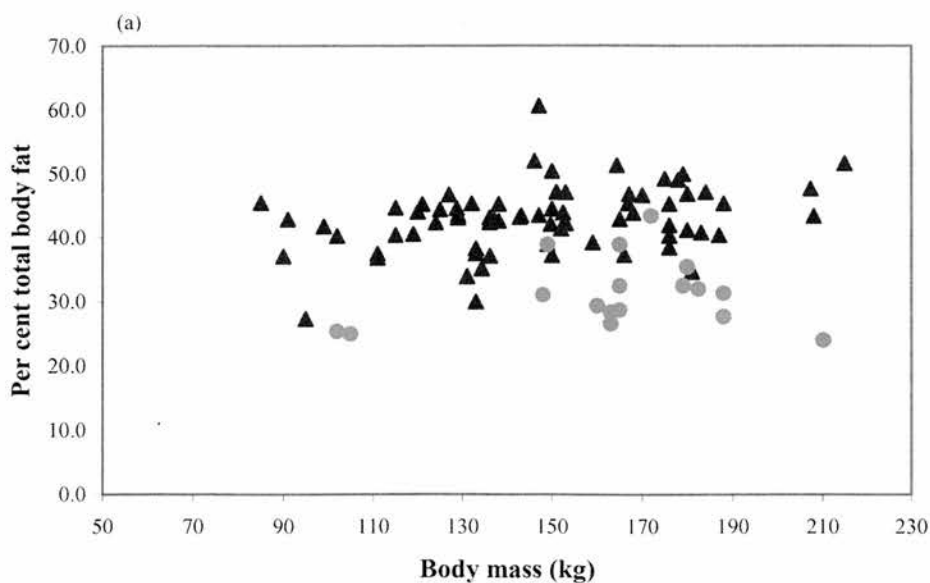


Fig. 3.12 Relationships between (a) mass loss rate and arrival mass and (b) duration and arrival mass during the moult for male and female 1-year old elephant seals.

At the beginning of the moult, mass was composed of 50.4 % water, 31.2 % fat and 16.4 % protein ( $n = 17$ ). In comparison to body composition at the mid-year haul-out, individuals at the moult had a lower percentage of body fat and a higher percentage of body protein (Fig. 3.13), indicating a growth in body tissue. There was no significant difference in per cent total body fat at the moult between individuals that had returned for the mid-year haul-out, and ones that had not ( $F_{1,15} = 0.332$ ;  $P > 0.05$ ). Changes in body composition during the moult were measured for only two individuals. One male lost 37 kg in body mass, which was comprised of 54.0 % water, 26.0 % fat and 17.9 % protein. One female lost 49 kg body mass, consisting of 30.4 % water, 60.6 % fat and 8.0 % protein. This may reflect sexual differences in partitioning of resources, or effects of a compositional difference at the beginning of the haul-out. This particular female had 10.5% more fat than the male thereby allocating fat as the main source of energy while the male also had to rely on protein stores.



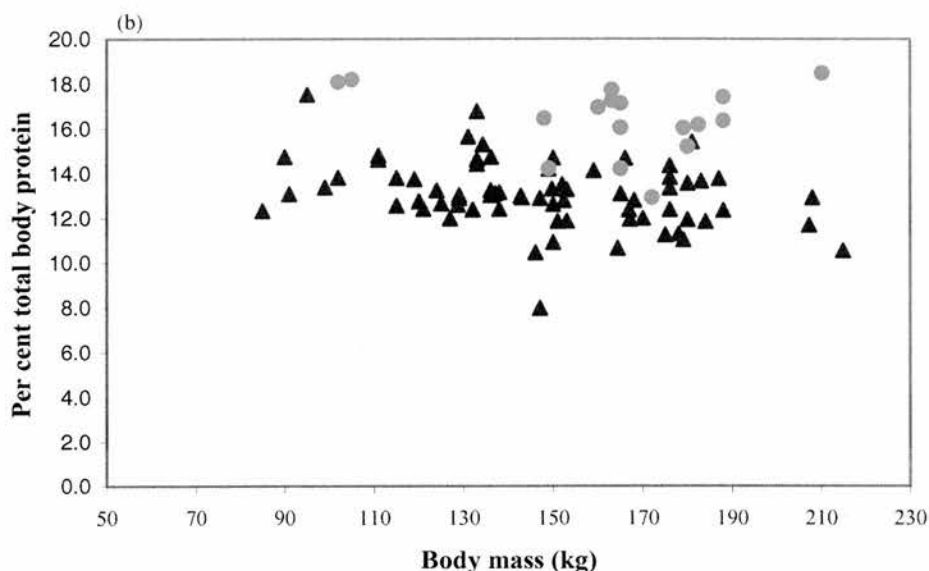


Fig. 3.13 Comparisons between (a) per cent total body fat and (b) per cent total body protein for the mid-year haul-out (triangles) and the moult (circles).

