POPULATION BIOLOGY, THERMOREGULATION AND SITE PREFERENCE OF THE NEW ZEALAND FUR SEAL, *ARCTOCEPHALUS FORSTERI* (LESSON, 1828), ON THE OPEN BAY ISLANDS, NEW ZEALAND

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ABSTRACT

Population biology, behavioural thermoregulation and site preference of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson, 1828) are described for the breeding colony on Taumaka, Open Bay Islands, Westland, New Zealand (43°52'S, 168°53'E), from data collected at irregular intervals between October 1974 and February 1977.

Sixteen fur seals (6 females : 10 males) were shot and aged by counting growth rings in a canine tooth. The age determinations suggest that females produce their first pup at age 5 years, and that bulls attempt to hold territories by age 8 years, but rarely are successful until about age 10 years. During their delayed 'social maturation', bulls may gain experience necessary to maximize reproductive success once territorial. A bull's territorial success ultimately depends on his fighting ability, which depends largely on the presence or absence of lower canine teeth. Canines are broken off during fighting; bulls without lower canines rarely defeat an opponent.

Females prefer sites on the rookery which provide pools of water, shade, and direct access to the sea. Both sexes use water and shade for cooling.

The theoretical 'mean' pupping date on Taumaka is 10 December. The sex ratio at birth is about 1:1. Males are heavier than females at birth, and are heavier and larger than females at mean age 55, 140, 235 and 290 days. Pups are weaned at about 300 days. Pup growth rates differed dramatically between 1974/75 and 1975/76. For example, male pups were about 22 percent heavier at 235 days in 1975/76 than in 1974/75. Differential growth rates probably are a consequence of food availability to lactating females and differing environmental temperatures between seasons.

Mortality to age 50 days is 20 percent. First year mortality may be 50 percent. Starvation may account for 70 percent of all deaths to age 50 days. Other causes of death include suffocation, drowning, trampling and predation. Human disturbance can kill pups indirectly by causing panic on the rookery. Tagging pups with monel metal cattle ear tags may increase mortality.

About 1400 pups are born on Taumaka annually. Using this figure for pup production, and incorporating reproductive data from other fur seal species (where none exist for the New Zealand fur seal), the estimated population of pups, females of breeding age and bulls on Taumaka is about 3700. The estimated population size associated with Taumaka, either through birth or by breeding on the rookery, is about 6000-6500. Using these estimates, and incorporating population data from the Northern fur seal, the estimated population growth rate on Taumaka is about 2 percent per annum.

CHAPTER ONE

GENERAL INTRODUCTION

The New Zealand fur seal (*Arctocephalus forsteri* Lesson) is one of eight recognized species within the genus (Repenning *et al.* 1971). Like all other members of the Arctocephalinae, it was exploited almost to extinction by commercial sealers during the early nineteenth century. Fur seals under New Zealand jurisdiction were given total protection in 1894, although there were limited harvests under governmental regulation in 1913-1916, 1922 and 1924. Under mounting pressure from the commercial fishing industry, some killing was permitted in 1946 in the vicinity of Stewart Island and in the south of the South Island; in all, 6187 fur seals of both sexes and various ages were taken (Sorensen 1969a). Fur seals within the New Zealand region[1] have received total protection since that time.

Early accounts of the New Zealand fur seal in New Zealand and Australia[2] were often anecdotal, and the literature deals primarily with problems of taxonomy, the species' natural history, and exploitation (e.g. Allen 1899; Chapman 1893; Clark 1873, 1875; Forbes 1892; Hector 1871, 1892; Hutton and Drummond 1904; McNab 1907; Thompson 1921; Waite 1909; Wood Jones 1925a, 1925b). Little detailed research on the biology of the New Zealand fur seal was undertaken until the early 1960's, when, in response to the accusations of fishermen that the fur seals were severely depleting commercial fish stocks, Street (1964) made a study of the fur seal's diet. He found that they were feeding principally on non-commercial species and cephalopods, and concluded that they posed no threat to the fishing industry. Since then, there has been a growing interest in the general biology of the species, which is reflected in studies undertaken on their diurnal rhythm (Stirling 1968a), history and management (Sorensen 1969a, 1969b), distribution and abundance (Crawley

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[1] The New Zealand region, as used in this thesis, includes North and South Island, New Zealand, Stewart Island, Chatham Island, and the New Zealand Subantarctic Islands, i.e. Antipodes, Auckland, Bounty, Campbell, Macquarie and Snares Islands.

[2] The fur seal of South and Western Australia has been shown to be conspecific with that found in the New Zealand region (see King 1968, 1969; Repenning *et al.* 1971; Shaughnessy 1970; Stirling and Warneke 1971). For this thesis, New Zealand fur seal will refer to the population found in the New Zealand region only, unless stated otherwise.

1972; Csordas and Ingham 1965; Falla 1965; King 1976; Stonehouse 1965; Wilson 1974a, 1974b), pup growth (Crawley 1975; Crawley and Brown 1971), mother-pup relations (McNab 1974; McNab and Crawley 1975; Wood 1970), vocalization (Brown 1974; Stirling and Warneke 1971), activity budgets (Crawley *et al.* 1977; Stark 1975), anatomy and physiology (Ling 1965, 1970; Miller 1975c; Wells 1978), prehistoric exploitation (Smith 1977), natural history (Crawley and Wilson 1976; Gaskin 1972; Marlow and King 1974), annual cycle (Ling 1969; Miller 1975a), evolution and systematics (King 1968, 1969; Miller 1975b; Shaughnessy 1970; Stirling and Warneke 1971), and aspects of their general behaviour (Gentry 1973, 1975; Miller 1971, 1974a, 1974b, 1974c, 1975d; Stirling 1970, 1971a, 1971b; Stirling and Gentry 1972).

Despite the research efforts noted above, in 1974 our knowledge of the population biology of the New Zealand fur seal, and of aspects either related to or likely to affect population biology, such as thermoregulation and site preference, was minimal. The importance of collecting data on population biology of marine mammals, apart from its basic scientific value, is that such data are essential for the development of sound conservation, exploitation or general management programmes. The growing world-wide interest in and concern for the welfare and survival of marine mammals has drawn attention to problems of legislation, conservation and management of marine mammals as well as to our lack of knowledge on certain aspects of their general biology (see Eberhardt 1977; Eberhardt and Siniff 1977; Gulland 1971; Scheffer 1973, 1975). However, the literature on population studies of marine mammals is continually growing, particularly for those species of commercial importance. The most studied pinniped of all is the Northern fur seal, which is harvested annually under international agreement. Research is continuing on various aspects of its population dynamics and general biology (e.g. Bartholomew 1953; Chapman 1961, 1964; Kenyon *et al.* 1954; Lander 1975; Marine Mammal Division 1977; Nagasaki 1961; North Pacific Fur Seal Commission 1975). To a lesser degree, the same has occurred with other pinniped species (e.g. Bertram 1940; Bigg 1969; Carrick and Ingham 1962b; Coulson and Hickling 1964; Hewer 1964; Laws 1953b, 1956a, 1956b, 1960; Lett and Benjaminsen 1977; Mansfield 1958; Mansfield and Beck 1977; Sergeant 1973; Siniff *et al.* 1977; Smith 1973; Stirling 1971c; Summers *et al.* 1975).

When this research programme began in 1974, it was felt by the Fisheries Research Division, Wellington, that attempts should be made to collect data 'relevant' to the population biology of the New Zealand fur seal, e.g. data on the reproductive ages of males and females, recruitment, mortality, growth rates, and reproductive rates. The original aims of this study, therefore, were to collect data on the population biology of the species, on which legislative considerations regarding the management of the species could be based should the question of management ever arise. With the introduction of the Marine Mammals Protection Act 1978, the likelihood of a management programme ever being required for the New Zealand fur seal diminished appreciably. Nevertheless, should the argument ever be advanced that fur seals are damaging a commercial enterprise (as was the situation which led to the 1946 open season) or that commercial exploitation of fur seals is both feasible and desirable, then basic knowledge of the general biology and, more importantly, of the population biology of the species is not only desirable, but necessary for the development of a sound management programme.

Following the above considerations, the principal objectives of this study were as follows:

1) to collect data on population biology, including: the number and sex of fur seals present on the rookery at different times during the breeding season; the sex ratio, growth rate and mortality of pups; and the ages at which males and females became sexually and socially (i.e. reproductively) mature (from autopsied animals killed under permit);
2) to identify preferred sites on the rookery and to establish which factors influence the selection of these sites (the quantity and quality of sites available could influence aspects of population biology, such as pup production, growth and survival, and the reproductive success of individual bulls);
3) to attempt to estimate the size of the breeding population on Taumaka; and, using data from other fur seal species whenever necessary, to speculate on the potential growth of the population on Taumaka and within the New Zealand region.

During the 1974/75 season, it soon became apparent that certain unforeseen constraints were going to necessitate a change in emphasis from the original aims of this study. It was originally planned to take a maximum of 100 adult fur seals over two years in order to collect data on their age and reproductive status. From previous behavioural studies, it was suggested that virgin females mated for the first time early in the season (Crawley and Wilson 1976; Miller 1975a). Females observed copulating early in the season before pupping commenced were to be killed in order to determine their age, to determine if they had just been mated for the first time, and to collect data on general reproductive biology. Other females were to be taken throughout the season, in order to collect additional data on reproduction. Bulls were to be taken early in the season before most territories were claimed, and also later in the season after most territories were occupied, in order to collect data on the age at which bulls first begin to attempt to hold territories, and the age at which they are successful in this endeavour. However, these aspects of the research programme were not carried out to their full extent for three reasons:

1) it was extremely difficult to retrieve animals shot on the rookery, or to autopsy these animals on the spot, without the danger of attack from territorial bulls. This difficulty increased as the breeding season progressed and bulls became more aggressive. A portable wire-mesh barrier was constructed for protection while on the rookery, but this was not successful; attacking bulls were able to penetrate the barrier with ease;
2) any disturbance by us on the rookery usually resulted in the females panicking and rushing to the sea. Repeated disturbances of this nature could be a factor in pup mortality (e.g. through trampling and abandonment) and may also have an effect on the population structure and reproductive success of the disturbed fur seals; and
3) it was felt that the collection of a large, random sample of animals of breeding age would have had too detrimental an effect on the stability of this breeding colony.

In addition to the effects noted above, the removal of a large number of breeding bulls may have resulted in a decrease in the overall age structure of bulls holding territories for the first time during the height of the breeding season. With these factors in mind, I felt that it was preferable to retain the study population on Taumaka in as near an undisturbed condition as possible, both for the general welfare of the colony, and for the sake of future research. The Taumaka colony is the best-studied population of New Zealand fur seals within the New Zealand region.

Because of the considerations noted above, finally only 6 female and 10 male adults were killed (under special permit issued by the New Zealand Wildlife Service, Department of Internal Affairs, Wellington); sufficient to provide an indication only of the age of first breeding in males and females. From these data, a working hypothesis was formulated on the age of sexual and social maturity in males, and sexual maturity in females (see Chapter 3 for details).

Because far fewer animals were killed than originally planned, there was a shift in emphasis in the overall theme of the thesis. This shift was away from reproductive biology and towards other aspects of population biology (pup growth and mortality) and aspects which affect population biology (behavioural thermoregulation and site preference).

Many data used in this thesis are from other pinniped species, particularly the Northern fur seal and the Cape fur seal. Both of these species are commercially exploited. In Alaska, bachelor Northern fur seal bulls (aged 3-4 years) are harvested annually. These individuals segregate themselves from the breeding animals, so that there is no disturbance to the rookery during the harvest. A harvest of this nature would have little effect on the structure of the breeding population on the rookery provided that the number of real and potential breeding bulls was not drastically reduced. If the number of potential territorial bulls was drastically reduced, then it follows that competition for rookery sites would decline. If this were to occur, then one could expect a possible decline in the age structure of territorial bulls. This in itself may not be too serious, provided that the behavioural patterns of the younger bulls did not alter or disrupt the breeding population of females. If the breeding pattern of females was disrupted, then this could affect the overall breeding success of the population, for example through missed pregnancies or an increase in pup mortality. A different harvesting strategy is followed for the Cape fur seal in South Africa. In this case, it is predominantly the pups (aged 6.5-10.5 months old) which are harvested. In management terms, a harvest of this nature may have no detrimental effect on the structure of the adult population, provided an 'excess' number of pups were not taken, and provided that there were no long-term adverse effects on the overall breeding population caused by disturbance during harvesting. It may be that the harvesting of pups would have little effect on overall pup mortality; there may be fewer pup deaths due to natural causes, with the difference made up by pups harvested. Were the pup harvest to result in a decrease in the overall population size of the population, then it is possible that the age at which males and females start breeding would decline. Such a situation may have occurred with Southern elephant seals, where the reproductive age of females and males of an exploited population (South Georgia) was less than the reproductive age of males and females from an unexploited population (Macquarie Island;

see Carrick *et al*. 1962).

Although the structure of an exploited population may differ from that of an unexploited population, and although the population structure of one species (e.g. the Northern fur seal) may differ from the population structure of another species (e.g. the New Zealand fur seal), the use of data from species other than the one under study can be justified provided that no data on the species in question are available, that the use of the data is suitably qualified and the results obtained from such data are given as speculative and subject to change. For example, data from the Northern fur seal have been applied to the Grey seal (Hewer 1964), Kerguelen fur seal (Payne 1977), and Cape fur seal (see Shaughnessy 1977).

The same argument holds true for the use of minimal data such as that for the New Zealand fur seal reproductive data in this thesis. Although it is undesirable that ideas about such subjects as the reproduction of the New Zealand fur seal should be based on what clearly are too few facts, unfortunately it is often necessary to proceed with such an exercise because the collection of more substantial information is either impractical or unjustified. In such cases, due recognition of the speculative nature of conclusions drawn must be made. Consequently deductions are presented in this thesis which are based on a small sample size, or are based on data from another pinniped species, but they are given as speculative, and should not be misconstrued as fact.

The age of each adult taken was established by counting growth rings in a canine tooth. This is an effective technique for aging most pinniped species, and has been shown to be effective for fur seals (see Klevezal and Kleinenberg 1967 for a review of the use of growth rings for aging mammals, including pinnipeds). Males were considered to be sexually mature if spermatozoa were present in the epididymes, and females were considered to be sexually mature if either a Graffian follicle or corpus luteum was present. Because the largest bulls collected were aged 10 years or older, and allowing for natural variation in the size of individual animals of the same age, it was assumed that all 'large' bulls observed were aged at least 10 years. Bulls which held territories during the height of the breeding season were considered to be socially mature.

Non-parametric statistical tests were used throughout this thesis for one or more of the following reasons. Either the data were of a nominal scale, they were not normally distributed, or they had unequal variances. These conditions make the use of parametric statistical tests undesirable.

All field studies were carried out on Taumaka, Open Bay Islands, Westland, at irregular intervals from October 1974 to February 1977.

This thesis is divided into discrete chapters, each of which has an introduction and discussion. To avoid needless repetition, the general methods used throughout the study are presented in one chapter, but additional methods sections are included in chapters where more details of specific methods are essential to understand the material. A general discussion is included at the end, which contains discussion and speculation on factors which may have an effect on the population structure of the New Zealand fur seal during the breeding season. The major findings of this research are listed in the summary, which follows immediately after the general discussion.

CHAPTER TWO

DESCRIPTION OF STUDY AREA AND METHODS

2.1. Description of study area

All field work was carried out on Taumaka, the larger of the two Open Bay Islands, located 4.8 km off the mouth of the Okuru River, Westland (43°52'S 168°53'E; Figures 2.1 and 2.2). The descriptions of topography, vegetation etc. which follow are for Taumaka, but in general they apply equally to Popotai, the smaller of the two islands.

(a) General description of Taumaka

Taumaka is composed of Oligocene limestone with some blue-grey marine siltstone (Mutch and McKeller 1964), and is covered by a glacial till ranging in depth from about 1.5-2.0 m (Burrows 1972). The island is about 12 ha in area, of which 10 ha is covered in bush, with the exposed rocks of the rookery making up the remaining 2 ha. The long axis of the island is orientated in a NE by SW direction. The sloping rocks of the rookery are found on the NW coast only; the remaining coasts consist of vertical cliffs of about 10-30 m height which drop directly into the sea. Although no beaches are found on these coasts, occasional large boulders are present which are used by non-breeding fur seals as resting platforms. Taumaka is divided by a channel at the SW end, which separates an area of about 0.5 ha from the rest of the island. Large permanently exposed rocks and extensive reefs, which are exposed at low tide, are found just offshore from the rookery and are used extensively by non-breeding fur seals (see Miller 1971; Wilson 1974a). Interspersed amongst the reefs are numerous deep channels, where pups play during low tides.

The vegetation is extensive and varied, but primarily consists of a tangled, almost impenetrable mass of kiekie (*Freycinetia banksii*) with a thin band of native bush about 10 m in width bordering the rookery. This band is comprised mostly of mahoe (*Melicytus ramiflorus*), hebe (*Hebe elliptica*) and seven-finger (*Schefflera digitata*), with some interspersed broadleaf (*Griselinia littoralis*), tree fuchsia (*Fuchsia excorticata*) and cabbage trees (*Cordyline australis*). Small, open areas (< 250 m^2) of sedge (*Carex comans*) are present, particularly on the NE and SW ends of the island. These areas are used by non-breeding fur seals and by females and pups later in the season. Fern banks consisting primarily of *Asplenium obtusatum* are common.

The vegetation on Popotai is similar to that on Taumaka, except that no kiekie is present.

Further descriptions of the islands, their vegetation and bird life can be found in Burrows (1972), Cockayne (1905) and Stirling and Johns (1969).

(b) Climate

The sea state and the following weather conditions were recorded daily: air temperature (°C), relative humidity, maximum air temperature for the previous 24 hrs, minimum air temperature for the previous 24 hrs, rainfall, wind direction and wind velocity. An attempt was made to make all daily weather observations between 0700 and 0800 hrs, New Zealand Standard Time, but because field work took precedence over meteorological observations, this was not always possible. These data are deposited with the Department of Zoology, University of Canterbury, Christchurch.

The climate of Taumaka is wet and windy, but generally mild. Mean monthly maximum and minimum air temperatures for 1974/75 and 1975/76 combined ranged from 17-25°C and 9-15°C respectively. Some rain fell **on** 59 percent of the days, and 1 mm or more rain fell on 46 percent of the days. The amount of rainfall ranged from 165-290 mm per month. These data are given in Table 2.1. Sea-breezes were persistent during the day, and occasionally winds as high as 65 km/hr were recorded.

TABLE 2.1. Mean maximum and minimum air temperatures and the amount of rainfall on Taumaka, Open Bay Islands, November-January, 1974/75 and 1975/76.

	1974/75			1975/76		
	Nov.	Dec.	Jan.	Nov.	Dec.	Jan.
Mean max. air temperature °C	20.3	22.5	25.0	17.4	18.3	20.6
Mean min. air temperature °C	11.3	13.9	14.7	10.0	9.3	11.2
Days with rainfall	16	19	18	18	19	18
Days with > 1.0 mm rainfall	11	14	13	16	17	11
Total rainfall (mm)	168.7	185.7	166.1	290.7	176.1	184.3
Max. 24 hr rainfall (mm)	30.3	32.0	40.4	43.6	30.7	28.6

(c) General description of the rookery

The rookery at Taumaka extends along the length of the N-NW coast, and ranges in width from less than 25 m to greater than 60 m (Figure 2.2). It is composed of sharp, irregular, limestone flats and rocks, with interspersed guts oriented in a NW-SE direction (i.e. at right angles to the long axis of the island), and occasional precipitous cliffs. Large boulders are scattered about the rookery, particularly in the vicinity of guts. The rookery is exposed to the prevailing winds and seas, but the effects of these are moderated by extensive offshore reefs. A fringe of native bush, much used by non-breeding fur seals, females and pups, adjoins the rookery along its length (Plate 2.1). Typical views of the rookery are given on Plate 2.2. For a general description of New Zealand fur seal habitat and distribution see Crawley and Wilson (1976) and Wilson (1974a).

Observations of fur seals were made at two areas, designated as Study Area I and Study Area II. Detailed descriptions of both are given in Chapter Five, Preferred Sites.

2.2. Methods

The general methods used are given below. A separate methods section is included in each chapter where additional details were deemed necessary.

(a) Logistics

(i) Access to Taumaka

Access to and from Taumaka was usually by helicopter. The pilot was able to land on a natural, sedge-covered clearing about 30 m from the hut, which expedited the shifting of gear and goods. When a helicopter was not available a fishing boat was hired. Gear was landed on a large rock at the base of a 10 m cliff situated about 50 m from the hut, and hauled up the cliff face by rope. Such landings were often difficult and time-consuming, particularly during rough seas and stormy weather. Regardless of the means of landing, disturbance of the fur seals on the rookery was minimal.

(ii) Living accommodations

A two-man hut measuring about 2.5 x 3.0 m was built on the island in 1969 for use by researchers. This was used throughout the study, and was enlarged to about 2.5 x 6.0 m in October 1975. Potable rain water was collected off the roof in sufficient quantities for all uses during each visit. Supplies for the summer were taken to the island on the first trip of the season, and fresh supplies were brought out during periodic visits by the helicopter pilot and during personnel change-overs. As a safety precaution, at least two people were on the island at all times.

(b) Observational studies

(i) Hides

All observations of fur seal behaviour at the two study areas were made from hides. At Study Area I, the hide consisted of a perch built on a tripod in amongst the bush during the 1974/75 season. This was replaced the following season by an enclosed wooden hide, large enough to hold two observers comfortably. The hide is elevated about 1 m above the rookery and, because area I is relatively open, it affords an unobstructed view of the entire study area (Plate 2.3.a). Access to the hide is through the bush from behind.

At Study Area II, the hide built in 1970 by E.H. Miller for his research on fur seal behaviour was renovated and used (see Miller 1971). It is an enclosed wooden structure, but can hold only one observer (Plate 2.3.b). It was built on a large rock in amongst the bush, so that the observer looks out over the bush and down onto the rookery. This is ideal, because area II is covered by large rocks and boulders and includes two guts. Were the hide level with the study area, the overall view would have been greatly impaired. An access track was cut through the kiekie to the rear of the hide, thus minimizing any disturbance to the fur seals.

The presence of an observer in a hide had no apparent effect on fur seal behaviour. Occasionally, they would be startled momentarily by our approach, but within minutes they would settle down and presumably return to their previous behavioural patterns. Were one to move about outside a hide, and in full view of the rookery, then a general panic by females would often ensue.

(ii) Observational schedule

When weather conditions permitted, observations were made between 0500-2000 hrs New Zealand Standard Time over two consecutive days at each of the study areas. During the 1974/75 season, the time spent in a hide on any one occasion varied, depending on the weather conditions and other ongoing research projects. The following season, a schedule was set up as follows: day one, in hide 0500-0900 hrs and 1300-1700 hrs; day two, in hide 0900-1300 hrs and 1700-2000 hrs. The four hours on - four hours off schedule allowed for observations to be made for all daylight hours over the two day period, and it set aside at least four hours a day for other research projects and camp duties.

No extensive night-time observations were made because of poor visibility on the rookery at night, and because of the possibility of attack from bulls lying on or near the track.

(iii) Observations from the hide

A census of all fur seals on the study area was taken every hour on the hour during observations. During the 1974/75 breeding season, 175 hourly censuses were taken at area I, and 225 at area II. The following season, 310 hourly censuses were taken at each study area. All fur seals present were arranged into classes, modified slightly from those given by Miller (1971) and Wilson (1974a), (see also Crawley and Wilson 1976), *viz.*:

Territorial bull: fully grown male, holding a territory on the rookery.

Bull: fully grown male, but not holding a territory on the rookery.

Subadult male (SAM): obviously a male, but lacking the size and thick, heavy neck of a bull.

Female: obviously female, based on external characteristics, i.e. size and general body shape.

Neuter: older than two years old, but sex indeterminate from a distance.

Yearling: between one and two years of age, distinguished early in the year by coat colour and size, but difficult to differentiate from a neuter later in the year.

Pup: pup of the season, i.e. up to one year of age.

During each census the position of each individual was marked on a map of the study area, and the following conditions recorded: date, time of day, air temperature, blackbulb temperature, cloud cover (as a fraction of 8, i.e. 1/8, 2/8, 3/8 ... 8/8) and an estimate of wind velocity and sea state. Air temperature was measured using a mercury bulb thermometer suspended in the shade in an exposed portion of the hide. Blackbulb temperature was measured using a standard blackbulb thermometer suspended in direct sunlight near the hide. The position of each fur seal in relation to shade, fresh water and the sea was recorded during each census when there was direct sunlight on the rookery. Study area maps were printed from freehand drawings for the 1974/75 season. For the following season, maps were printed from tracings of a photograph taken from the hide for each study area. Line drawings based on aerial photographs of the rookery would have been preferable, but no aerial photographs were available at the time.

Notes were taken on general biology and behaviour of the fur seals, including the arrival and departure of bulls and females; inter- and intrasexual conflict; the presence and extent of wounds; the presence or absence of lower canines on bulls; births; deaths; the movement of marked pups; copulations and attempted copulations.

Approximations of rock temperature were recorded from five locations on Study Area I during the 1975/76 season. Thermistors were placed in shallow holes chipped out of the rock, and embedded in concrete with the tip of the probe just under the surface. Cables from each thermistor led back to the hide, where they individually could be plugged into a read-out unit, which gave the temperature as a number on a potentiometer. The number was then converted to degrees C from a conversion table developed for each individual thermistor. The unit had an accuracy of ± 0.1°C. These data are not presented in this thesis, but will be used as baseline data for an investigation into fur seal thermoregulation.

(iv) Pups

Pups which wandered near the bush line of the study areas and were therefore readily accessible were captured, sexed, weighed, measured, given an individual temporary mark and released. Marked individuals were used to study pup movement. The measurements recorded are given later in this section. Pups were individually marked by fur-clipping. For example, pup 2HR had two spots clipped in a row on its head, and pup 1MB had one spot clipped on the middle of its back. The thermal properties of the coat were not greatly affected by clipping, because just the tip of the fur was cut. The marks showed up as grey spots against a dark brown to black background (Plate 2.4.a). They caused no apparent discomfort, and were plainly visible two months later. Many could still be recognized four months later, but with difficulty.

As many pups as possible from the entire rookery were caught during the first week of February (mean pup age 55 days) in 1975 and 1976, and from half the rookery in 1977. The pups were sexed, weighed, measured, permanently marked, temporarily marked for recognition at a distance and released. During return trips to Taumaka in May (mean pup age 140 days) and August (mean pup age 235 days) 1975 and 1976, and in September (mean pup age 290 days) 1976, pups were again captured, sexed, weighed and measured, but were given only a temporary mark before release.

In February, pups were easy to capture because they tended to hide under rocks or in cracks and guts as we approached. Once captured, they were easy to handle because of their small size. As the pups grew older, they often went into the sea as we approached, making their capture much more difficult. Also, the pups became much more difficult to handle as they grew larger. Consequently, our catch per unit effort decreased considerably after the weighing and measuring in February. Pup catch data for the study are given in Table 2.2.

TABLE 2.2. Number and sex of pups weighed and measured on Taumaka, Open Bay Islands.

		Males	Females
February	1975	253	262
May	1975	88	85
August	1975	94	81
February	1976	429	392
May	1976	92	68
August	1976	88	68
September	1976	88	79
February	1977	186	177

Pups were caught, measured, weighed and marked by a team of three to four persons. For consistency, I took all measurements and applied all marks or tags. The other members of the team took turns as catchers and recorder. All data were recorded on pre-printed forms, cut to fit a pocket-sized field notebook. The data were later transferred onto data cards for computer analysis.

Pups were caught by hand and were processed and released near the site of capture. They were weighed in either a hessian or a plastic fibre bag suspended from a hand-held spring balance (Salter, model 235). Weights were recorded to the nearest 50 g. The spring balance was periodically adjusted to compensate for the increased weight of the bag as it became wet. Plastic fibre bags were superior to hessian bags because their weight remained constant, no water being absorbed. The linear measurements taken were: anterior length of left foreflipper, curvilinear length and axillary girth (Committee on Marine Mammals 1967; Figure 2.3). Because of the difficulty in holding pups straight and still, standard lengths were not taken.

In February, pups were permanently marked by placing a monel metal cattle ear tag (Stockbrands Co. Pty Ltd, Mt Hawthorn, Western Australia) through the trailing edge of either the left (male) or right (female) foreflipper (Plate 2.4.b). Each tag had the letters FS and an individual four digit number stamped on one side, and Dept of Zoology, Univ. Canterbury, Christchurch, stamped on the other. Care was taken to place the tags through connective tissue only. A disinfectant was applied to the tag site as a precaution against infection. These tags were no longer used after 1975, because of doubt as to their effect on pup survival. For the following two seasons, pups were permanently marked by clipping off the cartilaginous tip of a digit on a hindflipper (Plate 2.4.c). This resulted in a year mark only, but apparently had no long-term adverse effect.

During trips to Taumaka subsequent to tagging, pups were temporarily marked during weighing and measuring by one of three methods. Either 'Raddle', a chalk-like stock marker, was rubbed onto their backs, or 'Aerosine', an aerosol stock marker, was sprayed onto their backs, or they were fur-clipped. The chalk-like stock marker was the least effective. It was difficult to apply when the pups were dry, and tended to wash or rub off once the pups were wet. The aerosol marker was better, though it tended to rub or wash off within a few hours of application. The best method was to clip a small patch of fur off a specific spot on the pup's back. Using this technique, there was no question as to whether or not the pup had previously been weighed and measured during the trip.

Fresh dead pups were collected from the rookery whenever opportunity permitted. The measurements taken and the data collected are given in the following section.

(v) Collection of specimens and autopsies

As part of this study, 10 male and 6 female adult fur seals were killed on Taumaka under a special permit issued by the Wildlife Service, Department of Internal Affairs, Wellington. All were shot in the head using a silenced .22 rifle. Immediately after death, the animal's body temperature was taken, both rectally and by plunging a mercury bulb thermometer through a knife cut into the pleural cavity. The animal was weighed to the nearest pound (later converted to kilograms) using a spring balance suspended from either a tripod or a tree limb, or from a heavy branch suspended between two rocks. The following linear measurements were taken, following the guide lines set by the Committee on Marine Mammals, American Society of Mammalogists (1967): standard length, curvilinear length, anterior length of left foreflipper, anterior length of left hindflipper, axillary girth and blubber thickness across the sternum (Figure 2.3). Gonads were removed and preserved in either Bouin's solution, or 10 percent seawater formalin. All uteri and bacula were collected, as were all skulls. The latter were cleaned in the field either by placing in the sea or by boiling. The length of the intestine was measured, and stomach contents collected. The weights of all major organs were recorded. Samples of blubber, muscle and liver were collected for future pesticide and heavy metal analysis. A gross examination for internal and external parasites was made, and those found (or representatives of those found) were preserved and returned to the Department of Zoology, University of Canterbury, as were all the other samples collected.

All dead pups collected were weighed and measured (following the same procedure as used for adults). A gross field autopsy was performed to try and determine cause of death. Either the entire skull was collected, or else the jaws were collected and preserved in 10 percent seawater formalin.

(vi) Aging technique

Each dead adult was aged by counting the growth rings, or 'increment lines', on etched and stained longitudinal sections of a canine tooth (Plate 2.5). The ability to age pinnipeds from growth rings in canine teeth was first recognized contemporaneously and independently by Laws (1953a) for the Southern elephant seal, and Scheffer (1950a) for the Northern fur seal. Since then, this technique has been successfully used for many, but not all, pinnipeds (see Klevezal and Kleinenberg 1967 and Laws 1962 for general reviews of age determination in pinnipeds based on growth rings in teeth and bone, and also Morris 1972 for a review of age determination in mammals). In the absence of known-age material, major growth rings were assumed to be annual. The procedures used for tooth preparation were based on those outlined by Carrick and Ingham (1962a) and Stirling (1969b).

While in the field, canine teeth were left in the skulls, which were cleaned of flesh and air-dried. In the laboratory, one canine tooth (the left lower when present, otherwise whichever intact canine tooth was present) was cut in half longitudinally using a thin bladed hacksaw. Each half was polished on progressively finer grades of emery paper while it was under water. The teeth were then etched and stained following a procedure modified from Stirling (1969b) as follows: 1) the sections were etched for 22 hours in a 5 part formic acid, 95 part 10 percent formalin solution, and 2) washed for at least 4 hours under flowing water; they were then 3) soaked for at least 4 hours in a solution of four drops 0.88 ammonia to 75 ml water, 4) stained for 5 seconds in a 0.125 percent solution of aqueous Thionin at 37°C and 5) left to air-dry.

The canine teeth of most pinnipeds have open pulp cavities which, because of dentine deposition, slowly close with age. The pulp cavity is roughly cone-shaped in the New Zealand fur seal; consequently the growth rings are cone-shaped as well. The cones become progressively shorter as deposition progresses. Therefore, it is important that the tooth is sectioned longitudinally. If transverse sections are cut, then there is a possibility that some of the growth rings will not be present on the section, i.e. some of the later deposition will have begun below the region of the transverse section.

Dentine deposition is layered, with alternating bands of dense columnar dentine and less dense marbled dentine (the latter referred to as vacuolar dentine by Stirling 1969b). Because the less dense marbled dentine is dissolved at a faster rate than the columnar dentine, alternating 'ridges' and 'valleys' appear on the etched sections. The dense columnar dentine has been shown to coincide with the breeding season, annual haul-out and moult of both adult and adolescent Southern elephant seals (Carrick and Ingham 1962a; Laws 1953a). From the samples of New Zealand fur seals collected, it appears that deposition of dense dentine begins during mid- to late summer, which roughly corresponds with the breeding season. Lesser bands appear between the ridges, and probably correspond to specific periods in the annual cycle (see Carrick and Ingham 1962a and Laws 1962).

Growth rings were counted with the aid of a binocular microscope using tungsten lighting for illumination. As a check on my counts, the same sections were given for interpretation to an independent observer experienced in counting growth rings in teeth and bone. For the 28 teeth used in this study, 57 percent (16/28) of our interpretations were the same, 79 percent (22/28) were within one year of each other, and 21 percent (6/28) were greater than one year apart. Where agreement could not be reached, my interpretations were used.

Sections of testes and epididymes of bulls collected were examined for the presence of spermatozoa. The sections were prepared following standard histological techniques, stained with Ehrlich's hematoxylin, and counter-stained with eosin. Ovaries were given a gross, macroscopic examination only.

(vii) Length of time on Taumaka and analysis of data

During this study, 282 days were spent on Taumaka, of which 232 days were during the months of October-February. The total number of days spent on Taumaka is summarized in Table 2.3.

TABLE 2.3. Dates spent on Taumaka, Open Bay Islands.

1974/75	1975/76	1977
25 Oct. - 8 Feb.	17 Oct. - 11 Feb.	29 Jan. - 4 Feb.
30 Apr. - 5 May	29 Apr. - 6 May	
2 Aug. - 10 Aug.	30 Jul. - 7 Aug.	
	25 Sep. - 1 Oct.	
	6 Dec. - 15 Dec.	

For convenience and ease of analysis, the breeding season was divided into dayblocks, each dayblock equalling five days (Table 2.4; see also Miller 1971, 1975a).

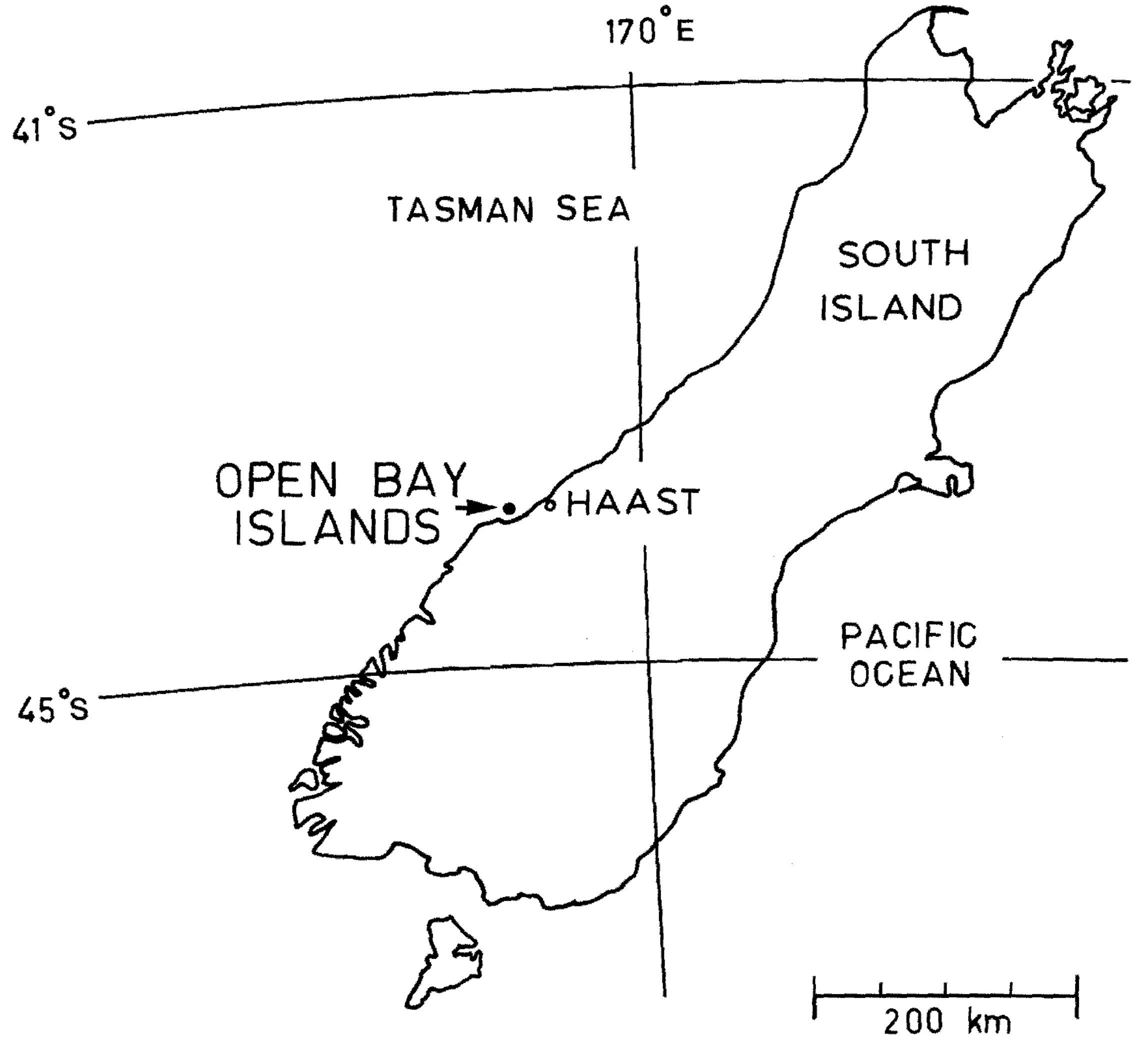
TABLE 2.4. Dayblocks and their corresponding dates.

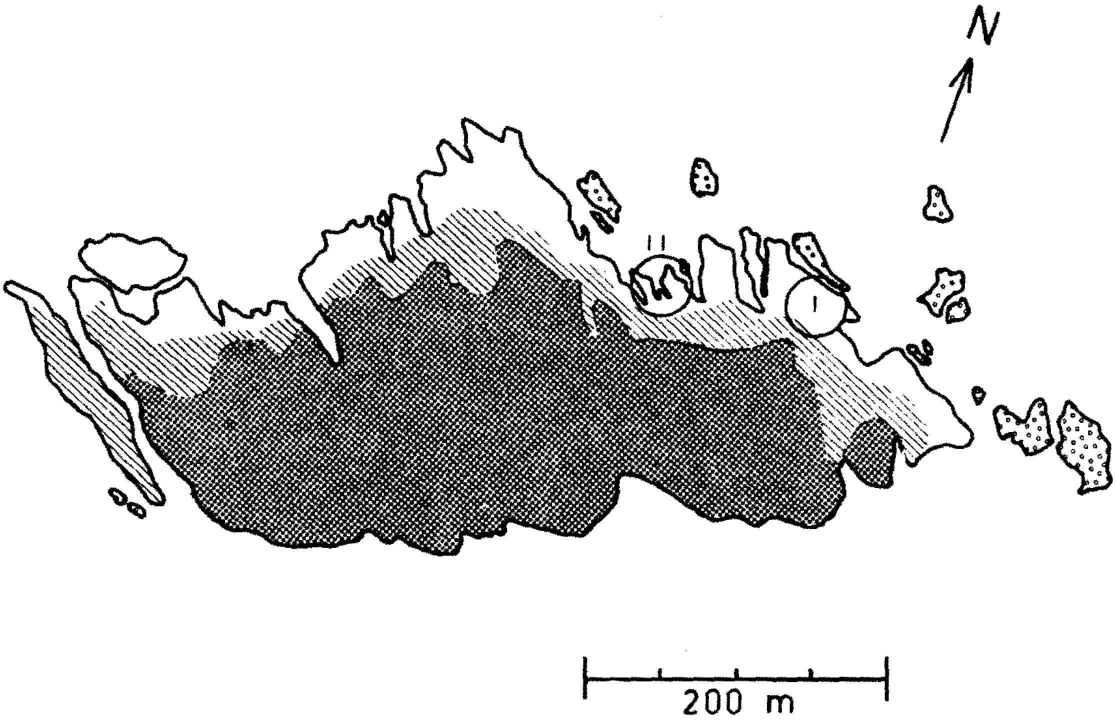
Dayblock	Dates (inclusive)	Dayblock	Dates (inclusive)
1	30 Oct. - 3 Nov.	11	19 Dec. - 23 Dec.
2	4 Nov. - 8 Nov.	12	24 Dec. - 28 Dec.
3	9 Nov. - 13 Nov.	13	29 Dec. - 2 Jan.
4	14 Nov. - 18 Nov.	14	3 Jan. - 7 Jan.
5	19 Nov. - 23 Nov.	15	8 Jan. - 12 Jan.
6	24 Nov. - 28 Nov.	16	13 Jan. - 17 Jan.
7	29 Nov. - 3 Dec.	17	18 Jan. - 22 Jan.
8	4 Dec. - 8 Dec.	18	23 Jan. - 27 Jan.
9	9 Dec. - 13 Dec.	19	28 Jan. - 1 Feb.
10	14 Dec. - 18 Dec.		

Statistical analyses followed the procedures set forth in Siegel (1956) or Sokal and Rohlf (1969). Where applicable, raw data were put on data cards and analysed using a Burroughs 6718 computer. All data cards are deposited with the Department of Zoology, University of Canterbury.

FIGURE 2.1. Location of Open Bay Islands (43°52'S, 168°53'E).

FIGURE 2.2. Map of Taumaka, Open Bay Islands, showing the location of Study Area I and Study Area II.
kiekie, ▦ scrub, ▧ rookery, □ offshore rocks. ⁘


170°E
41°S
TASMAN SEA
SOUTH ISLAND
OPEN BAY ISLANDS
HAAST
PACIFIC OCEAN
45°S
200 km


N
II
I
200 m

<u>FIGURE 2.3</u>. Measurements recorded for all dead specimens (blubber thickness over sternum not shown). Measurements marked by a star (★) were taken of live pups.

1. Curvilinear length.
2. Standard length.
3. Axillary girth.
4. Anterior length of foreflipper.
5. Anterior length of hindflipper.

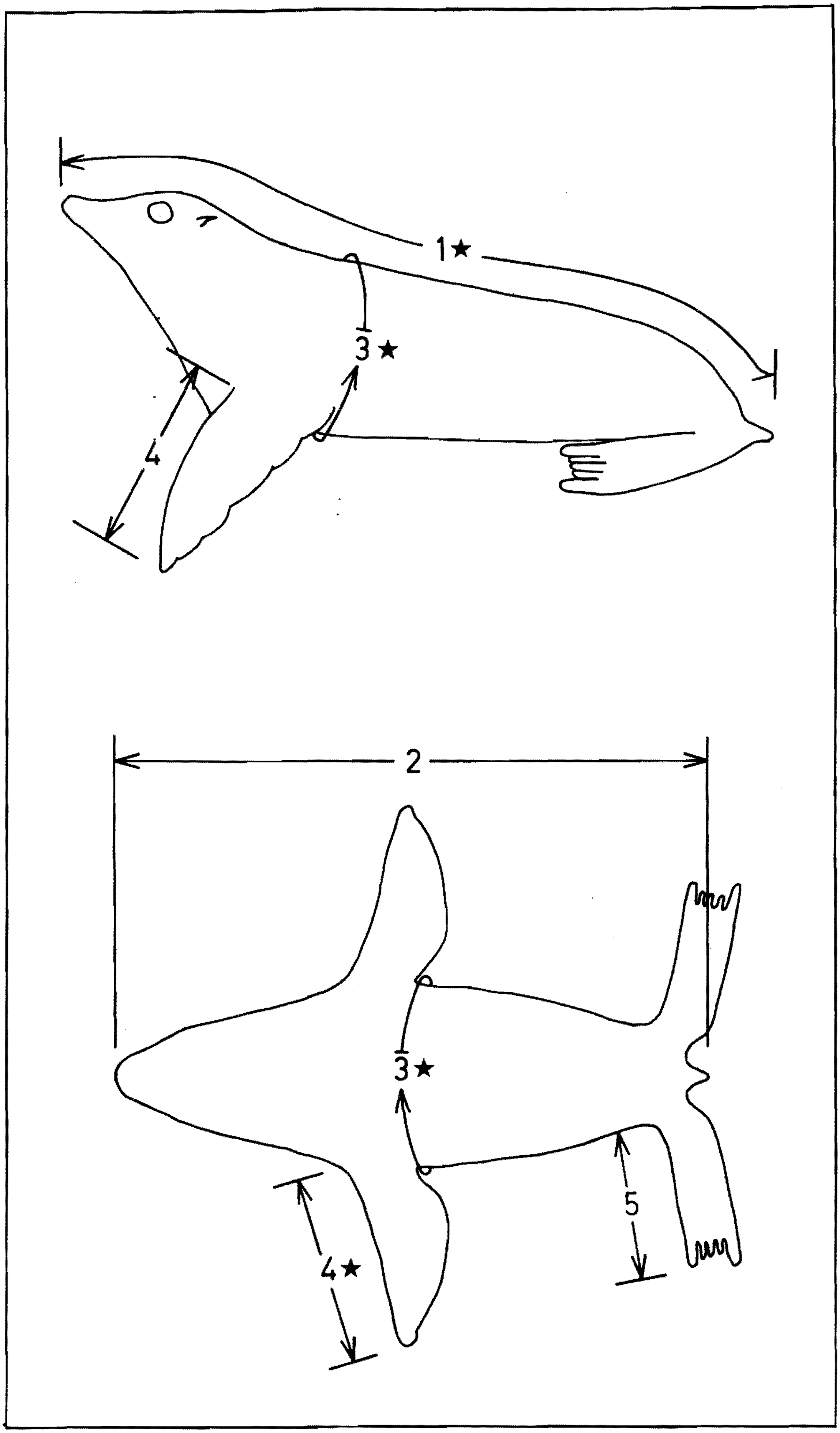

1★
3★
4
2
3★
4★
5

PLATE 2.1. Aerial view of a section of the rookery on Taumaka, showing: 1) the bush along the margin of the rookery, 2) the rookery (note the fur seals in the centre of the photograph), 3) a channel running through the offshore reef, and 4) the offshore reef. The bush and offshore reef are used by non-breeders, females and pups.