## Discussion

### *Factors affecting which animals haul-out*

Sex differences appear to be important. Differences in behaviour and development between male and female elephant seals have been recorded as early as during the post-weaning fast (Arnbom *et al.* 1993; Modig *et al.* 1997, McMahon *et al.* 1997). It is apparent that differences persist throughout their first foraging trip.

In our analysis of haul-out behaviour we could not account for individuals that were alive during the mid-year haul-out, did not return, and were not seen during the moult. We could only consider animals seen during the moult when examining factors that affected mid-year haul-out behaviour. Therefore, our results must be viewed in context.

Although the majority of underyearlings, which were sighted during the moult, returned for a mid-year haul-out in 2000, proportionally more males than

females returned. Average wean masses of males and females that returned were not different from the population averages, but females that returned had been significantly smaller at weaning than females that did not, while the average wean mass of males between the two groups was similar (Fig. 3.5). This is in contrast to the findings of Wilkinson and Bester (1990) who suggested that weaning mass had no influence on the likelihood of hauling out in the autumn on Marion Island. However, this could result from differences between the two populations (Macquarie Island and Marion Island) or differences between years. Furthermore, their study only considered the variation in masses of individuals that returned, and did not separate males from females, while this study compared returning individuals to ones that did not (i.e., those that were only seen during the annual moult).

We can only speculate as to why there would be a difference in weaning mass between females that returned and females that did not, but not in males. This could reflect differences in condition between individuals and the sexes however; there is no evidence of differences at weaning (Carlini *et al.* 2001). Even though mass differences influenced which individuals returned for the mid-year haul-out, they did not reveal a significant survival advantage of one sex over the other since there was no significant difference in numbers between the sexes at the time of the moult.

#### *Second mid-year haul-out*

All animals that were weighed at the second haul-out lost mass from the first haul-out. These seals were smaller than average at weaning and therefore may not have been able to forage as successfully, or they may have remained relatively close to the island during this intermediate trip and competed for food

resources with local populations of penguins and fur seals (see Goldsworthy *et al.* 2001). This could offer an explanation as to why Condy (1979) alleged that animals hauling out later in the winter appeared to have done more poorly.

### *Body Composition*

There are a number of methods available to measure body composition of individuals. Mass and condition indices may be adequate predictors of body composition in some animals (Costa *et al.* 1989; Arnould 1995; Hall *et al.* 2001) and useful in comparisons between populations (Bradshaw *et al.* 2000; Hall *et al.* 2001); however, they do not accurately represent the loss or gain of fat stores which is essential in determining energy acquisition and expenditure. On the other hand, hydrogen isotope dilution methods can accurately calculate lipid and protein stores by estimating total body water (Reilly and Fedak 1990; Arnould *et al.* 1996) and have been widely used in the study of body composition and energy metabolism in pinnipeds (Costa 1987).

To compare changes and utilization of resources between the first three haul-outs, and to determine if body composition affected which animals returned for the mid-year haul-out, body composition measurements were made for 75 individuals at weaning, and prior to departure. Unfortunately, due to inexplicable reasons, results were difficult to interpret and comparisons were not possible.

Overall, the primary loss during the mid-year haul-out was fat, which contributed the most to energetic requirements. Nevertheless, there were small losses in protein as well. However, smaller animals tended to lose absolutely more protein than larger animals and individual differences in composition also affected differences in the composition of mass loss. Maintaining an adequate blubber layer is necessary for thermoregulation (Ryg *et al.* 1988). Therefore,

smaller individuals and those with a lower fat content may rely more on protein stores (than larger or fatter individuals) for their energetic requirements, thereby sparing the blubber layer (Worthy 1983). These observed differences in the allocation of body stores could have implications on future stores and survival.

#### *Mass loss rates*

Mass loss rate increased steadily across all three haul-outs as per cent protein increased. There was a stronger relationship between mass loss rate and body mass for females than for males during each haul-out. Males are much more variable in their haul-out behaviour, as some actively engaged in social behaviour such as mock fighting (Arnbom *et al.* 1993; K.E. Wheatley unpubl. data). Therefore, mass loss rates of some individual males might be more inconsistent than others.

Carrick *et al.* (1962) suggested that returning for the mid-year haul-out might be advantageous in conditioning the organ-systems to be proficient in fasting and use of stored reserves. If this were the case than animals that returned for the mid-year haul-out would be more proficient “fasters” than animals that did not return. There were no obvious differences in mass loss rate during the moult between animals that returned for the mid-year haul-out and those that did not. However, power to detect minor differences was low.

One inherent bias in estimating mass by extrapolation using mass loss rate, is if mass loss rate changes during different periods of the fast. Arnbom *et al.* (1993) found that mass loss rate at the end of the post-weaning fast was lower than at the beginning of the fast, but higher than the middle of the fast. However, the difference between the calculated mass loss rate for the whole fast and the mass loss rate at the end of the fast was only  $0.16 \text{ kg} \cdot \text{day}^{-1}$ . During the midyear

haul-out loss rate increased toward the end of the fast by  $0.11 \text{ kg} \cdot \text{day}^{-1}$  ( $n = 1$ ). In this study, the average difference between the time of capture and the time of departure for the post-weaning fast was 6.3 days (range 0-26 days), for the mid-year haul-out was 2.8 days (range 0-12 days) and for the moult was 3.7 days (range 0-7 days). So, if mass loss rate differed it would have had negligible effects on the value of estimated mass.

#### *Haul-out durations*

Bell *et al.* (1997) suggested that the post-weaning fast duration might be critical in determining the time spent at sea. However, we found that only the departure date variable significantly affected date of arrival. Therefore, animals leaving later (regardless of fast duration) came back later. An additional test could include arrival mass or condition to determine if arrival date is affected by the condition an animal is in.

Haul-out duration differed between the post-weaning fast, mid-year haul-out and moult. Most weaners leave on their first foraging trip after losing ~30 % of their weaning mass (Wilkinson and Bester 1990; Arnborn *et al.* 1993; Carlini *et al.* 2001; this study). Although heavier weaners have higher mass loss rates, the rates are not higher relative to the amount of extra mass they possess; therefore, these animals can also remain ashore longer. There was a significant logarithmic relationship between the duration of the mid-year haul-out and arrival mass for both sexes indicating a possible “maximum” duration ashore. However, the correlation coefficient was very low. There was no correlation between body mass and duration of the moult for either sex. This could be an artefact of small sample size, or the fact that animals remain ashore simply long



enough to finish the moult, regardless of if they have sufficient energy stores to remain longer.

### *Moult*

Mid-year haul-out arrival date, duration and mass explained some of the variance in whether or not an animal returned for the moult. However, the biological significance is questionable. For example, the difference in the mid-year haul-out duration between the animals that did return for the moult and the animals that did not was only one day. McMahon *et al.* (2000) showed that weaning mass affected survival within the first-year for southern elephant seals on Macquarie Island. Therefore, it is not surprising the mid-year haul-out mass influenced whether or not an animal was seen during the moult. The fact that mid-year haul-out date influenced which animals were seen during the moult could indicate that subsequent condition and survival are affected by timing of the previous haul-outs.

### *Conclusions*

Although these results only cover one year, they suggest that differences between male and female southern elephant seals exist during the first foraging trip. The most obvious differences were in behaviour. However, the function of the midyear haul-out remains obscure since there was no apparent physiological or survival advantage in returning for the midyear haul-out. Carrick *et al.* (1962) suggested that the majority of survivors to later years were not seen in any winter. Clearly, by following the same animals for a number of years, advantages or disadvantages may become clearer.

Hindell (1991) has shown that differences in inter-annual survival rates of first-year seals do exist. These differences could be a direct or indirect response to inter-annual changes in the distribution of prey or variations in energy content of prey species (Mårtensson *et al.* 1996) either during initial foraging or in the total maternal resources supplied. Therefore, constant monitoring of which and how many underyearlings return in the first year may indicate inter-annual differences of successful foraging. To fully understand the significance of the mid-year haul-out, it is necessary to examine the condition of animals that are involved in consecutive years, and distinguish how this affects survival.

## Chapter 4

### General Discussion

The function of the midyear haul-out for southern elephant seals has been in debate for some years (Carrick and Ingham 1962; Carrick *et al.* 1962; Bryden 1969; Condry 1979; Ling and Bryden 1981). Considering the high energetic costs involved in returning to Macquarie Island, it seems probable that some purpose is served. Although there have been several broad descriptions and suggested hypotheses (see Chapter 1 Introduction), the significance of this haul-out on condition and survival has never been investigated. Detailed descriptions of physical and behavioural aspects may provide some indication.

There was a definite synchronization in haul-out behaviour between age and sex classes. Although there was some overlap in time spent ashore, this was reduced by different cohorts arriving ashore at different times. Hindell and Burton (1988) have reported similar patterns in haul-out behaviour of juveniles and adults during the moult; however, no consideration was given to specific age classes. Carrick *et al.* (1962) gave a detailed description of haul-out behaviour for the midyear haul-out and the moult, yet data were combined from three years of observations so inter-annual variability could have affected distributions. Therefore, it would be worthwhile to examine if the synchronization observed during the midyear haul-out persisted to the moult and if patterns differed in consecutive years.

If the midyear haul-out were necessary from a developmental viewpoint (see Chapter 1 hypotheses by Carrick and Ingham 1962; Carrick *et al.* 1962), then presumably all animals would participate, or otherwise incur a physiological disadvantage. Yet, in terms of mass gain, mass loss rate and body composition,

our results suggest that there were no differences at the time of the moult between animals that returned, and animals that did not. If the midyear haul-out were simply a “rest” period for animals that could not withstand prolonged periods at sea, this would indicate that within the first year differences already exist between males and females, since there were significant differences in wean mass of males and females that returned versus those that remained at sea.