1
2
3
4

PLATE 2.2. Typical views of the rookery. Note the use by resting fur seals of rocks elevated above the general level of the rookery.

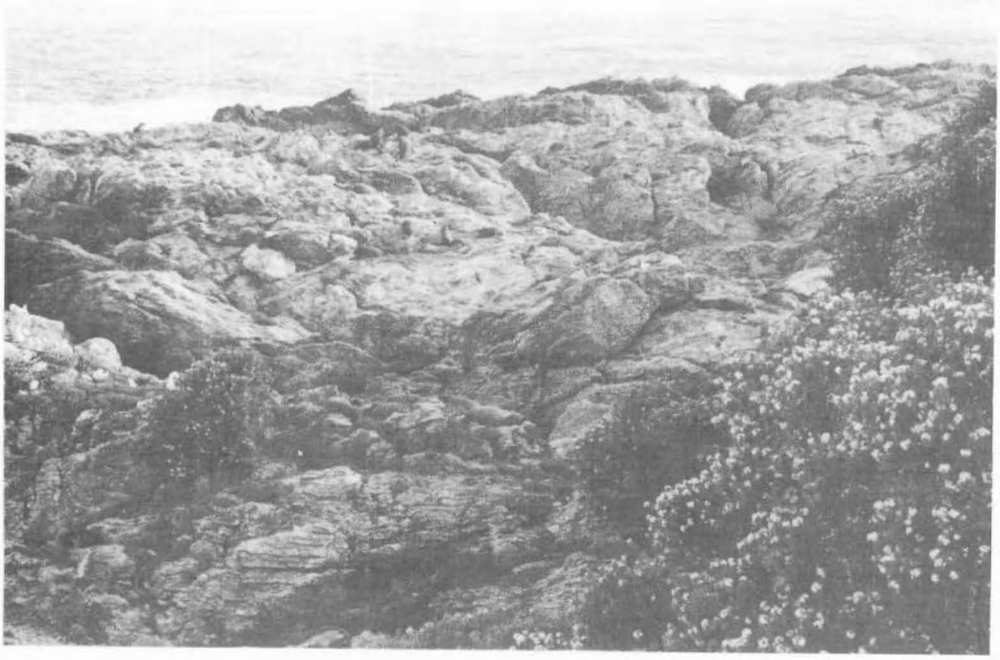
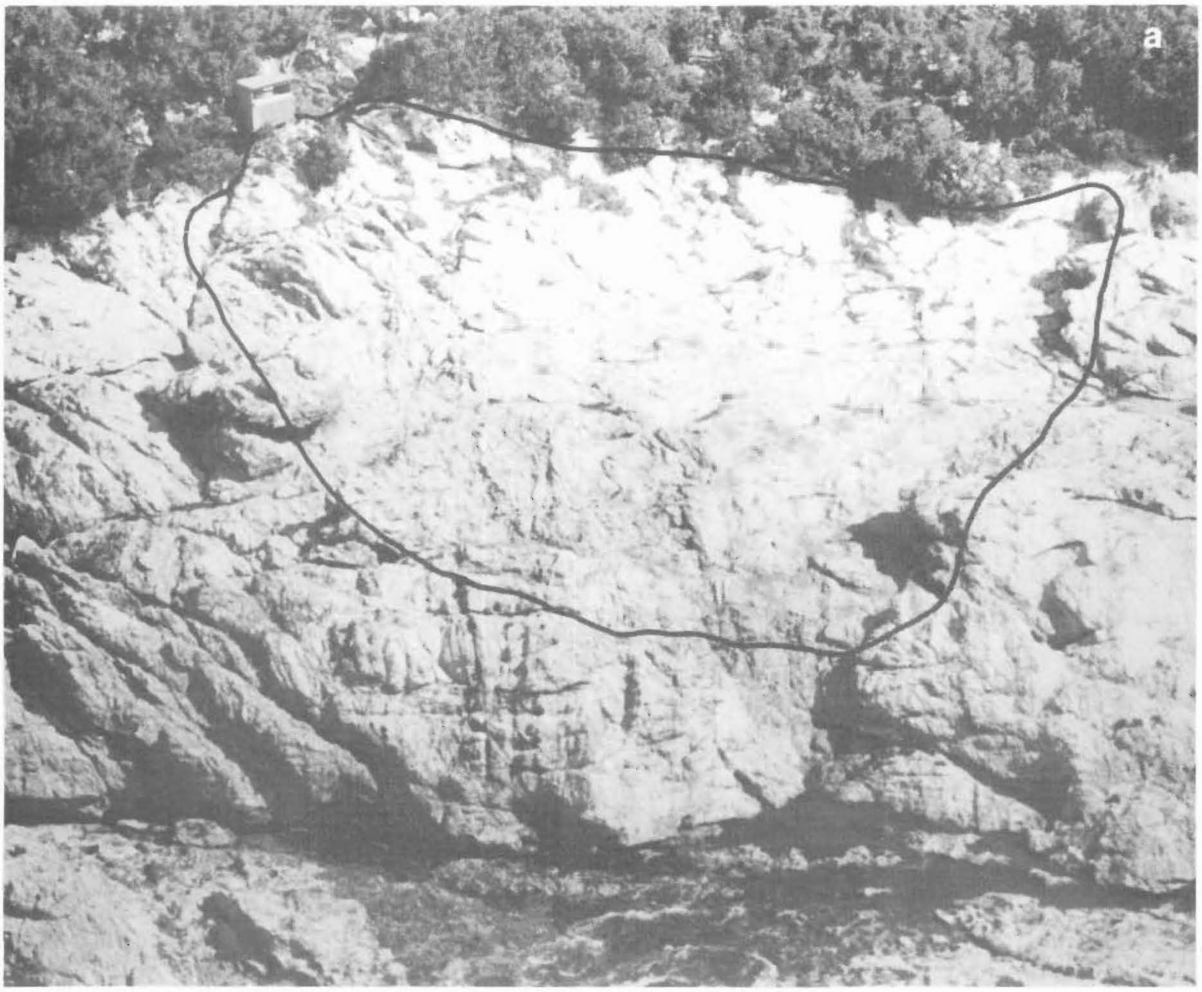


PLATE 2.3. Aerial views of study areas.

a. Study Area I. The border is outlined in black. The hide is at the upper left, providing a view across the rookery.

b. Study Area II. The border is outlined in black. The hide is at the mid-top; its position permits an observer to look down onto the rookery.


a

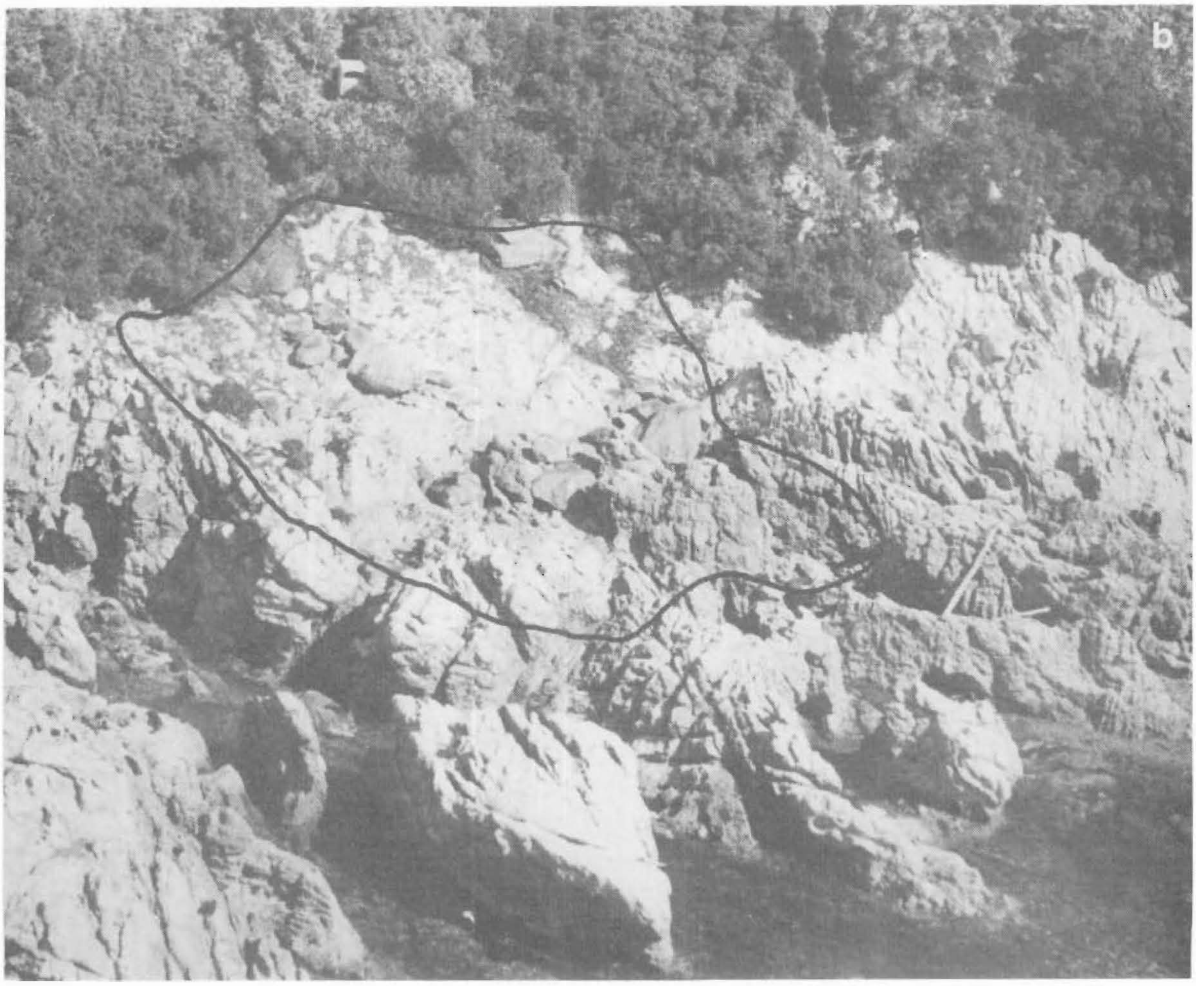

b

PLATE 2.4. Techniques used to mark pups temporarily (a) and permanently (b, c).

a. A pup temporarily marked by fur-clipping. Such marks were plainly visible after two months, but were difficult to recognize four months after clipping.

b. A pup permanently marked with a monel metal cattle ear tag. These tags may have adversely affected pup survival.

c. A pup permanently marked by clipping off the cartilaginous tip of a digit on a hindflipper. This technique resulted in a year-mark only, but had no apparent long-term adverse effect.


a

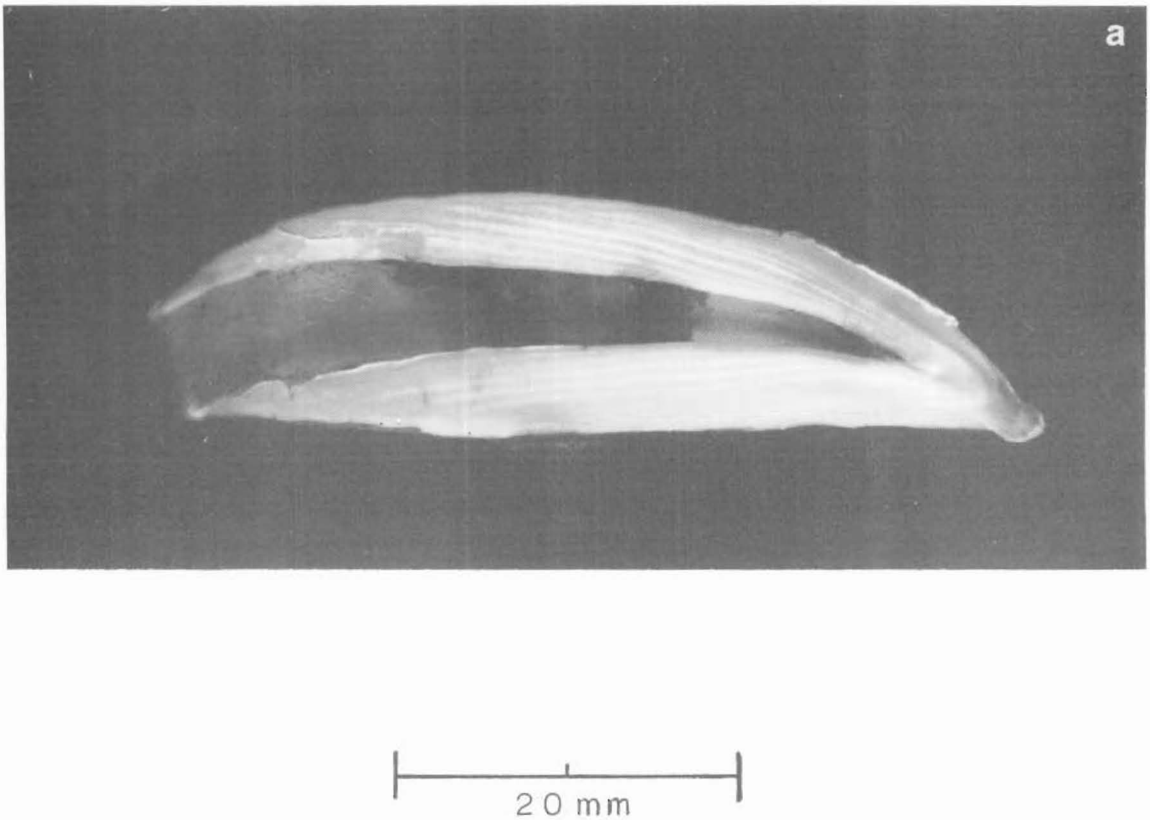

b

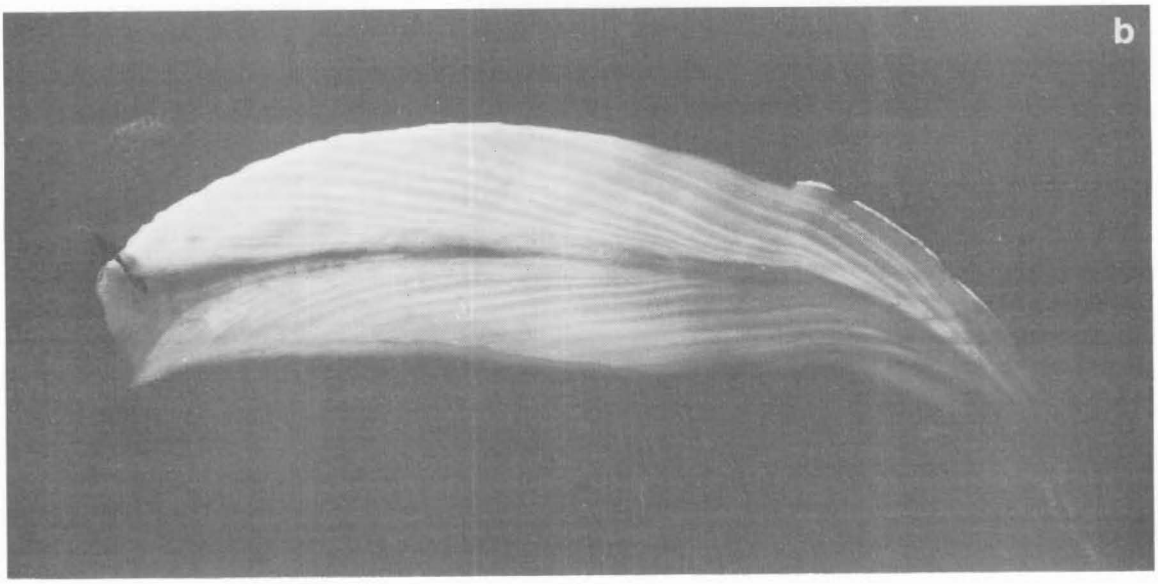

c

PLATE 2.5. Longitudinal sections of canine teeth, showing growth rings and the degree of closure of the pulp cavity with age.

a. Stained upper canine of a bull aged 8 years, with an open pulp cavity (specimen number DM733; photo by T.P. Williams).

b. Stained upper canine of a bull aged 15 years, with a closed pulp cavity (specimen number 2; photo by T.P. Williams).


a
20 mm


b

CHAPTER THREE

POPULATION BIOLOGY

3.1. Introduction

An understanding of the population dynamics of a species is vital for the development of a biologically sound management programme should one be required. An excellent example of this is the management programme developed for the Northern fur seal, the population dynamics of which are among the best known of any vertebrate (see e.g. Chapman 1961; Kenyon *et al.* 1954; Marine Mammal Division 1977; North Pacific Fur Seal Commission 1975). Although they are harvested annually, albeit under strict governmental regulation, the population is thriving. A similar situation occurs with the Cape fur seal in South Africa, although its population dynamics are not as well known as those of the Northern fur seal (see e.g. Rand 1955; Shaughnessy 1977). Because both of these species are commercially exploited, it is possible to collect large samples for aging purposes and the determination of reproductive condition. Although most other fur seal species are now totally protected from commercial exploitation, information about their population biology is still being collected (e.g. Bonner 1968; Fleischer 1978; Paulian 1964; Payne 1977; Tollu 1974; Vaz-Ferreira and Sierra de Soriano 1963).

A thorough understanding of population dynamics requires the following types of data: overall and age specific reproductive rates, reproductive age, age specific mortality, growth rates, sex ratio, and population size (for a review of pinniped reproduction, see Harrison *et al.* 1952, and Harrison and Kooyman 1968). Many of these data can be obtained by killing and examining a random sample of individuals from the population under study. Supporting data can be obtained from observational studies of known-aged (i.e. tagged) individuals, but this requires the continuation of a long-term tagging programme. In addition, in order to tag most animals, they must first be captured and then restrained. This is possible for both pups and adults of many pinniped species, e.g. the Weddell seal (Stirling 1966), but it is not possible for all species, including the New Zealand fur seal. Only pups could be tagged due to the timidness and speed of adults while on land, and their violent reaction when captured. Although pup tagging has been carried out sporadically on Taumaka since 1968, only four tagged fur seals older than yearlings have been seen on the rookery. Therefore, an analysis of the dynamics of the breeding population on Taumaka depended on the collection of a large random sample of adult fur seals. This was not possible because of the adverse effect it would have had on the breeding population. However, it was possible to answer two questions pertaining to the population dynamics of the New Zealand fur seal from data collected from a non-random, small sample of adults, *viz.*: 1) to get an indication only of the age of sexual maturity in males and females, and 2) to get an indication of the age of reproductive (i.e. social) maturity of males, should that be different from the age of sexual maturity. To obtain these data, ten bulls were killed early in the season as they became territorial, and six females were killed at irregular intervals during the year. Two of the females collected were shot very early in the season immediately after copulating. These data were of value in the calculation of population size and population growth (see Chapter Eight, Estimates of Population Size and Potential Growth) and for the description of the population structure during the breeding season (this chapter).

In addition, observational data were collected on the fluctuation in numbers of each age class of fur seals during the breeding season (i.e. bulls, females and pups), the presence or absence of lower canines in bulls and how this may have affected their territorial success, pup movement on the rookery, and the adult sex ratio. The data are presented separately for bulls, females and pups, with a final section on adult sex ratio. It is intended that they form part of the basis for an understanding of the population biology of the New Zealand fur seal during the breeding season.

3.2. Results and observations

(a) Bulls

(i) Fluctuation in numbers

Few bulls were present on Taumaka in May and August of 1975 and 1976, though considerably more were present in September 1976 (the island was not visited during September 1975). For example, on 5 August 1975 five bulls were on the rookery, but none appeared territorial. On 30 July 1976, four bulls were on area I and two were on area II, but again they appeared to be non-territorial. By September, bulls were beginning to arrive and claim territories; on 28 September 1976, 78 bulls were counted on the rookery. From these observations, it is clear that bulls must have been present on the rookery for several weeks by the time field studies commenced at dayblock 4 in 1974 (14 November) and dayblock 1 in 1975 (30 October). By dayblock 5 (15-23 November) most territories were occupied, but bulls continued to claim territories up until mid-December (see Chapter Four for an account of preferred sites). The number of territorial bulls was at a maximum between dayblocks 5 and 12, which coincided with the period of rapid increase and maximum numbers of females on the rookery. From dayblock 12 (24-28 December) on, bulls were beginning to leave their territories temporarily, and by dayblock 15 (8-12 January), territories were being abandoned. There were no territorial bulls on the study areas by 1 February during either of the two seasons. The last recorded occupied territory for either season was at Study Area I on 29 January 1976. The mean number of bulls seen on each of the study areas for both breeding seasons is graphed in Figures 3.1.a-d.

(ii) Age structure of territorial bulls

All 10 of the bulls collected during this study had mature spermatozoa in their epididymes, indicating that they were sexually, but not necessarily reproductively, mature. Four of the 10 were noticeably larger than the others, being over 110 kg in weight, and were territorial at the time of their collection. They were aged 10 years, 10 years, 12 years and 14 years. The six remaining 'smaller' bulls were under 100 kg in weight. One was in the bush when collected, and was not territorial; it was aged 7 years. Two of the remaining five bulls were aged 9 years, two were aged 10 years, and one was aged 11 years; all were territorial. The 11 year old individual was the lightest bull collected, weighing 49.5 kg. These data and the dates of collection are summarized in Table 3.1.

The majority of the early arrivals (i.e. those present in September, and those present when observations began) probably were under 100 kg in weight and between 7 and 10 years old. This subjective assessment of their weight and age was based on a visual comparison of the sizes of the living fur seals with the sizes of the fur seals shot and examined. Early arrivals were very aggressive during territorial maintenance, and repeatedly patrolled their territorial boundaries and gave territorial displays. It was not unusual for one of these presumably young bulls to defend an area which later in the season would constitute three or more territories. As the larger, and presumably more experienced, bulls began to arrive, they displaced the smaller bulls from their territories. Large bulls were occupying all the permanent territories by dayblock 5

TABLE 3.1. Age and territorial status of bulls collected on Taumaka.

Specimen number	Date collected	Age in years	Weight in kg	Territorial status
Z001	27 X 74	10	62.3	territorial
Z002	28 X 74	11	49.5	territorial
Z003	30 X 74	14	125.0	territorial
Z004	3 XI 74	9	77.7	territorial
Z005	5 XI 74	10	83.6	territorial
Z006	7 XI 74	7	70.9	not territorial
Z007	10 XI 74	12	150.9	territorial
Z009	7 I 75	10	114.8	territorial
Z014	29 X 75	9	95.9	territorial
Z016	10 XI 75	10	154.1	territorial

(19-23 November). Judging from the ages of the four 'large' bulls collected, the holders of permanent territories were probably aged 10 years or more. The large bulls defended their territories vigorously, but did not participate in territorial displays and patrols to the same extent as the smaller bulls. For a detailed account of territorial behaviour at Taumaka, see Miller (1971, 1974b, 1975a, 1975b).

The displaced smaller bulls either became non-territorial, tried holding territories in the bush, held very marginal territories (often not on the rookery proper), moved to the few offshore rocks, or left the area entirely, only to return to the rookery when the larger bulls began to abandon their territories in early to mid-January.

Although the 'young' bulls which held territories on the rookery either early or late in the season occasionally had the opportunity to copulate with receptive females, they did not show the same reproductive expertise as the 'older' bulls. For example, a young bull which had moved onto a territory after the voluntary departure of the large resident bull attempted to copulate with a receptive female on 11 January 1975. The female remained passive throughout. The bull made repeated attempts to mount the female, but he was never properly orientated to gain intromission. He was either too far forward to too far back, and at one time was making rapid pelvic thrusts in the vicinity of the female's left fore-flipper. He first mounted the female at 0613 hours, but finally gave up and went to sleep 28 minutes later. It is doubtful if this bull ever succeeded in impregnating the female during this attempted copulation.

Based on these data, it is hypothesized that sexually mature, but inexperienced, bulls probably begin to attempt to hold territories at the age of 8 or 9 years, but generally are successful only very early and late in the season. Bulls presumably gain experience during these attempts at being territory holders, and by the time they are 10 years old they probably are sufficiently mature, both physically and socially, to be able to take and hold a territory at the height of the breeding season.

(iii) Longevity of bulls

The oldest bull killed during this study was at least 14 years old. Four bulls found dead of unknown causes on Taumaka were aged, 10, 10+, 14+, and 15 years. The oldest of seven males, the skulls of which are held at the National Museum, Wellington, was 13+ years of age. Collection data for aged material are given in Appendix B.

(iv) Canines and territorial success

During territorial conflicts, bulls which inflicted the greatest amount of physical punishment usually were victorious. Physical damage was inflicted when a bull bit and shook his opponent, with the actual damage being caused by the canines, particularly the lower canines. The lower canines are larger and are more deeply embedded in the jaw than are the upper canines, and are continually sharpened by the process of thegosis, i.e. in this case by the rubbing of a lower canine against the corresponding upper canine (Plate 3.1.a-b).

Canines are broken off, either partially or at the gum line, during territorial conflicts (Plate 3.1.c). For example, a bull was observed to break off his left lower canine at the gum line when he struck his opponent on the left side of the head with his muzzle. During territorial displays, opponents often swing at each other without making contact. In this case, the bull which was struck appeared to be slightly off balance, and was not able to pull away soon enough.

Because the upper canines are not as visible as the lower canines, often it was not possible to determine their presence or absence on a live bull. Bulls missing one or both of their lower canines were commonly seen on and near the rookery. Of 33 non-territorial bulls checked for presence or absence of canine teeth during the height of the breeding season, 10 (30.3 percent) had both lower canines, eight (24.2 percent) had no lower canines, eight (24.2 percent) were missing their left lower canine, and seven (21.2 percent) were missing their right lower canine. Of the 80 territorial bulls observed, 58 (72.5 percent) retained both lower canines, four (5 percent) had no lower canines, five (6.25 percent) were missing their left lower canine, and 13 (16.25 percent) were missing their right lower canine. Bulls retaining either one or both of their lower canines were found throughout the rookery, but those with no lower canines were either located on very poor territories, were of short tenure, or both. The most 'preferred' territory on area I was held during the 1975/76 breeding season for 66 days by a bull missing his right lower canine. Two of the four territorial bulls with no lower canines seen during this same season held territories at either side of the head of a gut, but were present for only 6 and 13 days respectively. Both were gone by 25 November. The third territorial bull with no lower canines occupied a territory on area I from 16 to 30 December, but the territory was small (about 15 m^2) and was immediately adjacent to the bush line. The fourth territorial bull with no lower canines also held a territory on area I, from 18 November until 5 January. The territory was very narrow, and consisted of a slanting cut into the rocks with no more than 8 m^2 of reasonably level terrain. None of the four bulls was ever observed to be seriously challenged during its tenure. The bull which was on area I for 48 days eventually lost interest and abandoned his territory. The other three were probably driven off by force, though this was actually observed in one case only.

(b) Females

(i) Fluctuations in numbers

Fewer than 15 females were usually present at any one time at either of the two study areas until the end of dayblock 6, after which their numbers increased rapidly. The maximum was reached in 1974/75 by dayblock 13 (29 December - 2 January) at area I (54 females) and dayblock 11 (19-23 December) at area II (54 females), and in 1975/76 by dayblock 10 (14-18 December) for both areas (59 females for area I and 58 females for area II). Following these maxima, the number of females ashore at any one time gradually decreased, until fewer than 19 were ashore by dayblock 19 (28 January - 1 February; Figure 3.2.a-d).

(ii) Age and reproduction

Six females were collected during this study. Their age, the presence or absence of follicles and corpora lutea, and the volume of each ovary (± 0.5 ml) are given below, along with basic collection data. Ovary volumes were obtained by water displacement. Complete collection data are given in Appendix B. The following data are presented as a possible indication of reproductive condition at the time of collection, and whether or not the female may have been pregnant the previous year. No readily identifiable corpora albicantia were found in any of the ovaries examined.

The data for these females, in order of collection, are:

Z008: Collected on 12 November 1974; age 5 years; weight 30.6 kg; collected immediately after copulating. The left ovary (1.5 ml) contained no obvious follicles, though a corpus luteum measuring 9.6 mm x 5.0 mm was present. The right ovary (3.0 ml) contained two small follicles (1.0 mm and 1.3 mm in diameter respectively) and one large follicle (15.0 mm x 12.0 mm) which had either recently erupted or was about to erupt. This female was not seen with a pup.

Z010: Collected on 28 January 1975; age 7 years; weight 36.0 kg; collected from the large offshore rock located about 60 m to the N.E. of Taumaka. No pup was present. The left ovary (2.5 ml) contained no obvious follicles, but a corpus luteum was present, measuring 10.0 mm x 5.4 mm. The right ovary (2.5 ml) contained about 20 follicles, ranging in diameter from 1.0 mm to 4.6 mm, and one large follicle, measuring 11.1 mm x 9.3 mm.

Z011: Collected on 30 January 1975; age 4 years; weight 30.6 kg; collected from the large offshore rock located about 60 m to the N.E. of Taumaka. No pup was present. The left ovary (4.0 ml) contained over 40 follicles ranging in diameter from 0.8 mm to 4.1 mm, plus a corpus luteum measuring 11.8 mm x 6.9 mm. The right ovary (2.5 ml) contained about 12 follicles (range in diameter: 0.8 mm to 3.8 mm), but no corpus luteum.

Z012: Collected on 31 January 1975; age 8 years; weight 32.0 kg; collected from the large offshore rock located about 60 m to the N.E. of Taumaka. No pup was present. The left ovary (2.5 ml) contained no obvious follicles, but there was a corpus luteum measuring 5.3 mm x 5.8 mm. The right ovary (2.5 ml) contained five follicles (range in diameter: 1.0 mm to 2.5 mm), and a lobed corpus luteum measuring 11.4 x 7.5 mm.

Z013: Collected on 6 August 1975; age 12 plus years; weight 50.0 kg (with foetus present; foetus weight 0.85 kg); collected from the

N.E. end of Taumaka. No pup was present. The left ovary (2.5 ml) contained about 11 follicles (range in diameter: 1.2 mm to 2.8 mm). There was no readily discernible corpus luteum present. The right ovary (8.0 ml) contained one follicle (1.6 mm in diameter) and a corpus luteum measuring 16.6 mm x 14.6 mm. The foetus was in the right horn of the uterus.

Z015: Collected on 31 October 1975; age 4 years; weight 31.0 kg; collected at area I immediately after copulating. The left ovary (4.0 ml) contained one very large follicle, measuring 10.6 mm x 13.9 mm, which either had recently erupted or was about to erupt. No other follicles were present. The right ovary (3.0 ml) contained six follicles, five of which ranged in diameter from 13.0 mm to 2.5 mm, and the sixth was 5.8 mm x 5.1 mm. There was a band of pale tissue on one side of the ovary, but no obvious corpus luteum was present.

(c) Pups

(i) Fluctuation in numbers

Live pups first began to appear on the study areas during dayblock 5 (19-23 November) in 1974/75 and dayblock 4 (14-18 November) in 1975/76, after which their numbers increased rapidly to a peak and then declined. The maximum mean number of pups observed for any one dayblock differed between the study areas for the two years, occurring at or after dayblock 13 (29 December - 2 January) in three cases, and during dayblock 11 (19-23 December) in the fourth (range: 39-46 pups). The mean number observed for each dayblock decreased after dayblock 14 (3-7 January) in 1974/75, and although there was a similar decrease in 1975/76, it was not as extensive or pronounced (Figure 3.3.a-d).

(ii) Pup movement on the rookery

As pups grew older they wandered about the rookery, either singly, in pairs, or as part of a pup pod. They first began to gather into pairs during dayblock 8, and by dayblock 9 pods of three or more pups were common.

Although pups were able to roam freely on the rookery, most of their time was spent within 10 m of the area where they were last with their mothers. For example, on eight of the 10 days that pup 2HR-II was seen on area II, it was within a 6 m radius of a boulder group where it was recorded with its mother on three days, two of which were consecutive.

It was never observed more than 12 m from a location where it had been seen with its mother, and was never seen outside the borders of the study area. Pup 1MB-II was within a 5 m radius of one or the other of two areas, situated about 7 m apart, on 10 of the 11 days it was recorded. It was seen with its mother at both of these areas. It was more than 5 m away from one or the other of the two areas on three days only, but was never more than 15 m distant. At area I, pup 1H was usually at one or the other of two areas, about 17 m apart. It was with its mother at the first area on 27 December, 8 January and the morning of 9 January, after which they moved during the afternoon of the 9th to the second area. The pup subsequently was seen with its mother at the second area on 16 and 21 January, but was never recorded in the immediate vicinity of the first area again. Pup 1MB-I was the least localized in its travels, though it was recorded most often on the righthand side of Study Area I. It was seen with its mother only once (at the righthand side of Study Area I) out of 42 sightings recorded over eight days between 27 December and 9 January. It was found dead on 12 January. It had no measurable blubber across the sternum, which indicated that it probably had starved to death (see Chapter Seven, Pup Mortality).

Pups occasionally made relatively long excursions, but in no instance was a pup recorded further than 25 m from a location where it had been seen with its mother. The distance between sightings in any one day never exceeded 30 m.

(d) Adult sex ratio on the rookery during the breeding season

(i) 1974/75

A maximum of 54 cows was seen at any one time in 1974/75 at each of the two study areas. The greatest number of territorial bulls seen at any one time for the same period was 11 at Study Area I and 13 at Study Area II. These maxima resulted in a cow to territorial bull ratio of 4.9:1 for Study Area I and 4.2:1 for Study Area II. The mean number of occupied territories for December, the month with the greatest breeding activity, was 8.8 for Study Area I and 8.6 for Study Area II. This yielded a cow to occupied territory ratio of 6.1:1 for Study Area I and 6.3:1 for Study Area II. It was estimated that 66 pups were born on Study Area I and 61 were born on Study Area II (see Chapter Seven, Pup Mortality, for the calculation of birth estimates). Assuming that each cow produced one pup, and utilizing the mean number of occupied territories for the month of December for each study area, the cow to occupied territory ratio became 7.5:1 for Study Area I and 7.1:1 for Study Area II. Best (1973) determined that Cape fur seal females of breeding age had a fertility rate of 74 percent, based on data collected by Rand (1959) between 1954 and 1956. Assuming that the same is true for New Zealand fur seal females, and assuming that females of reproductive age which did not give birth to a pup nevertheless were present on the rookery, entered estrus, and were available to territorial bulls, then the ratio of cows to occupied territories was 10.1:1 for Study Area I (number of cows = 66/.74 = 89) and 9.5:1 for Study Area II (number of cows = 61/.74 = 82).

(ii) 1975/76

In 1975/76 a maximum of 59 cows was seen at any one time on Study Area I, and 59 on Study Area II. The greatest number of territorial bulls was 12 for Study Area I and 13 for Study Area II. These maxima resulted in a cow to territorial bull ratio of 4.9:1 at Study Area I and 4.5:1 at Study Area II. The mean number of occupied territories for December was 9.4 at Study Area I and 9.7 at Study Area II, which resulted in a cow to occupied territory ratio of 6.3:1 at Study Area I and 6.0:1 for Study Area II. An estimated 70 and 63 pups were born on Study Area I and II respectively. Accepting the same premise and following the same procedure as used for the 1974/75 data, then the ratio of cows to occupied territories was 7.4:1 at Study Area I and 6.5:1 at Study Area II. When applying the 74 percent estimate of fertility in the same manner as before, the cow to occupied territory ratio became 10.1:1 for Study Area I (number of cows = 70/.74 = 95) and 8.8:1 for Study Area II (number of cows = 63/.74 = 85).

It must be emphasized that these estimates are of adults of reproductive age only. They do not take into consideration idle bulls or immature individuals of either sex.

3.3. Discussion

(a) Bulls

Age structure and reproduction

Young, presumably inexperienced, bulls of many seal species commonly move onto the rookery after the older, experienced bulls depart, but usually it is the older, more experienced bulls which arrive first (e.g. the Northern fur seal, Kenyon and Wilke 1953; Kenyon *et al*. 1954; Steller sea lion, Orr and Poulter 1967; Southern elephant seal, Carrick *et al.* 1962). Young bulls of many species are found on the periphery of the 'harems' of experienced bulls, where they attempt to copulate with females (e.g. the Kerguelen fur seal, Bonner 1968; Southern sea lion, Hamilton 1934; California sea lion, Peterson and Bartholomew 1967; Northern fur seal, Scheffer 1950b; and the New Zealand sea lion, G.J. Wilson pers. comm. 1978). Occasionally they meet with success, but usually are driven off by the territory holder. The situation is slightly different with the New Zealand fur seal, in that presumably young bulls do not hold marginal or peripheral territories on the rookery proper. At Taumaka, this is because the large, experienced bulls control the available breeding areas on the island. This is usually the case within the New Zealand region, where most New Zealand fur seal rookeries are bordered by cliffs, gullies or other natural barriers (Wilson 1974a) which restrict or prevent the formation of peripheral territories by 'young' bulls. While 'young' bulls are present on Taumaka during mid-season, and occasionally copulate with receptive females, the opportunity for territorial maintenance on the periphery of 'organized harems' is lacking.

The early appearance of sexually mature, but young and presumably inexperienced, bulls on the rookery at Taumaka was initially recognized by Miller (1971) who broadly categorized bulls as early, intermediate and late arrivals. As a group, the early arrivals probably were young bulls between the ages of 7 and 10 years who were attempting to hold territories for the first, second, or perhaps third time. That bulls may first attempt to hold territories at about age 7 or 8 years is not unexpected, judging from the age of first breeding found in other pinnipeds. Kerguelen fur seal bulls first attempt to become territorial at about age 6 years (Bonner 1968). Northern fur seal bulls first become territorial at age 7 years, but they meet with little success until age 10 years (Johnson 1968), at which time they are in prime sexual and sociological condition (Scheffer 1950b). Southern elephant seal bulls at Macquarie Island first appear on land during the breeding season at age 6-9 years, but may not reach breeding bull status until age 14 years (Carrick *et al.* 1962). Grey seal bulls are sexually mature at age 8 years, but the majority of breeders are aged 10 years or more (Hewer 1964). Male Steller sea lions reach sexual maturity at age 6-7 years, but have little success in becoming territorial until age 9-10 years (Thorsteinson and Lensink 1962).

Young bulls are able to gain the social and reproductive experience necessary to improve their chances of success as territorial bulls during future breeding seasons by arriving on the rookery before the influx of large, experienced bulls, and by returning to the rookery after their departure. To a great extent, it is this social experience which enables older territorial bulls to defend their territories against young, less experienced challengers by bluff alone, as has been shown for the Northern fur seal (Bartholomew 1953).

Although it follows that reproductive success is contingent upon territorial success for males of polygynous pinniped species, it is reproductive success and not territorial success that is of primary importance to the overall benefit of the population. A bull which is capable of holding a territory but is unable to successfully copulate with every receptive female he attempts to mount is a detriment to the population as long as he remains territorial. Females may cross territorial boundaries and become impregnated by bulls in adjacent territories, but the potential for missed pregnancies is increased. Experience alone can not compensate for a physiological disfunction which has led to reproductive failure, but it can increase a 'normal' bull's chances of successfully copulating.

By being on the rookery shortly before the arrival and shortly after the departure of the experienced territorial bulls, young New Zealand fur seal bulls are able to copulate with females which enter estrus outside the regular breeding season. The importance of this is twofold: it not only enables young bulls to gain valuable reproductive experience, but it also increases the reproductive success of the population as a whole, because it is a means by which females entering estrus either early or late in the season can be impregnated.

Territorial success and canine teeth

The lower canine teeth of New Zealand fur seal bulls are used for intraspecific fighting during the breeding season. Bulls with one lower canine are capable of successfully defending a territory, but the loss of both lower canines reduces their chance of successful territory defence to virtually nil. Without these teeth, bulls are unable to damage their opponent, and it is the bull which inflicts the most punishment which usually is victorious. Some bulls are able to remain territorial by tenacity alone, i.e. by refusing to abandon a territory regardless of the amount of punishment received, but this is uncommon, and the tenure of such bulls is usually short (pers. ob.; Miller 1971).

Because of the relative ease with which lower canines are broken off, and judging from the maximum age of bulls found dead on the rookery, it is unlikely that bulls are able to remain territorial for more than three to five seasons, and are probably territorial for fewer. Johnson (1968) found that few Northern fur seal bulls are territorial after age 15 years, but he made no mention of the condition of their canine teeth. Thorsteinson and Lensink (1962) found that over 90 percent of the Steller sea lion territorial bulls they studied were aged 9 to 13 years. They theorized that the 'erosion' of canine teeth may have been a factor in preventing older bulls from remaining territorial. Judging from the small canines of females, and from the otherwise healthy outward appearance of bulls missing both lower canines, it is apparent that these teeth are not needed to obtain food; nor are they necessary for survival in the seal's physical environment, as is the case with the Weddell seal which uses its upper canines and incisors to maintain holes in the ice (Stirling 1969b).

(b) Females

Pregnant females feed heavily at sea just prior to arriving on the rookery to pup (Miller 1975a), which accounts for the low number of females ashore between the end of October, when observations began, and the fourth week in November. Females remain ashore a little over one week after pupping, after which they go to sea to feed, return to suckle their pup, depart for the sea, and so on, staying away from the rookery for progressively longer periods of time. This is reflected in the gradual decrease in numbers of females ashore after mid- to late December. From the end of January until September or October, the number of females ashore probably remained relatively constant at about 25-30 percent of the total number of cows with pups.

Age and reproduction

The female reproductive data collected, albeit limited, are the basis for the hypothesis that New Zealand fur seal females come into estrus for the first time at about age 4 years, and have their first pup at about 5 years. Both four year old females collected appeared to have ovulated for the first time that year. This is in general agreement with the Northern fur seal from the eastern Pacific, which normally begins to breed at age 4 years, though there are isolated cases of females aged 2 and 3 years breeding for the first time (Abegglen and Roppel 1959; Chapman 1961). Cape fur seal females were originally thought to have their first pup at age 3 years, based on the aging of females by the degree of closure of cranial sutures (Rand 1955). More recently it has been shown that they do not have their first pup until age 4 years or older (Shaughnessy 1977). Female Kerguelen fur seals become sexually mature earlier than the other fur seals discussed; 57 percent are pregnant at age 3 years, and all are fully recruited into the breeding population by age 5 years (Rayne 1977). The earlier age of first breeding in females of this species is thought to be a consequence of the rapid expansion of the population as compared with the more stable Northern fur seal population (Payne *op. cit.*). If this is so, then the implication is that the New Zealand fur seal population on Taumaka is either stable, or nearly stable. This possibility is discussed in more detail in Chapter Eight, Estimates of Population Size and Potential Growth.

Ovaries of New Zealand fur seal females are very similar in gross anatomy to those of other fur seal species, e.g. the Northern fur seal (Craig 1964) and the Cape fur seal (Rand 1955), and will not be discussed in detail here. However, some general observations are worth mentioning.

The alternation of ovulation between ovaries found in the New Zealand fur seal also occurs in most pinniped species (Northern fur seal, Pearson and Enders 1951; Cape fur seal, Rand 1955; Southern elephant seal, Laws 1956b; Weddell seal, Mansfield 1958; Grey seal, Backhouse and Hewer 1964; and the Ringed seal, Smith 1973). The occurrence of corpora albicantia is more variable, but has been described in the ovaries of female Northern fur seals, where they may last two to four years (Craig 1964); Cape fur seals, where they last for about 25 months (Rand 1955); and in numerous phocids, e.g. the Ringed seal, where they disappear after two years (Smith 1973); the Harbour seal, where they last for one to four years (Bigg 1969); and the Grey seal, where they last for about one year (Backhouse and Hewer 1964). That corpora albicantia were not positively identified in the ovaries of females collected during this study does not necessarily mean that none was formed, but rather that they may be difficult to identify, or that they may be present for a short time only, as in the Grey seal.

Corpora lutea were readily identifiable, and were a means by which ovulation, and possibly pregnancy, could be determined for at least two breeding seasons, i.e. the season in which the female was collected (as shown by a Graafian follicle or a corpus luteum in one ovary) and the previous season (as shown by a corpus luteum in the other ovary).

From previous behavioural studies, it was assumed that virgin females usually mated for the first time early in the season (pers. ob.; Crawley and Wilson 1976; Miller 1975a). The few female reproductive data collected support this assumption. This is consistent with what is known of the Cape fur seal (Rand 1955), but is contrary to the recorded breeding habits of virgin Northern fur seal females (Craig 1964; Enders *et al.* 1946) and virgin Amsterdam Island fur seal females (Paulian 1964), which mate late in the season after the mating of non-virgin females. However, Paulian (*op. cit.*) suspected that some virgin females were mated early in the season as well. Like virgin Cape fur seal females (Rand 1955), virgin New Zealand fur seal females as a class (not individually) may remain in estrus over a longer period of time than non-virgin females. If so, then it is possible that virgin females are mated both during and after the breeding season. Considering the rapid breakdown of the social system at the end of the breeding season, it is likely that many virgin females on the rookery are mated prior to the influx of pregnant females about to give birth. It is also likely that some virgin females are mated in the general vicinity of, but not on, the rookery by young bulls and non-territorial bulls, but at present there are no data to substantiate or refute this suggestion.

(c) Pups

Mortality alone was not enough to account for the decline in numbers of pups seen at any one time after dayblock 14; rather the decline was a consequence of both the pups' growing independence and the warm summer temperatures, particularly during the 1974/75 breeding season. As pups grew older, they played near the sea during fine weather or amongst the rocks on the rookery, where they were often obscured from view. Also, pups sheltered in amongst the rocks during hot sunny days, where they likewise were out of view.

The tendency of pups to remain near the site where they were last with their mothers has obvious survival value. A female returning from a feeding trip at sea goes to where she and her pup were last together, but makes no attempt to locate her pup; at best she may emit a pup attraction call which often is answered by several pups, none of which may be her own. A pup therefore stands a better chance of being reunited with its mother if it is relatively sedentary. Should a female and her pup not be reunited before the female returns to the sea to feed, not only does the pup miss vital food, but the probability that the female will not return to the same area increases. The greatest single cause of pup mortality appears to be starvation (see Chapter Seven, Pup Mortality), so any means by which a pup is able to locate its mother is to the pup's advantage. As pups grow older, no doubt they travel further afield, but they probably still remain in the same general vicinity where they were last with their mothers. Northern fur seal pups stay near their birth site, though they may wander as far as 75 yd (68.5 m) from this area (Bartholomew 1953, 1959).

(d) Adult sex ratio on the rookery during the breeding season

Any one territory may have been held sequentially by several bulls during a breeding season. Consequently, a cow:territorial bull sex ratio may be determined for a specific time from one census only, or refer to the whole season if the ratio was calculated for the total number of bulls which held territories during the time when the counts were made. When the sex ratio is meant to relate the number of cows to the number of bulls present at any one time, a more descriptive and accurate term such as 'occupied territory' should be used in place of territorial bull, i.e. cows:occupied territory.

The total number of cows on the rookery is not necessarily the same as the number of estrus cows available to territorial bulls. To determine the latter, it is necessary to know the number of available cows which copulated but did not pup, which pupped but did not copulate, which pupped and also copulated, and which neither pupped nor copulated. The collection of all these data is difficult, if not impossible. Nevertheless, sex ratios are of value as long as the technique used in their calculation is given.

When calculating a sex ratio for New Zealand fur seals based on the total number of births to the mean number of occupied territories, Miller (1971, 1975a) estimated a ratio of 6.1:1 at Taumaka, Crawley and Wilson (1976) estimated a ratio of 5:1 at the Snares Islands, and Stirling (1971a) estimated a ratio of 6-8:1 at South Neptune Island, Australia. These data imply that the adult sex ratio of this species while on the rookery during the breeding season is about the same throughout its range. Whether this was historically the case is not known, but it is likely that previous to its indiscriminate slaughter, the number of available cows to each occupied territory was considerably higher. This is all the more likely when one considers that 60,000 skins were taken from the Antipodes Islands by one vessel alone between 1804 and 1805, and that 11,000 skins were taken over a four year period from a group of islands tentatively identified as the Open Bay Islands (McNab 1907). The total population of this species in the New Zealand region is now estimated to be about 40,000 individuals (Crawley and Wilson 1976).

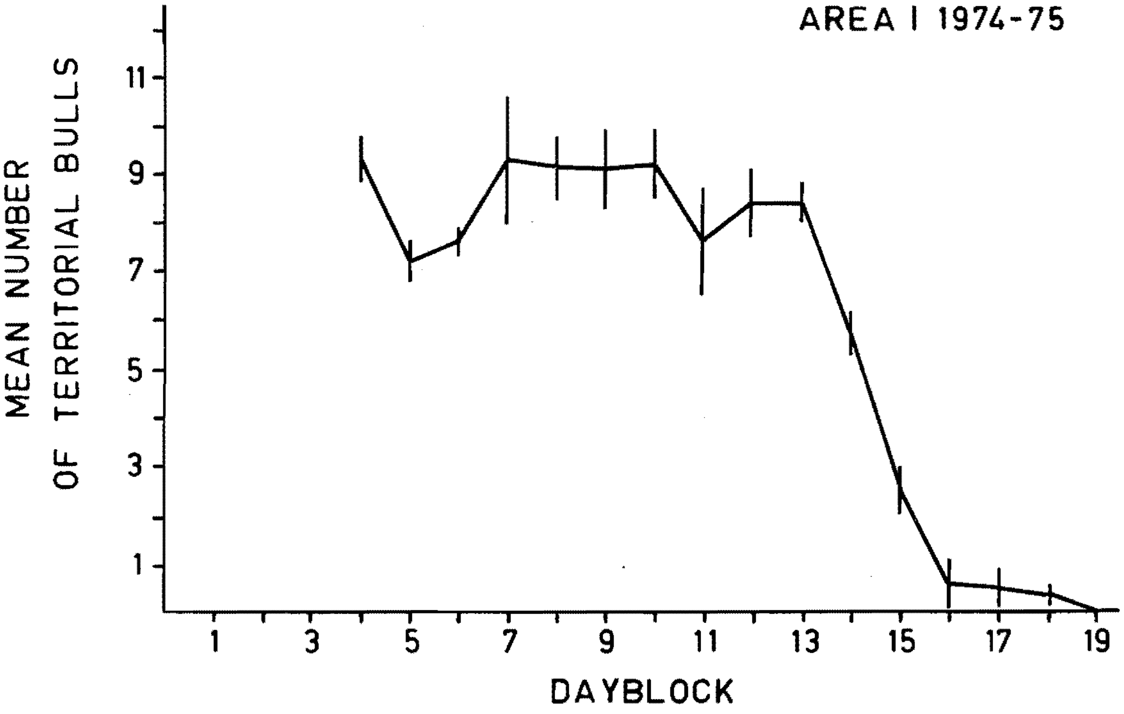
When using the direct census technique (i.e. direct counts of the seals on the rookery), Vaz-Ferreira (1956) estimated that the sex ratio of South American fur seals was 4.7-6.4:1. Based on estimates of the number of pups born, Paulian (1964) calculated that the sex ratio of the Amsterdam Island fur seal was about 6-8:1. Bonner (1968) estimated that the sex ratio of the Kerguelen fur seal at South Georgia was 11.5-15.75:1 for the years 1957-1961 (omitting 1959), and suggested that the average 'harem' of an undisturbed population would include about 15 cows. Recent estimates from South Georgia indicate that the average 'harem' size is about 10 cows (Payne 1977). Hamilton (1934) estimated by the direct census technique that the Southern sea lion had a sex ratio of 6.3:1, and Marlow (1975) estimated the sex ratios of the Australian sea lion and the New Zealand sea lion to be 3.7:1 (range: 1-8:1) and 27.5:1 (range: 10-50:1) respectively at the height of the breeding season. The greatest breeding adult sex ratio of all the otariids is found in the Northern fur seal, which has an average 'harem' size of between 40 and 50 cows for every territorial bull (= occupied territory; Kenyon *et al.* 1954).

The sex ratio of New Zealand fur seals at the rookery is similar to that found in most other otariids. Judging from the sex ratio of the Kerguelen fur seal at South Georgia, which is a rapidly expanding population, and the Northern fur seal, an increase in the number of females per occupied territory can be expected should the population as a whole substantially increase.

FIGURE 3.1. Mean number of territorial bulls on the study areas, per dayblock. Vertical lines equal 95% confidence limits. Observations began at dayblock 4 in 1974/75.

a. Study Area I, 1974/75 breeding season.

b. Study Area II, 1974/75 breeding season.


AREA I 1974-75
MEAN NUMBER OF TERRITORIAL BULLS
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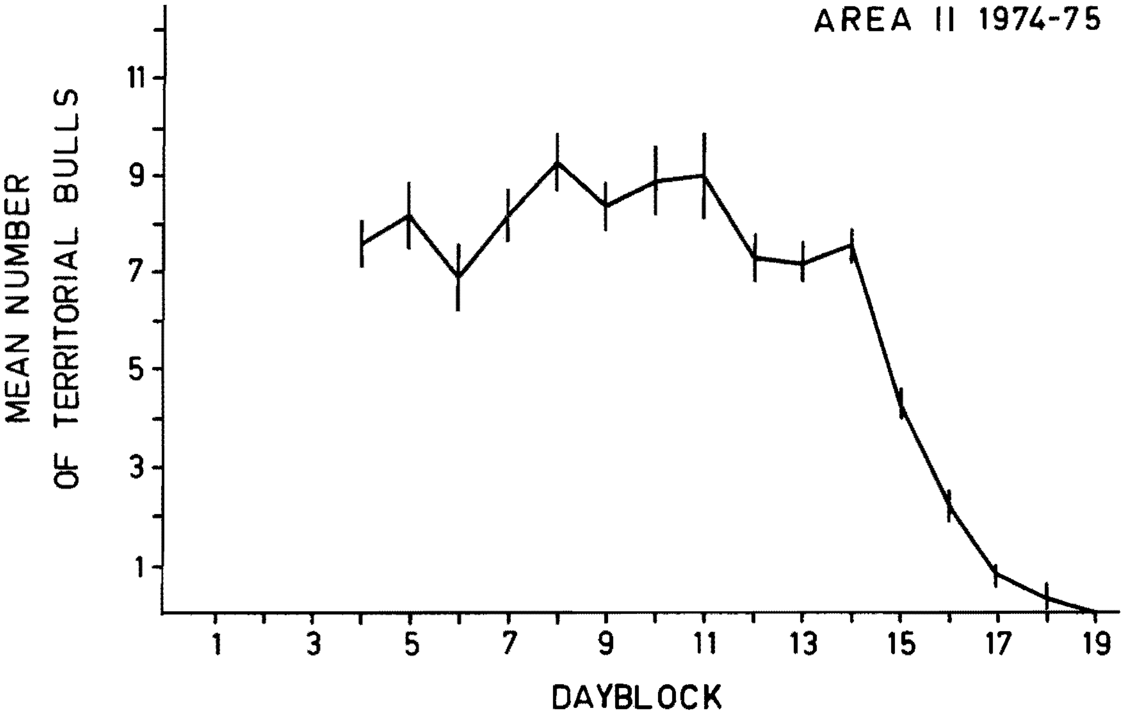
AREA II 1974-75
MEAN NUMBER OF TERRITORIAL BULLS
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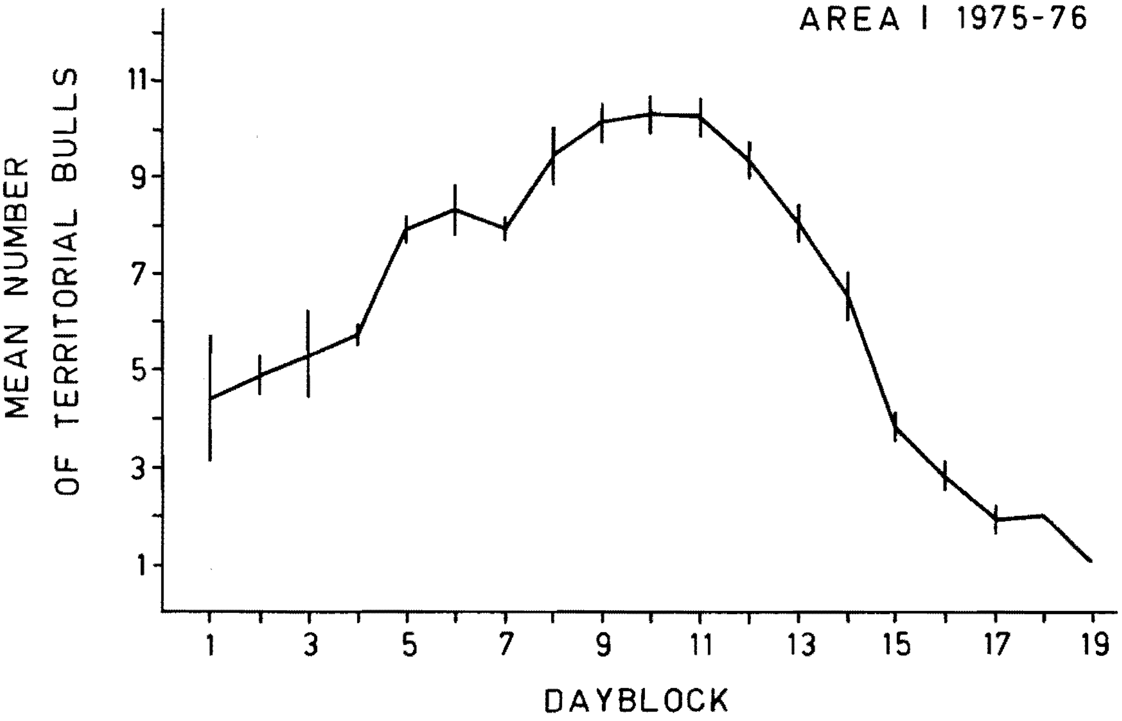
FIGURE 3.1. Continued.

c. Study Area I, 1975/76 breeding season.

d. Study Area II, 1975/76 breeding season.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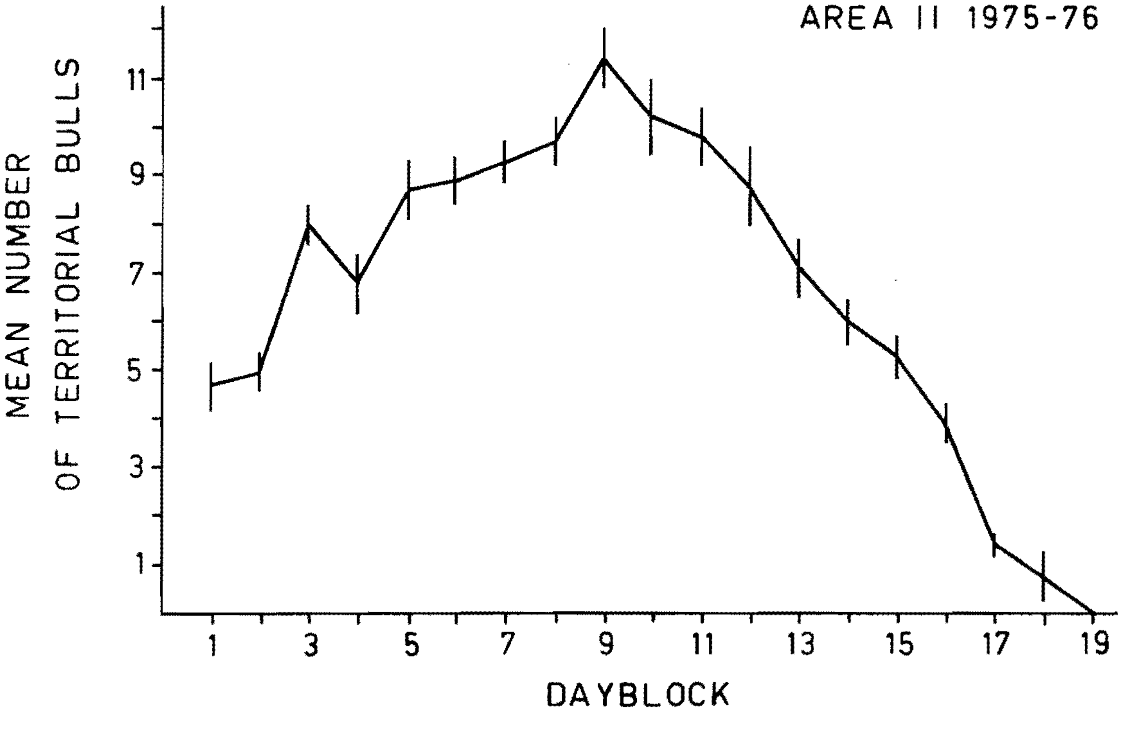
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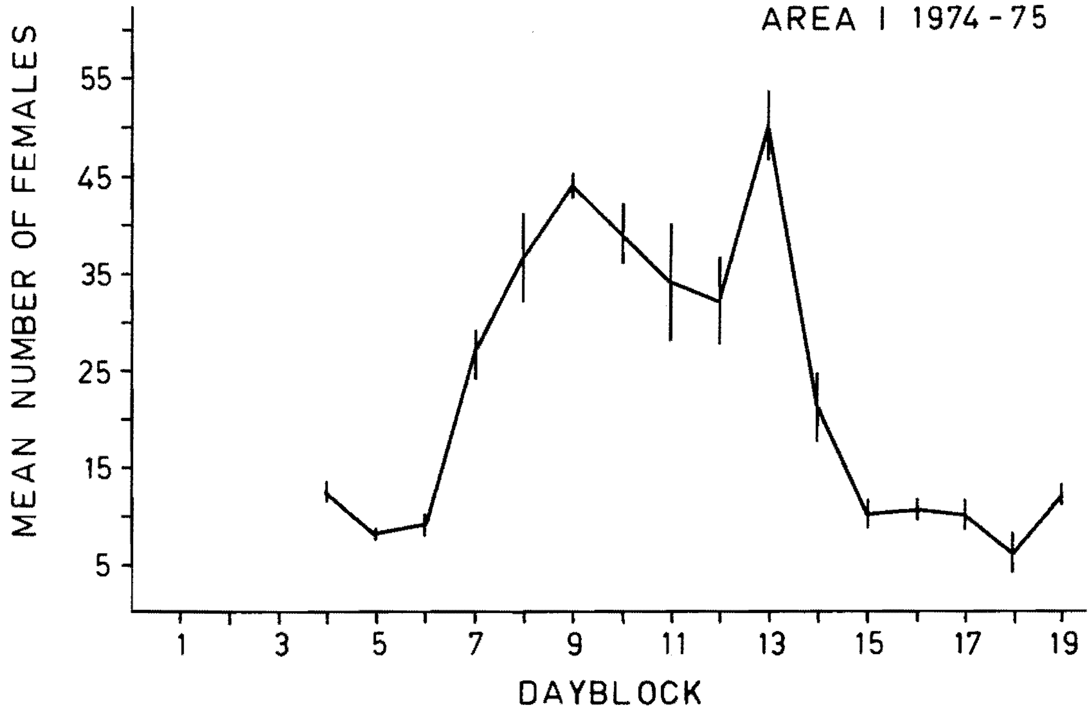
FIGURE 3.2. Mean number of females on the study areas, per dayblock. Vertical lines equal 95% confidence limits. Observations began at dayblock 4 in 1974/75.

a. Study Area I, 1974/75 Breeding season.

b. Study Area II, 1974/75 breeding season.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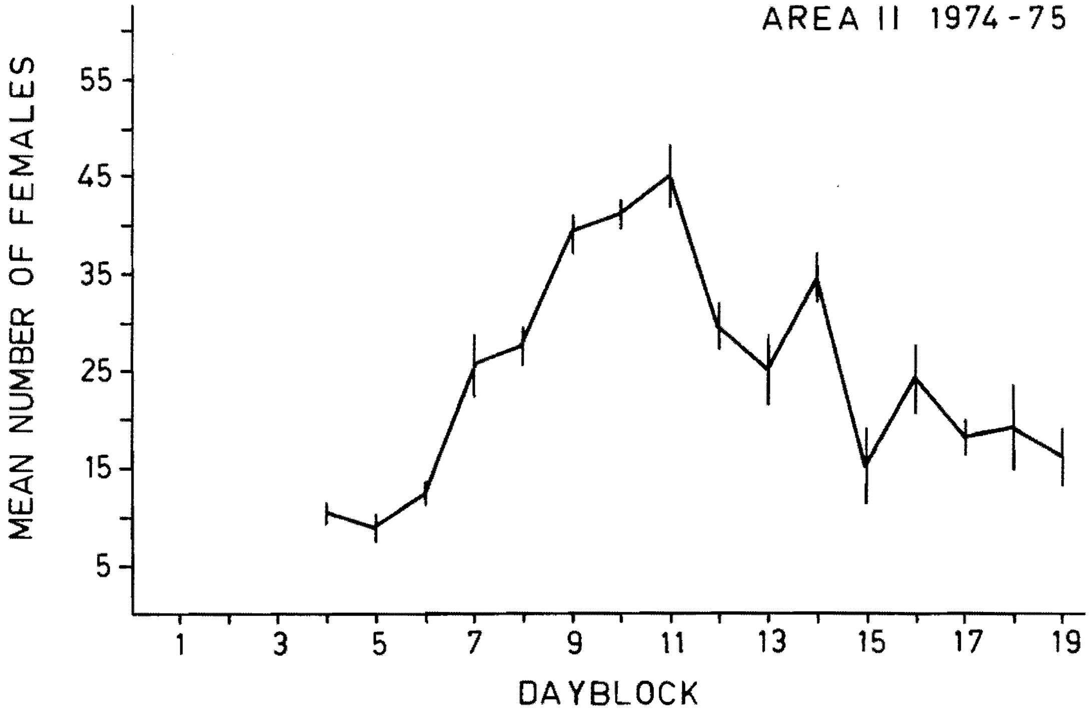
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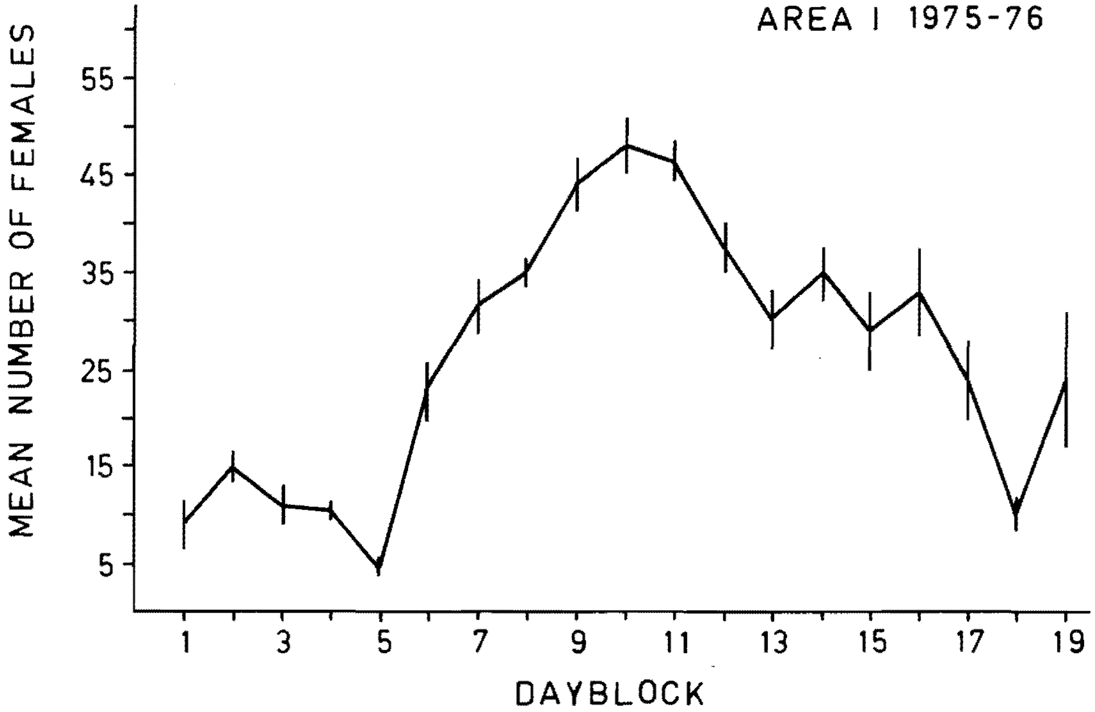
__FIGURE 3.2__. Continued.

c. Study Area I, 1975/76 breeding season.

d. Study Area II, 1975/76 breeding season.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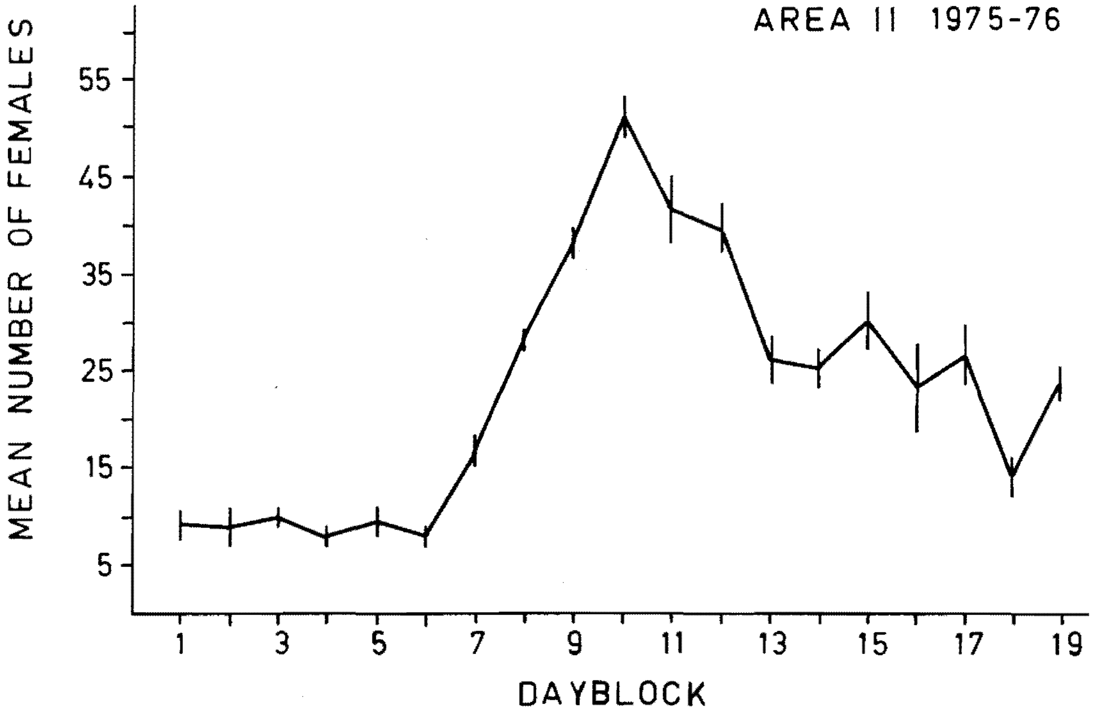
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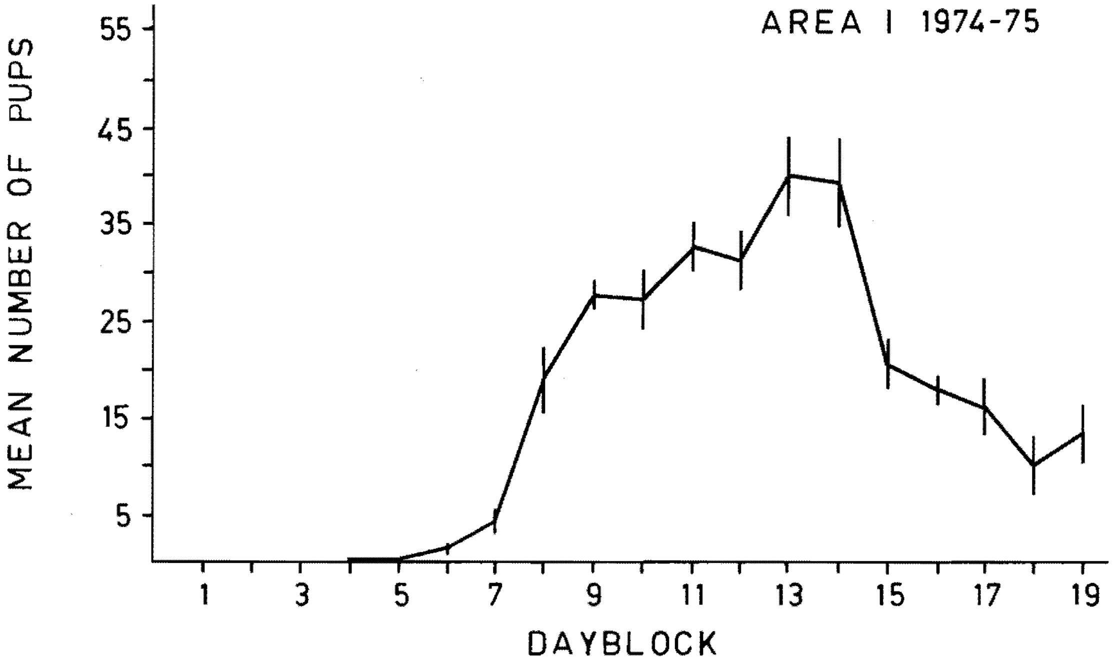
FIGURE 3.3. Mean number of pups on the study areas, per dayblock. Vertical lines equal 95% confidence limits. Observations began at dayblock 4 in 1974/75.

a. Study Area I, 1974/75 breeding season.

b. Study Area II, 1974/75 breeding season.


AREA I 1974-75
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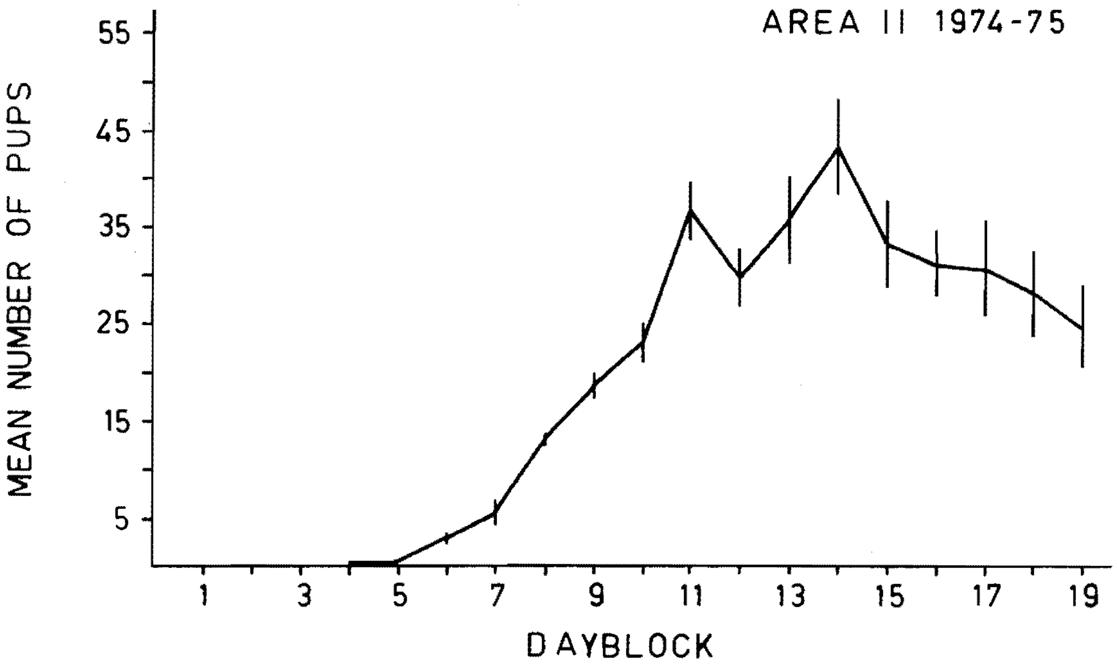
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MEAN NUMBER OF PUPS
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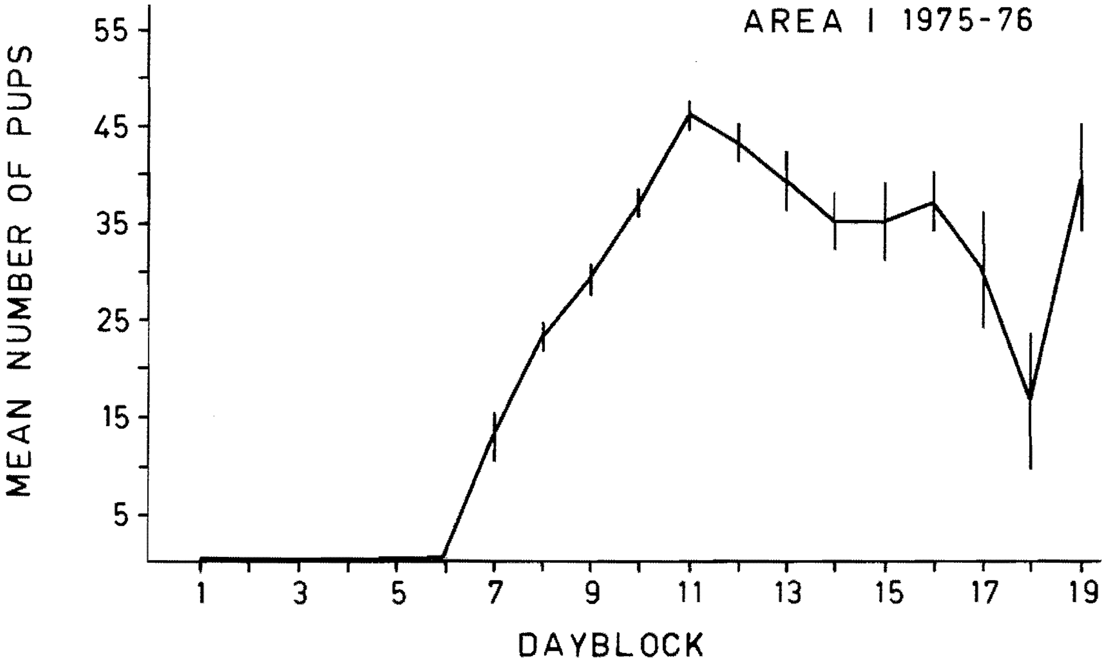
FIGURE 3.3. Continued.

c. Study Area I, 1975/76 breeding season.

d. Study Area II, 1975/76 breeding season.


AREA I 1975-76
MEAN NUMBER OF PUPS
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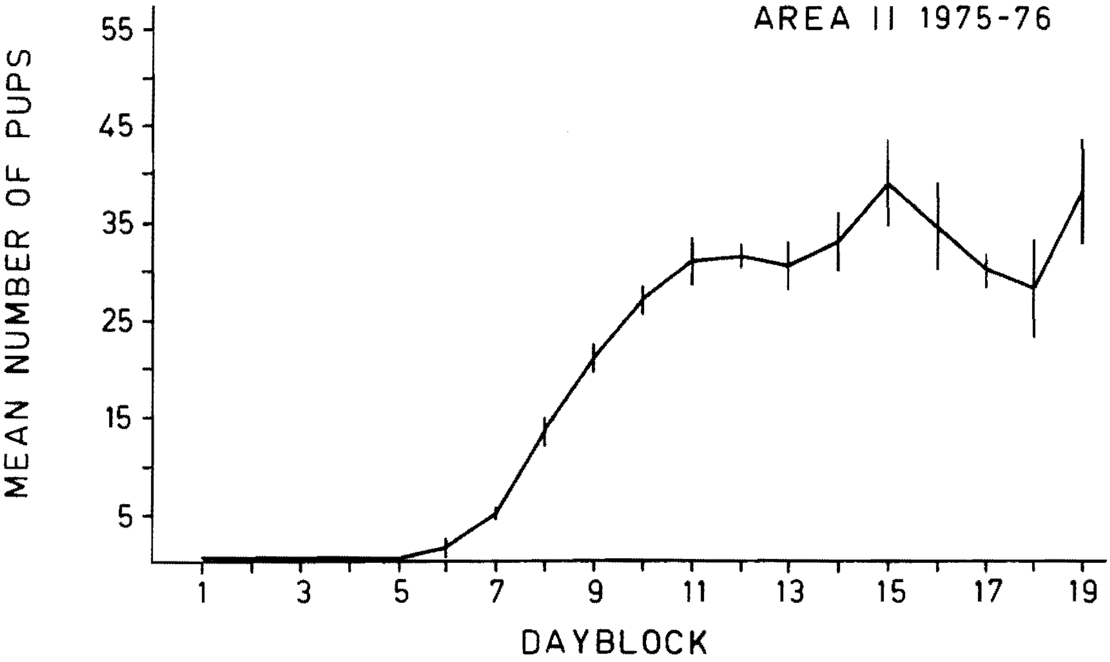
AREA II 1975-76
MEAN NUMBER OF PUPS
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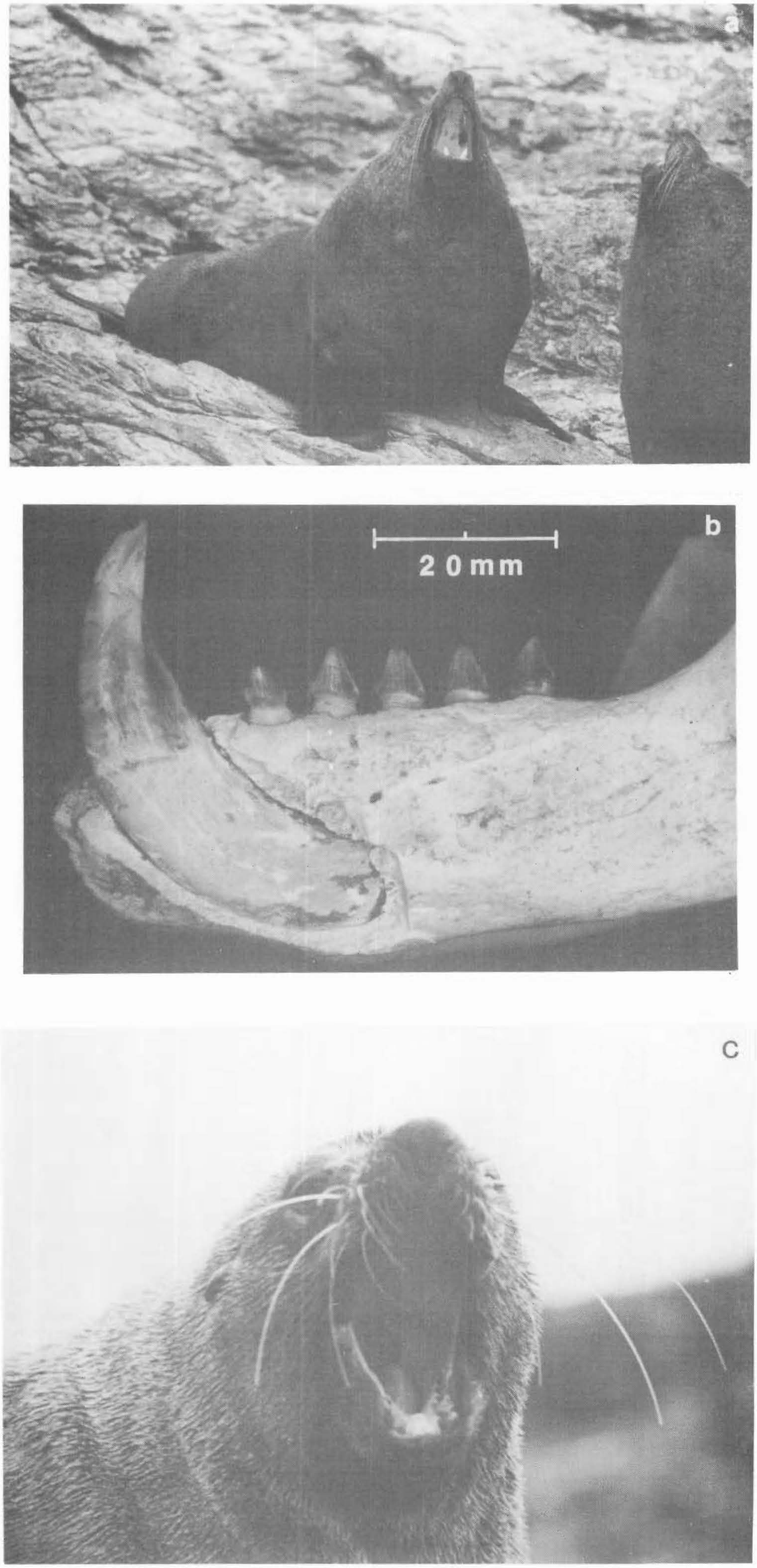
DAYBLOCK

PLATE 3.1. Lower canines of bulls.

a. A territorial bull with both lower canines (photo by M.C. Crawley).

b. Greater than half the length of a lower canine is embedded in the jaw. Canines are broken off, not knocked out, during intrasexual fighting. Note the sharp edge of the lower canine, caused by rubbing against the corresponding upper canine.

c. An adult male with both lower canines broken off near the gum line; otherwise, it apparently was in excellent health. It was not territorial.


a
b
20 mm
c

CHAPTER FOUR

THE USE OF SHADE AND WATER AS AIDS DURING BEHAVIOURAL THERMOREGULATION

4.1. Introduction

Fur seals have little difficulty in retaining body heat at cold temperatures because of their thick underfur and subcutaneous blubber layer. However, the insulative efficiency of the underfur and blubber makes the dissipation of excess metabolic heat difficult. Northern fur seals begin to show definite signs of heat stress when air temperatures reach 12°C; the activity of bulls decreases, and behavioural thermoregulation increases, i.e. females begin to temporarily abandon the rookery and panting and flipper waving become more frequent (Bartholomew and Wilke 1956). New Zealand fur seals neither pant nor flipper wave, but they do make use of the terrain on which their colonies are located in order to counter heat stress. This is accomplished by their moving into pools of water, to damp or wet areas, by moving into the shade, or by temporarily leaving the rookery altogether and entering the sea (pers. ob.; Gentry 1973; Miller 1971; Stirling 1970). Similar behaviour is common among other fur seal species (Bartholomew 1966; Bonner 1968; Eibl-Eibesfeldt 1960; Peterson *et al.* 1968; Rand 1967; Vaz-Ferreira and Palerm 1961). There is considerable literature on behavioural thermoregulation and the physiology of thermoregulation in pinnipeds, so the topic will not be dealt with here (e.g. Irving 1973; Irving and Hart 1957; Irving *et al.* 1962; Matsuura and Whittow 1974; Odell 1974; White and Odell 1971; Whittow *et al.* 1971; Whittow *et al.* 1972). Rather, the degree to which the terrain plays a role in enabling fur seals to counter heat stress is measured by assessment of the percentage of bulls, females and pups totally in the sun as air and blackbulk temperatures increased.

4.2. Methods

Air temperature and, when possible, blackbulb temperature were recorded at the time of each census. When there was direct sunlight on the rookery, each fur seal censused was categorized as being either totally in the sun, partially in the sun, totally in the shade, and/or partially in the water. The last three categories were pooled because they are means by which these fur seals counter heat stress. This resulted in two basic thermoregulatory categories: those totally in the sun (= sun) and those not totally in the sun (= other). The temperature data recorded were divided into four arbitrary ranges, *viz.* low, moderate, medium and high (Table 4.1). No air or blackbulb temperatures were recorded in the low ranges during the 1974/75 season. During the 1975/76 season air temperatures were recorded in the low and moderate ranges only, but blackbulb temperatures were recorded in all four ranges.

TABLE 4.1. Temperature ranges recorded at Taumaka, in degrees C.

Range	Air temperature	Blackbulb temperature
Low	12.5 - 16.5	20.0 - 25.0
Moderate	16.6 - 20.5	25.1 - 30.0
Medium	20.6 - 24.5	30.1 - 35.0
High	24.6 - 29.0	35.1 - 42.0

4.3. Results

(a) 1974/75

(i) Air temperature

There was a significant difference ($p < 0.001$) in the number of bulls females and pups in the sun as air temperature increased during the 1974/75 breeding season. The percentage of females and pups in the sun declined steadily with increasing air temperature from 47 percent and 36 percent respectively at the moderate range, to 28 percent and 21 percent respectively at the high range. The percentage of bulls in the sun did not show a similar steady decline with increasing air temperature, but instead showed an increase of 4 percent from the medium to the high range, after a decline of 26 percent from the moderate to the medium range. These data are summarized in Table 4.2.

(ii) Blackbulb temperature

The change in the percentage of bulls and females in the sun with increased solar radiation followed a different pattern. After an initial decrease in the percentage of bulls (13 percent decrease) and females (1 percent decrease) in the sun from the moderate to the medium blackbulb temperature range, the percentage increased from the medium to the high range by 13 percent and 6 percent respectively. The percentage of pups

TABLE 4.2. The number and percentage of bulls, females and pups totally in the sun (= sun) and not totally in the sun (= other) by air temperature ranges, 1974/75 breeding season.

	Bulls		Females		Pups	
	Sun	Other	Sun	Other	Sun	Other
Moderate	182(53%)	162(47%)	445(47%)	493(53%)	233(36%)	418(64%)
Medium	44(27%)	121(73%)	284(36%)	502(64%)	289(28%)	752(72%)
High	16(31%)	36(69%)	74(28%)	185(72%)	81(21%)	301(79%)
χ^2	34.876		40.272		26.488	
d.f.	2		2		2	
p	<0.001		<0.001		<0.001	

in the sun declined steadily as blackbulb temperature increased, from 35 percent at the moderate range to 26 percent at the high range. There was a significant difference between the number of bulls and pups in the sun and those not in the sun as the blackbulb temperature increased ($p < 0.02$), but there was no significant difference for the females ($p > 0.05$). These data are summarized in Table 4.3.

TABLE 4.3. The number and percentage of bulls, females and pups totally in the sun (= sun) and not totally in the sun (= other) by blackbulb temperature ranges, 1974/75 breeding season.

	Bulls		Females		Pups	
	Sun	Other	Sun	Other	Sun	Other
Moderate	67(48%)	72(52%)	150(39%)	232(61%)	123(35%)	231(65%)
Medium	75(35%)	141(65%)	302(38%)	493(62%)	262(30%)	604(70%)
High	91(48%)	99(52%)	297(44%)	380(56%)	192(26%)	536(74%)
χ^2	9.429		5.504		8.308	
d.f.	2		2		2	
p	<0.02		>0.05		<0.02	

(b) 1975/76

(i) Air temperature

Air temperatures during the 1975/76 season were not as high as during the previous season, and were within the low and moderate ranges only. There was a significant difference ($p < 0.001$) between the number of bulls, females and pups in the sun and the number of those not in the sun as the air temperature increased. The percentage of those in the sun was higher at the low range than at the moderate range. These data are summarized in Table 4.4.