Although we cannot explain the function of the midyear haul-out on Macquarie Island, our results suggest that if some benefit is served, it is clearly restricted to the juvenile population. Although the number of animals ashore may decrease with age, this could be confounded by mortality of individuals within the population over several years. However, we found that as females matured to breeding age, there was a significant decline in the number returning and residence time ashore. Although some adult females did return, the haul-out did not appear to play the same role as it did for juveniles. The number of males tapered off more slowly, but by the age of six, as a number of males were beginning to show up during the breeding season, the number ashore for the mid-year haul-out was noticeably reduced. Our age categories did not include males that would be actively breeding. However, considering the energetic costs incurred during the breeding season, like females, most adult males probably did not return for the midyear haul-out.

Overall, there was a significant difference in behaviour and physiology between males and females that returned for the midyear haul-out. McMahon *et al.* (1997) has described precocious development in females at the time of weaning and several others have described differences in behaviour during the post-weaning fast (Arnbom *et al.* 1993; Modig *et al.* 1997). Our study suggests

that these differences persist through all age classes and may be related to females reaching sexual maturity much earlier than males.

Arrival date, duration and mass of the mid-year haul-out influenced which underyearling elephant seals returned to Macquarie Island for the moult. It would be useful to test for this in other age classes returning for the mid-year haul-out. Nevertheless, this indicates that differences in haul-out behaviour may be a useful indicator of the condition and survival of the animals involved.

The model developed with this data set can potentially be applied to data sets of other phocid seals to examine movement rates and haul-out behaviour. Results may have implications towards population ecology, conservation and management of the species.

Appendix

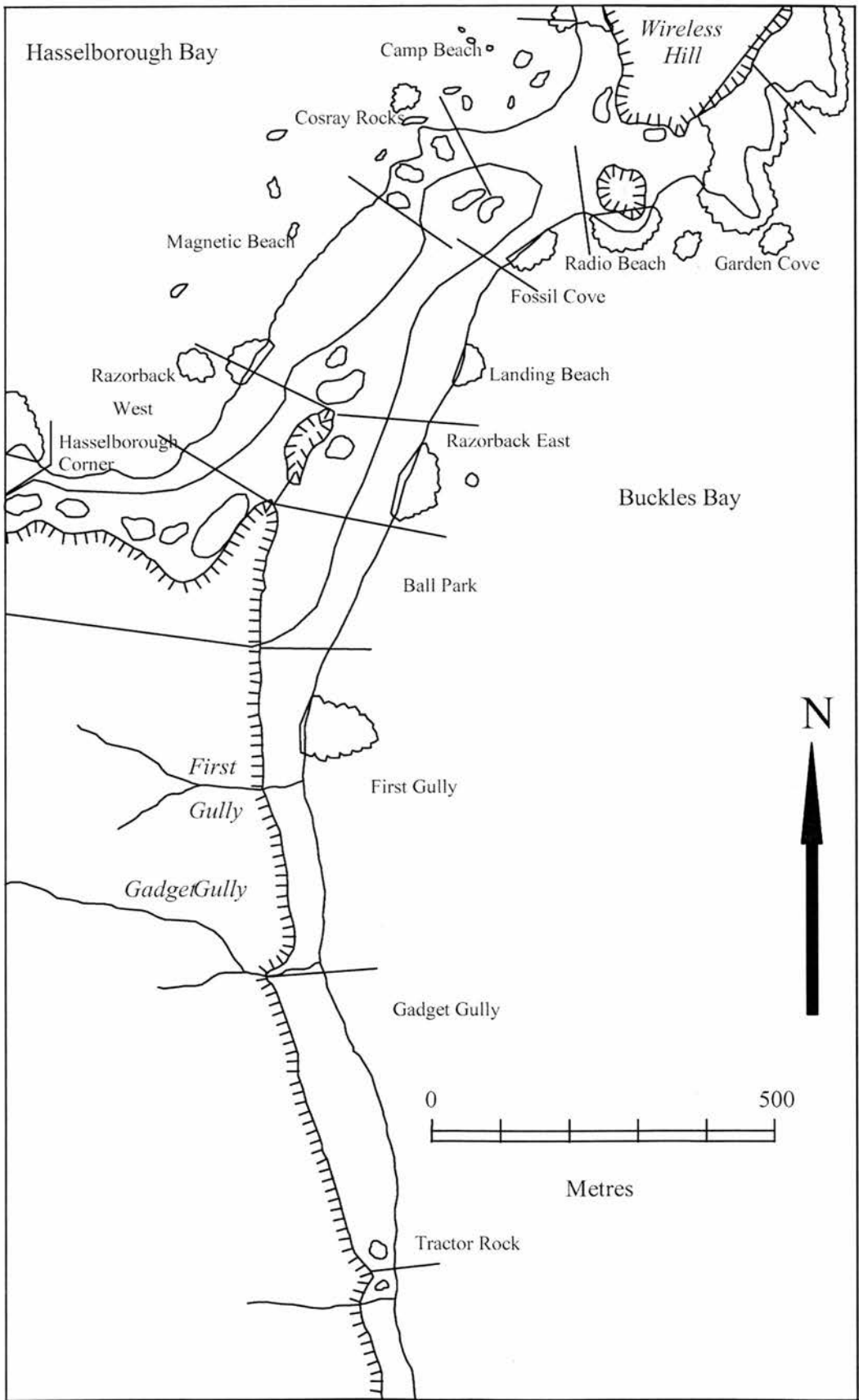


Fig.1 Map of the Isthmus study area on Macquarie Island.