TABLE 4.4. The number and percentage of bulls, females and pups totally in the sun (= sun) and not totally in the sun (= other) by air temperature ranges, 1975/76 breeding season.

	Bulls		Females		Pups	
	Sun	Other	Sun	Other	Sun	Other
Low	397(54%)	340(46%)	1273(53%)	1110(47%)	804(54%)	682(46%)
Moderate	200(41%)	288(59%)	983(44%)	1247(56%)	767(38%)	1274(62%)
χ^2	19.648		40.211		95.065	
d.f.	1		1		1	
p	<0.001		<0.001		<0.001	

(ii) Blackbulb temperature

There was a significant difference ($p < 0.001$) between the number of bulls, females and pups in the sun and the number of those not in the sun as the blackbulb temperature increased, such that there was a steady decline in the percentage of those in the sun with increasing temperature. The most dramatic change was that for bulls, which decreased from 62 percent in the sun at the low range to 16 percent at the high range, a difference of 46 percent. The percentage of females and pups in the sun decreased from 61 percent for females and 59 percent for pups at the low range to 31 percent and 29 percent respectively at the high range, or a difference of 30 percent in each case. These data are summarized in Table 4.5.

4.4. Discussion

Otariids not only make use of shade and water for behavioural thermoregulation, but rely on posture as well (see Gentry 1973). In addition, they leave the rookery temporarily and enter the sea if temperatures get too high (Bartholomew 1966; Gentry 1973; Peterson and Bartholomew 1967). Consequently, inconsistencies in the use of shade and water for thermoregulation by the New Zealand fur seal often are the result of the fur seal's relying on alternative thermoregulatory means, such as changes in posture, and also whether or not they are wet, and the length of time

TABLE 4.5. The number and percentage of bulls, females and pups totally in the sun (= sun) and not totally in the sun (= other) by blackbulb temperature ranges, 1975/76 breeding season.

	Bulls		Females		Pups	
	Sun	Other	Sun	Other	Sun	Other
Low	132(62%)	82(38%)	451(61%)	286(39%)	241(59%)	166(41%)
Moderate	287(51%)	271(49%)	1069(52%)	993(48%)	804(51%)	764(49%)
Medium	139(41%)	201(59%)	647(42%)	914(58%)	467(34%)	915(66%)
High	5(16%)	27(84%)	32(31%)	72(69%)	23(29%)	56(71%)
χ^2	38.298		101.959		136.231	
d.f.	3		3		3	
p	<0.001		<0.001		<0.001	

since they were previously wet. Nevertheless, fur seals on Taumaka rely heavily on shade and water provided by the irregular, rocky terrain of the rookery to counter heat stress (Plate 4.1). During every census, some individuals were using either one or the other, even at air and blackbulb temperatures as low as 12.5°C and 20.0°C respectively. In general, the dependence on the terrain for shade and water increased as both air and blackbulb temperatures increased. This was particularly evident during the 1975/76 breeding season, although the situation was not so clear during the previous season.

The increase in the percentage of bulls and cows totally in the sun as blackbulb temperatures increased during the 1974/75 breeding season is difficult to explain. This season was considerably warmer overall than the 1975/76 season, which probably was why relatively few females and bulls were ashore and few pups were in view during the later part of the summer (as shown in Figures 3.1-3, Chapter Three, Population Biology). Once wet, they would be able to remain in the sun longer than if they were dry.

Perhaps more importantly, there were more than twice as many samples of blackbulb temperatures than air temperatures in the high range during the 1974/75 season. This then, suggests that the fur seals had a stronger negative response (i.e. resorted to either shade or water) to increasing air temperatures than to increasing blackbulb temperatures, and that, in the case of females at least, repeated wetting in the sea increased their tolerance to high insolation.

The slight increase in percentage of bulls totally in the sun between the medium and high air temperature ranges was not statistically significant ($\chi^2 = 0.332$, $p > 0.05$), and consequently was not considered sufficient to cast doubt on the overall trend shown by bulls.

These data indicate that the use of the terrain by the New Zealand fur seal as an aid during behavioural thermoregulation increased as temperature increased. Even at the low temperature ranges, about 40 percent or more of the fur seals present were either partially in the shade, totally in the shade, or in some water. Shade and standing water play a vital role in the ability of fur seals to counter heat stress. The presence of shade and water is therefore a determining factor in why New Zealand fur seal rookeries are found on exposed, rocky coasts. The importance of standing water to territorial bulls for cooling purposes was recognized by Stirling (1970, 1971a), who suggested that its presence could be an important factor in a bull's ability to remain territorial. There is little doubt that this is the case, as demonstrated by New Zealand fur seal bulls on territories without water, who are the first to leave their territories temporarily at high air temperatures. The significance of shade and standing water to site preference is discussed more fully in Chapter Five, Preferred Sites, and in Chapter Nine, Final Discussion.

PLATE 4.1. The use of water (a) and shade (b) by adult male fur seals as thermoregulatory aids (photo (a) by M.C. Crawley). Note bull in (b) drinking from a small pool of rainwater.


a

CHAPTER FIVE

PREFERRED SITES

5.1. Introduction

The Arctocephalinae are different from most pinnipeds in that their colonies are always found on rocky coasts and never on sand or open shingle beaches (general habitat descriptions are available for most fur seal species, e.g. Bartholomew 1966; Bonner 1968; Hubbs and Norris 1971; Paulian 1964; Peterson *et al.* 1968; Rand 1967; Vaz-Ferreira 1956). Within the New Zealand region, New Zealand fur seal colonies are located on broken, irregular coastlines which contain numerous angular rocks and boulders, and are usually exposed to the prevailing winds and seas (Crawley and Wilson 1976; Wilson 1974a). However, little is known about their specific site preferences on the rookery. In this chapter, sites (i.e. territories) on Study Areas I and II are assessed according to their physical characteristics and according to preference shown for them as determined by the presence and number of females on each site per dayblock. Preferred pupping sites at the two study areas are also given. The significance of the physical characteristics held in common by preferred sites is discussed in terms of the fur seal's ability to remain ashore for extended periods of time during the breeding season. Because there was no difference in site preference between the 1974/75 and 1975/76 breeding seasons, only data from the latter season are given.

5.2. Methods

(a) Division of study areas

Study Areas I and II were divided into sections, each of which roughly corresponded to what was at one time or another a territory held by an individual bull (Figures 5.1.a and 5.5.a). Not all of these sections were always occupied by a bull; on occasion some bulls held two or more adjacent sections, either totally or in part, while other sections were sometimes unoccupied.

For each dayblock, the census taken when the most females were present was regarded as representative of that dayblock. This usually resulted in the maximum sample sizes recorded and it was during these times that maximum social pressure was on females who were trying to secure a site on the rookery.

(b) Assessment of sites

(i) According to physical and biological parameters

Sites were assessed according to the characteristics of each section. The site descriptions, based on physical and biological characteristics recorded, were:

1) No standing border: no large rocks or bush on any border.
2) Bush border: bush present on at least one border.
3) Rock border with 'cave': rocks or rock ledges formed at least one border, and contained at least one large indentation or 'cave'.
4) Rock border without 'cave': same as number 3 above minus the 'cave'.
5) Rarely with standing water: water rarely collected, even after a heavy rain.
6) Standing water present intermittently: standing water usually, but not always, present.
7) Permanent standing water present: standing water always present.
8) Ground cover present: grass or similar vegetation covered at least part of section.
9) Two or more bulls between section and sea: passage to and from the sea necessitated passing two or more bulls other than the home territory holder.
10) At least one bull between section and sea: the same as number 9 above, except that one or more bulls between section and sea.
11) Indirect access to sea: no more than one bull between section and sea.
12) Direct access to sea: no bull (other than territory holder) between section and sea.
13) Resting platform present: presence of conspicuously raised area on which bulls preferred to rest.
14) No shade: shade never present on any part of section.
15) Shade present: some shade present at least part of the time.
16) Subject to sea wash: at least part of section covered by sea wash during storms.
17) Rarely subject to sea wash: section usually secure from sea wash during storms.

(ii) According to the females' site preference

Site preference was determined independently by two methods, both of which were based on the presence or absence of females. Firstly, the sites were ranked in descending order of preference by the number of representative dayblocks during which females were present, minus the number of pairs of adjacent dayblocks when females were not present. This compensated for the different sizes of the sections by ranking according to the presence or absence of females only. Secondly, site preference was determined according to the total number of females present on each section, which was calculated by adding the number of females present for each representative dayblock. This method did not take into account size differences between the sections, nor did it take into account fluctuations in the number of females present at different times during each dayblock.

The characteristics of each section (as listed in (i) above) were then compared, to determine which characteristics were common to the 'preferred' sites, i.e. the sites which contained females most often, or which contained the greatest 'number' of females.

5.3. Results and observations

(a) Study Area I

(i) Description of study area

Study Area I covered about 655 m^2, and had a large, open central region of about 490 m^2 surrounded by rock structures varying in height from 1-5 m. These extended along about 56 m of its 125 m periphery. Half of the structures included some kind of overhang or shallow cave (Plate 5.1; Figure 5.1.b). One area (A, Figure 5.1.b) included a steep, sloping cave of 2-3 m depth with an approximate 45° downward slope. Sea water usually was present at the bottom of this cave during high tides and storms.

A permanent large pool of about 8.5 m^2 was on the far left side of the study area, and a smaller pool, which never exceeded 1 m^2 in area, was at the right of the study area. Depending on the amount of rain, puddles of standing water usually were present over most of the study area, except for the central sections nearer the bush line. Water never collected in this area (B, Figure 5.1.b).

There was one route of direct access to the sea, known as the passage (C, Figure 5.1.b), and an indirect route located to the right of the study area (D, Figure 5.1.b). Females passing through the indirect route were often harassed by young bulls, some of which were not territorial. All other access involved moving some distance overland through occupied territories.

Although the open portion of the study area contained no obstructions, it nevertheless was very irregular and broken, with a vertical drop of about 8.5 m from the bush line to the sea (Figures 5.1.b and 5.1.c). Because of this slope, and because of the limited direct access to the sea, storm-induced sea wash never reached more than 6 m into the area.

(ii) Site preference

1) By class of fur seal

BULLS: Six bulls were already on the study area at the start of dayblock 1 (30 October - 3 November), but with one exception they were small and probably less than 10 years old (see Chapter Three, Population Dynamics). The only large territorial bull was to the left of the passage (section 4). The two smallest bulls present held territories against the bush line and did not remain for the entire dayblock. On 1 November, only three bulls were present: one to the left of the passage (section 4), one to the left of the study area (section 1/2; in front of a rock forming what was called penguin cave) and one to the right of the hide (section 7). Figure 5.2.a represents 31 October.

By dayblock 3 (9-13 November), three large territorial bulls were present: the one to the left of the passage (section 4), one to the right of the passage (section 5) and the one by penguin cave (section 1/2). The remaining occupied territories were similar to those occupied during dayblock 1, except that two small, and presumably young, bulls had taken up residence on the central region (sections 10 and 11).

A large, newly-arrived, territorial bull moved onto section 3 (by the one large pool) during dayblock 4 (14-18 November), and by dayblock 5 (19-23 November) large territorial bulls, which probably were 10 years old or older, were occupying the territories held continuously from this point on throughout the season (all were against the rocks bordering the periphery of the study area; Figure 5.2.b).

By dayblock 8 (4-8 December), the maximum number of bulls which held territories against the rock periphery were present and, two dayblocks later, the maximum number of bulls were present on the study area

(Figure 5.2.c).

Bulls in the central open region were more inclined to rest near to, rather than away from, the bush edge during dayblock 12 (24-28 December), and by dayblock 13 they were beginning to leave their territories temporarily and enter the sea. Only four bulls were not leaving their territories for short visits to the sea by dayblock 14 (3-7 January). These held territories to the left of the passage (section 4), by the large pool (section 3), by penguin cave (section 1/2) and to the right of the hide (section 7/8).

Some territories were beginning to be abandoned in dayblock 15 (8-12 January), particularly those on the flat central region, but three were continually maintained. They were to the left of the passage (section 3/4), by penguin cave (section 1/2) and to the right of the hide (section 8). By dayblock 16 (13-17 January), only three bulls remained on the study area. They were located between the large pool and the passage, by penguin cave and by the indirect access to the sea (Figure 5.2.d). These territories were held until dayblock 19 (28 January - 1 February), though not necessarily by the original bull, at which time only the area to the left of the passage remained occupied (Figure 5.2.e).

Bulls preferred to lie on elevated ground, even if it was elevated by only a few centimetres. Consequently, they would usually lie entirely on a rock, or rest their head on a rock. Of 183 records of resting bulls, 158 (86.3 percent) were elevated at least slightly.

FEMALES: From dayblock 1 (30 October - 3 November) to dayblock 5 (19-23 November), the number of females present on the study area declined as they went to sea for a final feeding trip before pupping. Those which remained were mainly located on the sections with the most direct access to the sea, i.e. sections 4, 6, 7 and 8 (Figure 5.2.a and 5.3). This decline was especially pronounced on section 4, which contained the greatest percentage of females early in the season.

From dayblock 5 (19-23 November) towards mid-season, the number of females increased steadily as they arrived ashore to give birth. The most obvious increases took place on those sections with the most direct access to the sea (sections 4, 6, 7 and 8), particularly section 4.

An increase in the number of females on section 1 occurred after increases on sections 4 and 3. The peak number of females on section 1 was roughly three dayblocks behind the peak on sections 3 and 4, and followed the slight increase in number of females on section 2 (Figure 5.3).

Females increased in numbers on the less populated sites as the season progressed and additional females continued to arrive. Much of the increase in the number of females on sections 10 and 11 was due to an 'overflow' of females from sections 3 and 4. During the last half of the season, females moved inland towards the bush line, causing a decline in numbers on sections near the sea. The number of females present on sections away from the seaward side of the rookery, but which had an indirect access to the sea (i.e. sections 6, 7 and 8) did not reflect this decline (Figure 5.3).

Females also preferred to rest on elevated ground, even if it was only a few centimetres above the surrounding terrain. Of 710 records of resting females, 631 (88.9 percent) were of females on elevated ground.

YEARLINGS: Yearling distribution was similar to that of the females, which was not surprising as many were still suckling. They were seen most commonly between the large pool and the passage and in the vicinity of the hide until dayblock 5 (19-23 November). After this they were rarely present.

PUPS: As might be expected, pup distribution matched that of females. After dayblock 10 (14-18 December), pups left on their own began to form into pods, particularly in the areas by the bush to the left of the hide, near the passage and on the rocks over penguin cave. As pups grew older, they began to form pods by the large pool to the far left of the study area, but seldom settled in the open, exposed, central regions. Later in the season during particularly bad weather, pups would move up into the bush and onto the raised rocks to the far left and right of the study area (Figure 5.2.e).

Pups also preferred to be elevated while resting, but not to the same degree as either the bulls or females. Of 537 sightings, 422 (78.6 percent) were at least partially on raised rocks.

SUBADULT MALES (SAM): Subadult males were occasionally on the study area during the early and late parts of the season, but were rarely on the rookery for any length of time. When present, they tended to remain in the vicinity of the indirect access to the sea.

NEUTERS: Neuters (those individuals which could not be positively sexed at a distance) were most abundant during the early part of the season and were usually on the rocks behind section 4 (see Figure 5.2.b) and in the bush by the hide. With the exception of one individual during dayblock 9 (9-13 December), neuters were not seen on the study area between dayblocks 7 (29 November - 3 December) and 14 (3-7 January). As bulls became less territorial, later in the season, neuters began to reappear on the study area.

2) According to physical and biological parameters of the sections

The physical and biological characteristics of each of the 13 sections and their order of preference by females are summarized in Tables 5.1 and 5.2 respectively.

Based on the presence or absence of females, section 4 was the most preferred, followed by sections 6, 7 and 8 as a group, then sections 10, 1 and 3. Based on the number of females present, section 4 was again the most preferred, followed by sections 8, 3, 7, 1 and 6. Four characteristics were generally held in common by sections 1, 3, 4, 5, 6, 7 and 8, i.e. all were bordered on at least one side by some kind of rock structure, five of the seven always contained standing water and standing water was usually present on the other two, four of the six had either a direct or indirect access to the sea (the remaining two required passing at least one bull in order to reach the sea), and all provided some shade.

3) Preferred pupping sites

On Study Area I, 26 births were recorded. Of these, 22 were seen either in progress or the new pup was seen within minutes of birth, three of the new pups were seen within 24 hours of birth, and one was seen within 48 hours of birth. These births were concentrated in six regions, which in decreasing order of numbers of births recorded were: section 4 (14 births, 53.8 percent), section 8 (5 births, 19.2 percent), section 3 (3 births, 11.5 percent), section 1 (2 births, 7.7 percent), section 6 (1 birth, 3.8 percent) and section 13 (1 birth, 3.8 percent; Figure 5.4).

The first four recorded births were on section 4, which was used for pupping throughout the season. On section 8, the first recorded birth was six days after the first on section 4, and section 8 was also used as a pupping site throughout the season. Recorded births on section 3 were during mid-season, and those on section 1 were during the later part of the season. The single births recorded for sections 6 and 13 took place early in the season.

As sections 4 and 8 not only contained the majority of births, but were used as pupping sites throughout the season, then it is assumed that

TABLE 5.1. Physical and biological parameters present on each of the 13 sections of Study Area I.

		Section number												
	Physical parameter	1	2	3	4	5	6	7	8	9	10	11	12	13
1.	No standing border		x								x	x	x	
2.	Bush border	x						x	x	x				x
3.	Rock border with 'cave'	x		x	x	x	x							
4.	Rock border without 'cave'			x	x			x	x					
5.	Rarely standing water									x				x
6.	Intermittent standing water					x	x				x	x	x	
7.	Permanent standing water	x	x	x	x			x	x					
8.	Ground cover													
9.	Two or more bulls between section and sea									x	x			x
10.	At least one bull between section and sea	x	x	x								x	x	
11.	Indirect access to sea						x	x	x					
12.	Direct access to sea				x	x								
13.	Resting platform present	x	x	x	x	x	x	x	x	x	x	x	x	x
14.	No shade		x								x	x	x	
15.	Shade present	x		x	x		x	x	x	x				x
16.	Subject to sea wash													
17.	Rarely subject to sea wash	x	x	x	x	x	x	x	x	x	x	x	x	x

TABLE 5.2. Order of female preference for sections on Study Area I (see also Figure 5.3).

			Section number												
			1	2	3	4	5	6	7	8	9	10	11	12	13
A.	The number of representative dayblocks during which females were present minus the number of pairs of adjacent dayblocks when females were not present (a), and order of preference (b) (see Figure 5.3).	(a)	13	6	11	19	10	16	16	16	10	14	7	4	8
		(b)	4th	9th	5th	1st	6th	2nd	2nd	2nd	6th	3rd	8th	10th	7th
B.	Total number of females present by representative dayblock for the entire season (a), and order of preference (b) (see Figure 5.3).	(a)	46	10	60	161	21	45	51	83	26	36	21	7	29
		(b)	5th	11th	3rd	1st	10th	6th	4th	2nd	9th	7th	10th	12th	8th

they were the two most preferred sites. One thing these two sections had in common which the other sections where births were recorded did not, was that they had the most direct access to the sea, with section 4 (containing 53.8 percent of the births) bordering on the only direct access.

Females about to give birth did not appear to prefer any particular site within a preferred section, though generally they did prefer to be near some irregularity, such as a rock or log.

(b) Study Area II

(i) Description of study area

Study Area II covered about 525 m^2 of irregular, broken terrain containing numerous rocks and boulders plus two large guts (Plate 5.2; Figure 5.5.a). Although both guts filled partially with water at high tide, the upper reaches usually remained dry. During storms which coincided with high tides sea wash often reached to the head of both guts, but especially the one on the right.

There were three routes of direct access to the sea: one through each of the two guts, and one, known as the exit, through a gap in the rocks at the far right side of the study area (designated as A, B and C respectively on Figure 5.5.b). Some cross-over occurred through an opening between the two guts. The one route of indirect access to the sea was over the ridge forming the border on the right side of the study area (D, Figure 5.5.b).

Standing water was always present in four small pools, three by the exit and one near the centre of the study area. The three pools near the exit were fed largely by sea spray and never exceeded 2 m^2 in area, whereas the other was fed by rain water and never exceeded 1 m^2 in area. A large pool was located to the mid-left, just outside the border of the study area.

Few fur seals were ever seen on top of the rocks separating the two guts (E, Figure 5.5.b), but fur seals used the large rocks to the right rear of the study area (F, Figure 5.5.b).

Study Area II had a vertical drop of about 7.5 m from the bush line to half way down the right gut (Figure 5.5.c) and was, with the exception of the two guts, safe from sea wash.

Vegetation consisted of one small *Hebe elliptica* on the ridge forming the border on the right side of the study area, the predominantly *Hebe* border on the landward side of the study area, and areas of peaty earth containing a sparse herbaceous growth (primarily of *Lepidium oleraceum* and *Tillaea moschata*) which was dispersed over the rocks on the upper reaches of the area.

(ii) Site preference

1) By class of fur seal

BULLS: Four bulls were already present on the study area by dayblock 1, three of them on the 'rookery' proper. These three were located in the left gut, the right gut and by the exit (sections 6, 8 and 2 respectively), while the fourth was on the high rocks to the rear right side (section 1). This latter area was occupied throughout the season by one or more bulls, but their tenure was usually short. The three bulls on the rookery proper were all large and probably were at least 10 years old (see Chapter Three, Population Dynamics). They were joined by three others during the following dayblock, who took up territories by the rocks to the left of the entrance to the left gut (section 5), by the central 'ring' of rocks (section 4), and to the right rear of the study area (section 3; Figure 5.6.a).

There were few additions until dayblock 5, when one additional bull moved into each of the two guts. The new bull in the left gut remained towards the seaward side (section 7), while the bull in the right gut was pushed up into the near right corner and into section 9. A third bull tried to hold a territory in the left gut during dayblock 6, but was unsuccessful. Other than that, there was little change. A third bull moved into the right gut during dayblock 9 (Figure 5.6.b), but by dayblock 12 only 1 remained.

During dayblock 14, the bull in the central region (section 4) abandoned his territory, as did one of the two bulls in the left gut, and the bull on the territory to the near right side (section 3). The bull on the rocks to the left of the entrance into the left gut (section 5) abandoned his territory by dayblock 16, and by dayblock 17 only two bulls remained; one each in the left and right gut. Territorial bulls were no longer present by dayblock 18.

FEMALES: The number of females on area II remained reasonably constant (i.e. 9-14 individuals) during the first five dayblocks. They were located principally in the vicinity of the exit (section 2), the rocks of the central region towards the guts (section 4) and the two guts (sections 6 and 8; Figure 5.6.a, and 5.7). The percentage of females by the exit was greatest at the beginning of the season, but then steadily declined.

Additional females began arriving from dayblock 7, and tended to congregate in areas where large rocks and boulders were present, i.e. sections 2, 3, 4, 5, 6, 8 and 10 (Figures 5.6.b and 5.7). Although some of the greatest concentrations of females occurred close to the heads of the two guts, the guts themselves were not used to the same degree as were sections 2, 3, 4, 5 and 10.

After dayblock 10, many females (and their pups) began to frequent the area towards the bush line on sections 4 and 5 (Figure 5.6.c). This region was elevated above the rest of the study area, and was covered by rocks and peat which contained a scattered herbaceous growth of *Lipidium oleraceum* and *Tillaea moschata*.

The seaward end of the left gut (section 7) was seldom used by females until dayblock 13, and then not extensively. The far end of the right gut was rarely used, probably because there were no adequate resting places. Females began using the ridge to the right of the study area during dayblock 11, but never in great numbers.

Section 9 was rarely used. It was a small, steeply sloping section with few resting places. The high rocks to the rear of the study area (section 1) were seldom used by females until dayblock 15, and then not intensively.

During stormy weather, females and their pups left the guts and rested among the major rock groupings (Figure 5.6.d).

Females resting on elevated ground accounted for 752 of the 863 sightings (87.1 percent).

YEARLINGS: Yearlings were rarely seen after dayblock 4. The few that were present (the maximum counted at one time was 10, during dayblock 1) were seen by the exit and on the rocks behind the exit (section 2).

PUPS: When not in pods, pup distribution was basically the same as female distribution. Pups first began to form into pods during dayblock 10, particularly on the areas by the rocks in the rear central region (sections 3 and 4) and by the ridge to the right (section 3). By dayblock 12, pups were forming pods by the rocks to the left of the entrance to the left gut (section 5), by the rocks to the right of the head of the right gut and on the rocks behind the exit (section 2). During good weather, pups from dayblock 13 onward played in the calm sea water at the far end of the guts (especially the left gut).

Pups were particularly common on the rocks behind the exit, on the elevated areas by the bush line in sections 4 and 5, and on the ridge to the right by dayblock 15. However, there was no place where pup pods were not found at one time or another.

Of 544 records of resting pups, 363 (66.7 percent) were of pups on elevated ground.

SUBADULT MALES AND NEUTERS: Subadult males and neuters were rarely seen on this study area, and when seen were usually by the sea's entrance into the guts and, in the case of neuters, on the ridge to the right.

2) According to the physical and biological parameters of the sections

The physical and biological characteristics of each of the 10 sections and their order of preference by females are summarized in Tables 5.3 and 5.4 respectively.

Sections 2, 4 and, to a lesser degree, 8, were used throughout the season, and sections 3, 5, 10 and, to a limited degree, 6, were used extensively after dayblock 6 (i.e. after the end of November; Figure 5.7). Seals on all of the sections in area II had reasonable access to the sea, rocks, boulders, shade and water. Only sections 1, 9 and 7 were rarely used. Section 7 flooded at high tide, and lacked adequate resting sites. Section 1 was very high and provided little or no cover. It was used by bulls who were resting and not necessarily holding the area as a territory. Section 9 was very small and steep, and provided barely enough room for the resident territorial bull.

3) Preferred pupping sites

On Study Area II, 34 births were observed totally or in part, or within 24 hours of taking place. Births occurred in all sections (range: 3-7 births per section) except 1, 7 and 9. When the locations of the recorded births were divided into eight birth site regions based on natural groupings about some characteristic terrain, a very definite pattern of preference emerged. In decreasing order of number of births recorded, these regions were: on the rocks at the head of the two guts (region F, 8 births, 23.5 percent), on the rocks on the central part of the study area, and at the head of the right gut (regions D and G respectively, 7 births each, 20.6 percent each), on the central right of the study area, by the rocks to the left of the head of the left gut, and in the left gut (regions B, E and H respectively, 3 births each, 8.8 percent each),

TABLE 5.3. Physical and biological parameters present on each of the 10 sections of Study Area II.

		Section number									
	Physical parameter	1	2	3	4	5	6	7	8	9	10
1.	No standing border	x									
2.	Bush border			x	x	x					
3.	Rock border with 'cave'										
4.	Rock border without 'cave'		x	x	x	x	x	x	x	x	x
5.	Rarely standing water	x								x	
6.	Intermittent standing water										x
7.	Permanent standing water		x	x	x	x	x	x	x		
8.	Ground cover				x	x					
9.	Two or more bulls between section and sea										
10.	At least one bull between section and sea				x	x					
11.	Indirect access to sea			x			x			x	x
12.	Direct access to sea	x	x					x	x		
13.	Resting platform present	x	x	x	x	x	x	x	x	x	x
14.	No shade	x									
15.	Shade present		x	x	x	x	x	x	x	x	x
16.	Subject to sea wash						x	x	x		
17.	Rarely subject to sea wash	x	x	x	x	x				x	x

TABLE 5.4. Order of female preference for sections on Study Area II (see also Figure 5.7).

			Section number								
		1	2	3	4	5	6	7	8	9	10
A.	The number of representative dayblocks during which females were present minus the number of pairs of adjacent dayblocks when females were not present (a), and order of preference (b) (see Figure 5.7).										
	(a)	-3	19	13	19	12	16	4	17	-7	12
	(b)	7th	1st	4th	1st	5th	3rd	6th	2nd	8th	5th
B.	Total number of females present by representative dayblock for the entire season (a), and order of preference (b) (see Figure 5.7).										
	(a)	9	100	96	110	54	39	17	55	1	48
	(b)	9th	2nd	3rd	1st	5th	7th	8th	4th	10th	6th

on the rocks towards the rear right of the study area (region C, 2 births, 5.8 percent) and by the exit (region A, one birth, 2.9 percent; Figure 5.8).

Regions D, F and, to a lesser degree, G, were used as birth sites throughout the season. These regions combined contained 65.7 percent of the recorded births. The remaining regions were sites of few births and, with the exception of region H, were used as pupping sites during mid-season only, i.e. during the second and third weeks of December. Regions D, F and G had two factors in common: they all had direct or indirect access to the sea, and they were composed of very irregular terrain with concentrations of large rocks and boulders. These characteristics were the two most important factors determining birth site preference on area II.

5.4. Discussion

'Preferred site' territories, or those which ultimately were to have the greatest densities of females, were the first to be held by territorial bulls. This was especially obvious at Study Area I. Assuming that the greatest competition amongst bulls was for sites preferred by females (see Chapter Nine, Final Discussion), then this implies that: 1) either bulls 'instinctively' knew which areas would ultimately contain the greatest density of females, or 2) that bulls had been on the rookery before and from experience knew which areas females preferred, or 3) that bulls had the same, or nearly the same, site requirements.

It is unlikely that instinct alone accounted for socially mature bulls knowing which specific areas on the rookery were preferred by females (see Chapter Three, Population Biology, for a discussion of social maturity in bulls). Rather, experience probably played an important role in site preference, in which case recognition of preferred sites by bulls is at least partially learned. Bulls make their first real attempt at being territorial at age 7 or 8 years, but are rarely successful until about age 10 years. This gives bulls two to four years to gain the experience necessary to choose and maintain a territory successfully. The most preferred territory on area I was the first to be held by what appeared to be a socially mature bull of at least 10 years of age. New Zealand fur seal bulls probably return to the same rookery every, or nearly every, breeding season. One bull, which was easily identified by a badly damaged right foreflipper, although not on the rookery *per se*, was seen on the same rock for three consecutive breeding seasons (pers. ob.; M.C. Crawley *pers. comm.* 1976). Site fidelity has been shown for many pinnipeds, including the Grey seal (Bonner *in* Anderson *et al.* 1975), Northern fur seal (Kenyon 1960; Peterson 1968) and Cape fur seal (Rand 1967). Until more data from permanently marked seals are collected, observations on site fidelity must remain speculative. However, experience has been shown to play an important part in territory choice by the Northern fur seal (Peterson 1968).

Bulls and females ashore have many of the same site requirements. Both sexes are subject to thermal stress, which makes areas containing shade and water highly desirable (see Chapter Four, The Use of Shade and Water as Aids during Behavioural Thermoregulation). Therefore, bulls probably are drawn initially to locations on the rookery by similar thermoregulatory requirements to those of females, but experience from previous breeding seasons may play an important role in directing bulls to the sites most preferred by females.

There is little doubt that female New Zealand fur seals have definite site preferences. This was particularly obvious at Study Area I, which had a greater diversity of territory types than Study Area II. Females arriving early in the season tended to head for specific locations, and later arrivals spread to other localities as the more preferred sites became crowded. Data on the amount of crowding New Zealand fur seal females will tolerate are limited, but it appears that at least one body length (1.1-1.3 m) between individuals is desired (pers. ob.; Gentry 1973; Miller 1971). It has been suggested that newly-arrived females of many seal species orient towards other females rather than towards specific sites (Bartholomew 1953; Bonner 1968; Carrick *et al.* 1962; Fogden 1971; Laws 1956a; Marlow 1975). It is unlikely that this is the case with New Zealand fur seal females because of their low tolerance to crowding. A concentration of females on an area could, in fact, act as a deterrent to later arrivals. This apparently is what happened at Study Area I, where there was a progressive increase in the number of females moving away from section 4 as the area became more crowded, rather than the degree of crowding on section 4 becoming more intense.

It is unlikely that females orient towards specific bulls. The tenure of territorial bulls can be very short, and females, either individually or as a group, gave no indication of moving to other territories whenever a resident bull on a particular territory was replaced. Rather, females orient towards specific sites on the rookery which fulfil their terrain requirements.

Relief from thermal stress (i.e. heat stress) is the single most important criterion in site preference. The shade and water provided by the terrain were used extensively during behavioural thermoregulation. Territories near the sea are the first to contain females on the open breeding beaches of the Northern fur seal (Bartholomew and Hoel 1953). This probably is because females retreat into the sea whenever there is a break in the almost continual cloud cover and the air temperature reaches 12°C (Bartholomew and Wilke 1956). The presence of shade has been shown to play an important part in the determination of site preference by the Guadalupe fur seal, though the presence of standing water is also important (Peterson *et al.* 1968).

When shade, rocks and standing water are all present, it is ease of access to the sea which determines the most preferred sites. Such access is of no real importance to territorial bulls, but females routinely leave the rookery either to cool off, groom or to go on feeding trips. With direct access to the sea, females are less subject to harassment from bulls, as there are no 'free' lanes of access to and from the rookery as found on rookeries of the Northern fur seal (Bartholomew 1953), South American fur seal (Vaz-Ferreira 1956), and Cape fur seal (Rand 1967). No free lanes of access are found on rookeries of the Australian population of the New Zealand fur seal (Stirling 1971a), Kerguelen fur seal (Bonner 1968) or Amsterdam Island fur seal (Paulian 1964).

Females probably have a high degree of rookery fidelity, though to date there are no data to substantiate this supposition. Rookery fidelity is common in pinnipeds, and has been shown in the Australian population of the New Zealand fur seal (Stirling 1971b), Northern fur seal (Kenyon 1960; Peterson 1968), Cape fur seal (Rand 1967), Grey seal (Cameron 1971) and Weddell seal (Stirling 1969a).

There was no evidence that females pupped in specific sites because other females had previously pupped in the same location, as has been suggested for the New Zealand fur seal (Miller 1971) and the Australian sea lion (Marlow 1975). Rather, females about to pup preferred to be near some irregularity in the terrain, which caused the majority of births to be grouped in specific regions.

Females avoided much of the intraspecific conflict found on the more preferred sites by moving to areas higher up on the rookery (but not into the bush) during the later part of the breeding season. By this time bulls were less territorial, and females were rarely bothered by them as they travelled to and from the sea. Also, females were far enough apart so that intrasexual conflict was at a minimum.

Territorial behaviour is more highly developed in the Arctocephalinae than in any other otariid. New Zealand fur seal bulls may be ashore for up to 60 consecutive days during the breeding season. To maintain thermal neutrality when ashore, fur seals must be able to retain or dissipate body heat as the environmental conditions dictate. The retention of body heat is facilitated by their dense underfur and subcutaneous blubber layer, but the dissipation of excess metabolic heat is more difficult. For this, fur seals usually resort to lying either totally or partially in shade or water, or in some species by flipper-waving or panting (Bartholomew 1966; Bartholomew and Wilke 1956; Gentry 1973; Peterson *et al.* 1968; Vaz-Ferreira and Palerm 1961; Vaz-Ferreira and Sierra de Soriano 1963). Consequently, I agree with Wilson (1974a; *pers. comm.* 1978) that most fur seal species are found on rocky coasts because of their particular thermoregulatory requirements, i.e. their reliance on the terrain for aid in cooling by behavioural means. This is usually accomplished through their large hind flippers (Bartholomew and Wilke 1956; Harrison and Kooyman 1968; Irving *et al.* 1962). Many otariids which breed on sandy beaches frequently return to the sea to cool off, or locate their territories at the sea's edge, flip sand over their bodies, or roll in damp sand (Peterson 1968; Peterson and Bartholomew 1967; Vaz-Ferreira 1975a, 1975b). Because of the fur seal's dense underfur, sand flipping or rolling in damp sand would be ineffective.

It has been suggested that hunting pressure may have had an influence on the present location of Amsterdam Island fur seal rookeries (Marsallon 1969), and may have encouraged the Guadalupe fur seal to use caves (Peterson 1968; Peterson *et al.* 1968). There is no evidence to suggest that New Zealand fur seals ever utilized any other type of habitat than exposed rocky coasts.

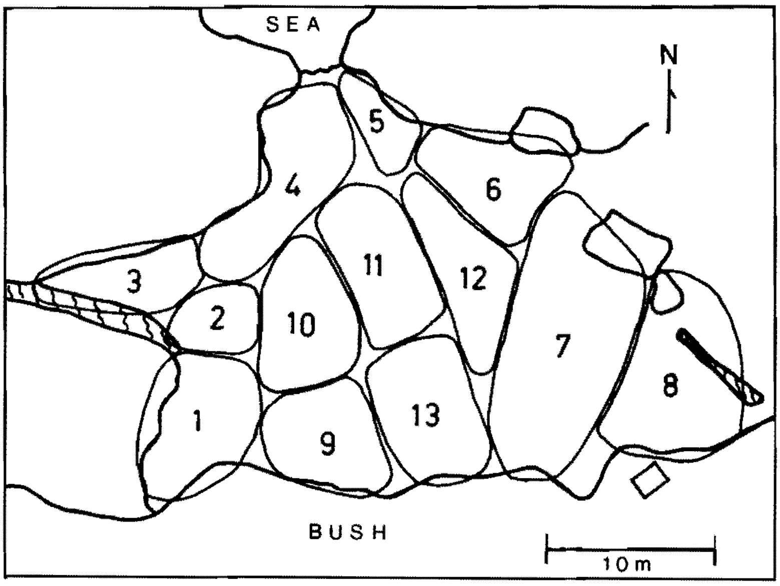
Therefore, New Zealand fur seals prefer sites on the rookery with rock or boulder cover which provides shade and standing water in the form of small pools or puddles for use during behavioural thermoregulation, and easy access to the sea. In the case of the two guts at Study Area II, it probably was the negative attribute of flooding when storms coincided with high tides that made them less desirable than they might otherwise have been. The presence of females on section 10 at Study Area I was largely due to an overflow of females from the adjacent and more preferred site, section 4, and not to the characteristics of the section itself. Section 5 on area I had all the attributes of a 'preferred' site, but because of its small size and steeply sloping cave, it could hold only a few females.

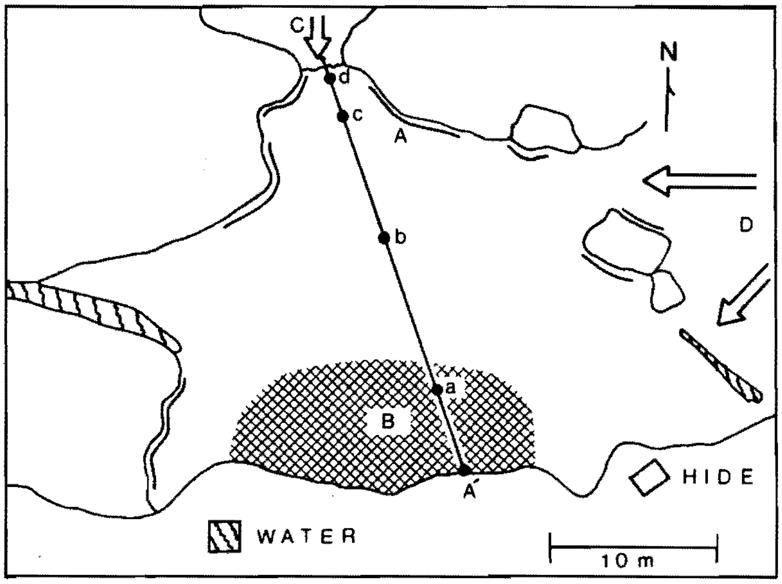
FIGURE 5.1. Study Area I.

a. General outline of territories (= sections) which were held by individual bulls sometime during the breeding season.

b. A) Location of cave of 2-3 m in depth, which slopes down at an angle of about 45°. B) Location where rain water never collects. C) Direct route of access to and from the sea. D) Indirect route of access to and from the sea. A'-B') Line of the profile given in Figure 4.1.c. Double solid lines mark areas where caves or overhangs are present.

c. Profile of study area, showing the vertical drop from the bush line to the sea.


SEA
N
5
4
6
3
11
12
2
10
7
8
1
9
13
BUSH
10 m


C
d
c
A
N
D
b
a
B
A´
HIDE
WATER
10 m

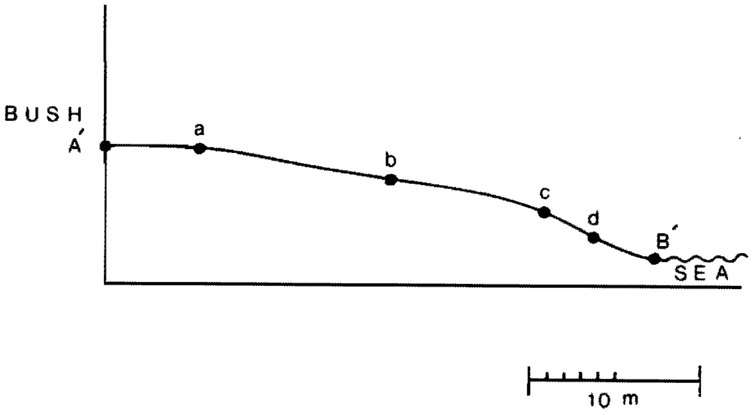
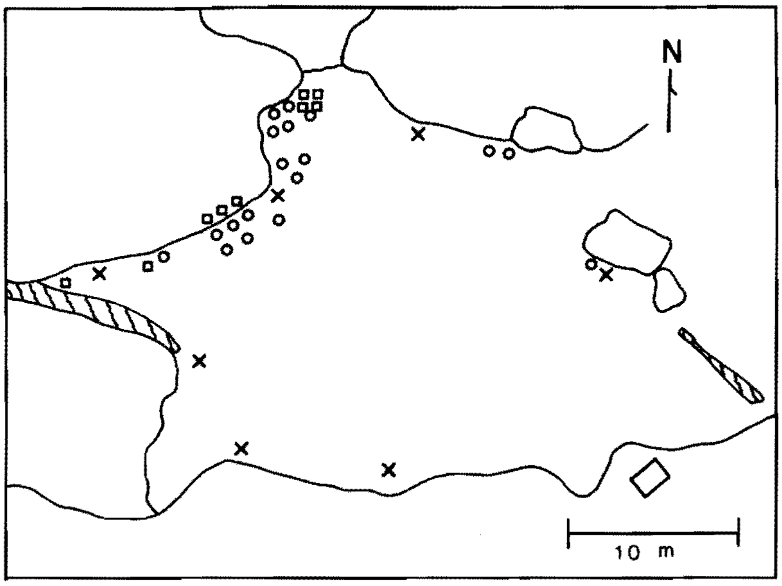

BUSH
A´
a
b
c
d
B´
SEA
10 m

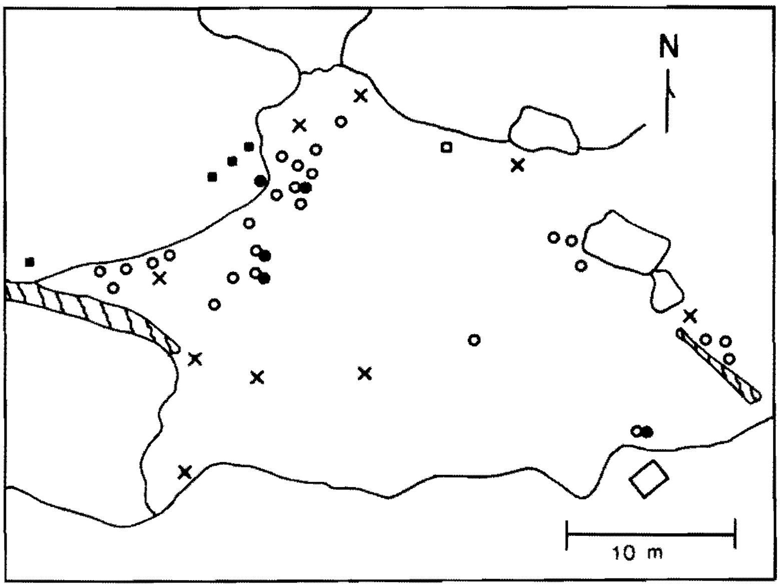
FIGURE 5.2. Location map of bulls ✕ , females ○ , yearlings □ , neuters ■ , and pups ● on Study Area I.

a. 31 October 1975, 0900 hours New Zealand Standard Time, dayblock 1.

b. 28 November 1975, 1100 hours New Zealand Standard Time, dayblock 6.

c. 16 December 1975, 1000 hours New Zealand Standard Time, dayblock 10.


N
10 m


N
10 m

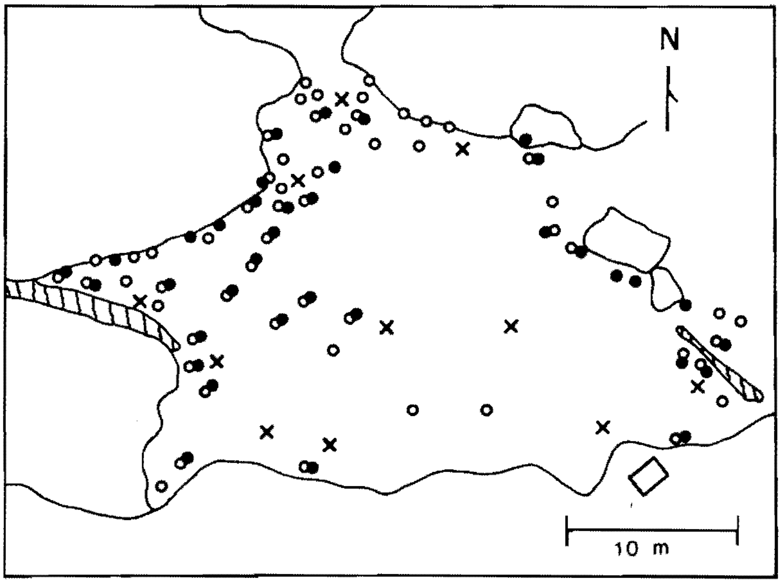
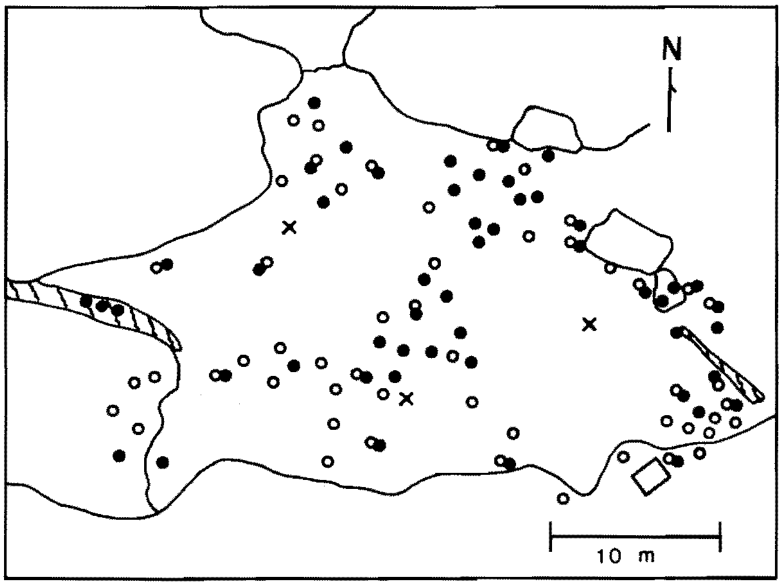

N
10 m

FIGURE 5.2. Continued. Bulls ✕ , females ○ , pups ●.

d. 17 January 1976, 1300 hours New Zealand Standard Time, dayblock 16.

e. 29 January 1976, 1000 hours New Zealand Standard Time, dayblock 19.


N
10 m

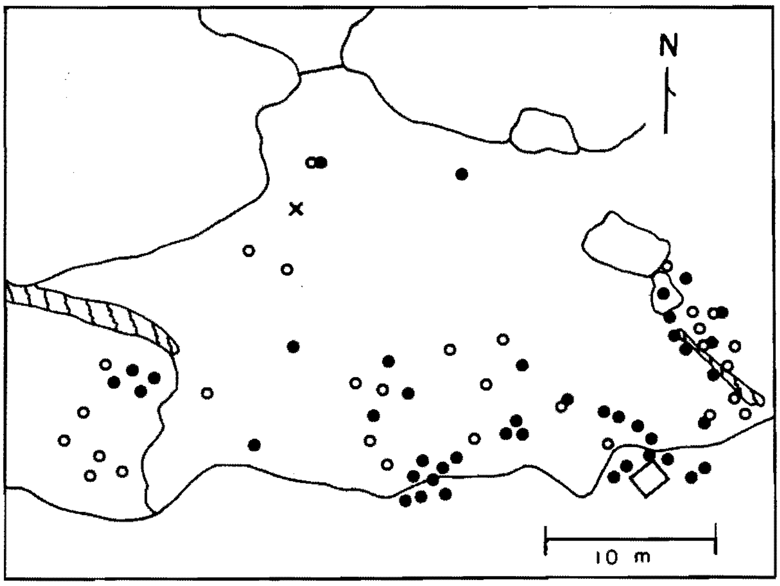

N
10 m

FIGURE 5.3. Number of representative females on each section of Study Area I, per dayblock.

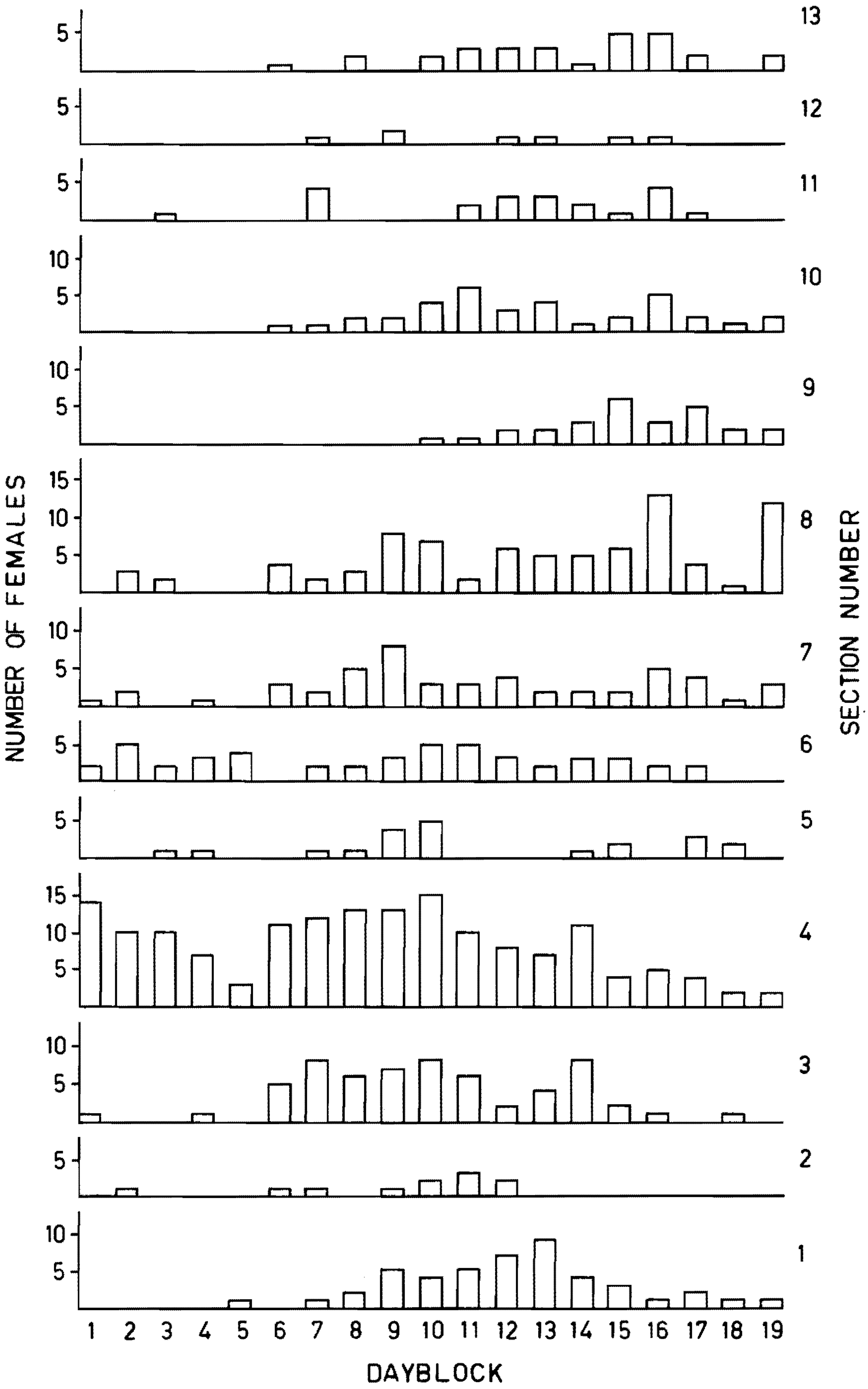
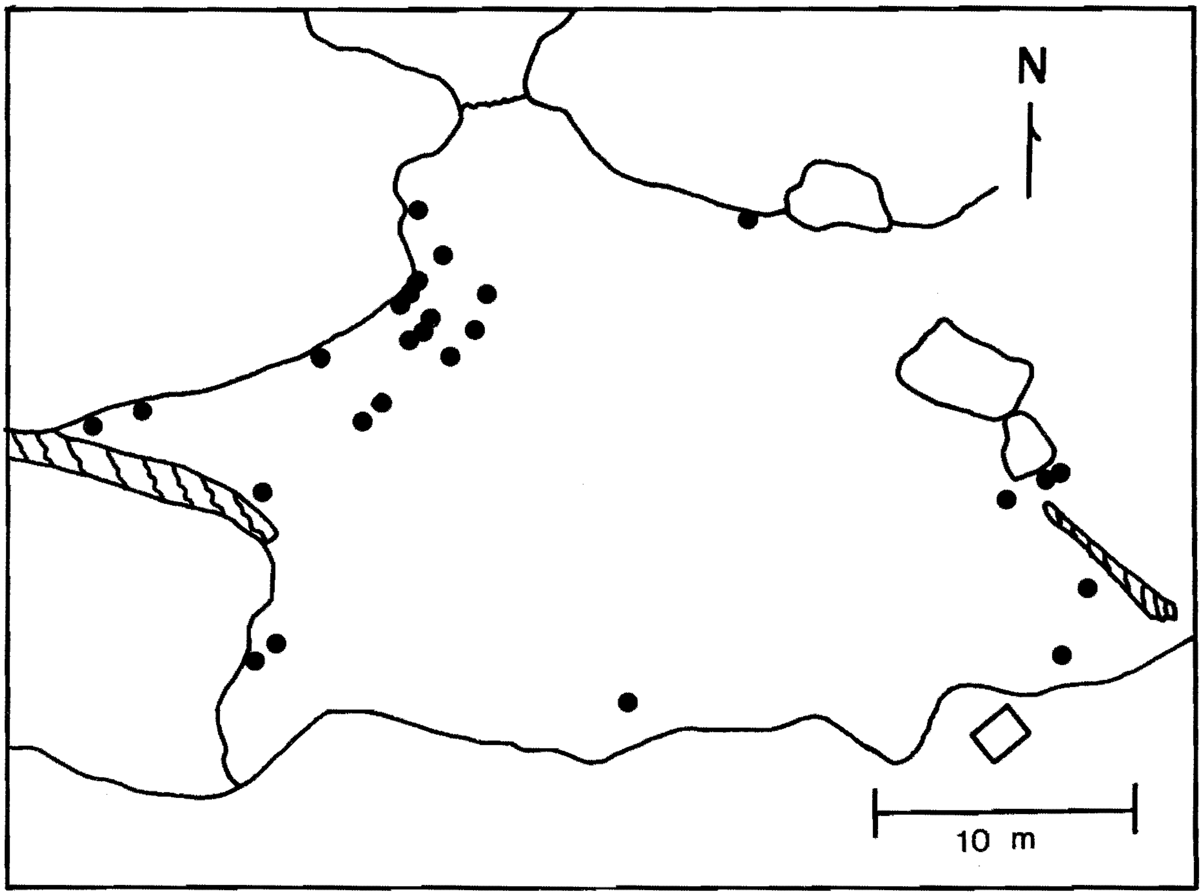

NUMBER OF FEMALES
SECTION NUMBER
DAYBLOCK
13
12
11
10
9
8
7
6
5
4
3
2
1
5
10
15
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19

FIGURE 5.4. Locations of recorded births on Study Area I, 1975/76 breeding season.

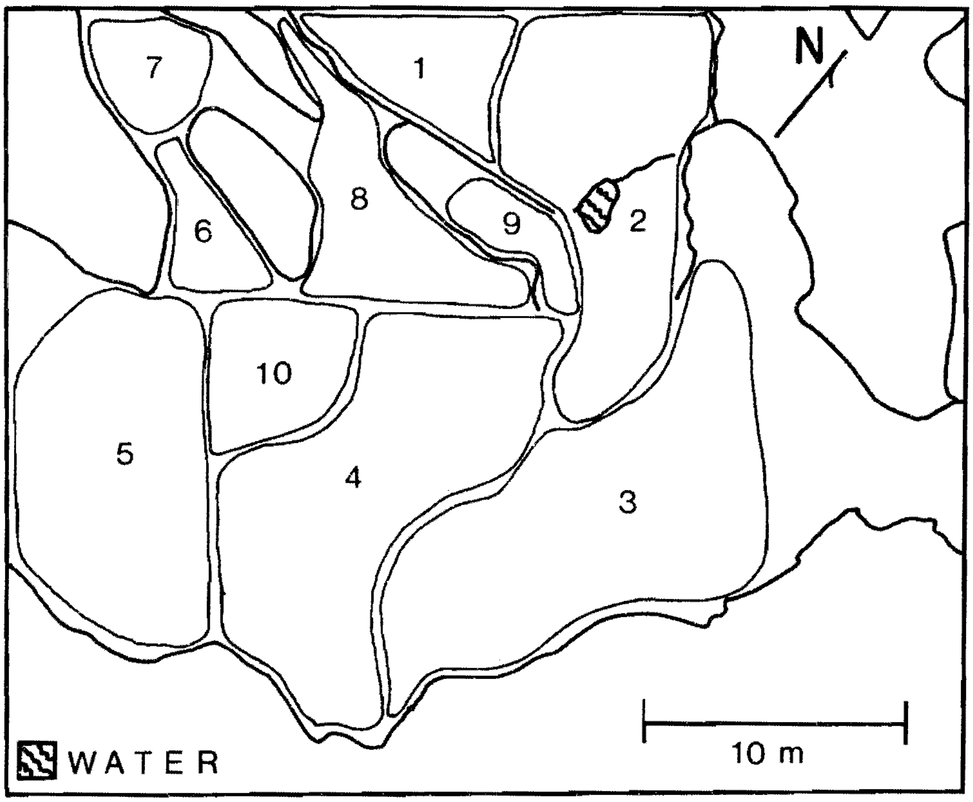

N
10 m

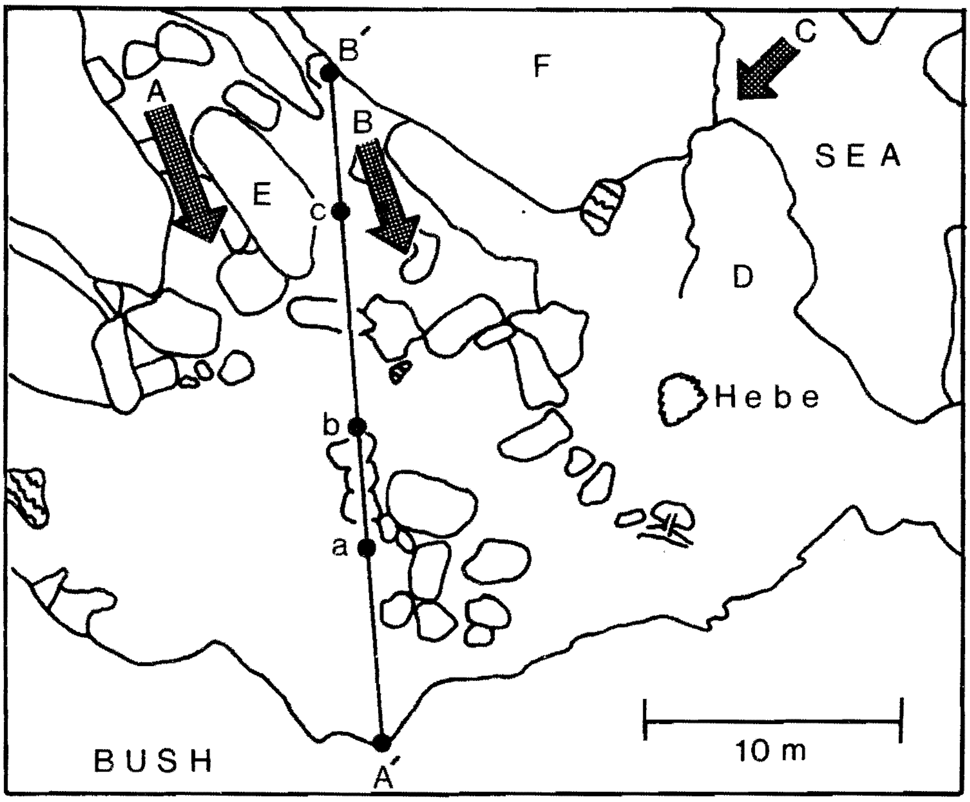
<u>FIGURE 5.5</u>. Study Area II.

a. General outline of territories (= sections) which were held by individual bulls sometime during the breeding season.

b. A, B, C) Three routes of direct access to and from the sea. D) Ridge, forming the border on the right side of the study area. E) Large rock structure separating the two guts. F) Rocks used occasionally by females and non-territorial or transient bulls. A'-B') Line of the profile given in Figure 4.5.c.

c. Profile of the study area, showing the vertical drop from the bush line to the sea.


N
1
2
3
4
5
6
7
8
9
10
WATER
10 m


B′
F
C
A
B
SEA
E
c
D
Hebe
b
a
BUSH
A′
10 m

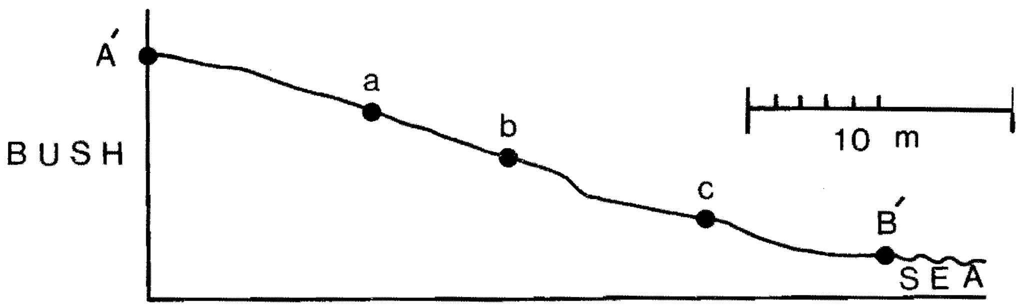
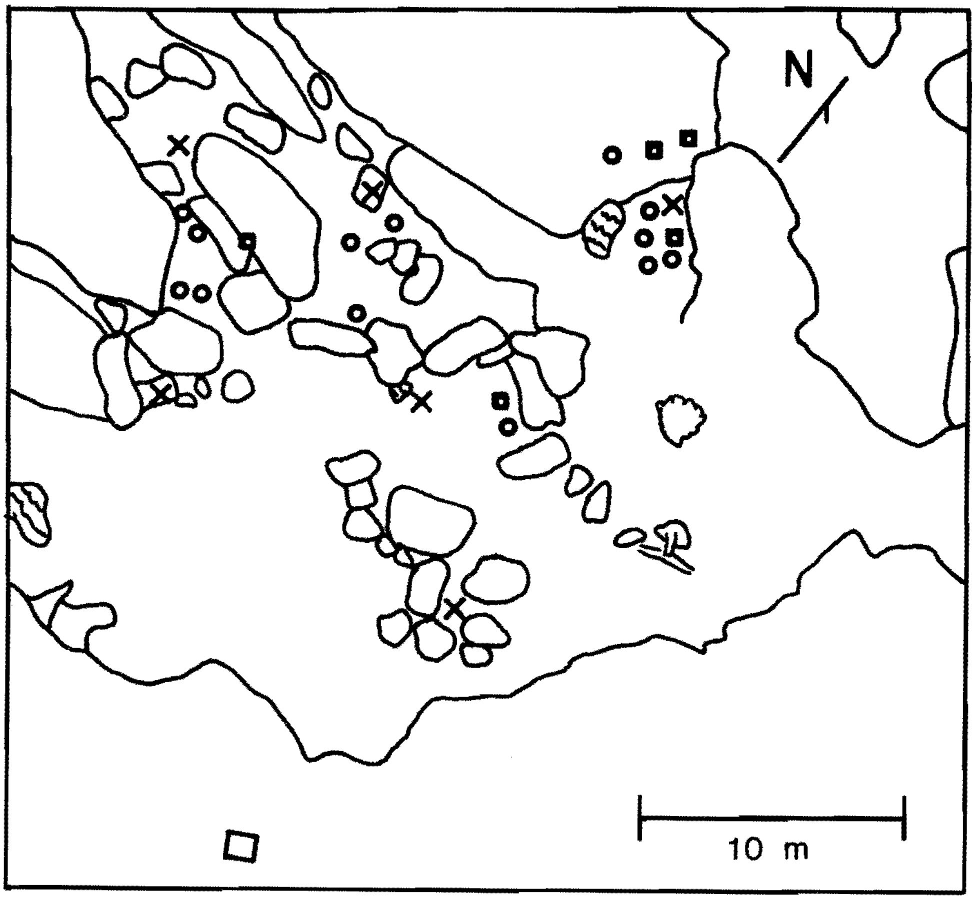

A′
a
b
c
B′
BUSH
SEA
10 m

FIGURE 5.6. Location map of bulls ✕ , females ○ , yearlings □ , and pups ● on Study Area II.

a. 4 November 1975, 1300 hours New Zealand Standard Time, dayblock 2.

b. 11 December 1975, 1600 hours New Zealand Standard Time, dayblock 9.


N
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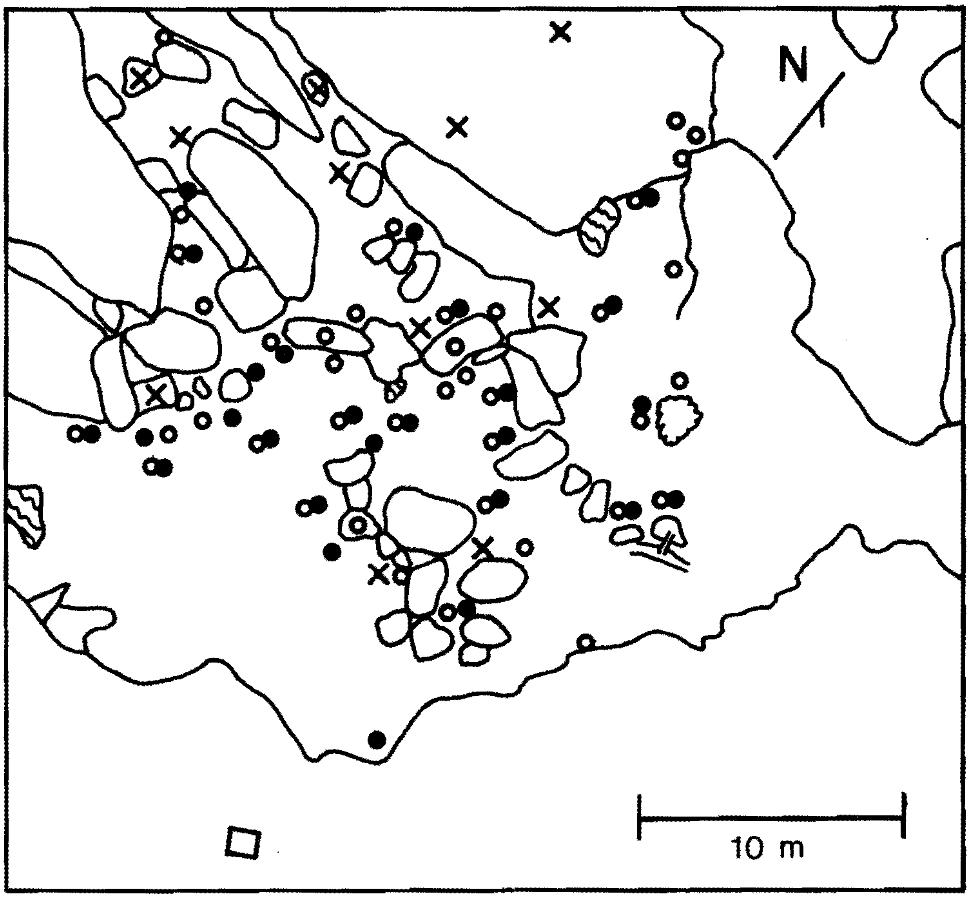
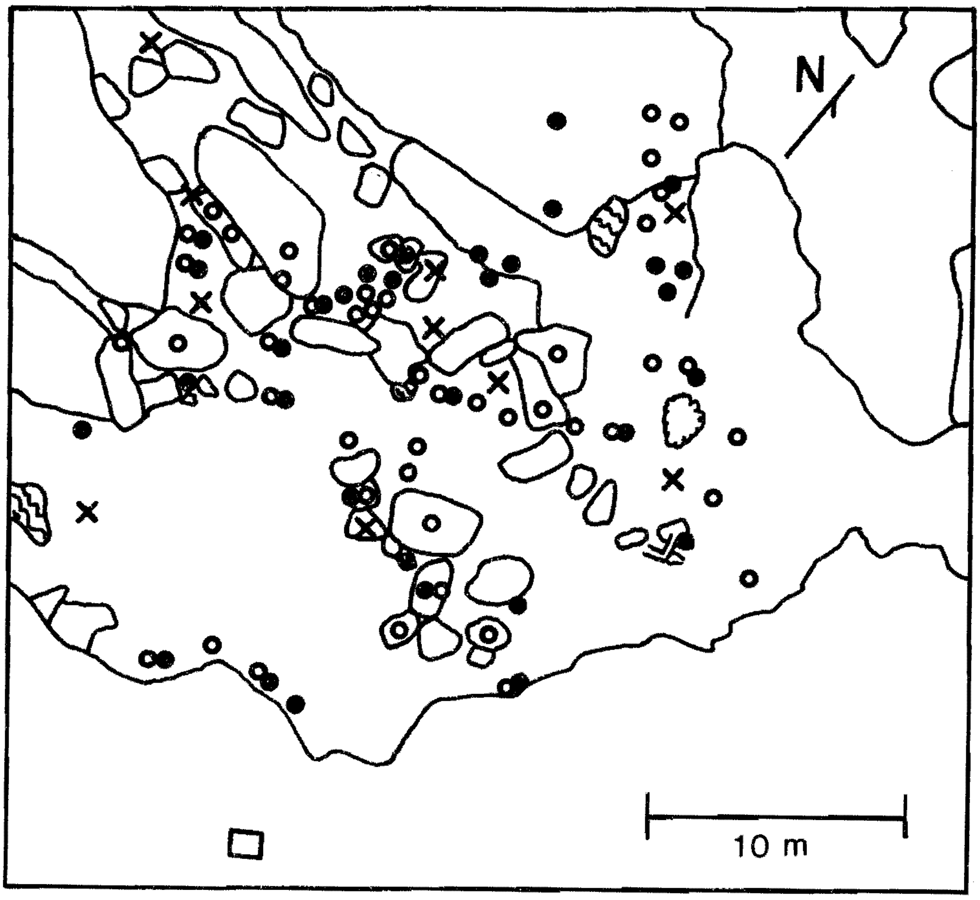

N
10 m

__FIGURE 5.6.__ Continued. Bulls ✕ , females ○ , pups ● .

c. 24 December 1975, 1600 hours New Zealand Standard Time, dayblock 12.

d. 29 January 1976, 1300 hours New Zealand Standard Time, dayblock 19.


N
10 m

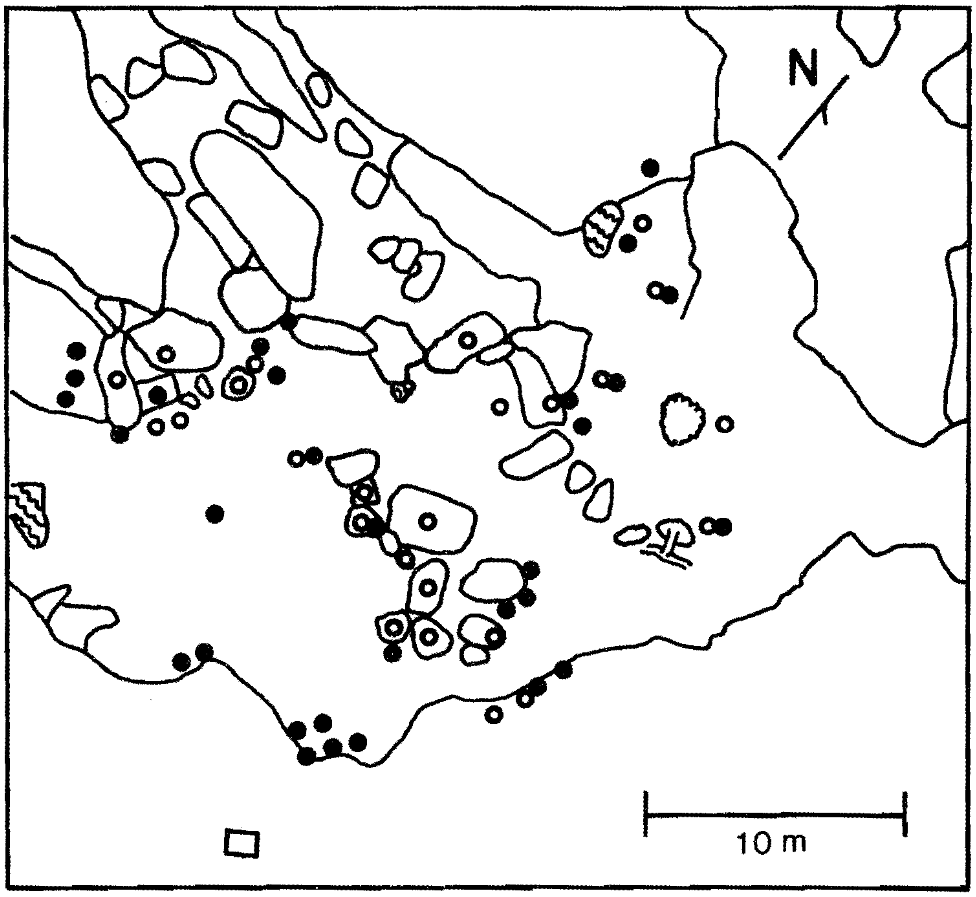
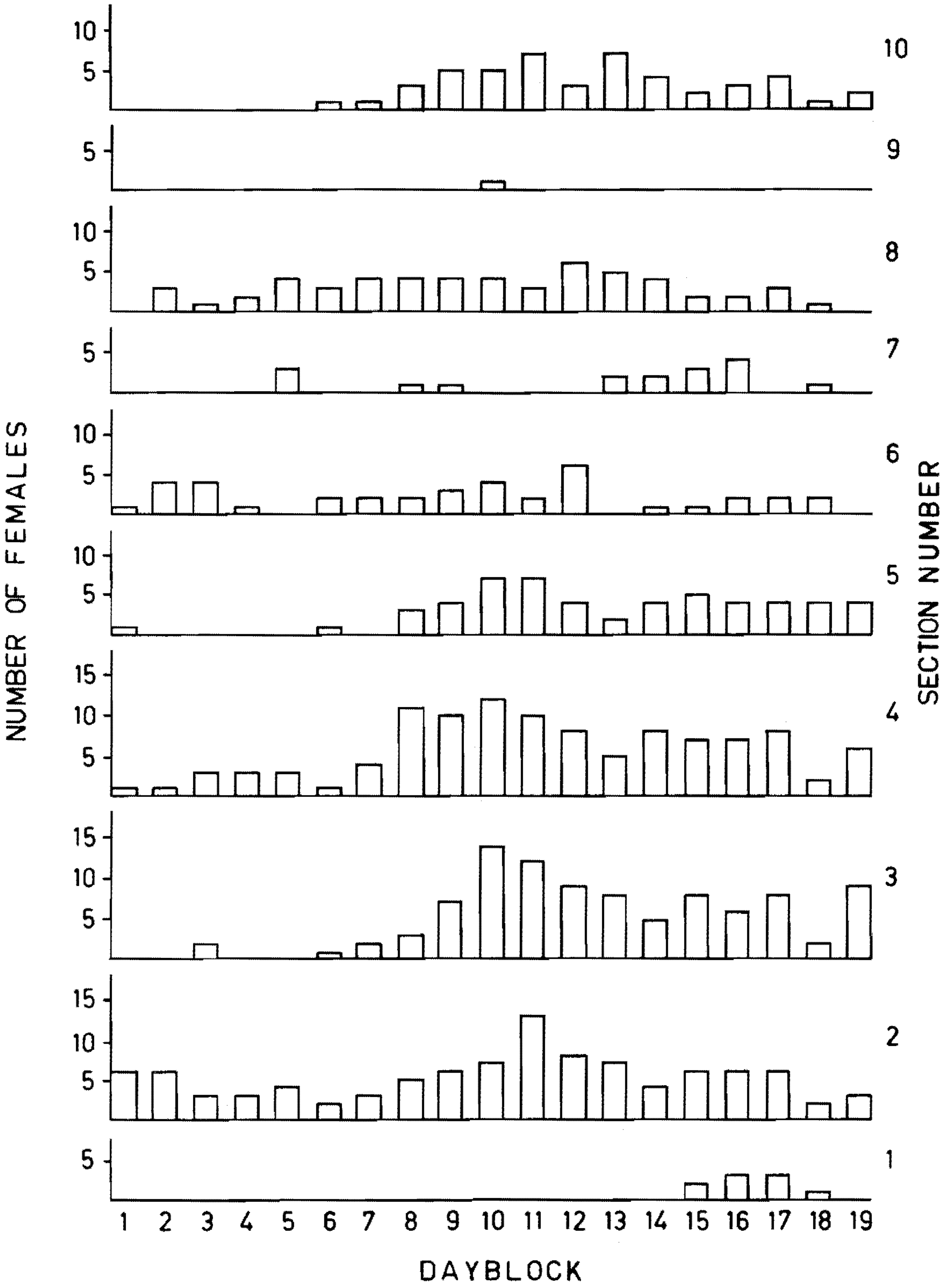

N
10 m

FIGURE 5.7. Number of representative females on each section of Study Area II, per dayblock.


NUMBER OF FEMALES
SECTION NUMBER
DAYBLOCK
10
9
8
7
6
5
4
3
2
1
5
10
15
1
2
3
4
5
6
7
8
9
10
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19

FIGURE 5.8. Locations of recorded births on Study Area II, 1975/76 breeding season, in relation to birth site regions (A-H).

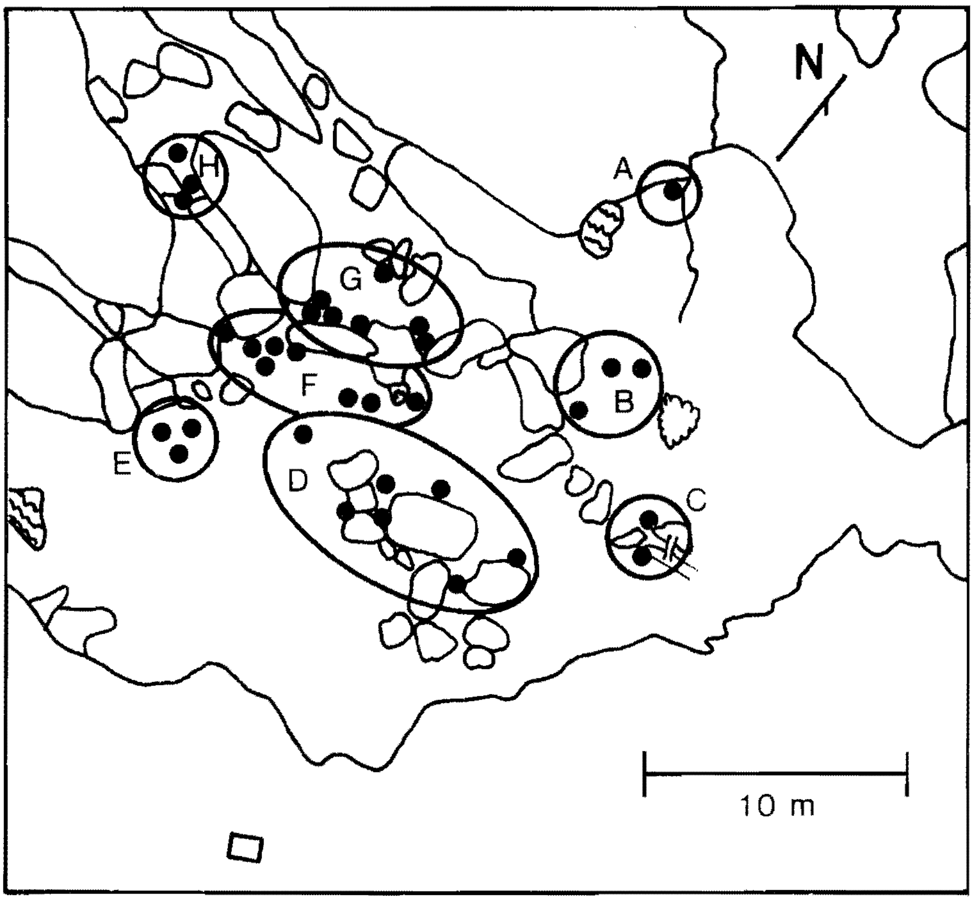
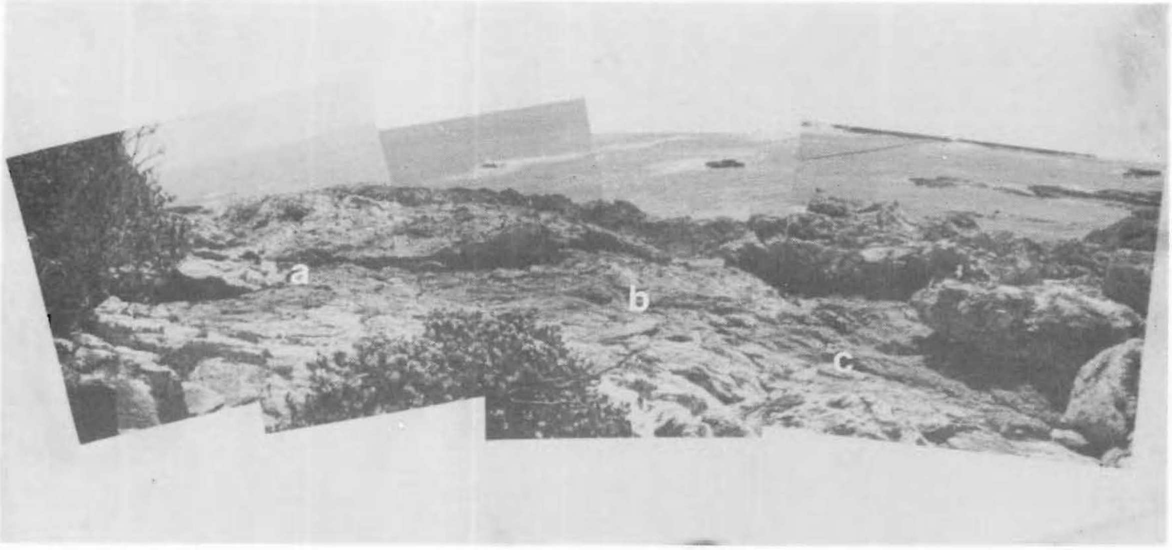

N
A
H
G
F
B
E
D
C
10 m

PLATE 5.1. Composite photograph of Study Area I, taken from the hide. Note pools of water (a, b, c), caves and overhangs, exposed offshore reefs, and the general ruggedness of the terrain. Photo taken 23 December 1974, 1300 hours New Zealand Standard Time.

PLATE 5.2. Composite photograph of Study Area II, taken from the hide. Note the pools of water (a, b, c), the two guts (d, e), the general irregularity of the terrain in comparison with Study Area I, and the use of elevated ground and rocks by resting fur seals. Photo taken 22 December 1974, 0630 New Zealand Standard Time.


a
b
c


e
b
c
d
a

CHAPTER SIX

PUP GROWTH

6.1. Introduction

Growth curves, based on data collected from commercial and scientific harvests, have been developed for several species of pinnipeds, e.g. the Northern fur seal (Scheffer and Wilke 1953), the Southern elephant seal (Bryden 1968a; Carrick *et al*. 1962; Laws 1953b), the Harbour seal (Bigg 1969), the Ringed seal, Ribbon seal and the Bearded seal (Tikhomirov 1971), but for most species no growth data are available. In his review of growth and development in marine mammals, Bryden (1972) commented on this general lack of data, and attributed it to the problems encountered by early workers in accurately aging specimens and to general difficulties which arise when working with such inaccessible animals. These particular constraints do not apply to the New Zealand fur seal, but because of the protected status and relative scarcity of the species, and because the collection of sufficient specimens from Taumaka (150-200 animals) in the time available would have had too deleterious an effect on the study population, data for the construction of growth curves were not collected. However, because of their long suckling phase (about 300 days), it was possible to follow pup growth from birth to shortly before weaning. Crawley (1975) reviewed pup growth in New Zealand fur seals, but because of limited data many of his conclusions were speculative. Therefore, a comprehensive investigation into pup growth was undertaken in order to describe general growth patterns and any differential growth between years.

For this study, growth refers to the production of new biochemical units as defined by Brody (1964: 486). The data are presented both as absolute increases in size between sampling periods, and also as relative increases, i.e. the percentage increase from the previous sampling period. Weight and curvilinear length were measured at birth, and weight, curvilinear length, anterior length of left foreflipper and axillary girth were measured at 55, 140, 235 and 290 days.

Most growth in pinnipeds before weaning involves an increase in weight, but in some, such as the Grey seal (Coulson and Hickling 1964), there is little or no length increase during this period. Because of this, and because of the difficulty in taking accurate length measurements from living pups, the major emphasis is on weight change as a measure of growth.

Growth differences between the sexes are compared, as are growth differences between the years studied. Factors possibly affecting pup growth are presented, as is the effect sea temperature may have had on the fur seals' primary food source, squid, and the effect high air temperatures may have had on the growth of pups while on land.

Coulson and Hickling (1964) were among the first to suggest that there is a minimum weight necessary for survival over the period from weaning to nutritional independence. Minimum survival weights for each age category of New Zealand fur seal pups sampled are given, including the minimum weight necessary for survival from weaning to nutritional independence.

6.2. Results and observations

(a) Pup birth dates

(i) Mean birth dates

The theoretical mean birth date for the two main study areas was 10 December in both 1974 and 1975 (Table 6.1). This date was calculated by taking the day on which the most pups were seen at any one time and working back to the day on which 50 percent of this number of pups was first observed.

TABLE 6.1. Mean birth dates at Taumaka, Open Bay Islands.

1974/75 season		1975/76 season	
Mean for area I	7 December	Mean for area I	8 December
Mean for area II	14 December	Mean for area II	11 December
Overall mean	10.5 December	Overall mean	9.5 December

(ii) Pup births 1974/75

On 4 November 1974, the entire rookery was searched but no pups were seen. The first pup seen was found dead on 10 November and was probably newly-born as it had not been seen in the area the previous day. A second pup, also dead, was found on 11 November in area II, and a third dead pup in area I on 18 November. The first live pups on areas I and II were seen on 22 and 23 November respectively, although one was seen on 19 November elsewhere on the rookery. There was a steady increase in pup numbers from this date on, with a maximum density during dayblock 14 (3-7 January).

(iii) Pup births 1975/76

The situation in 1975 was similar to that in 1974. No pups were seen during a search of the rookery on 29 October and 5 November. The first pups, one alive and three dead, were seen on 15 November. Two more dead pups were seen on 17 November, and on 19 November the first pup of the season for area II was recorded, but it too was dead. No further pups were noticed at area II until 25 November, when a live pup was seen. The first pup born on area I was observed alive on 21 November. After this, there was a rapid increase in pup numbers on both study areas until dayblock 11 (19-23 December), after which the rate of increase slowed appreciably. The maximum pup density observed at any one time for the season at areas I and II was during dayblocks 16 (13-17 January) and 17 (18-22 January), respectively.

Some births occurred very early in the season. On 29 and 30 September 1976, three apparently stillborn pups were collected at Taumaka (see Chapter Seven, Pup Mortality), and on 29 September, a well cared for female pup was found. She had no umbilical cord and her coat was beginning to turn slightly brown ventrally, suggesting that she was approximately one week old.

(b) Weight and measurement differences between male and female pups

At intervals from February 1975 through February 1977, pups along the length of Taumaka were weighed and measured. Assuming a mean birth date of 10 December, the approximate ages of the pups at the time of their weighing and measuring were 55 days in February, 140 days in May, 235 days in August and 290 days at the end of September.

At 55, 140 and 290 days, males were significantly heavier and larger in all dimensions measured than females ($p < 0.05$; Mann-Whitney U Test; Siegel 1956). At 235 days there was no significant difference in axillary girth ($p > 0.05$; Table 6.2).

Fifty-four male and 47 female New Zealand fur seal pups were weighed and measured by D.S. Horning, G.D. Fenwick, P.M. Sagar and J.L. Woods at the Snares Islands (48°07'S, 166°35'E) on 7 February 1977 (approximate age 55 days). Males were significantly heavier and larger than females in all dimensions measured except axillary girth (Table 6.2).

TABLE 6.2. Weights and measurements of male and female pups.