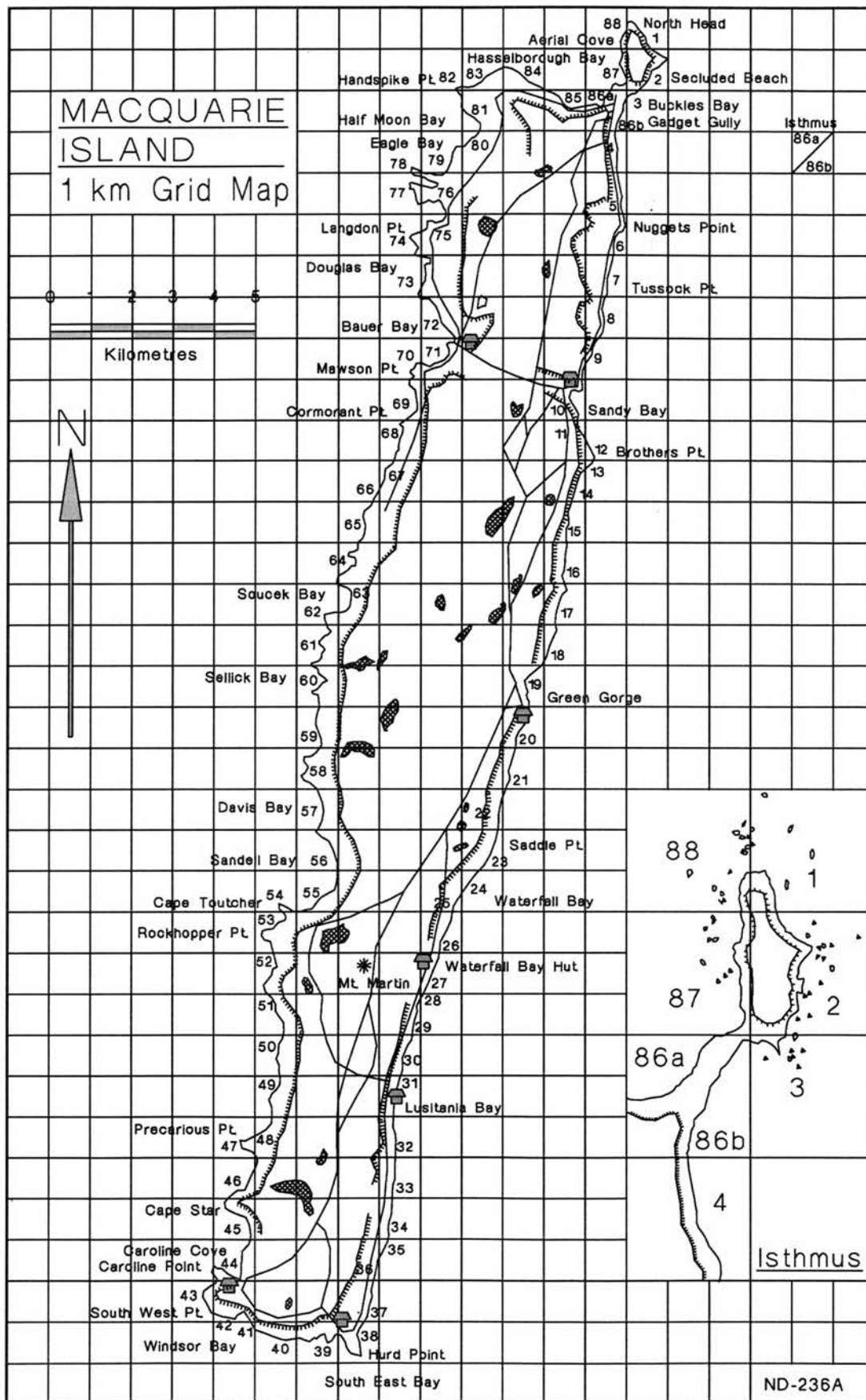
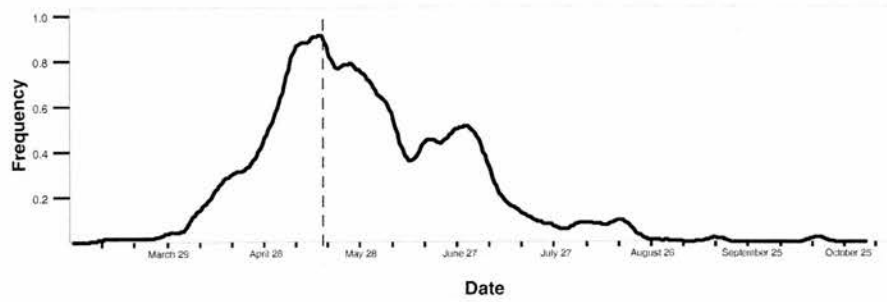
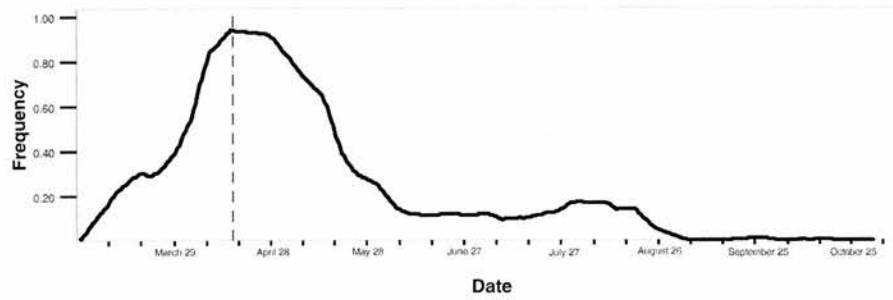