			1975					1976					1977			
Measurement	Sex	n	$\bar{x}$ ±	s.e.	z	p<	n	$\bar{x}$ ±	s.e.	z	p<	n	$\bar{x}$ ±	s.e.	z	p<
TAUMAKA:	55 DAYS															
Weight	M	253	6377	81.4	4.74	0.001	429	7215	68.1	9.29	0.001	186	7395	101.7	5.61	0.001
	F	262	5827	76.6			392	6294	58.5			177	6574	89.4		
c.l.	M	253	717.5	2.92	5.71	0.001	429	728.4	2.59	9.32	0.001	186	731.4	3.22	5.79	0.001
	F	262	693.2	2.75			392	695.5	2.35			177	702.9	3.27		
a.l.l.f.	M	253	213.3	0.71	4.97	0.001	429	214.6	1.38	9.27	0.001	186	211.3	0.88	6.74	0.001
	F	262	208.0	0.71			392	205.1	0.56			177	202.8	0.76		
a.g.	M	253	457.9	2.32	2.87	0.002	429	484.4	1.62	7.74	0.001	186	491.4	2.43	5.80	0.001
	F	262	448.4	2.22			392	465.8	1.57			177	471.5	2.34		
TAUMAKA:	140 DAYS															
Weight	M	88	7256	168.2	2.93	0.002	92	11085	214.5	3.11	0.001					
	F	85	6573	178.2			68	10092	205.3							
c.l.	M	88	741.5	5.59	2.37	0.009	92	822.9	5.99	3.49	0.001					
	F	85	724.6	5.59			68	790.8	5.81							
a.l.l.f.	M	88	234.1	1.24	3.51	0.001	92	244.1	1.72	4.71	0.001					
	F	85	226.7	1.44			68	232.0	1.55							
a.g.	M	88	516.1	5.60	3.06	0.001	92	582.2	4.88	2.77	0.001					
	F	85	492.4	5.04			68	566.0	4.06							

TABLE 6.2. continued

TABLE 6.2. continued

			1975					1976			
Measurement	Sex	n	$\bar{x}$ ± s.e.		z	p<	n	$\bar{x}$ ± s.e.		z	p<
TAUMAKA:	235 DAYS										
Weight	M	94	10067	304.8	2.42	0.008	88	12337	350.1	1.97	0.024
	F	81	9060	318.2			68	11274	375.5		
c.l.	M	94	808.0	6.36	3.07	0.001	88	861.9	7.59	2.27	0.012
	F	81	772.6	8.23			68	833.5	7.05		
a.l.l.f.	M	94	239.7	1.78	2.66	0.004	88	251.7	1.86	3.03	0.001
	F	81	232.2	2.03			68	244.3	7.32		
a.g.	M	94	567.1	6.97	1.28	n.s.	88	633.3	7.34	1.60	n.s.
	F	81	553.0	7.20			68	615.4	8.14		
TAUMAKA:	290 DAYS										
Weight	M						88	14063	373.4	2.72	0.003
	F						79	12607	348.2		
c.l.	M						88	851.4	6.73	3.41	0.001
	F						79	813.0	7.03		
a.l.l.f.	M						88	258.5	1.65	3.77	0.001
	F						79	249.8	1.79		
a.g.	M						88	647.0	7.00	2.38	0.009
	F						79	621.3	7.29		

TABLE 6.2. continued

TABLE 6.2. continued

Measurement	Sex	n	1977 $\bar{x}$ ±	s.e.	z	p<
SNARES ISLANDS: 55 DAYS						
Weight	M	54	8011	219.6	1.85	0.032
	F	47	7403	162.4		
c.l.	M	54	727.7	7.43	2.03	0.021
	F	47	704.3	6.80		
a.l.l.f.	M	54	219.6	1.66	2.97	0.002
	F	47	212.2	1.98		
a.g.	M	54	495.2	5.20	1.36	n.s.
	F	47	484.4	5.03		

(c) Pup growth

(i) Weight

Because of the aggressive nature of territorial bulls, and in many cases newly-parturient females, it was very difficult to catch and weigh newly-born pups. An estimated birth weight of 3.7 kg (range: 2.9-4.1 kg) was calculated from the weights of two dead and three live pups, all of whom still retained some soft umbilical cord and appeared to be full term. Although this weight was less than that reported for the Australian population of the New Zealand fur seal and for other fur seal species (Table 6.3), it was similar to the 3.5 kg figure (5 males, 5 females: range: 2.75-4.6 kg) reported by Crawley (1975) for pups from Taumaka. Crawley's weights were combined with mine to give a mean birth weight of 3.9 kg (range: 3.25-4.6 kg) for seven males and 3.3 kg (range: 2.75-3.8 kg) for eight females. Males were significantly heavier than females ($n_1 = 7$, $n_2 = 8$, $U = 12$, $p < 0.036$; Mann-Whitney U Test, Siegel 1956).

Using these birth weights, in 1974/75 the relative weight gain from birth to 55 days was 76 percent for females and 64 percent for males. The absolute weight gain from birth to 55 days for both sexes was similar. From 55 to 140 days and from 140 to 235 days males gained more weight, both absolutely and relatively, than did females (Table 6.4).

Throughout 1976, males consistently gained more absolute weight between weighings than did females, with a maximum daily increase (of 13 g per day) between 140 and 235 days. From birth to 55 days and from 55 to 140 days females had the greater relative weight increases. From 140 to 235 days the relative weight increase between the sexes was similar and from 235 to 290 days the relative weight increase of males exceeded that of females, but only by 2 percent (Table 6.4).

In 1977, males gained 64 g per day from birth to 55 days as compared to 59 g per day for females but, as in 1975 and 1976, females had the greater relative weight gains (Table 6.4).

In 1977, females doubled their birth weight in about 55 days. Males in 1977, and both sexes in 1976, increased their birth weight by 85-90 percent in their first 55 days. In 1975, neither sex doubled its birth weight until sometime after 140 days (Table 6.4).

In 1975, the rate of weight increase between 55 and 140 days slowed considerably for both sexes. It then accelerated again from 140 to 235 days to approximately 75 percent of the growth rate from birth to 55 days. This same pattern of accelerated growth, a slowing, then another period of accelerated growth was present in 1976, except that the period of slower

TABLE 6.3. Birth weights of other fur seal species. All weights are in kg unless otherwise specified.

Species	Male pups			Female pups			Sexes combined			Source
	Mean	Range	n	Mean	Range	n	Mean	Range	n	
Northern fur seal *C. ursinus*	5.4	4.1-7.1	23	4.8	3.3-6.0	16				Scheffer and Wilke (1953)
Cape fur seal *A. pusillus*	15.4lb (7.0kg)	15.3-15.5lb (6.95-7.04kg)	3	14.0lb (6.36kg)	13.0-14.0lg (5.91-6.36kg)	2				Rand (1956)[1]
Amsterdam Island fur seal *A. tropicalis*	4.94	3.60-6.10	25	4.021	3.300-4.550	29				Paulian (1964)
Kerguelen fur seal *A. gazella*							5.2	4.1-6.7	4	Bonner (1968)[2]
New Zealand fur seal in Australia *A. forsteri*	4.41	± 0.66	25	4.11	± 0.47	16				Stirling (1971b)

[1] Mean derived from figures of selected pup weights during their first week of life; p. 15, Table E3.

[2] Mean derived from figures presented on Table X, p. 62.

growth took place between 140 and 235 days (Figure 6.1).

(ii) Curvilinear length

Of the three linear measurements taken, curvilinear length was by far the most suspect. Whereas the values obtained in the measurement of foreflipper length and axillary girth were reasonably independent of the way the pup was held, the measurement of curvilinear length was not. From experience, it was found that the most accurate curvilinear length values were obtained when pups were held as still and as straight as possible. It takes considerable strength to do this, especially with larger pups. This imprecision of measurement is demonstrated in the curvilinear length data collected in 1976. For both sexes, the mean length at 290 days was less than at 235 days (Table 6.2). These data are of value for comparison between males and females measured at the same time, but they are unsuitable for comparison of pups measured at different times. Consequently, pup growth in curvilinear length is presented here only for pups to age 235 days. These data are inconclusive, and give only a general indication of the trend of length increase.

Utilizing data on curvilinear length at birth from Crawley (1975, *pers. comm.* 1977; 5 males, range: 495.0-600.0 mm, $\bar{x} = 550.0$; 5 females, range: 470.0-595.0 mm, $\bar{x} = 550.0$ mm) and data I collected from one male (600.0 mm) and two female (510.0 mm and 520.0 mm) newly-born pups, a mean curvilinear length at birth of 558 mm (range: 495.0-600.0 mm) for six males and 540 mm (range: 470.0-595.0 mm) for seven females was obtained. There was no significant difference in curvilinear length at birth between the sexes ($n_1 = 6$, $n_2 = 7$, $U = 14$, $p > 0.05$).

Based on these figures, males in 1975 had a slightly greater absolute increase in length than females from birth to 55 days, although the relative increase was 28 percent for both sexes. Between 55 and 140 days, females had greater absolute and relative increases in length, but this trend was reversed between 140 and 235 days (Table 6.4).

In 1976, males had greater absolute and relative length increases than did females between birth and 55 days, but from 55 to 140 days, and from 140 to 235 days, females had a slightly greater gain in length, in both absolute and relative terms (Table 6.4).

In 1977, males gained 3.2 mm per day from birth to 55 days, while females gained 3.0 mm per day. Males had the greater relative length increase by 1 percent.

(iii) Anterior length of left foreflipper

Insufficient data were available to obtain an acceptable estimate of mean foreflipper length at birth, due to the difficulties mentioned earlier in getting to newborn pups.

In 1975, from 55 days onwards, the absolute and relative increases in foreflipper length between the sexes were similar.

In 1976, from 55 to 140 days and from 235 to 290 days, both sexes had similar absolute and relative increases in foreflipper length. Between 140 and 235 days, females had the greater absolute and relative gains. For both years studied, the increases were greatest between 55 and 140 days (Table 6.4).

(iv) Axillary girth

As with foreflipper length, insufficient data were available to obtain a meaningful estimate of axillary girth at birth.

In 1975, both the absolute and relative girth increase of males were greater than those for females between 55 and 140 days, but the opposite was true between 140 and 235 days.

The pattern was slightly different in 1976. Between 55 and 140 days, females had a slightly greater increase in absolute and relative girth than males. From 140 to 235 days, males had the greater absolute increase, but again it was slight. The greatest difference in girth increase took place between 235 and 290 days, when males had a daily girth increase of 0.2 mm, as compared to 0.1 mm for females (Table 6.4).

(d) Geographic variation in pup growth

In 1977, males on the Snares Islands aged 55 days were significantly heavier ($n_1 = 54$, $n_2 = 186$, $U = 3890.0$, $p < 0.006$) and had a significantly longer foreflipper ($n_1 = 54$, $n_2 = 186$, $U = 3068.0$, $p < 0.001$) than their counterparts on Taumaka. Females on the Snares Islands were significantly heavier ($n_1 = 47$, $n_2 = 177$, $U = 2462.0$, $p < 0.001$) and larger in all categories except curvilinear length (anterior length left foreflipper: $n_1 = 47$, $n_2 = 177$, $U = 2393.0$, $p < 0.001$; axillary girth: $n_1 = 47$, $n_2 = 177$, $U = 3123.5$, $p < 0.004$).

(e) Comparison of growth between years

Pups were significantly larger in 1976 than in 1975, with the exception at 55 days of foreflipper length in males and curvilinear length in females. This difference was so great, that with the exception of foreflipper length in females, pups of both sexes were larger at 140 days in

TABLE 6.4. Absolute weight and measurement gains, relative weight and measurement gains, and daily weight and measurement gains for male and female pups between birth, ages 55, 140 and 235 days in 1974/75 and 1975/76, and 290 days in 1976.

Year	Sex	Period	Absolute increase	Relative increase (%)	Daily increase
WEIGHT INCREASE (g)					
1975	M	B-55	2491	64	45
	F		2521	76	46
	M	55-140	879	14	10
	F		746	13	9
	M	140-235	2811	39	30
	F		2488	38	26
1976	M	B-55	3329	86	60
	F		2988	90	54
	M	55-140	3870	54	46
	F		3789	60	47
	M	140-235	1252	11	13
	F		1182	12	12
	M	235-290	1726	14	31
	F		1333	12	24
1977	M	B-55	3509	90	64
	F		3268	99	59
CURVILINEAR LENGTH INCREASE (mm)					
1975	M	B-55	159	28	2.9
	F		153	28	2.8
	M	55-140	24	3	0.3
	F		32	4	0.4
	M	140-235	66	9	0.7
	F		48	7	0.5
1976	M	B-55	170	30	3.1
	F		156	29	2.8
	M	55-140	94	13	1.1
	F		95	14	1.1
	M	140-235	39	5	0.4
	F		43	5	0.5
1977	M	B-55	173	31	3.2
	F		163	30	3.0

TABLE 6.4. continued

TABLE 6.4. continued

Year	Sex	Period	Absolute increase	Relative increase (%)	Daily increase
ANTERIOR LENGTH LEFT FOREFLIPPER INCREASE (mm)					
1975	M	55-140	21	10	0.2
	F		19	9	0.2
	M	140-235	6	2	0.1
	F		6	2	0.1
1976	M	55-140	30	14	0.4
	F		27	13	0.3
	M	140-235	8	3	0.1
	F		12	5	0.1
	M	235-290	7	3	0.1
	F		5	2	0.1
AXILLARY GIRTH INCREASE (mm)					
1975	M	55-140	58	13	0.7
	F		44	10	0.5
	M	140-235	52	10	0.5
	F		61	12	0.6
1976	M	55-140	98	20	1.2
	F		100	22	1.2
	M	140-235	51	9	0.5
	F		49	9	0.5
	M	235-290	14	2	0.2
	F		6	1	0.1

1976 than at 235 days in 1975. Comparative weight data for 1974/75 and 1975/76 are given in Figure 6.1.

At 55 days in 1977, males were not significantly heavier or longer than males in 1976, but females in 1977 were significantly heavier and larger than females in the previous year.

(f) Factors possibly contributing to annual variation in growth

(i) Meteorological conditions

The mean maximum and minimum daily air temperatures on Taumaka and at Haast (the nearest official meteorological station, about 12.5 km from Taumaka) were higher throughout the 1974/75 summer than during the 1975/76 summer (Figure 6.2 and 6.3). When comparing December 1974 with December 1975, Haast had a 4.2°C difference in mean air temperature and a 3.8°C difference when comparing January 1975 with January 1976. Although comparable temperatures for Taumaka were higher than those for Haast, the differences for the two years were similar, i.e. a difference of 4.4°C for December and 3.5°C for January.

Late in the summer, fewer pups were seen at any one time in 1974/75 than in 1975/76. Also in 1974/75, females made more trips to the sea, presumably to cool off, which could have decreased the amount of time they spent with their pups.

In order to quantify the amount of time females spent ashore on each study area, the number of returning females was divided by the total number of females on the study area, resulting in a percent 'turn-around' (Figure 6.4). Returning females, rather than those departing, were counted because their wet coats made them easier to recognize. Only data from dayblock 10 (14-18 December) onwards were used, because females arriving earlier in the season could have been new arrivals rather than returnees.

At area I, the percent turn-around was much higher in 1974/75 (22 percent) than in 1975/76 (9 percent). The percent turn-around at area II was only slightly higher in 1974/75 (18 percent) than in 1975/76 (13 percent).

(ii) Food availability

Squid was the most prevalent food item found in the stomachs of adult fur seals collected on Taumaka. Samples of squid beaks taken from the stomachs of two different adults were identified by M.J. Imber (New Zealand Wildlife Service, Wellington) as *Nototodarus sloani sloani*.

Uda (1959) has shown that the abundance of squid varies greatly with differing hydrographic conditions, but that they generally are most abundant in cool water, i.e. between 10° and 17°C, with an optimum around 14° to 15°C, and where there is a 5°C gradient in the upper 100 m of water. To determine how the availability of squid off the west coast of South Island may have been affected by hydrographic conditions in 1974/75 and 1975/76, temperature-depth data for January (the month for which the most extensive hydrographic data were available) for the two years were compared.[1] Only data collected at the hydrographic station closest to Open Bay Islands for each of the two years are presented, as the data for the other stations are similar (Figure 6.5).

In 1975 (station 36; 43°59'S, 168°00'E; about 75 km from Open Bay Islands), there was a 6°C gradient in the upper 100 m of water, from about 14°C to 20°C (Figure 6.5.a). Offshore surface temperatures in February varied from between 18° to 19°C in the Open Bay Islands, Jackson's Head area.

In 1976 (station 10; 44°24'S, 167°24'E; about 135 km from Open Bay Islands), there was at most a 3°C gradient in the upper 100 m of water, from about 14° to 16°C (Figure 6.5.b). Offshore sea surface temperatures in the Open Bay Islands, Jackson's Head area in January were between 14° and 16°C, and in February were about 16°C.

Even though the temperature gradient in 1975 was closer to the optimum, the cooler water in 1975/76 apparently was more favourable for squid. The Japanese squid fishery off New Zealand caught 0.3 tons of *N. sloani sloani* per unit effort during December 1974, and 1.5 tons per unit effort during December 1975. In January 1975 and 1976, the catches per unit effort were 1.7 and 2.0 tons respectively (Kawakami 1976b cited by Okutani 1977).

(g) Pup weight distributions

(i) 1974/75

The weight distribution of males in 1975 became skewed to the right as the year progressed. Although not apparent at 55 days, by 235 days the skew was obvious and significant ($g_1 = 0.603$, s.e. = 0.267, $p < 0.001$; Sokal and Rohlf 1969). The percentage of lighter pups decreased at each successive weighing as expected for a normal growth situation (Figure

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[1] Hydrographic data were provided by Dr P. Roberts, Fisheries Research Division, Ministry of Agriculture and Fisheries, Wellington.

6.6.a). The same general trends were present for females in 1975, except that the right hand skew became significant at 140 days ($g_1 = 0.572$, s.e. = 0.261, $p < 0.05$; Figure 6.6.b).

Some of the attrition in the lower weight ranges must have been due to pups losing weight and very likely dying. Of 17 tagged pups which were weighed at 55, 140 and 235 days, one lost weight continuously and one lost weight between the second and last weighing.

(ii) 1975/76

A markedly different situation developed during 1976. Weight distributions of males and females never deviated significantly from a normal distribution. Whereas the frequency of males in the lower weight ranges decreased throughout 1975, the frequency of males in 1976 in the 5-8 kg weight range increased between 140 and 235 days. No males were collected in the 5-7 kg range at 290 days, but there was an increase in the frequency of males in the 7-8 kg range (Figure 6.7.a). A similar but even more pronounced situation occurred with females in 1976. Ten percent were in the 7-8 kg range at 140 days, slightly more than 1 percent were in the 6-7 kg range, and none was in the 5-6 kg range. By 235 days, there was a slight increase in the frequency of females in the 6-7 kg range but, most importantly, about 4.5 percent of the females fell within the 5-6 kg range. No females were in the 5-7 kg range by 290 days, but the frequency in the 7-8 kg range had increased slightly to about 11 percent (Figure 6.7.b).

(iii) Minimum survival weights

Based on these data, minimum survival weights for pups before weaning are: 55 days, 3 kg for males and females; 140 days, 4 kg for males and females; 235 days, 5 kg for males, 4 kg for females. As 1976 was an exceptionally good year for pup growth, relative to 1975, it was more difficult to assign a minimum survival weight for 290 days. Assuming that pups weighed at this age included some close to or at the minimum survival weight, then this would be about 7 kg for both sexes.

Pups probably need to weigh a minimum of 8-9 kg in order to survive the transition from weaning to nutritional independence. This is the point on the weight distribution histograms at 290 days where the weights of both males and females again began to increase (Figures 6.7.a and 6.7.b). If this is the case, then pups weighing less than 8 kg may not have the energy reserves necessary for survival. Consequently, in 1976, about 10 percent of the pups alive at weaning may not have had the energy reserves necessary to survive to total independence.

6.3. Discussion

A mean birth date of about 10 December is consistent from year to year and tends to coincide with the peak density of females on the rookery. Miller (1971) calculated a mean birth date of 9 December based on his study at Taumaka in 1970/71. This is what one might expect, judging from the short arrival to pupping interval found in the New Zealand fur seal (2.1 days, McNab and Crawley 1975; Miller 1975a), and by the sudden increase in the number of cows about mid-December.

Other pinnipeds also have a precisely-timed pupping period. The mean birth date of the Kerguelen fur seal on South Georgia did not vary by more than one day over a five year period (Payne 1977), and that of the Harbour seal on Sable Island, Nova Scotia, by not more than five days over a three year period (Boulva 1975). Again, this is what one might expect from a group where reproductive success is contingent on reproductively active individuals converging on a particular location at a specific time of the year.

Ninety percent of the pups were born within six weeks at Taumaka, whereas 90 percent of the Kerguelen fur seal births at South Georgia occurred in half that time (Payne 1977). The harsher climatic conditions at South Georgia no doubt necessitate a more circumscribed reproductive schedule. Kerguelen fur seal pups are weaned in about four months (Payne 1977), in contrast with those of the New Zealand fur seal which are weaned in about 300 days.

Considering the pronounced sexual dimorphism in the size of adult New Zealand fur seals, it was not surprising to find that male pups were significantly heavier than female pups at all weighings. Crawley (1975) found a similar weight difference in pups at 40, 50 and 60 days, but found no significant difference at 240 days. The small size of his sample (31 males; 33 females) may have biased his results, hence his observations were speculative.

A comparison of relative weight gains is in many ways more meaningful than a comparison of absolute weight gains. A large disparity in relative weight gains between conspecifics of different size but of the same age, as is the case with male and female New Zealand fur seal pups, could result in a survival advantage for that group with the greater gain. For example, assuming that much of the weight increase in pups is in the deposition of blubber, as has been shown for the Harp seal (Sivertsen 1941) and the Grey seal (Amoroso and Matthews 1952), then the group with the greater relative gain would be in a better position to survive the transition from weaning to nutritional independence, as they would have a more substantial blubber reserve relative to their size. Such a marked dissimilarity in relative weight increase did not occur between male and female New Zealand fur seal pups, implying that there was no differential survival advantage based on 'fitness' between the sexes. How dissimilarities in weight between comparable time periods for the two years studied may have affected pup survival is discussed later in the chapter. The relative weight gains of male and female Weddell seal pups calculated by Bertram (1940) from data collected by Lindsey (1937) also were similar.

Male fur seals appear to weigh more at birth than do females (Table 6.3). This also is true of the Southern sea lion (Vaz-Ferreira 1976), but is not uniformly true throughout the otariids, e.g. the birth weights of male and female Steller sea lions are similar (Scheffer 1945). Stirling (1971b) found that although male New Zealand fur seals in Australia were heavier at birth than females, the difference was not significant. It is possible that the significant difference found in this study was a consequence of the small sample size (7 males; 8 females) compared to Stirling's (25 males; 16 females).

The period of slower weight gain found between periods of more rapid weight gains in both years is as yet unexplained. It is unlikely that it coincided with the pups learning to become competent swimmers or with the pups learning to catch prey for themselves, as it occurred at different times in the two years, and in 1975 it occurred before the pups were confident in the water. It may have been the result of some behavioural change in either the mother, pup or both, but as yet there are no detailed studies of mother-pup behaviour from shortly after birth until weaning. Also, it could have been the result of a change in the composition of the mothers' milk. Such changes have been shown to occur for the Southern elephant seal as the breeding season progressed (Bryden 1968b).

The most rapid weight gains for both sexes were between birth and 55 days, though they never approached the gains of 74 g and 61 g per day for males and females respectively recorded by Crawley (1975) for New Zealand fur seal pups from birth to 60 days, or the gain of 70 g per day for the first three months (excluding the first 10 days when the pups grew faster due to their mothers continual presence) found in Kerguelen fur seals (Bonner 1968).

Birth weight doubling times were highly variable for the two years, and ranged from 55 to over 140 days. Crawley (1975) gave a doubling time of 55 days for New Zealand fur seal pups on Taumaka, while Bonner (1968) reported 70 days for Kerguelen fur seal pups. Male Cape fur seal pups grow at a faster rate than females, and double their birth weight by the second month (Rand 1956). The Steller sea lion doubles its birth weight by the seventh week (Scheffer 1945). The birth weight doubling time for phocids is considerably shorter, e.g. 11 days for the Southern elephant seal on Signy Island (Laws 1953b); 18.6 days for males and 16.7 days for females of the same species on Macquarie Island (Carrick *et al.* 1962); from 17 days (Kenyon and Rice 1959) to three weeks (Wirtz 1968) for the Hawaiian monk seal; 10 days for the Weddell seal (Stirling 1968b) and four to five days for the Harp seal (Sivertsen 1941). The shorter doubling time found in the phocids is a consequence of their shorter lactation phase.

The greatest increase in curvilinear length took place between birth and 55 days. From birth to 60 days, Crawley (1975) recorded an average daily gain of 3.7 mm for male and 3.5 mm for female New Zealand fur seal pups on Taumaka. Mathisen *et al.* (1962) found that the Steller sea lion increased in standard length by about 30 inches (760 mm) from a mean birth length of 39.6 inches (1006 mm) in the first year; an increase of 76 percent. For the same species, Scheffer (1945) recorded a 25 percent increase in length within seven weeks of birth. This is in contrast with the Grey seal, which changes little in length from birth to weaning (Coulson and Hickling 1964).

Although there were no data on foreflipper length at birth, it was likely that maximum growth took place during the first 55 days, as the growth rate declined appreciably after 140 days. Likewise, the greatest gains in axillary girth took place in the earlier part of the year. If axillary girth is accepted as a measure of fitness as well as growth (Usher and Church 1969), then there was no appreciable difference in the degree of 'fitness' between the sexes for any one year (the same conclusion as was derived from the relative weight data).

Fewer pups were seen late in the summer of 1975 than in 1976 (see Chapter Three, Population Biology , Figure 3.3). The high air temperatures experienced in 1975 relative to 1976 apparently caused the pups to become less active and to seek shelter from the heat to a greater degree than during the following year. Females made more trips to the sea to cool off in 1975, which probably decreased the amount of time mothers spent with their pups. When ashore, cows spend 60 percent of their time interacting with their pups, of which half was spent suckling (Stark 1975). While most cows in 1974/75 were ashore long enough for their pups to receive sufficient nutrition, pups may not have had the opportunity to suckle as long as they might otherwise have had, had the cows been ashore longer. Unfortunately, no data were collected which could substantiate or refute this possibility. However, if this was the case, then conceivably it could have resulted in a slower absolute growth of pups in 1975 relative to 1976.

Bryden (1968b) stated that the variation in birth weight of the Southern elephant seal on Macquarie Island between two years was probably the result of annual differences in the quantity of food available to pregnant cows. If so, then the availability of food to the mothers could also have an effect on post-natal pup growth.

Squid is a major food item of New Zealand fur seals (Falla *in* Csordas and Ingham 1965; Sorensen *in* Bailey and Sorensen 1962; Street 1964) and was the most abundant and prevalent food item found in the stomachs of adults collected at Taumaka. Samples of squid beaks taken from two different individuals were made up entirely of *Nototodarus sloani sloani*, which is an abundant species in the nearshore waters of New Zealand (Kawakami 1976a). Areas of upwelling, such as those off the west coast of the South Island (Stanton 1971), are favourable grounds for squids (Uda 1959), but the overall hydrological conditions favoured by squids (Uda 1959) were more prevalent during the 1975/76 summer than during the 1974/75 summer. This is reflected in the catch statistics of the Japanese squid fishery. During December 1974, 0.3 tons of *N. s. sloani* were caught per unit effort off the New Zealand coast, while 1.5 tons were caught per unit effort during December 1975. The catch per unit effort for January 1975 and 1976 was similar (1.7 and 2.0 tons per unit effort respectively; Kawakami 1976b cited by Okutani 1977: 43, Table 3.3). The total catch off the west coast of the North and South Island was ca. 9,530 t for 1974/75 and ca. 19,460 t for 1975/76 (T. Kawakami *pers. comm.* 14 March 1978). Therefore, lactating cows probably were able to feed on *N. s. sloani* with less effort in December 1975, than in December 1974. Consequently, the mothers probably were in excellent condition, which was reflected in their milk supply and ultimately in their pup's growth. Payne (1977) recognized the need for an adequate food supply within range of Kerguelen fur seal breeding colonies on South Georgia, and suggested that a decrease in food availability may be a causative factor in reduced pregnancy, slow growth rates and high mortality. Gaskin (1973) has shown that sperm whale catches in the New Zealand region were greatest where hydrological conditions were favourable for squid concentrations.

The greater pup growth in 1976 was probably due to the combined effect of cooler air temperatures and more favourable hydrological conditions. This is discussed in greater detail in Chapter Nine, General Discussion.

The more rapid growth rate in 1976 gave these pups a distinct post-weaning survival advantage over pups of the previous season. Coulson and Hickling (1964) found a positive correlation between growth rate and survival of Grey seal pups. The percentage of pups found alive after five weeks (having been independent of their mothers for approximately 17 days, and therefore regarded as being successfully reared to independence) increased as their growth rate prior to weaning increased. They found a survival rate of 50 percent for pups which gained 1.0-1.9 lb (0.45-0.86 kg) per day, and 100 percent survival for pups with gains greater than 3.9 lb (1.77 kg) per day.

Pups in 1976 were significantly heavier (at least to 235 days) than pups in 1975. Therefore, if pups in 1976 began to lose weight later in the year, they would have been able to sustain a greater weight loss than pups in 1975. Pups losing weight in 1975 reached the minimum survival weight sooner, after which they either died or else regained weight (three of 17 individually marked pups in 1975 lost weight between 55 and 140 days, then gained weight between 140 and 235 days).

A pup which received adequate nutrition for survival prior to weaning would not necessarily be able to survive once weaned. A Grey seal pup which does not weigh at least 65 lb (29.5 kg) before going to sea is unlikely to survive the first winter (Bonner 1970). This is slightly over double their birth weight, which is about the same for the 8 kg minimum survival weight at weaning suggested for the New Zealand fur seal. This figure is quite possibly too low, and will need revision as further mortality data become available.

<u>FIGURE 6.1.</u> Mean weights of male and female pups at age 55, 140 and 235 days in 1975 and 1976, and 290 days in 1976; shaded rectangles = male, open rectangles = female, rectangle = ± one standard error, vertical line = 95% confidence limits, number to left of rectangle = sample size.

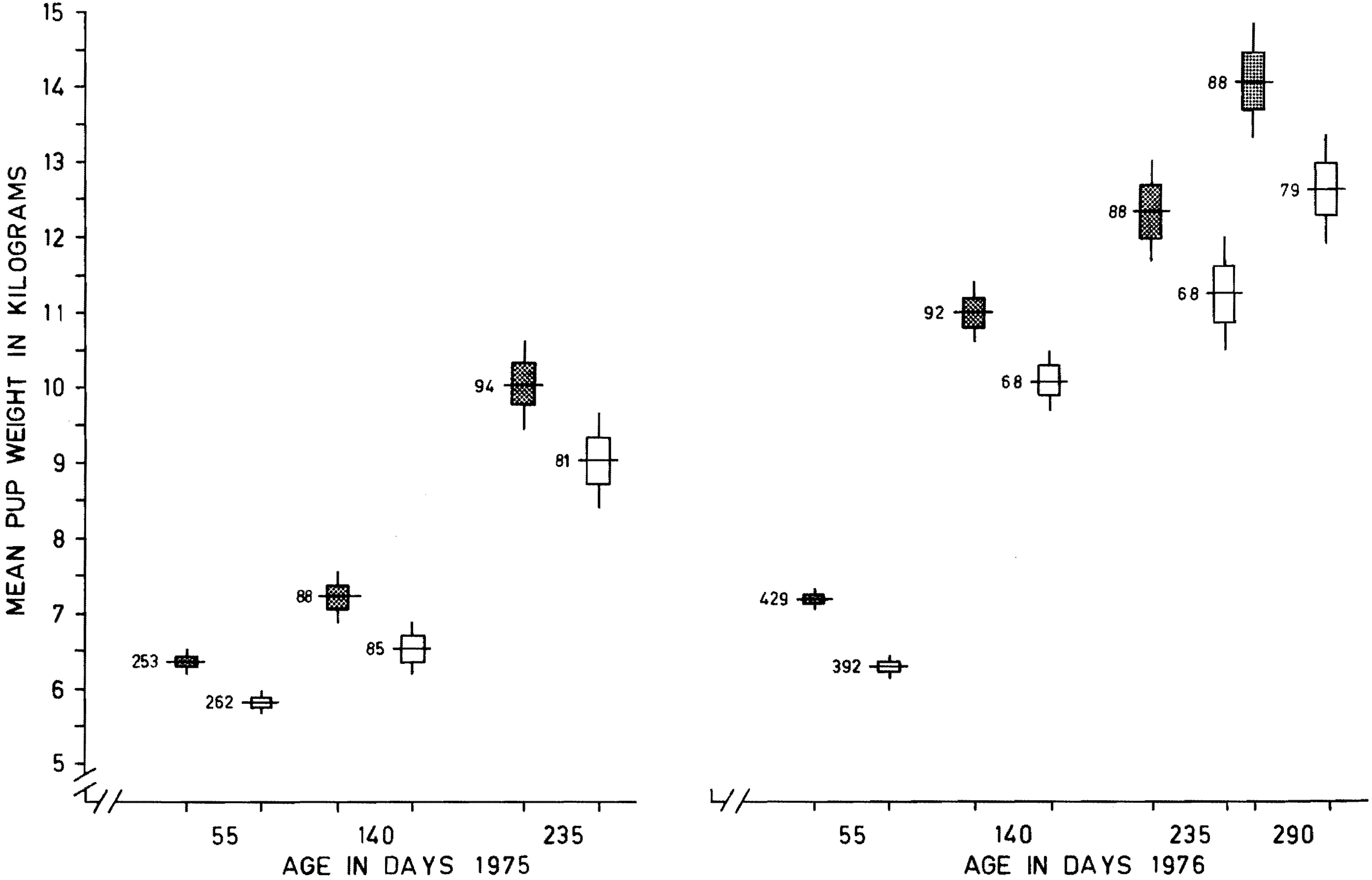
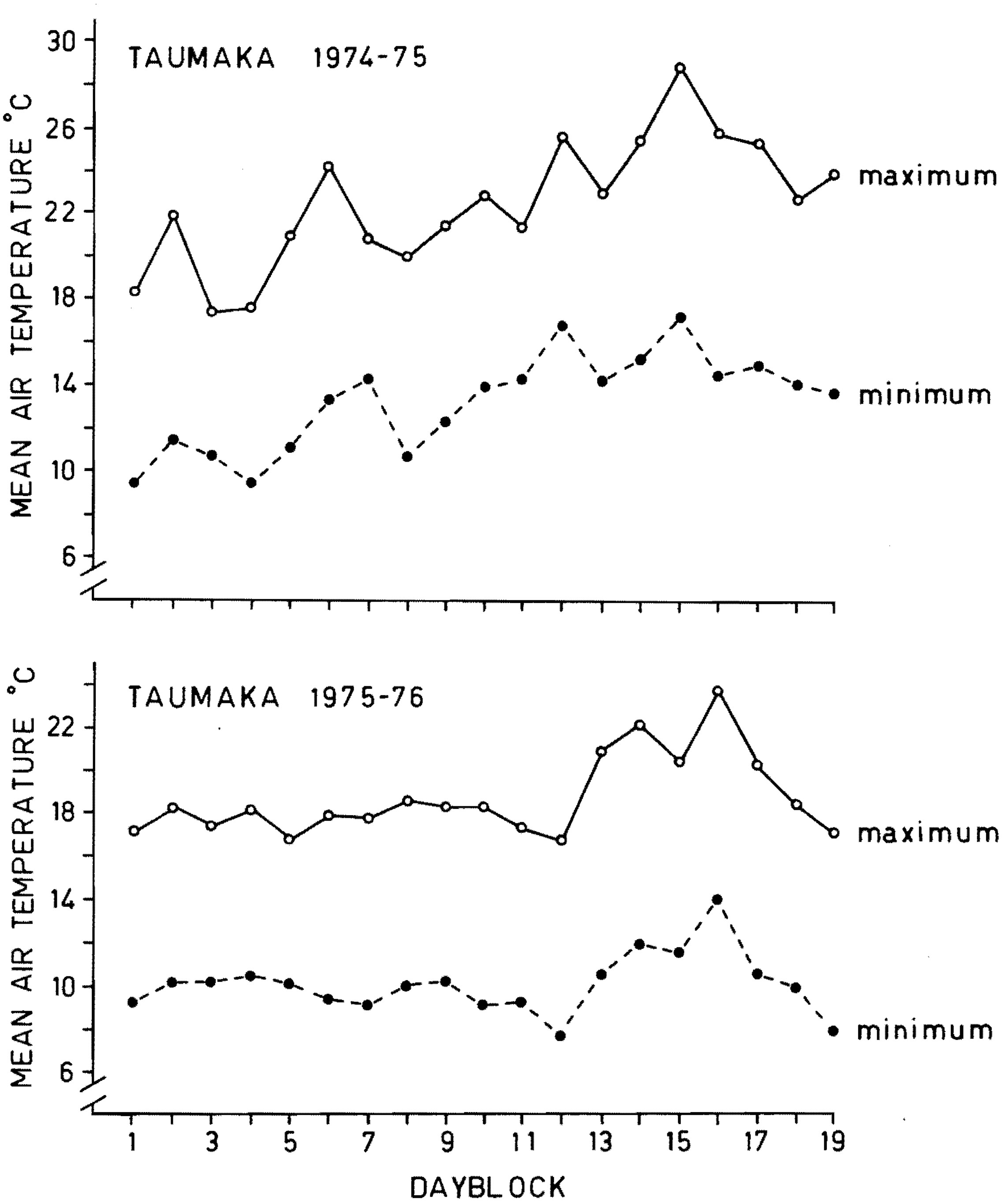

15
14
13
12
11
10
9
8
7
6
5
MEAN PUP WEIGHT IN KILOGRAMS
253
262
88
85
94
81
55
140
235
AGE IN DAYS 1975
429
392
92
68
88
68
88
79
55
140
235
290
AGE IN DAYS 1976

FIGURE 6.2. Mean maximum and minimum air temperatures at Taumaka for the 1974/75 and 1975/76 breeding seasons, by dayblock.

FIGURE 6.3. Official monthly mean air temperatures for Haast Township (42°52'S, 169°00'E), October 1974-August 1976 (New Zealand Meteorological Service, Wellington).


TAUMAKA 1974-75
MEAN AIR TEMPERATURE °C
30
26
22
18
14
10
6
maximum
minimum
TAUMAKA 1975-76
MEAN AIR TEMPERATURE °C
22
18
14
10
6
maximum
minimum
1
3
5
7
9
11
13
15
17
19
DAYBLOCK

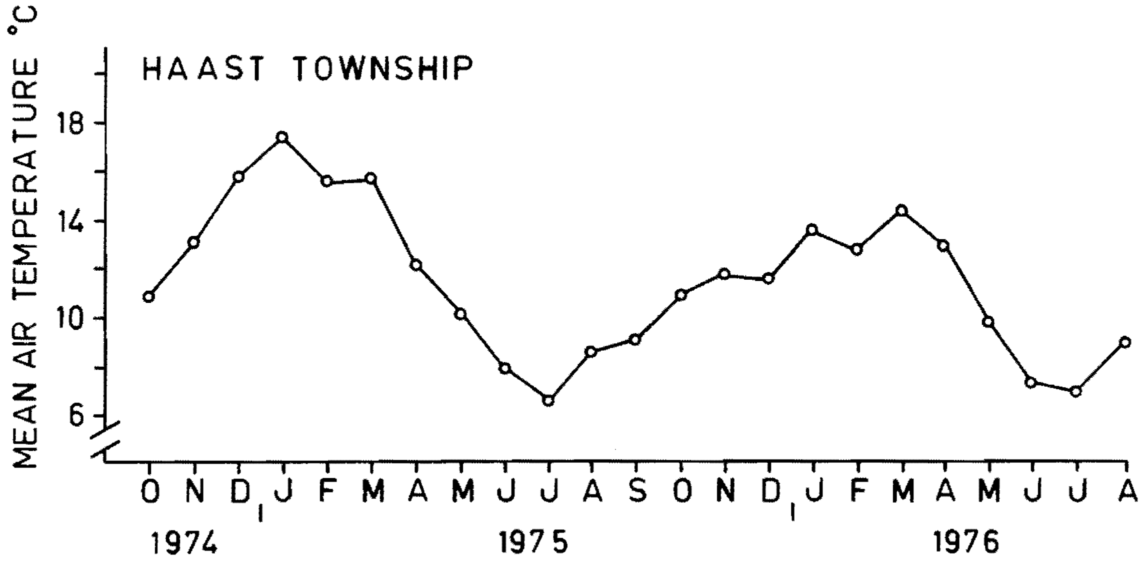
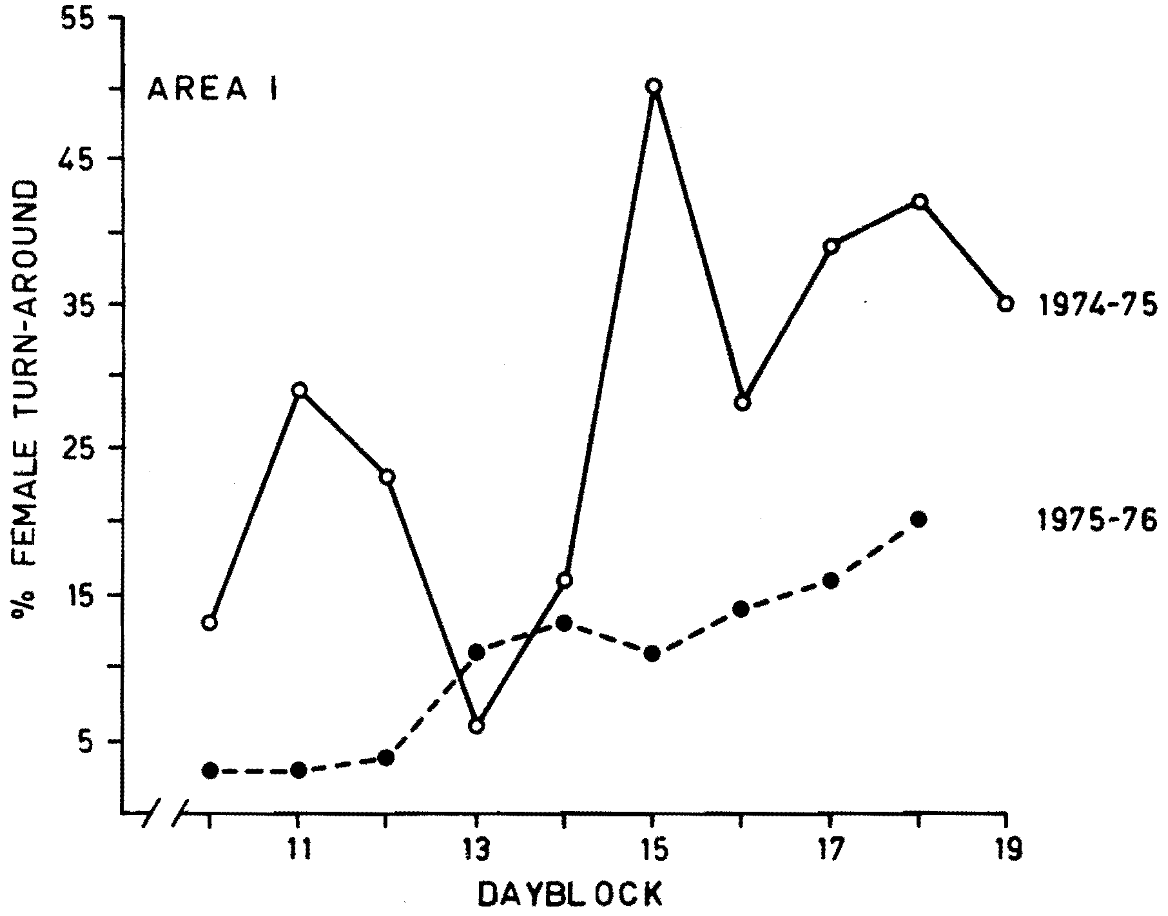

HAAST TOWNSHIP
MEAN AIR TEMPERATURE °C
18
14
10
6
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
1974
1975
1976

FIGURE 6.4. Percent 'turn-around' of females at each study area for dayblocks 10-19 (percent turn-around = $\frac{\text{number of females returning from the sea}}{\text{total number of females present}}$).

a. Study Area I, 1974/75 and 1975/76 breeding season.

b. Study Area II, 1974/75 and 1975/76 breeding season.


AREA I
% FEMALE TURN-AROUND
55
45
35
25
15
5
11
13
15
17
19
DAYBLOCK
1974-75
1975-76

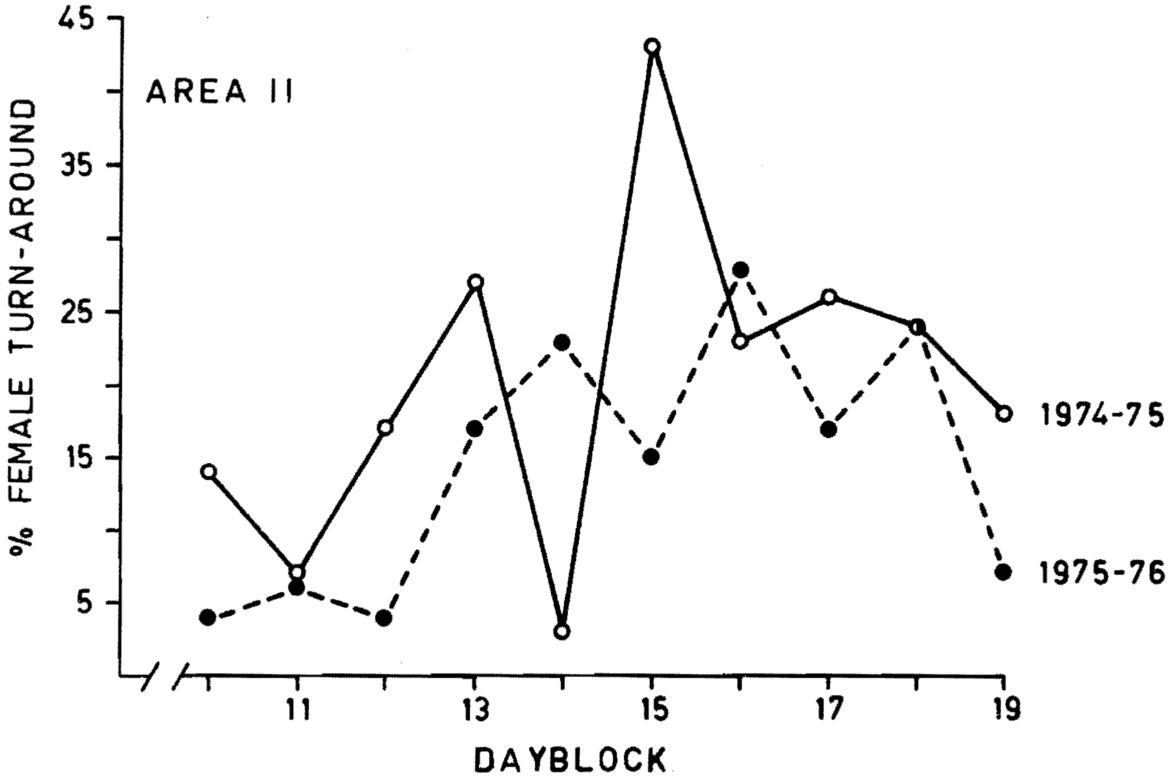

AREA II
% FEMALE TURN-AROUND
45
35
25
15
5
11
13
15
17
19
DAYBLOCK
1974-75
1975-76

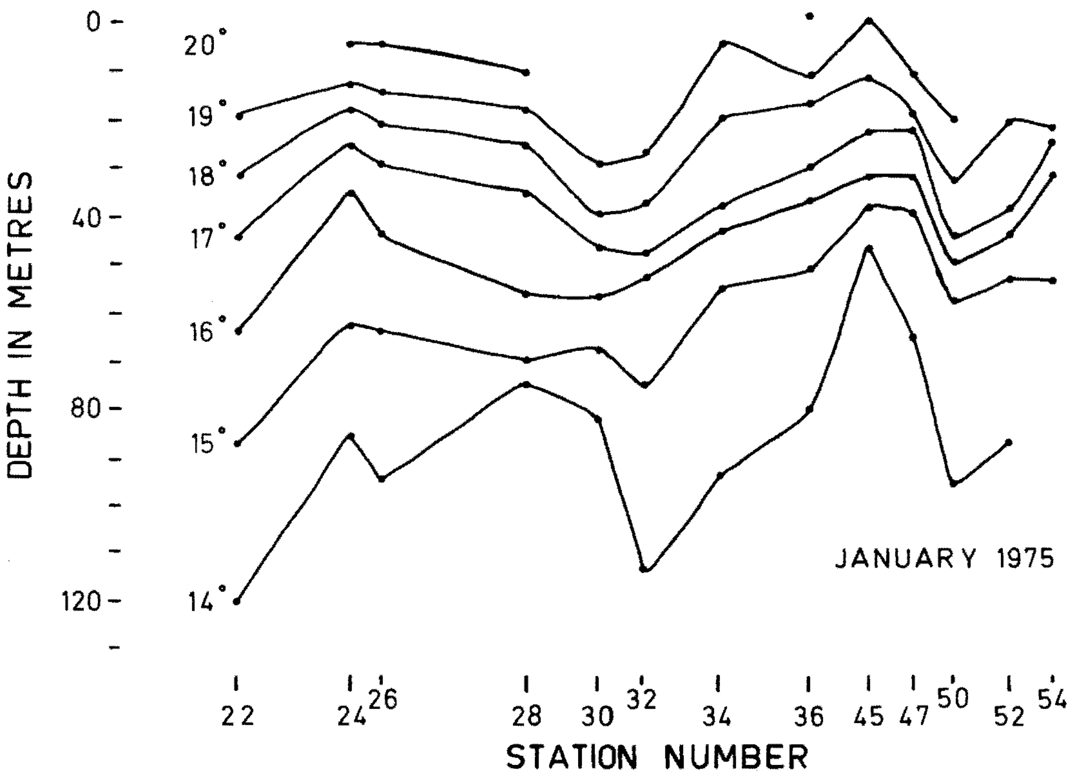
FIGURE 6.5. Temperature-depth recordings off the west coast of South Island. (Data supplied by Dr P. Roberts, Fisheries Research Division, Ministry of Agriculture and Fisheries, Wellington).

a. January 1975

Station number	Location
22	41°04'S 167°58'E
24	41°38'S 168°00'E
26	41°48'S 167°56'E
28	42°32'S 167°56'E
30	42°55'S 168°00'E
32	43°09'S 168°02'E
34	43°32'S 168°00'E
36	43°59'S 168°00'E
45	44°17'S 167°30'E
47	43°31'S 167°28'E
50	44°43'S 167°27'E
52	45°00'S 166°54'E

b. January 1976

Station number	Location
6	46°15's 165°30'E
10	44°24'S 167°24'E
16	42°30'S 169°03'E
27	40°48'S 170°09'E
34	40°15'S 172°06'E


DEPTH IN METRES
0
40
80
120
20°
19°
18°
17°
16°
15°
14°
JANUARY 1975
22
24
26
28
30
32
34
36
45
47
50
52
54
STATION NUMBER

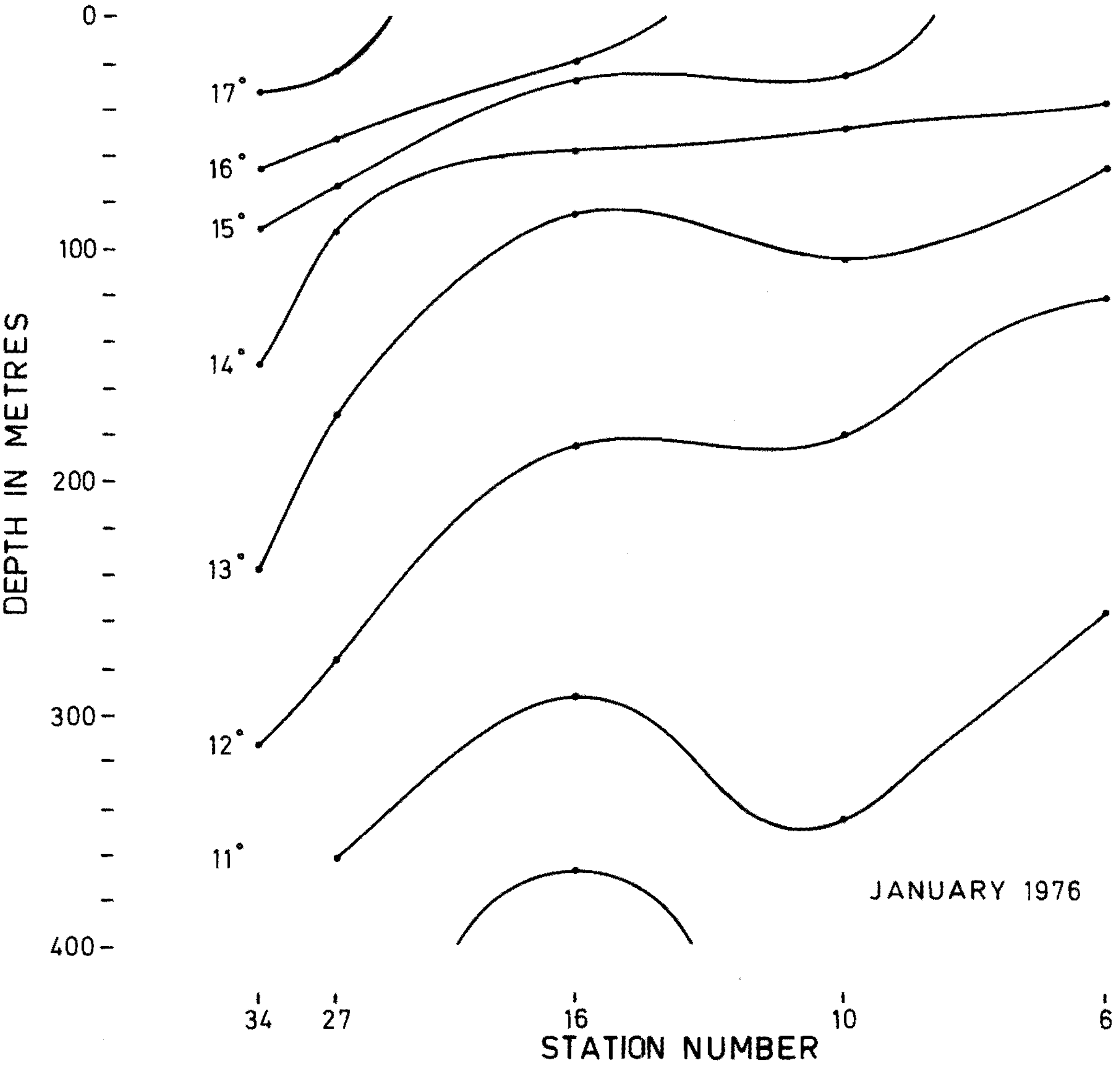

DEPTH IN METRES
0
100
200
300
400
17°
16°
15°
14°
13°
12°
11°
JANUARY 1976
34
27
16
10
6
STATION NUMBER

FIGURE 6.6. Weight distributions of male and female pups at ages 55, 140 and 235 days in 1975.

a. Males. Note the significant ($p < 0.001$) skew to the right at age 235 days.

b. Females. Note the significant ($p < 0.001$) skew to the right at age 140 days.

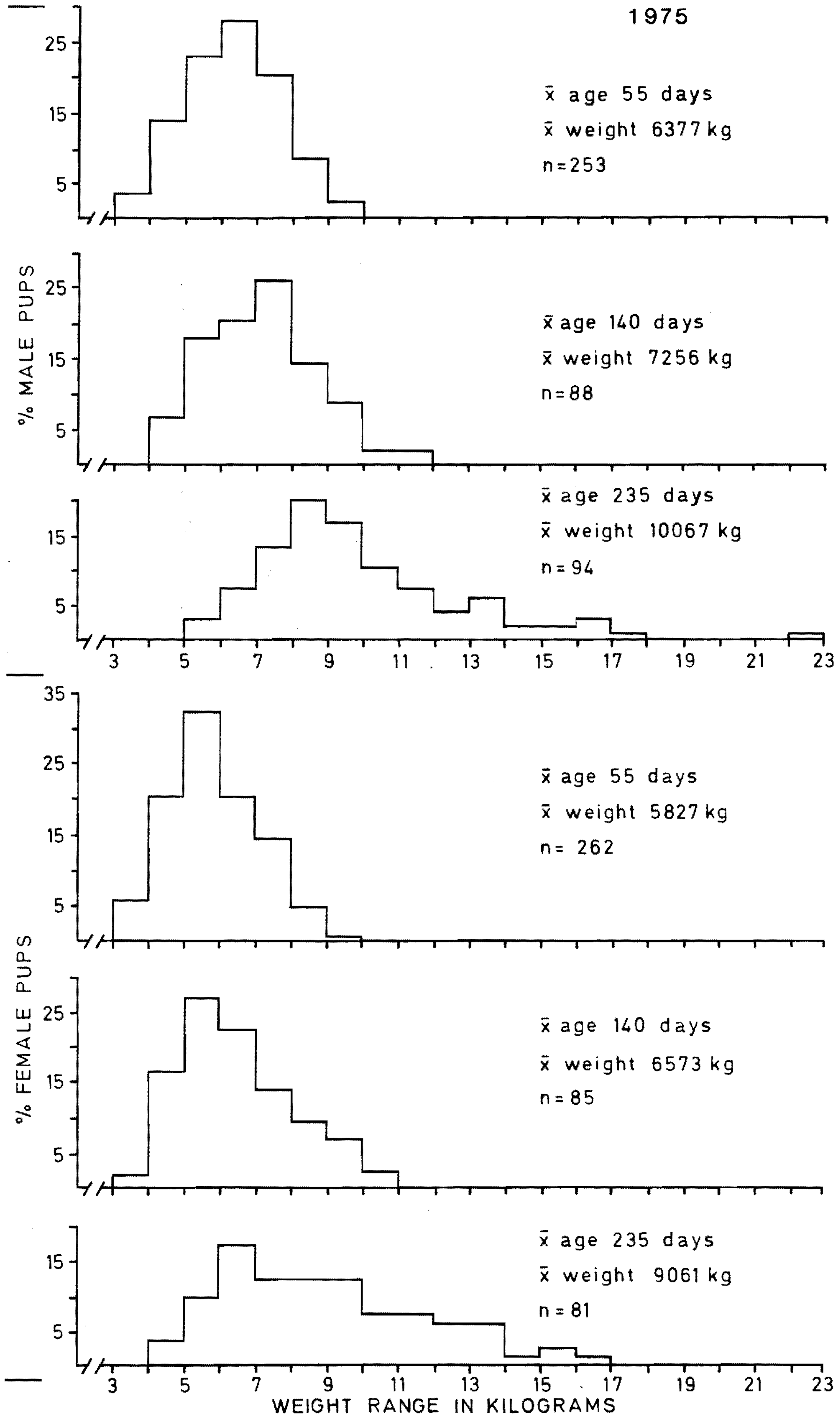

1975
x̄ age 55 days
x̄ weight 6377 kg
n=253
% MALE PUPS
x̄ age 140 days
x̄ weight 7256 kg
n=88
x̄ age 235 days
x̄ weight 10067 kg
n=94
x̄ age 55 days
x̄ weight 5827 kg
n= 262
% FEMALE PUPS
x̄ age 140 days
x̄ weight 6573 kg
n=85
x̄ age 235 days
x̄ weight 9061 kg
n=81
35
25
15
5
3
5
7
9
11
13
15
17
19
21
23
WEIGHT RANGE IN KILOGRAMS

FIGURE 6.7. Weight distributions of male and female pups at ages 55, 140, 235 and 290 days in 1976.

a. Males.

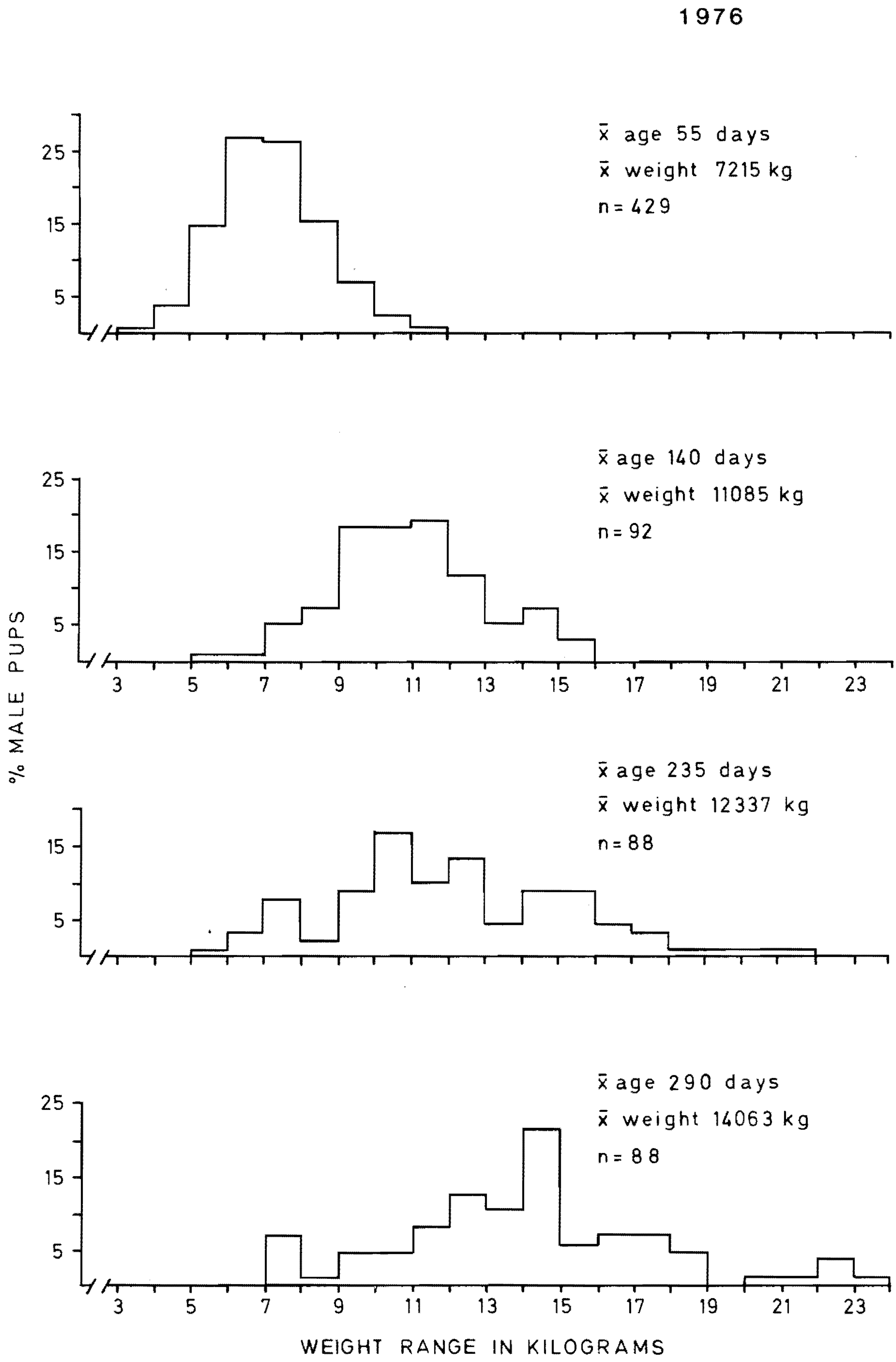
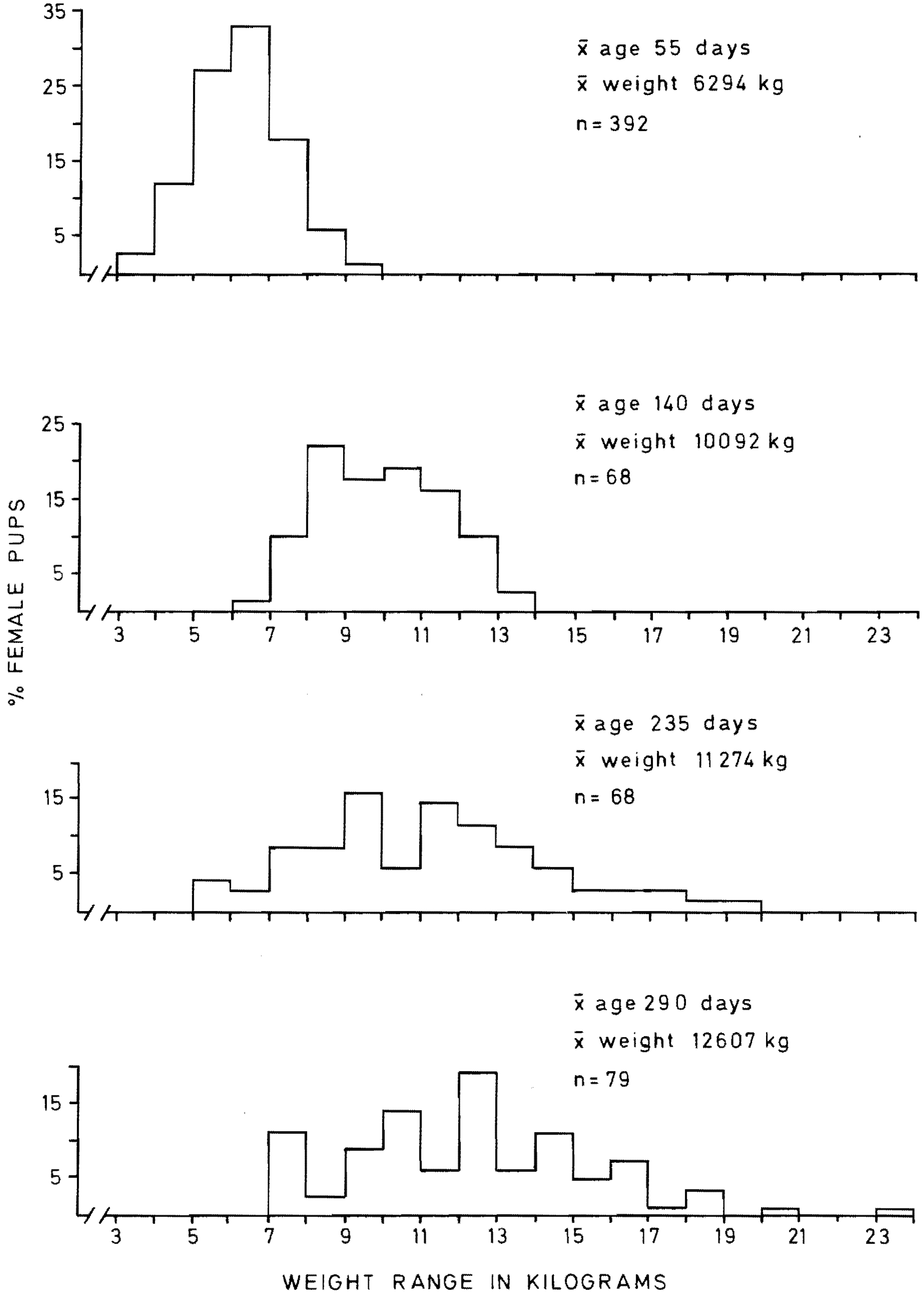

1976
x̄ age 55 days
x̄ weight 7215 kg
n = 429
x̄ age 140 days
x̄ weight 11085 kg
n = 92
x̄ age 235 days
x̄ weight 12337 kg
n = 88
x̄ age 290 days
x̄ weight 14063 kg
n = 88
25
15
5
% MALE PUPS
3
5
7
9
11
13
15
17
19
21
23
WEIGHT RANGE IN KILOGRAMS

FIGURE 6.7. Continued.

b. Females.

1976


x̄ age 55 days
x̄ weight 6294 kg
n = 392
35
25
15
5
x̄ age 140 days
x̄ weight 10092 kg
n = 68
25
15
5
3
5
7
9
11
13
15
17
19
21
23
% FEMALE PUPS
x̄ age 235 days
x̄ weight 11 274 kg
n = 68
15
5
x̄ age 290 days
x̄ weight 12607 kg
n = 79
15
5
3
5
7
9
11
13
15
17
19
21
23
WEIGHT RANGE IN KILOGRAMS

CHAPTER SEVEN

PUP MORTALITY

7.1. Introduction

The quantification of mortality is basic to an understanding of population dynamics. However, the causes of death are many and varied and are difficult to quantify. For some species, the estimates made of mortality rates are of doubtful validity, but for others, reliable estimates do exist, e.g. for the Grey seal (Bonner and Hickling 1971; Coulson and Hickling 1964; Hewer 1964, 1974; Summers *et al.* 1975), the Southern elephant seal (Carrick *et al.* 1962; Carrick and Ingham 1962b; Laws 1953b), the Harbour seal (Bigg 1969), the Ringed seal (Smith 1973), the Weddell seal (Siniff *et al.* 1977; Stirling 1971c), the Kerguelen fur seal (Payne 1977) and the most extensively studied pinniped of them all, the Northern fur seal (Chapman 1964; Marine Mammal Division 1977; North Pacific Fur Seal Commission 1975).

In this chapter, data are presented on mortality rates of pups from birth to about 300 days, and the suspected causes of death, both natural and those caused by human disturbance are discussed. The causes of mortality and the mortality rates are compared with those of other fur seal species, e.g. the Kerguelen fur seal, the Amsterdam fur seal, and the Northern fur seal, and with selected phocid species, e.g. the Southern elephant seal and the Grey seal.

7.2. Methods

Quantitative mortality data were collected in two ways:

1. For the period from birth to 50 days, the number of dead pups in the two study areas were counted. Together, these two study areas comprised about 6 percent of the total rookery area and contained between 5 and 6 percent of the breeding population. When weather conditions permitted, several censuses were made daily on one or the other of the study areas, and the location of living and dead seals was mapped. The pup mortality rates (= cumulative mortality loss over a defined period of time) calculated were considered to apply to the entire pup population.

2. Calculation of pup mortality rates up to 290 days was based on estimates of the decline in numbers of living pups on the entire rookery. Pup mortality beyond approximately 300 days could not be determined as pups began to leave the island at that age. For each study area, an estimate of the total number of pups born was calculated as follows:

total pups born = (total number of dead pups seen) + (maximum number
of live pups seen at any one time) - (number of
dead pups seen after maximum live pup count)

Estimates of pup mortality to 50 days (until the end of January, when observations on the study areas ceased) were calculated by:

$$\text{pup mortality to 50 days} = \frac{\text{total number of dead pups}}{\text{total number of pups born}}$$

It is probable that more pups were born than were counted, but it is also probable that more pups died than were counted, so these estimates were accepted as representative of the true values for each of the two study areas.

During February 1975, 253 male and 262 female pups of average age 55 days (mean birth date 10 December; see Chapter Six, Pup Growth, for its calculation) were tagged on the posterior edge of either the left (male) or right (female) foreflipper with numbered monel metal cattle eartags (Stockbrands Co. Pty Ltd, Mt Hawthorn, Western Australia). In February 1976, 429 male and 393 female pups were given a year-mark only, by removing the cartilaginous tip of the second digit of the left hindflipper.

After the pups were marked at 55 days, a census was taken of pups over the entire rookery. Assuming that we could have captured all marked and non-marked pups that we were able to touch, and knowing how many pups were originally marked, an estimate of the total pup population at the time of marking was calculated by using the Peterson estimate:

$$N = \frac{M(n + 1)}{m + 1}$$

where N is an estimate of the total population size, M is the total number of marked pups, n is the sample size, and m is the number of marked pups in the sample.

The standard error of the estimate was calculated by:

$$\text{S.E.} = \sqrt{\frac{M^2(n + 1)(n - m)}{(m + 1)^2(m + 2)}}$$

The Peterson estimate assumes that there was no differential mortality between marked and non-marked pups from the time marking began until the census was completed; that no immigration or emigration took place for that time; and that marked pups were as easy to catch as non-marked pups. The three assumptions are most likely correct, as mortality probably was minimal over such a short period (about 5 days); young pups avoid the open sea, so no immigration or emigration could occur; and all pups fled when approached, so it is unlikely that marked pups were any easier or harder to 'capture' than non-marked pups. Therefore, these population estimates are thought to be realistic.

By assuming that the mean mortality rate to 50 days for the two study areas was true for the whole rookery, and having estimated the pup population at 55 days, the total number of births on Taumaka was calculated.

During subsequent trips to Taumaka (at mean pup ages of 140 and 235 days in 1975 and 1976, and also 290 days in 1976 only), pups were counted while the observer walked the length of the rookery. Because of the extreme disturbance it would have caused, no effort was made to climb into deep gullies or look under rocks for pups. Various other factors also affected census accuracy. For example, on warm, clear days, fewer pups were out in the open than on cooler, more overcast days; and as pups grew older, they spent more time by the sea or in tidal pools, where the irregular terrain of the rookery obscured them from view. Consequently, it was difficult to estimate accurately the total pup population. Crawley and Brown (1971), when using the same census technique, suggested a 20 percent under-count, but this most certainly was an under-estimate of the error. During February 1975, about 50 percent of all pups were tagged. By greatly increasing search efforts, 64 percent were marked during February 1976. This indicates that one could expect an under-count of as high as 50 percent during subsequent pup censuses. Therefore, estimates of the total number of pups were made by doubling the total pup count for each census. The high census count in August 1976 (at 235 days) was due in part to the rough seas present at the time of the census which forced pups away from the sea to where they were more easily seen. It was assumed that more than 50 percent of the pups were counted during the August 1976 census, but, for consistency, the total count was doubled when calculating the total population estimate.

7.3. Results

The collection of mortality data during the breeding season was difficult. Movement onto the rookery was curtailed because of the disturbance it caused, and because of the danger of attack from territorial bulls; most dead pups could therefore not be marked or retrieved. Consequently, specific results are given only for overall mortality rates, and for those mortality factors for which quantifiable data were collected. Other, non-quantifiable, causes of mortality are reviewed in the discussion.

(a) Mortality rate estimates to 50 days

In 1975, proportionally more pups died on area I than on area II (26 *versus* 15 percent), but the following summer, the reverse was true

(24 percent for area II *versus* 20 percent for area I). For the two years together, there was no significant difference in pup mortality between the two areas ($x^2 = 1.63$, $p > 0.05$) so the data were combined for further analysis. The estimated pup mortality up to 50 days was 21 percent, which for convenience was rounded to 20 percent (Table 7.1).

TABLE 7.1. Pup mortality to age 50 days, as a percentage of total births.

	1974/75 Area			1975/76 Area			Years and areas combined
	I	II	I&II	I	II	I&II	
A. Maximum number of pups counted alive at any one time	53	57	110	57	54	111	221
B. Total number of dead pups counted	17	9	26	14	15	29	55
C. Total number of dead pups counted before maximum count of live pups	13	4	17	13	9	22	39
D. Total number of pups born (A + C)	66	61	127	70	63	133	260
E. Percent mortality $(\frac{B}{A + C})$	25.8	14.8	20.5	20.0	23.8	21.8	21.2

(b) Mortality rate estimates to 290 days

For 1975, pup population estimates were: total born, 1319; at 55 days, 1055 (± s.e. = 83); at 140 days, 716; at 235 days, 758. The 1976 pup population estimates were: total born, 1628; at 55 days, 1273 (± s.e. = 57); at 140 days, 892; at 235 days, 1242; at 290 days, 984). These data suggest that there was little pup mortality after 140 days. This conclusion is supported by the number of dead pups counted during each visit to Taumaka. In 1975, 36 dead pups were counted at 140 days and 9 were counted at 235 days. In 1976, only three badly decomposed pups were found at 140 days, 2 dead pups were found at 235 days, and 3 at 290 days.

The population estimates given above indicate that in 1975 there was a 42 percent mortality rate to 235 days, and in 1976 there was a 40 percent mortality rate to 290 days (the maximum pup ages for which data were collected).

(c) Causes of mortality

(i) Starvation

Two dead pups, both with umbilical cords still attached, had 6 mm and 4 mm of blubber across the sternum respectively, suggesting that pups have about 5 mm of blubber either at, or shortly after birth.

Two males and one female accidently killed by us when they were about 50 days old had an average blubber thickness across the sternum of 17.1 mm (range: 17.0-18.0 mm). They appeared to be average to slightly above average in size, suggesting that at 50 days pups of either sex with at least 15 mm of blubber across the sternum are in good condition.

Twenty fresh, dead pups were collected during January and early February for weighing and measuring. None had milk in its stomach. Eleven (55 percent) had no measurable blubber across the sternum, three (15 percent) had 5 mm or less, and the remaining six (30 percent) had between 5 mm and 10 mm of blubber. Assuming that blubber acts as a food reserve (Young 1976), this suggests that the 11 pups with no blubber had starved to death. Whether starvation was the sole cause of death for the remaining 9 pups is unknown, but it is probable that it was a contributing factor.

Assuming that pups with 5 mm or less of blubber had starved to death, then starvation accounted for 70 percent of the mortality to 50 days.

For the above analysis, data from three dead pups collected in December were not used. They were probably all very young, and two still retained umbilical cords.

(ii) Mortality caused by human disturbance

a. Pup handling

There is evidence from studies of the Northern fur seal that pup handling can have an adverse effect on pup growth; in 1966 handled pups were significantly lighter ($p < 0.05$) 13 days after handling than non-handled pups (Marine Mammal Biological Laboratory 1969). To see if handling affected New Zealand fur seal pups in a similar manner, the weights of marked and non-marked pups were compared. Apparently it did not, as there was no significant difference between the weights of marked and non-marked pups at 140 days (85 days after marking) in 1975 and 1976 ($p > 0.05$; Mann-Whitney U Test; Siegel 1956).

b. Tagging

In February 1975, pups on Taumaka were tagged with monel metal cattle ear tags. Although every effort was made to apply the tags in such a way that they would cause the least harm and discomfort, it was seen in May 1975, during the first return trip to Taumaka, that the tags were working in the wounds, preventing proper healing. Seventy-seven percent (43 of 56) of the tagged pups recaptured showed some indication of either suppuration or incomplete healing at the tag site. In August of the same year (180 days after the pups had been originally tagged), 75 percent (46 of 61) of the pups had incompletely-healed tag wounds.

Pup recapture data were tested to see if tagging had increased pup mortality. The ratio of tagged to non-tagged pups was calculated by taking a pup census within one day after tagging. As all pups ran when approached, it was unlikely that tagged pups were any more wary of our presence than non-tagged pups.

In 1975, the expected ratio was calculated by averaging the separate counts made at the same time by two different observers (85 tagged, 87 non-tagged; 76 tagged, 83 non-tagged). There was no significant difference between the two censuses ($\chi^2 = 0.09$, $p > 0.05$), so the expected ratio was accepted as representative of the true ratio. From this, it was determined that 49 percent of the pups were tagged.

In 1975, there was a significant difference in a goodness-of-fit test between the actual and expected ratios of tagged to non-tagged pups (number tagged:number non-tagged) at 140 days (72:102; $\chi^2 = 4.044$, $p < 0.05$) and at 235 days (67:108; $\chi^2 = 8.039$, $p < 0.01$) such that there were fewer tagged pups than expected. In 1976, there was no significant difference in a goodness-of-fit test between the actual and expected ratios of marked (64 percent) to non-marked (36 percent) pups at 140 days (96:64; $\chi^2 = 1.111$, $p > 0.05$), 235 days (92:65; $\chi^2 = 1.988$, $p > 0.05$) and 290 days (114:53; $\chi^2 = 1.318$, $p > 0.05$). The only difference in pup handling between the two years was that pups in 1976 were permanently marked by digit clipping rather than by tagging.

7.4. Discussion

The mortality rate estimates and factors which contributed to, or were thought to have contributed to, pup mortality are discussed below.

The mortality factors are divided into two major groups, *viz.* natural mortality, which includes starvation, stillbirths, suffocation in the amnion, drowning, trampling, microbial infection and predation; and mortality caused by human disturbance, which includes pup handling, human presence and tagging.

(a) Mortality rate estimates

As the two study areas were thought to be representative of the rookery, the 20 percent mortality to 50 days of pups in the study areas should apply to the total pup population of Taumaka. The mortality rate to 300 days of 40 percent is more speculative. It is based on population estimates of the remaining pups at specific times, and is therefore directly dependent on the accuracy of these estimates. Nevertheless, the estimated 40 percent mortality to 300 days probably approximated the actual mortality.

There was no apparent pattern as to when most pup deaths occurred during the first 50 days, but the mortality rate was greatest during this period. Of the remaining 20 percent mortality, most probably died before 140 days. The first 15 days are the most critical for Amsterdam Island fur seals (Paulian 1964), and Northern fur seal pup mortality is greatest during the first few weeks of life (Kenyon *et al.* 1954).

With a 40 percent mortality to 300 days, the first year mortality could be in the vicinity of 50 percent. If this is correct, then deaths on land made the greatest contribution to first year mortality. Many other seal species have a similar first year mortality, but the deaths on land can be of considerably less significance. For example, the Northern fur seal in recent years has had a first year mortality of 31.9 to 61.9 percent, but an on-land mortality of 4.8 to 11.1 percent (North Pacific Fur Seal Commission 1975). These pups leave for the sea after about four months (Baker *et al.* 1970). The Southern elephant seal on Macquarie Island has a first year mortality of 40-50 percent, and a birth-to-weaning mortality of 2 to 16 percent (Carrick *et al.* 1962). They are weaned in about 23 days (King 1964). On land mortality of Grey seal pups ranges from 14.9 to 35 percent, depending on the rookery (Bonner and Hickling 1971; Coulson and Hickling 1964; Summers *et al.* 1975), and first year mortality is about 60 percent (Hewer 1964, 1974). They are weaned in about 17 days (Coulson and Hickling 1964). This does not mean that New Zealand fur seal pups survive better than those of other species at sea, but only that they are at sea for a relatively short period of time during their first year of life.

Kerguelen fur seal pup mortality is about 6 percent while on land at South Georgia (Bonner 1964, 1968) and 23.9 percent for the first year (Payne 1977); a first year mortality of slightly less than half the estimate for the New Zealand fur seal. However, the South Georgia population is increasing rapidly, whereas the New Zealand fur seal population on Taumaka is either stable or increasing slowly (see Chapter Eight, Estimate of Population Size and Potential Growth).

(b) Natural mortality

(i) Starvation

There is little doubt that starvation is a major cause of pup deaths, but without detailed studies of other causes of mortality, it is extremely difficult to quantify. Nevertheless, it is reasonable to assume that the 11 pups with no blubber over the sternum starved to death. Considering that the three apparently healthy and robust pups accidently killed had 17-18 mm of blubber over the sternum, it is likewise reasonable to assume that pups with 5 mm or less of blubber were at least weakened by lack of food.

Starvation is probably the greatest cause of pup deaths in many seal species, including the New Zealand sea lion (Marlow 1975), Southern elephant seal (Carrick *et al.* 1962; Carrick and Ingham 1962b), Grey seal (Bonner 1975), Tasmanian fur seal (Warneke 1975) and Kerguelen fur seal (Bonner 1968). Next to hookworm infestations, starvation is the most prevalent cause of pup mortality in the Northern fur seal (Marine Mammal Division 1977; Nagasaki 1961).

Starving New Zealand fur seal pups often attempt to suckle surreptitiously from any available female, but females will knowingly suckle only their own pups. Adoptive suckling is not common in phocids, and is rare in otariids. It has never been reported in the Arctocephalinae (see Burns *et al.* 1972; Carrick *et al.* 1962; Fogden 1968, 1971; Stirling 1975a).

It is possible that by late August (approximate age eight months) many pups are able to nourish themselves. By May (the time of the first trip to Taumaka after the February marking), pups were confidently swimming about in inshore waters. Here they would have ample opportunity to learn to catch fish, though it is uncertain as to when they are able to do this successfully. Small fishes were regularly seen in close to shore. Best and Shaughnessy (1975) tentatively suggested that Cape fur seal pups were able to survive on their own from between seven and eight months of age.

(ii) Stillbirths

On 29 and 30 September 1976, one dead male and two dead female pups were collected on the rookery. Each weighed less than 2 kg and had very little hair. Although they were not dissected to see whether or not they had ever breathed, it is probable that they were stillborn. Because few dead pups similar in appearance were seen, stillbirths probably made only a small contribution to the overall mortality. On St Paul Island, in the Pribilof group, five of the 379 (1.3 percent) dead Northern fur seal pups collected in 1968 were stillborn (Marine Mammal Biological Laboratory 1970).

(iii) Suffocation in the amnion

New Zealand fur seals make no attempt to clean their pups immediately after birth (pers. ob.; Stirling 1971b), but despite this, death by suffocation in the amnion appears to be rare. None was observed during this study, but two instances were reported from Taumaka during the 1973/74 summer (McNab and Crawley 1975). Amsterdam Island fur seals (Paulian 1964) and Kerguelen fur seals (Bonner 1968) occasionally do attempt to clean their pups, but, in the latter species at least, deaths due to suffocation still result.

(iv) Drowning

Even pups less than three weeks old are remarkably adroit at scrambling out of the wash of high seas, but they are nevertheless in danger of being swept off the rookery during stormy weather. There is no hope for those washed out to sea, and little hope for those washed back ashore unless they are quickly reunited with their mothers. Drowning accounts for some pup mortality on Taumaka (pers. ob.; McNab 1974), but the nature of the terrain is such that most pups are born out of the reach of high seas. Also, females will remove their young pups from the sea's wash, as will female South American fur seals (Vaz-Ferreira 1965a), but at no time did cows place themselves between their pup and the sea's wash, as was reported for female Grey seals (Darling 1947).

In some seal species, drowning can account for a high percentage of pup mortality. At Amsterdam Island in 1955/56, 58 percent of the Amsterdam Island fur seal pups on the Plateau de la Recherche rookery were drowned (Paulian 1964). This mortality rate was exceptionally high, and occurred because the females pupped closer than usual to the sea's edge during a period of fine weather and calm seas.

(v) Trampling

An obvious disadvantage of the gregarious breeding found in the otariids is that pups may be trampled on by larger seals. New Zealand fur seal bulls are indifferent to pups (pers. ob.; Stirling 1971a), to the extent that they make no attempt to avoid them when moving about the rookery. However, pups learn to take evasive action even when as young as one to two weeks old. This lack of overt aggression towards pups is not universal in otariids. For example, overt aggression by bulls is a cause of pup death in the South American sea lion (Vaz-Ferreira 1965b) and the Northern fur seal (Bartholomew 1953), as is overt aggression by cows as well as bulls in the Australian sea lion (Marlow 1975) and the Grey seal (Coulson and Hickling 1964).

Early in the season, pups avoid trampling by sheltering amongst rocks or by congregating in open areas (pers. ob.; Crawley and Wilson 1976), but later they escape by running away, foregoing any cover offered by the terrain. Pups usually do not appear to be harmed by being trampled, but they risk receiving internal injuries which may not be immediately apparent, and some pups are fatally crushed (Stark 1975). Older pups will often bite bulls which trample on them.

Accidental pup trampling is known for the South American fur seal (Smith 1927), Amsterdam Island fur seal (Paulian 1964) and Kerguelen fur seal (Bonner 1968), as well as for other seal species (Morejohn and Briggs 1973; Orr and Poulter 1967; Sorenson 1950).

(vi) Microbial infection

With the exception of one pup with a badly infected umbilicus, none was seen with obviously infected wounds (excluding tag wounds). Pups commonly had eye infections during the first few months, but they appeared to clear up once the pups ceased playing in fetid pools and began playing in the sea. Microbial infection accounted for 11.5 percent (24 of 208) Northern fur seal pup deaths in 1969 on St Paul Island (Marine Mammal Biological Laboratory 1969). The pathology of the Northern fur seal is now under study (Marine Mammal Division 1975). Until pathological studies are made on the New Zealand fur seal, the extent of death due to infection will remain unknown, but it is unlikely that it is a major contributor to pup mortality.

(vii) Predation

With the exception of humans, seals in the New Zealand region have no natural terrestrial predators and no aerial predators. Once they go to sea, they may be preyed upon by sharks, killer whales and other seal species. Such predation is unquantifiable, but probably accounts for a large portion of the mortality of immature fur seals. For example, a great white shark (*Carcharodon carcharias*) caught in a fisherman's net off the Fiordland coast had two small fur seals in its stomach (W. McIvor *pers. comm.* 1975), and two seven-gill sharks (*Heptranchias cepedianus*) caught in a fisherman's trawl both contained fur seal parts (P. Eggling *pers. comm.* 1976). Whether these fur seal parts were from individuals killed or scavenged is unknown, but sharks are undoubtedly capable of catching fur seals. A small female fur seal with a series of three very severe gashes across her pelvis was observed pulling her way up the rocks at Taumaka during the austral summer of 1975/76. Such wounds could easily have been shark inflicted.

Adult fur seals were seen swimming in the same vicinity as seven-gill sharks, and while they were obviously aware of the sharks and alert to their presence, they showed no signs of flight. Conversely, the sharks paid no obvious attention to the fur seals. Perhaps it is the small, immature, or incapacitated fur seals which tend to be attacked. If so, then pups first venturing into the sea would be subject to more intense shark predation than other age classes. Sharks are known to prey upon other fur seal species, e.g. the Tasmanian fur seal (Warneke 1975), the South American fur seal (King 1964) and the Cape fur seal (Rand 1956). Shark attack is a major cause of death in the Hawaiian monk seal (Kenyon 1973).

Killer whales (*Orcinus orca*) generally are not found in the vicinity of Open Bay Islands, but are commonly seen further south. Because severe wounds are rarely seen on New Zealand fur seals, Csordas and Ingham (1965) suggested that either killer whales do not prey upon them or else fur seals seldom escape if attacked. It is unlikely that killer whales would forego fur seals as food. Rather, a fur seal injured by an attack would stand little chance of escape.

Fur seal parts, including one small pup, have been identified in the regurgitation of New Zealand sea lions from the Snares Islands (M.W. Cawthorn and D.S. Horning *pers. comm.* 1977). It is apparently not uncommon for Steller sea lions to attack Northern fur seal pups (Marine Mammal Division 1974, 1975, 1976). Leopard seals prey upon fur seals, but because there is very little overlap in their ranges such predation is undoubtedly low.

(c) Mortality caused by disturbance

Even if handling did not affect pup growth adversely, human presence was itself enough to cause pup deaths. When startled, adults and pups alike will panic and run, often precipitating a general stampede. Because of this, three pups were inadvertently killed during weighing and tagging operations. Two suffocated when trapped beneath a pile of pups under a large rock and the other was killed when a fleeing female leapt on it. On another occasion, a pup was killed when it ran off the edge of a 10 m high cliff onto the rocks below.

Such deaths can be minimized by not disturbing fur seals on the rookeries unless absolutely necessary during the first two months following pupping. After February, the immediate effect of human disturbance is not as critical, as by then the pups are more able to fend for themselves.

The capture of fewer tagged pups than expected at age 140 and 235 days in 1975 suggests that one or more of three things may have happened. Either tagged pups became more difficult to catch; or they suffered a greater mortality than non-tagged pups; or the original censuses from which the calculated ratio was obtained were inaccurate. The first possibility is highly unlikely, as there was no significant difference between the two independent counts, though more counts would have been desirable. Based on these limited data, the second alternative appears to be the most likely, although a count of dead pups made in May 1975 does not support it. Of 36 dead pups counted, 19 were tagged and 17 were not, which was not significantly different from the expected ratio of 49 percent tagged to 51 percent non-tagged ($\chi^2 = 0.21$, $p > 0.05$).

Although the evidence is not conclusive, the inference from the recapture data that tagging did increase pup mortality was considered sufficient to warrant the discontinuation of the use of monel metal cattle ear tags. In the Northern fur seal these tags have been found to interfere with circulation and to damage an important muscle in swimming, the flexor carpi ulnaris (Keyes 1966); they also have been shown to increase pup mortality (Chapman 1964; Chapman and Johnson 1968; Marine Mammal Biological Laboratory 1970). The tags are no longer used on Northern fur seal pups (G.Y. Harry Jnr *pers. comm.* 1975).

CHAPTER EIGHT

ESTIMATES OF POPULATION SIZE AND POTENTIAL GROWTH

8.1. Introduction

Crawley and Brown (1971) estimated that there were 2750 (range: 2000-3000) fur seals on Taumaka during the breeding season, including pups. Three years later, Wilson (1974a) estimated that there were 3575 (range: 2700-3900) fur seals on Taumaka and Popotai combined, of which 825 (range: 700-900) were on Popotai. Both of these estimates were based on an initial pup census with correction factors for mortality, pregnancy rates and the number of immature females taken into account. These correction factors were based on data from the Northern fur seal (Kenyon *et al.* 1954) and the Cape fur seal (Rand 1955). Crawley and Brown (*op. cit.*) questioned the accuracy of their estimate, and attributed its probable inaccuracy to a basic lack of knowledge about the New Zealand fur seal.

Many authors have suggested that the New Zealand fur seal population is increasing in numbers and expanding its range, based on circumstantial evidence and direct counts (Csordas and Ingham 1965; Falla 1965; Stirling 1968a; Stonehouse 1965). Gaskin (1972) expressed caution in accepting this suggestion. Rather, he proposed that the increase in numbers at various locations may be nothing more than the redistribution of a stable population. Wilson (1974a) made a survey of New Zealand fur seal colonies within the New Zealand region, and came to the conclusion that the population is increasing, but slowly.

In this chapter, estimates of the population size on Taumaka during the breeding season are given, based primarily on pup counts and estimates of total pup production made during the two years of the study. The population estimate calculated is given first, followed by the rounded estimate in square brackets. These population estimates include pups, females of breeding age, territorial bulls (= occupied territories) and 'surplus' bulls only, as few immature fur seals (other than pups) are on the rookery during the height of the breeding season. A more speculative estimate of the total number of fur seals associated with Taumaka, either through birth or through breeding on the rookery, is also given.