Fig. 2 Grid map of Macquarie Island.

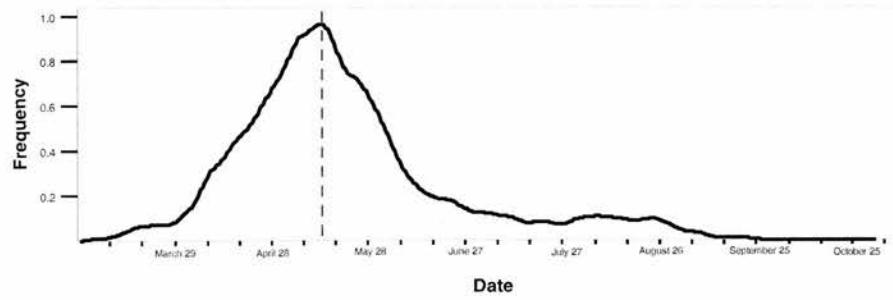
(a) Underyearling males



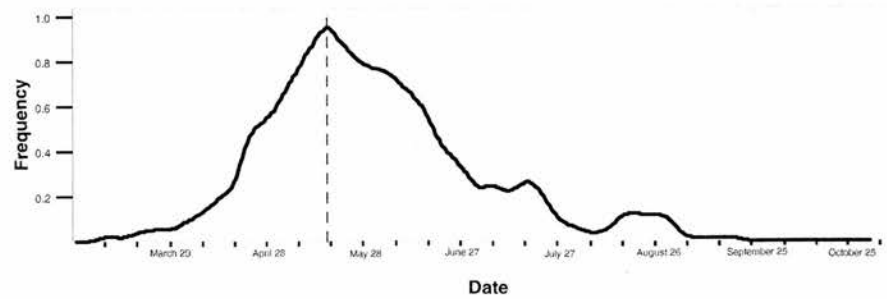
(b) 1 - year old males



(c) 2 - year old males



(d) 3 - year old males





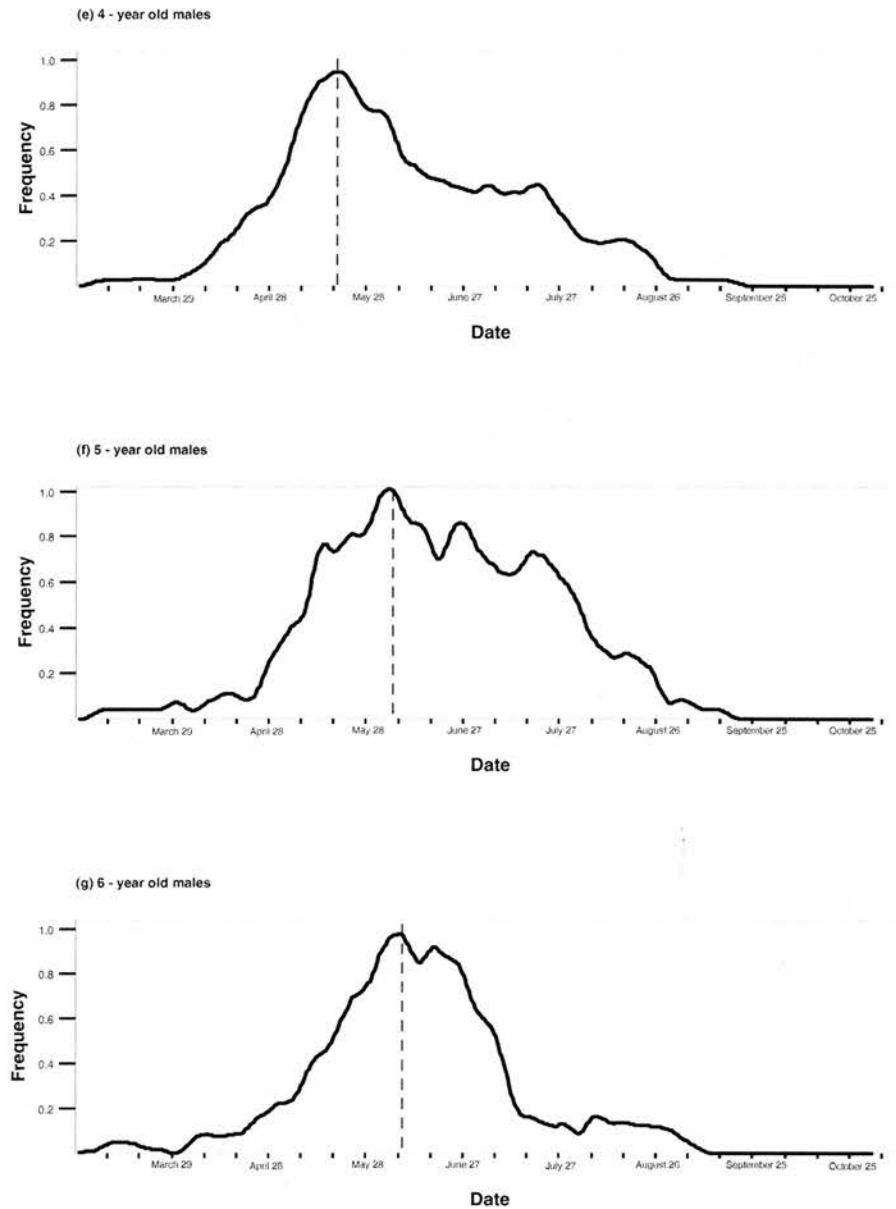
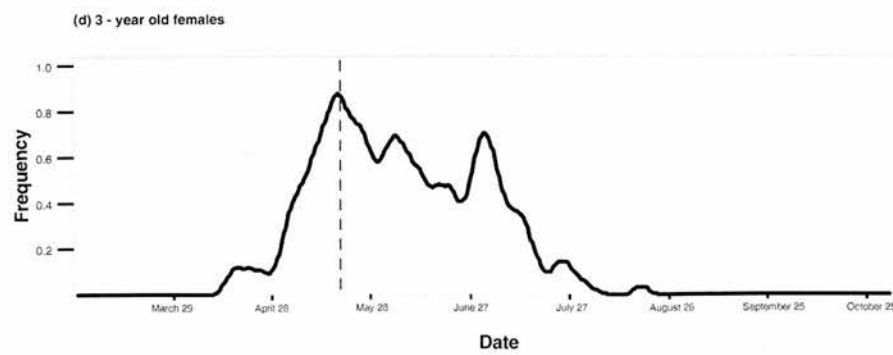
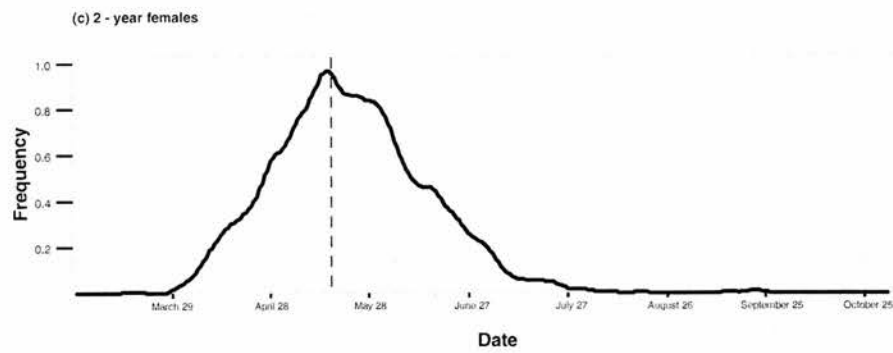
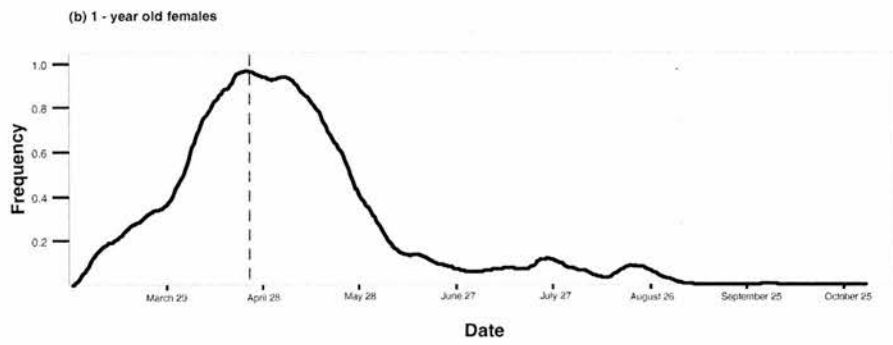
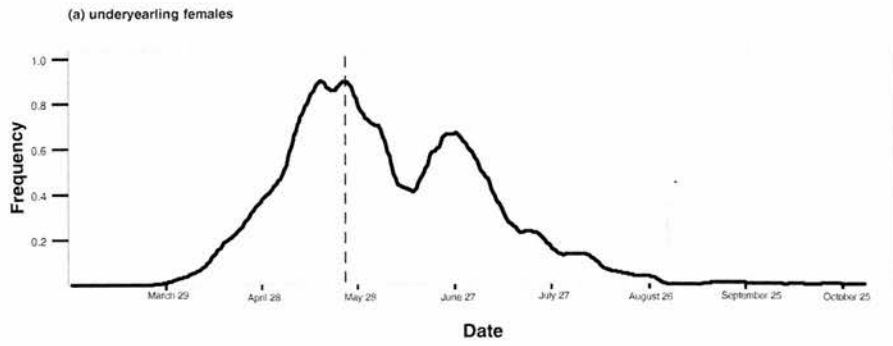


Fig. 3 Standardized curves for the total number of male elephant seals shore (underyearling to 6-years old) for the mid-year haul-out.



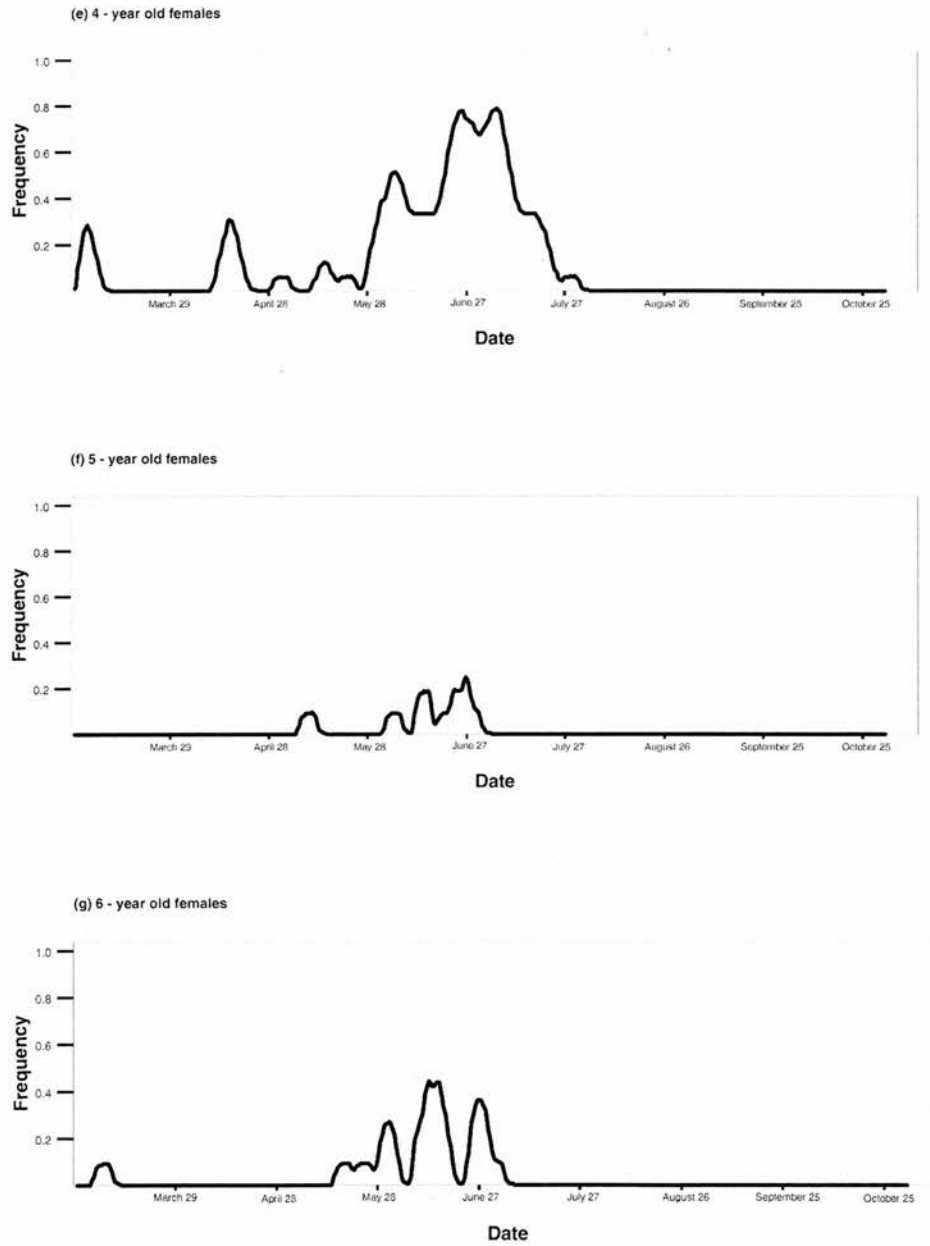


Fig. 4 Standardized curves for the total number of female elephant seals shore (underyearling to 6-years old) for the mid-year haul-out.

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