Population growth estimates are presented in this chapter, and are based on survival and pregnancy rates of the Northern fur seal, the first year survival rate calculated during this study, and theoretical first year survival rates. Although the population growth data are entirely speculative, they do give an indication of the possible or potential growth rates of the colony on Taumaka, and for New Zealand fur seals in general.

8.2. Results

(a) Population estimates during the breeding season

(i) 1974/75

An estimated 1303 pups were born on Taumaka during the 1974/75 breeding season (see Chapter Seven, Pup Mortality, for the calculation of this estimate). If every cow present had one pup, then there was an equal number of adult females, i.e. 1303. From this assumption, and based on a cow to occupied territory ratio of 7.3:1 (calculated from the sex ratios given for areas I and II in Chapter Three, Population Dynamics), there was an average of 178 (1303/7.3) occupied territories on the island. Assuming that only one bull occupied each territory for the entire season, then the resultant total of pups (1303), cows which bore pups (1303) and territorial bulls (= occupied territories; 178) was 2784 [2780] individuals.

The overall fertility rate (= pregnancy rate) of Cape fur seals was estimated to be 74 percent (Best 1973). If cows on Taumaka had a similar overall pregnancy rate to that of the Cape fur seal, and if those which were not pregnant were nevertheless on the rookery, then 1761 (1303/0.74) cows were present. From this, a population estimate for pups (1303), females of breeding age (1761) and territorial bulls (= occupied territories; 178) of 3242 [3250] was calculated.

A mean maximum of 12 territorial bulls was seen at any one time for the study areas combined. The mean number of occupied territories for the study areas combined during the month of December (the height of the breeding season) was 8.6. If every potential territorial bull was on the rookery at the time of the maximum territorial bull counts, then there were 3.4 'extra' bulls for every 8.6 territorial bulls, for a total of 70 'surplus' bulls (178/8.6 x 3.4). When the 'surplus' territorial bulls were included in the population total, the revised population estimate was 3312 [3300]; pups (1303), females of breeding age (1761), territorial bulls (= occupied territories; 178) and 'surplus' bulls (70).

These values are summarized in Table 8.1.

(ii) 1975/76

In 1975/76, an estimated 1628 pups were born on Taumaka. Based on the same assumptions as previously, at least an equal number of cows was present. The mean cow to occupied territory ratio was 7.0:1 for this season, which yielded a total of 232 (1628/7.0) occupied territories. Assuming that only one bull occupied each territory for the entire season, the resultant total for pups (1628), cows which bore pups (1628) and territorial bulls (= occupied territories; 232) was 3488 [3500] individuals.

Assuming that 74 percent of the cows were pregnant and each bore one pup, then there were 2200 (1628/0.74) cows present. The estimated total for pups (1628), females of breeding age (2200) and territorial bulls (= occupied territories; 232) was then 4060 individuals.

The mean maximum number of bulls for both study areas combined was 12.5 and the mean number of territorial bulls for the month of December was 9.5. Therefore, there were at least 3.0 'extra' bulls per 9.5 territorial bulls, or a total of 73 (232/9.5 x 3.0) 'surplus' bulls. Together with the previous estimate, this yielded an estimate for pups (1628), females of breeding age (2200), territorial bulls (= occupied territories; 232) and 'surplus' bulls (73) of 4133 [4130] individuals.

These values are summarized in Table 8.1.

TABLE 8.1. Population estimates for the breeding colony at Taumaka, Open Bay Islands.

	1974/75	1975/76	Approximate $\bar{x}$
A. Pups, cows which bore pups, and territorial bulls (= occupied territories)	2780	3500	3150
B. Pups, females of breeding age, and territorial bulls (= occupied territories)	3250	4060	3650
C. Pups, females of breeding age, territorial bulls (= occupied territories) and 'surplus' bulls	3300	4130	3700

(b) Estimates of population growth

Population growth was based on the female cohort of the population, and was estimated by means of a computerized growth model based on the Leslie Matrix (K.W. Duncan, Department of Zoology, University of Canterbury, Christchurch). Consequently, only data for females were used, and no limits were placed on the environment. The model was assigned 21 age classes (each age class = 1 year), was run for 50 iterations (i.e. '50 years') and required three major categories of data. They were: 1) the proportion surviving at the end of each age class, 2) the average number of births per individual for each age class, and 3) the initial number of individuals in each age class.

Estimated first year survival was .50 (see Chapter Seven, Pup Mortality, for the calculation of mortality rates), and the 'average' number of females born per season (730) was calculated from birth estimates made during the 1974/75 and 1975/76 breeding seasons. Northern fur seal data were used for the remainder of the survival rate estimates (Kenyon *et al.* 1954) and pregnancy rate estimates to age class 20 (North Pacific Fur Seal Commission 1962). Age class 21 was assigned a very low pregnancy rate, and it was assumed that there was no survival to age class 22. The number of individuals alive at the beginning of each age class, other than age class 1, was left at 0; the model calculated these data from the information supplied for age class 1, and from the survival and pregnancy rates provided. Because pregnancy rate estimates for the Northern fur seal differed between the eastern and western Pacific, both sets were used. These data were halved in order to compensate for the birth of males in the population. It was assumed that the sex ratio at birth was 1:1 (see Chapter Six, Pup Growth), and that there was no differential mortality between the sexes. Survival and pregnancy rates are summarized by age class in Table 8.2.

Population growth rates obtained when using first year survival values of .40 (western Pacific Northern fur seal data only), .50, .60, .70, .75 and .80 are given in Table 8.3.

8.3. Discussion

Population estimates of fur seals on Taumaka were based on total pup production (see Chapter Seven, Pup Mortality, for the calculation of these estimates). Although the estimates of pup production were more accurate than those made previously, there was a high degree of variability between the estimates for the two seasons studied; i.e. there were 20 percent more pups born in 1975/76 than in 1974/75. Nevertheless, the mean of the

TABLE 8.2. Survival and pregnancy rates per age class, based on the Northern fur seal. Rates in parentheses compensate for male births in the population; the population growth model was based on the female cohort only.

Age class	[1]Survival rates	[2]Pregnancy rates for the Northern fur seal, Eastern Pacific		[2]Pregnancy rates for the Northern fur seal, Western Pacific	
1	.50	.00		.00	
2	.72	.00		.00	
3	.92	.00		.00	
4	.94	.04	(.02)	.50	(.25)
5	.95	.45	(.225)	.80	(.40)
6	.95	.75	(.375)	.85	(.425)
7	.95	.85	(.425)	.90	(.45)
8	.95	.85	(.425)	.90	(.45)
9	.95	.90	(.45)	.90	(.45)
10	.95	.90	(.45)	.90	(.45)
11	.95	.90	(.45)	.90	(.45)
12	.88	.80	(.40)	.80	(.40)
13	.88	.80	(.40)	.80	(.40)
14	.88	.80	(.40)	.80	(.40)
15	.88	.80	(.40)	.80	(.40)
16	.88	.80	(.40)	.80	(.40)
17	.88	.60	(.30)	.60	(.30)
18	.88	.60	(.30)	.60	(.30)
19	.88	.30	(.15)	.30	(.15)
20	.88	.30	(.15)	.30	(.15)
21	-	.002	(.001)	.002	(.001)

[1] Values for age class 2-20 are taken from Kenyon *et al*. (1954: 40; Table 15).

[2] Values for age class 1-20 are taken from the North Pacific Fur Seal Commission (1962: 41; Table 23). The rate for age class 21 is an arbitrary value chosen to terminate the programme.

TABLE 8.3. Estimated population growth rates for the New Zealand fur seal on Taumaka, Open Bay Islands, based on theoretical first year survival rates and the first year survival rate calculated from this study, with the remaining survival rates and the pregnancy rates per age class based on the Northern fur seal (Kenyon *et al.* 1954; North Pacific Fur Seal Commission 1962; * = no value, i.e. value could not be determined by this model).

First year survival	Estimated population growth based on Northern fur seal data, Eastern Pacific	Estimated population growth based on Northern fur seal data, Western Pacific
.40	*	1.0077
.50	1.0176	1.0346
.60	1.0382	1.0580
.70	1.0564	1.0791
.75	1.0648	1.0888
.80	1.0728	1.0982

estimates for the number of pups, cows which bore pups and territorial bulls (= occupied territories) for the two seasons gives a good indication of the actual number on Taumaka during the breeding season.

The overall pregnancy rate of .74 given by Best (1973) for the Cape fur seal may be close to that of New Zealand fur seal females, but it is doubtful whether females of breeding age which did not pup or had lost their pup remained on the rookery for the entire season. New Zealand fur seals are very intolerant of each other and require at least one body length distance between them. Consequently, there is no obvious reason why females without pups should remain on the rookery once they had entered estrus and copulated. Rand (1959) suggested that Cape fur seal cows which had lost their pups tended to leave the rookery, and Miller (1975a) suggested the same for New Zealand fur seal cows. Therefore, the value calculated when applying the correction factor for pregnancy rate resulted in an estimate which included the number of females of breeding age which were probably on the rookery at some time during the breeding season, but were not necessarily on the rookery for the entire breeding season.

There probably were far more 'surplus' bulls present than were accounted for by the estimation technique used. Nevertheless, the population estimate which took into account the number of 'surplus' bulls as well as the 74 percent pregnancy rate correction factor gave the best indication of the number of pups and adults of breeding age which use the rookery during the breeding season, but are not necessarily on the rookery for the entire season.

These estimates are conservative, and possibly are too low. The greatest error is in the estimation of the number of bulls and of cows without pups. Consequently, they will require continual revision as more data become available on the population dynamics of the New Zealand fur seal. However, they do give a reasonable estimate of the population size of pups and fur seals of breeding age which use the rookery during the breeding season.

Bonner (1968) suggested that the total population of Kerguelen fur seals on South Georgia was equal to four times the number of pups born. Johnson (1972) suggested the same relationship for the Northern fur seal. If this relationship holds true for the New Zealand fur seal, then the total population associated with Taumaka should be in the vicinity of 5860 pups, juveniles and adults.

If about 1460 pups are born annually on Taumaka, and the sex ratio at birth is 1:1, then there is an annual production of 730 female pups. With a first year mortality of 50 percent, 365 female pups are alive at the end of their first year. Kenyon *et al.* (1954) estimated that second year mortality of Northern fur seal females was about 28 percent and third year mortality was about 8 percent. When applying these values to New Zealand fur seal females, 263 females are alive at the end of their second year, and 239 are alive at the end of their third year. These females begin to enter the breeding population at the end of their fourth year (see Chapter Three, Population Biology). Therefore, 867 [865] (365 + 263 + 239) additional females are associated with the population on Taumaka which were not taken into account when the population estimates for the breeding season were made.

Kenyon *et al.* (1954) calculated the natural mortality rate for Northern fur seal males. These data are given in Table 8.4. If 730 males are born annually on Taumaka, and first year mortality is 50 percent, then 365 male pups are alive at the end of their first year. By their tenth year, surviving males reach territorial bull status. When the mortality rates calculated by Kenyon *et al.* for male Northern fur seals are applied to male New Zealand fur seals for ages 2 through 9 years, this results in 1912 [1910] (365 + 253 + 232 + 218 + 208 + 197 + 187 + 143 + 109) additional males which are associated with the population at Taumaka, but were not taken into account when the population estimates were made (Table 8.4).

TABLE 8.4. Number of New Zealand fur seal males surviving to age class 9, based on: 1) an initial population size of 730, 2) the first year mortality rate calculated from this study, and 3) male Northern fur seal mortality rates for age class 2-9 (Kenyon *et al.* 1954: 38, Table 14).

Age class	Mortality rate	Number of surviving males
-	-	730
1	.50	365
2	.3075	253
3	.08	232
4	.06	218
5	.05	208
6	.05	197
7	.05	187
8	.2365	143
9	.2365	109

When these 'extra' males and females are added to the population estimate of 3700 fur seals (calculated from the estimates of pups, females of breeding age, territorial bulls and surplus bulls for the two seasons of the study; ((3312 + 4133)/2), the total population associated with Taumaka (i.e. fur seals either born on or breeding at the rookery) becomes 6475 individuals. If males are considered to reach territorial bull status at age 7 years (see Chapter Three, Population Biology), then the overall population estimate becomes 6035 fur seals. In the absence of sufficient data on the population dynamics of the New Zealand fur seal, it appears that the relationship suggested by Bonner (1968) for the Kerguelen fur seal, and by Johnson (1972) for the Northern fur seal gives a conservative but rough estimate of the total number of New Zealand fur seals associated with a given rookery.

Population estimates for the average number of fur seals on Taumaka can be divided into four categories. These categories and their respective values are: 1) pups, females which bore pups and territorial bulls (= occupied territories) = 3150; 2) pups, females of reproductive age and territorial bulls (= occupied territories) = 3650; 3) pups, females of reproductive age, territorial bulls (= occupied territories) and 'surplus' bulls = 3700; and 4) those fur seals associated with the rookery, i.e. were either born on or are breeding at Taumaka = 6200 ((6455 + 6025)/2) = 6240). Therefore, the breeding population on Taumaka, plus pups, is between 3000 and 4000 fur seals. The number of fur seals associated with Taumaka, either through birth or by breeding on the rookery, but which are not necessarily at or even near the rookery at any one time, is between 6000 and 6500.

First year mortality of New Zealand fur seals is about 50 percent (see Chapter Seven, Pup Mortality). Females may begin to enter estrus at age 4 years, and produce their first pup at age 5 years (see Chapter Three, Population Biology). This suggests that New Zealand fur seal pregnancy rates may be similar to those of the Northern fur seal in the eastern Pacific than in the western Pacific. If so, then the population on Taumaka has a growth rate of 1.0176, or an annual growth of about 2 percent.

If New Zealand fur seal first year survival is in fact greater than .50, then the theoretical population growth rate would increase accordingly (see Table 8.3). However, it is unlikely that this is so. At best, first year survival is no greater than .60, and about .50 is probably close to the actual value (see Chapter Seven, Pup Mortality).

Payne (1977) suggested that the Kerguelen fur seal population on South Georgia is growing at a rate of 16.8 percent per annum. He estimated that first year mortality is 23.9 percent; slightly less than half that estimated for the New Zealand fur seal. He also estimated an average adult mortality (i.e. mortality after age 1 year) of 7.9 percent for use in his model. Further, he found that females entered the breeding population at age 3 years, with a pregnancy rate of .55. New Zealand fur seals probably do not have their first pup until age 5 years.

If the data used for the New Zealand fur seal population growth estimates are accurate, then it is unlikely that the population will reach the growth rate suggested for the Kerguelen fur seal at South Georgia; at least not in the foreseeable future. The New Zealand fur seal population is probably increasing, but at a very slow rate, i.e. about 2 percent per annum. For the population growth rate to increase substantially, either mortality (particularly first year mortality) must decline, the pregnancy rate must increase, the age of first breeding in females must decline, or a combination of these factors must take place. There is no evidence that any of these conditions are occurring, though they may well be. The collection of these types of data will require a continual monitoring of the colony on Taumaka.

Gaskin (1972) is correct in suggesting that there has been a redistribution in the overall New Zealand fur seal population, but the numbers involved are probably few. For example, the number of New Zealand fur seals on Macquarie Island has increased from 174 counted during the summer of 1950 to 474 counted during the summer of 1963 (Csordas and Ingham 1965). No births were recorded at Macquarie Island previous to 1955, but some have been recorded since then (Csordas and Ingham *op. cit.*). This suggests that a resident breeding population may be establishing itself on the island.

CHAPTER NINE

GENERAL DISCUSSION AND SUMMARY

9.1. Introduction

The purpose of this thesis was to investigate aspects of the population structure of the New Zealand fur seal during the breeding season. Towards this end, data have been presented in the previous chapters on the objectives of the study, as given in Chapter One, General Introduction. The intent of the General Discussion is to discuss in greater detail topics which may have had an effect on the population structure of the New Zealand fur seal during the breeding season, and to speculate on their significance. The topics discussed are: 1) delayed maturation and reproductive success in males; 2) mate selection and female gregariousness; 3) site preference; 4) the significance of a long suckling phase; 5) factors affecting pup growth prior to weaning; 6) lack of pup defence by females; and 7) population growth.

Conclusions arising from this research are listed in the summary as individual statements. Each statement is followed by a chapter reference which directs the reader to the chapter or chapters where the original data are presented and discussed.

9.2. General discussion

Many of the implications of polygyny are discussed below, as they apply to the population structure of the New Zealand fur seal. For a discussion on the origin of polygyny in pinnipeds, see Bartholomew (1952, 1970), Bertram (1940), McLaren (1967), Nutting (1891), Peterson and Bartholomew (1967), Repenning (1976) and Stirling (1975b). For this discussion, polygyny is defined as the condition where more individual females contribute gametes to zygotes during the breeding season than individual males (Wiley 1974a: 202), and does not imply any pair bond formation (Lack 1968: 5; Vernor and Wilson 1966: 143).

(a) Delayed maturation and reproductive success in males

The delayed maturation of males relative to females is a common occurrence in polygynous species (see Estes 1974: 191; Geist 1971). The significance of delayed maturation to the evolution of polygyny was reviewed by Wiley (1974a) who termed the phenomenon 'sexual bimaturism'. Wiley (1974a: 216, 1974b: 708) suggested two conditions which could have lead to its development: 1) a high risk of mortality during reproduction, and 2) an increase in fecundity with age. Both of these conditions could be factors in the delayed social maturation of male polygynous pinnipeds. If this is the case, then experience can play an important role in minimizing their effect.

Bulls of polygynous pinnipeds generally do not reach their maximum size until the onset of reproductive maturity (Bryden 1972: 47; Scheffer and Wilke 1953: 131 ff), i.e. males are physiologically sexually mature long before they are able to enter the breeding population successfully. The attainment of sexual maturity involves an increase in testosterone levels during the breeding season, with its concomitant increase in aggression and sex drive. Reproductive success of New Zealand fur seal bulls (as well as bulls of other polygynous pinniped species) is directly linked to their ability to take and hold a territory. This usually requires some degree of intrasexual combat. During combat, the advantage goes to the larger bull, everything else being equal. Although there is no direct evidence of a bull killing his opponent, death arising from intrasexual combat in mammals is more prevalent than was once believed (Geist 1971: 130, 228 ff and references therein). New Zealand fur seal bulls often receive extensive wounds, which may include broken jaws, the loss of an eye, damaged flippers, etc. Such wounds could increase mortality by being sites of infection, by preventing or inhibiting feeding, or by generally rendering the bull more susceptible to predation while at sea. By not getting involved in territorial combat with large, experienced bulls, early survival of young bulls could be enhanced. During their delayed social maturity, young New Zealand fur seal bulls hold territories early and late in the season, and fight with other young, more evenly-matched, bulls. They are thus able to gain the experience necessary to compete successfully for territories during subsequent breeding seasons.

If the maximum reproductive potential of a bull is to be realized, then it is imperative that he be able to copulate successfully with every receptive female within his territory, regardless of his length of tenure. Inexperienced bulls do not have the reproductive expertise of experienced bulls; consequently one can expect a decrease in their reproductive (i.e. copulatory) efficiency. The number of seasons that a New Zealand fur seal bull remains territorial is probably few, i.e. not more than three to five, and perhaps fewer. For a bull to make the greatest contribution to the gene pool, his reproductive efficiency must be at a maximum. During the period between the attainment of sexual and reproductive (social) maturity, a bull is able to gain the reproductive experience necessary to help ensure his greatest chance of reproductive success once he becomes territorial. For New Zealand fur seal bulls, this experience can be gained on the rookery in two ways: 1) by moving onto the rookery before the arrival and after the departure of the large territorial bulls, in which case young bulls are in a position to copulate with cows which enter estrus either early or late in the season, and 2) by surreptiously copulating with cows on the margin of the rookery.

The experience gained between the time bulls become sexually mature and the time they become reproductive mature increases their fighting ability (see Miller 1975b) and reproductive finesse, which in turn maximizes their reproductive success.

The physiological stress on territorial fur seal bulls must be high, for they do not feed and rarely drink while they are fasting. The increased bulk (much of which is in the form of blubber) of reproductively mature males provides the energy reserves necessary to maximize their reproductive and aggressive vigour, which in turn enhances their reproductive success (Bartholomew 1970: 551 f).

Once bulls gain the size and experience necessary to become territorial, the number of seasons that they are able to do so ultimately depends on their fighting ability. In turn, this depends on the presence or absence of their canine teeth, particularly their lower canine teeth. New Zealand fur seal bulls are unable to punish their opponent sufficiently when fighting to ensure victory without at least one lower canine. Because of the ease by which canine teeth are broken off during intrasexual conflict, it is unlikely that these bulls are able to remain territorial for more than three to five seasons, and probably are territorial for fewer; Northern fur seal bulls are able to hold territories for an average of 1.5 breeding seasons (Peterson 1968: 39). Consequently, the number of years that a territorial bull is able to contribute to the gene pool is few when compared to the number of years females are able to produce pups. However, because bulls are able to copulate with numerous females per season, each individual territorial bull potentially has a greater impact on the gene pool than each individual female; but not all territorial bulls copulate. Miller (1975b: 181) found that slightly less than 50 percent of New Zealand fur seal bulls copulate, and Le Boeuf (1974: 165 f) found that less than one-third of the resident Northern elephant seal bulls copulate. The fecundity of those which do copulate is high. Bartholomew (1970: 551) stated that the fecundity of territorial Northern fur seal bulls is about 25 times that of cows. That New Zealand fur seal bulls are unable to remain territorial for more than three to five years is therefore a means by which genetic variability within the population is enhanced. By undergoing a delayed maturity, bulls are able to gain the social and reproductive experience necessary to maximize their individual reproductive success and their individual effect on the gene pool once they became territorial.

(b) Mate selection and female gregariousness

Mate selection is generally divided into two broad categories. The first is intrasexual selection, where members of one sex compete for the opportunity to mate with members of the other, and the second is epigamic or intersexual selection, where the members of one sex choose members of the other (see Ralls 1977: 919; also Darwin 1901: Chapter 8; Huxley 1938). Direct mate selection by females occurs in many bird and mammal species (Orians 1969: 590; Ralls 1977: 920), but does not occur in the polygynous pinnipeds (Peterson 1968: 38). However, Cox and Le Boeuf (1977) found that indirect mate selection by female Northern elephant seals does occur, through female incitation of competition between males. Females will protest an attempted copulation, which motivates adjacent bulls to interfere. Competition between bulls follows, with the most dominant bull usually being the one to copulate. Miller (1975b: 184) suggested that gregariousness in female New Zealand fur seals acts as an indirect mechanism for mate selection by inciting competition between bulls for areas which hold the greatest number of females. Only the most 'fit' bulls become territorial in these preferred areas, and consequently perform the majority of copulations. In addition, intrasexual competition between females for preferred sites ensures that the most 'fit' females are in a position to copulate with the most fit bulls. I agree with Miller's suggestion that this form of indirect mate selection does occur in the New Zealand fur seal. In all probability, it also occurs in other polygynous pinniped species as well. Stirling (1971c: 157 f) suggested that a similar condition occurs in the Weddell seal.

New Zealand fur seal bulls become aware of the sites preferred by females in one of two ways. Either they arrive after the females and can see where the majority are located, or else they know of these areas from previous seasons on the rookery, perhaps during their delayed maturation. In all probability, both situations occur, although the former probably occurs less often; most bulls are on the rookery before the arrival of most females. The latter assumes that site fidelity occurs in bulls, but this apparently is the case (see Miller 1975b: 184 and references therein; Peterson 1968: 31 f). It seems, then, that experience plays an important role in the reproductive success of New Zealand fur seal bulls through their ability to determine or recognize sites preferred by females.

Bartholomew (1970: 555) suggested that selection favours gregariousness in females because it assures the reproductive success of their male progeny; the females would be mated by genetically fit, i.e. territorial, bulls through the exclusion of less successful, or non-territorial bulls. This 'marginal male effect' assumes that bulls which are unable to hold a territory are genetically inferior to those which are able to hold territories. As pointed out by Miller (1971: 226) and Stirling (1975b: 206), non-territorial bulls are not necessarily genetically inferior to territorial bulls, but rather they may be too young (or too inexperienced) to do so. However, even with time, some of the bulls on the margin of the rookery may never reach the size and aggressiveness necessary to obtain territorial bull status. Therefore, what female gregariousness does accomplish is to maximize the probability that the majority of cows will be impregnated by proven genetically fit or 'superior' bulls.

(c) Site preference

Orr (1965: 163) suggested that pinnipeds use inaccessible beaches because of a history of pressure from terrestrial predators, including man. With the exception of predation on Ringed seals by polar bears (*Ursus maritimus*) and, to a lesser degree, arctic foxes (*Alopex lagopus*; Smith and Stirling 1975; Stirling and McEwan 1975), predation on pinnipeds by terrestrial predators is slight (see King 1964; Scheffer 1958). New Zealand fur seals have no terrestrial predators, and there are known extinct terrestrial predators within the New Zealand region (R.E. Fordyce, *pers. comm.* 1978). Likewise, there is no evidence that hunting pressure from man has caused major relocations of fur seal rookeries, though hunting pressure from man may have reinforced the timidness found in New Zealand fur seals. This suggestion is discussed in more detail later in the chapter.

Ling (1969) stated that there is little spatial or temporal overlap in terrain requirements in different species of pinnipeds using the same island, and pointed out that this was necessary for optimal use of the environment. There is no overlap in breeding areas of the New Zealand fur seal and other pinniped species within the New Zealand region. Interspecific competition for breeding localities therefore has no bearing on New Zealand fur seal rookery location; virtually all accessible terrain types are open for colonization, with perhaps the exception of some sand

and shingle beaches at the Auckland Islands and Macquarie Island where New Zealand sea lions and Southern elephant seals, respectively, breed. Rather, the location of fur seal rookeries in general, and New Zealand fur seal rookeries in particular, is based on the fur seal's thermoregulatory requirements while on land. Fur seals dissipate excess body heat by various behavioural means which often require the use of thermoregulatory aids such as pools of water or shade (see Gentry 1973; Vaz-Ferreira and Palerm 1961). Without these thermoregulatory aids, the length of time they are able to remain ashore is considerably shortened. This could result in a bull's inability to remain territorial (Stirling 1971a: 257), and also affect his reproductive success. In Australia, of the New Zealand fur seal bulls seen to copulate, those holding territories which contained water averaged 3.6 copulations per male, while those without water averaged 1.7 copulations per male (Gentry 1973: 82).

Other pinniped species also dissipate excess body heat by a variety of behavioural means, including lying on damp sand, flipping sand over their bodies, and by positioning their territories near the sea's edge (Laws 1956a: 20; Peterson 1968: 12; Peterson and Bartholomew 1967: 65; Vaz-Ferreira 1975a: 224, 1975b: 260; Vaz-Ferreira and Sierra de Soriano 1963: 8). Because of the dense underfur of the fur seal, sand flipping and digging into the sand are ineffective means of alleviating heat stress. Therefore, rookery locations and, secondarily, preferred sites on the rookery are those which best fulfil the fur seal's thermoregulatory requirements, i.e. those which provide shade, water, or both. The Northern fur seal is an exception to this generalization. However, temperatures rarely exceed the comfort range at their breeding colonies in the North Pacific. When this does occur, Northern fur seals thermoregulate by flipper waving and, when the solar insolation or air temperatures get too high, by retreating to the sea.

If the requirements for shade and water are fulfilled, then site choice depends on the ease of access to and from the sea. Females will routinely go to sea to feed or to counter heat stress. Because bulls will try and prevent females which enter their territory from escaping, the fewer territories females have to cross, the less harassment they receive. The amount of harassment females do receive may have an effect on pup growth and survival. Bryden (1968b) suggested that this was the case with the Southern elephant seal at Macquarie Island, where pups have a higher mortality and slower growth than Southern elephant seal pups on the less disturbed rookeries at the Falkland Islands Dependencies. This is entirely speculative for the New Zealand fur seal, and must await further research into thermoregulation and its associated behaviour. It is apparent that females must congregate in order to take advantage of the limited number of sites which provide at least the shade they require while on land. Consequently, the thermoregulatory requirements of *Arctocephalus* females may act as a positive reinforcement for gregariousness, as well as a density-dependent regulator of the population size.

(d) Length of suckling phase

The length of time from birth until nutritional independence in otariids is long when compared with that in phocids. With the exception of the odobenids, the most protracted obligate birth to weaning phase is in the Arctocephalinae. In the New Zealand fur seal, weaning takes place between 8 and 10 months of age. The extended suckling phase present in the Arctocephalinae is due in part to the relatively mild climate found throughout their range. With few exceptions, there are no severe seasonal changes which would make rapid weaning advantageous. The shortest suckling phase in the fur seals is that found in the Northern fur seal, where pups are weaned in about 3 months (Scheffer and Wilke 1953: 131). This is necessitated by the oncoming winter season. During the fall, females and immature males migrate to the relatively warmer waters further south. Bulls are able to remain in the north because of their large size (relative to females) and thick subcutaneous layer of blubber. The Kerguelen fur seal is weaned in about 4 months (Payne 1977: 68), but again this is at least partially necessitated by the onset of winter. Like the Northern fur seal, these fur seals spend the majority of the year at sea.

Extended nutritional dependence in young usually implies some degree of parental care, but this is certainly not the case in the New Zealand fur seal. Although there has been some controversy over the possibility of paternal care by California sea lions at the Galapagos Islands (Barlow 1972, 1974; Miller 1974c), it is generally accepted that polygynous pinniped species show no paternal care whatsoever. Female New Zealand fur seals will defend their pups for the first few days following birth, but after that pups are abandoned at the first sign of danger. The significance of this to the overall reproductive strategy of New Zealand fur seals is dealt with later in the discussion.

Even without increased parental care, the extended suckling phase of fur seals has survival value. The long suckling phase enables pups to become skilled swimmers and to learn how to capture prey before leaving the rookery. By being able to rely on their mothers for nutrition while gaining swimming and hunting skills, they are not immediately thrust in a 'swim and hunt or perish' situation as commonly occurs in the phocids.

There is no direct evidence that New Zealand fur seal pups capture prey while still suckling, as has been suggested for the Cape fur seal (Best and Shaughnessy 1975: 6), but this probably is the case. Even if pups are rarely able to catch small fish, they nevertheless gain hunting and swimming skills, simply by chasing them about. Therefore, the general aquatic skills acquired by pups while still suckling improve their chances for survival once they are fully independent and have left the rookery.

Another factor which favours a long suckling phase is the decreased physiological stress placed on nursing females. Fur seal females are small, and do not have the energy reserves necessary to fast for extended periods of time. This is particularly true if the females were nursing pups during the fast. Because the suckling phase in fur seals generally is not restricted by climatic factors, and assuming that there is an abundant food supply near the rookery year-round, then there is no apparent evolutionary pressure towards a short suckling phase and rapid pup growth. Consequently, this did not act as a selective force for large body size in females, which would have been required to provide the necessary energy to maintain their own metabolism, yet provide sufficient nutrition to support rapid growth in their pups. Females are therefore able to remain healthy and fit throughout the year, rather than having a period of reduced fitness immediately after fasting and suckling their young.

(e) Pup growth prior to weaning

Growth implies a quantitative increase in size, the rate of which can be highly variable. The growth and growth rate of immature animals are controlled by one or more of several factors, including hormonal control, and behavioural and environmental factors, but the most important factor determining growth rate is nutrition (Blaxter 1968: 329). Poor prenatal nutrition can result in offspring which are underweight at birth, deformed or stillborn (see Everitt 1968: 133 and references therein). Nevertheless if females are sufficiently well nourished during their pregnancy to produce normal, viable offspring, then they are sufficiently well nourished to provide enough milk for growth. This has been shown by Mirone *et al.* (1948) for laboratory mice. However, the rate of growth of suckling offspring can be affected by the quality and quantity of its mother's nutrition. Human babies born in England during

World War II were heavier and longer during their first year than were babies born prior to the war. Mirone *et al.* (1948: 139) attributed this to the improved overall nutrition in England during the war years. Consequently, the abundance of food of proper nutritional value available to females will be reflected in the birth weights and growth rates of their pups.

Low availability of prey species near the rookery could affect the nutrition of pups through their mothers in two ways. Firstly, a decrease in prey availability could result in a decrease in the amount eaten by the female per unit effort. The calories produced would be needed for milk production as well as the maintenance of the female. If the caloric intake were sufficiently low, then one could expect a decrease in the overall condition of the female, which could result in a decrease in milk production. Secondly, if a female had to travel farther afield or stay out longer to feed, then the time between nursings would be increased. This in turn would result in fewer feeds for pups, which in turn could result in a slower growth rate. Consequently, variations in the abundance of food species available to lactating mammals can be reflected in the growth rates of their offspring. This has been suggested for the Northern fur seal (Chapman 1961: 361), and I suggest that it was one of the factors which contributed to the difference in growth rates of suckling New Zealand fur seal pups recorded during the two seasons of this study. This is not to suggest that there was a 'shortage' of squid available to the fur seals during the 1974/75 season, but only that the hydrographic conditions were more favourable for squid during the following season. This resulted in an increase in the availability of squid within range of the rookery. Considering the present size of the fur seal population in the New Zealand region compared to what it must have been prior to commercial exploitation, it is unlikely that food availability is a factor limiting its growth, commercial fisheries not withstanding.

All muscular activity produces heat, including the process of eating. As environmental temperatures increase, metabolic heat production increases with high levels of feeding. If feeding levels remain high at environmental temperatures above the zone of thermoneutrality (the "...range of temperature within which the environment has no effect on heat production." Fuller 1969: 85 f), a thermoregulatory burden is placed on the body to dissipate the excess metabolic heat by behavioural or physiological means, or both. Consequently, the ability to withstand high environmental temperatures is lowered by high levels of feeding (Fuller 1969: 87 f).

In addition, warm air temperatures may affect milk production in lactating females. This has been shown in dairy cows, where an increase in air temperature from 16°C to 35°C reduced daily milk production from 12.2 kg to 7.7 kg, with a reduction in casein content from 2.1 to 1.8 percent and a reduction in non-fat solids from 8.1 to 7.6 percent (Brody 1964: 295). Bryden (1968b: 746) found that female Southern elephant seals at Macquarie Island produced less milk than those at the Falkland Islands Dependencies, but suggested that this was due to the greater intraspecific disturbance at Macquarie Island rookeries. This could be the case, but availability of food could also have been a factor, perhaps in conjunction with the disturbance. Bryden (*op. cit.*: 745) further suggested that the difference in birth weights of Southern elephant seal pups between seasons at Macquarie Island was a consequence of food available to pregnant females.

Therefore, the combined effect of high air temperatures and low squid abundance during the 1974/75 season (relative to the 1975/76 season) was sufficient to have caused the difference in the observed growth rates by one or more of the following four means: 1) a decrease in the quantity of milk produced by lactating females; 2) a decrease in the quality of milk produced by lactating females; 3) a lengthened nursing cycle; or 4) a decrease in feeding by pups because of the high environmental temperatures. It must be re-emphasized that this is relative to the 1975/76 season, and that the growth rates observed during this study are well within the range one might expect in a natural population.

(f) Lack of pup defence by females

The seemingly total disregard shown by female otariids towards the defence of their pups is perplexing. Female New Zealand fur seals will unhesitatingly abandon their pups and flee for the sea at the first sign of danger. However, otariids are not unique among higher vertebrates in this respect. A similar situation occurs in the California condor (*Gymnogyps californianus*), where adults will abandon their nest at the slightest disturbance. Mertz (1971) suggested that the survival of the adult condor is more important to the survival of the species than survival of the young, because of the condor's low reproductive rate and long lifespan. A bird which abandons the nest survives to nest again, whereas a bird which remains at the nest may be killed. Consequently, the former bird's contribution to the population will be greater than the latter's. A similar survival mechanism may have evolved in the early otariids.

New Zealand fur seals have no terrestrial predators, and there is no paleontological evidence of there ever having been large terrestrial predators in the New Zealand region. However, pup abandonment and retreat to the sea by females could have appeared early in otariid evolution as an escape response to terrestrial predation. The phylogeny of pinnipeds is poorly understood, but the known fossil record indicates that they originated in the North Pacific Basin and that the otariids first appeared during the Miocene (see Mitchell 1975; Repenning 1975; Repenning and Tedford 1977). This was a time when large terrestrial predators were present (see Romer 1966). By abandoning their pups and retreating to the sea, female survival was assured. This is assuming that females would be safe from pursuit once in the water. Females would then be able to produce another pup the following year.

Judging from the Northern fur seal, female New Zealand fur seals have a relatively low reproductive rate and long lifespan. The average number of pups produced per individual Northern fur seal female is 5.4 in a lifetime (Peterson 1968: 39). Further, pinnipeds as a group are adapted for a life at sea. Their mobility on land is poor in comparison with terrestrial mammals, as is their sense of smell (King 1964: 124). However, their senses of sight and hearing while on land are generally good (Jamiesen and Fisher 1972: 259; Repenning 1972: 316). The latter two characteristics are important in intrasexual behaviour during the breeding season, but they also could be advantageous in detecting terrestrial predators, particularly on rookeries where offshore breezes make olfactory detection difficult. The usual reaction of prey species when confronted by a predator is flight. The same reaction no doubt holds true for pinnipeds, but this is difficult on land. When preyed upon, if females were to try and take their pups with them, or try and hide their pups, their chances of escape without a confrontation with the predator would be slight. The females probably would be killed by the terrestrial predators because of their poor mobility while on land and lack of effective defensive weapons. By abandoning their pups, female fur seals, like the condor, would live to reproduce again, which would result in the greatest individual contribution to the population. The 'flight reaction' found in the New Zealand fur seal probably was reinforced during modern times by the hunting of fur seals by the early Maoris and later by the commercial sealers, though it is unlikely that such predation had any effect on rookery location.

This suggestion for the origin of pup abandonment in the face of real or potential danger is entirely speculative. However, were terrestrial predation a factor in ancestral adult mortality, then it would provide a mechanism to ensure the greatest individual contribution to the gene pool by females and, ultimately, to the growth of the population.

(g) Population growth

Mertz (1971) has shown that species with a low reproductive rate and long lifespan can not withstand increased adult mortality and retain stable population numbers. He used the California condor as an example, and suggested that susccesful condor populations are those with an adult survival of at least .85. While the reproductive rate of fur seals is not as low as that of the condor, nor are fur seals as long-lived, the basic assumption is still valid; increased adult mortality will inhibit any increase in the potential growth rate of the population, as long as all other biological and environmental considerations remain the same. The same conclusion was drawn for marine mammals in general by Eberhardt and Siniff (1977: 186). A low reproductive rate in conjunction with natural mortality was sufficient to maintain the original New Zealand fur seal population size within the limits set by the environment because of the large number of fur seals involved. Even with density-dependent environmental factors removed, the drastically reduced adult population now present is not capable of producing enough progeny to reflect a major increase in the growth rate of the population as a whole (see also Cole 1954). In the case of the New Zealand fur seal, about 50 percent of the pups born are female. The available data indicate that females do not produce their first pup until they are at least 5 years. If female longevity and individual pup production are similar to those of the Northern fur seal, then they may live as long as 30 years and have an average of 5.4 pups in a lifetime (Baker *et al.* 1970: 11; Peterson 1968: 39). For this discussion, it will be assumed that this is the case. A lowering of the age at first breeding can increase the rate of population growth considerably in species with a high reproductive rate (Cole 1954: 123; Lewontin 1965: 85). Although the reproductive rate of fur seals is not as high as that for many other vertebrate species, one might expect an increase in the intrinsic rate of population increase concurrent with a decrease in the age of first breeding in females; again, provided that there were no limits on the environment. Eberhardt and Siniff (1977: 186) suggested that the age at first breeding may not be very important in the regulation of population size in marine mammals.

Rather, they suggested that population size increase is more dependent on increased survival of immature individuals and a high adult survival. While Eberhardt and Siniff may be correct, because of the relatively low reproductive rate of marine mammals, there nevertheless is little doubt that a lowering of the age at first breeding in females in conjunction with an increase in first year survival would lead towards a rapid increase in population size, as has occurred with the Kerguelen fur seal on South Georgia (Payne 1977).

Because the total number of New Zealand fur seals is very low compared to what it was prior to commercial exploitation, it is unlikely that density-dependent factors which might otherwise have regulated population size are having any effect on population growth (see Lack 1954). Therefore, two speculative conclusions can be drawn from the above. The first is that the intrinsic rate of population increase will continue to be low until such a time that there is a decrease in the age of first breeding in females, or perhaps more importantly, an increase in first year survival, or both; and the second is that based on these population growth estimates, and what is now known about its general biology, the New Zealand fur seal is not capable of withstanding any commercial or large scale exploitation, either now or in the foreseeable future. With this in mind, it can be concluded that the population is increasing, and is in no imminent danger of wide scale or regional extinction.

9.3. Summary

(1) Territorial bulls are already present on the rookery by the end of October, but do not reach their maximum numbers until the third week of November. Bulls begin to leave their territories temporarily during the last week of December, and begin to abandon their territories during the second week of January. No territorial bulls are on the rookery after the end of January. Few bulls are at Taumaka outside the breeding season (Chapter 3).

(2) Growth rings which may be used for aging purposes are present in the canine teeth of New Zealand fur seals (Chapter 2).

(3) Bulls probably are sexually mature by age 7 years, but probably are not reproductively mature (i.e. are not able to hold territories and enter the breeding population) until about age 10 years (Chapter 3).

(4) Experience probably plays an important role in a bull's territorial and reproductive success. Young bulls gain this experience, in part, by being on the rookery before the arrival and after the departure of the older, more experienced territorial bulls. By being on the rookery at these times, young, inexperienced bulls are able to copulate with females which enter estrus outside the regular breeding season. The importance of this is twofold. Firstly, it enables young bulls to gain valuable social and reproductive experience, and secondly, it increases the reproductive success of the population as a whole by ensuring that bulls are present to impregnate females which enter estrus either early or late in the season (Chapter 3 and 9).

(5) The territorial success of bulls is based on their fighting ability. This in turn is contingent on the presence or absence of their lower canine teeth. Without at least one lower canine, bulls are unable to inflict enough damage on their opponents to ensure victory. Because of the ease with which canine teeth are broken off during intrasexual combat, it is unlikely that bulls are able to remain territorial for more than three to five seasons, and are probably territorial for fewer (Chapter 3 and 9).

(6) The oldest bull aged during this study was 15 years old. The oldest female aged during this study was 12+ years old (Chapter 3).

(7) Few females are ashore prior to the third week of November, after which their numbers rapidly increase. The maximum number ashore at any one time is reached at about the end of December or early January. By the end of January, few females are ashore at any one time (Chapter 3 and 5).

(8) It is hypothesized that females first begin to enter estrus at age 4 years, and produce their first pup at age 5 years. The overall reproductive rate per age group is unknown (Chapter 3).

(9) Live pups are first seen on the rookery during the third week of November, but the maximum number of live pups observed at any one time does not occur until the third or fourth week of December. The theoretical mean pupping date on Taumaka is 10 December (Chapter 3, 5 and 6).

(10) Pups wander freely about the rookery, but rarely travel more than 10 m from the spot where they were last with their mothers (Chapter 3).

(11) Because of the uncertain tenure of territorial bulls, the term 'occupied territory' is more appropriate when referring to adult sex ratios than the term 'bull'. Otherwise, it must be made perfectly clear what the term 'territorial bull' is meant to designate. At Taumaka, the ratio of females which produced pups to occupied territories is about 7.1:1; the ratio of females of reproductive age to occupied territories probably is about 9.5:1 (Chapter 3).

(12) All age classes of New Zealand fur seal make use of shade and water as thermoregulatory aids to help dissipate excess body heat. This is of extreme importance in site preference on the rookery (Chapter 4, 5 and 9).

(13) Females prefer sites on the rookery which provide the shade and water necessary for cooling. If these requirements are fulfilled, then preferred sites are those with the most direct access to the sea (Chapter 4, 5 and 9).

(14) It is unlikely that females pup in specific sites solely because other females had done so. Rather, females prefer to pup near some irregularity in the terrain (Chapter 5).

(15) Because of the difficulty in taking linear measurements on live pups, weight is the best measure of growth. Males are heavier than females from birth until about age 300 days, which is the approximate age of weaning. No data are available on growth beyond age 300 days, but it is likely that males continue to be heavier and larger than females of the same age (Chapter 6).

(16) In general, males are significantly longer, greater in girth and have a longer foreflipper than females from age 55 days until about 300 days (Chapter 6).

(17) The growth rate of suckling pups can differ from year to year. This may be caused by one or both of the following two factors: 1) variations in the quantity or quality of milk available to the pups, and 2) differences in environmental temperatures between years. The more food available to females, the more food potentially available to pups, either through a shortened time span between the periods a female is ashore, or through a greater quantity or quality of milk. High environmental temperatures may cause pups to suckle less frequently (Chapter 6 and 9).

(18) Approximate minimum survival weights for pups prior to weaning are: 55 days, 3 kg for males and females; 140 days, 4 kg for males and females; 235 days, 5 kg for males, 4 kg for females; 290 days, 7 kg for males and females. Pups probably need to weigh a minimum of 8 to 9 kg in order to survive the transition from weaning to nutritional independence (Chapter 6).

(19) The mortality rate of suckling pups is greatest prior to age 50 days, with an actual mortality of about 20 percent. Mortality to age 290 days is about 40 percent. First year mortality is about 50 percent (Chapter 7).

(20) The greatest single cause of pup mortality probably is starvation, which may account for 70 percent of all deaths to age 50 days. Other natural causes of pup mortality include stillbirths, suffocation in the amnion, drowning, trampling, predation and general misadventure (Chapter 7).

(21) Human presence can cause pup deaths, either through the disturbance and panic it can cause on the rookery, or through the handling and tagging of pups. Monel metal cattle ear tags may increase pup mortality, probably through infection at the tagging site. Because of the shape of the monel metal cattle ear tags, and because of the rough treatment tag sites receive due to the rocky terrain of the rookery, tagging wounds often do not heal properly. Freeze branding has great potential as a means of permanently marking pups, but until the technique is perfected, digit clipping is the safest procedure (Chapter 2 and 7).

(22) About 3150 pups, cows which bore pups, and territorial bulls (= occupied territories) are present on Taumaka during the breeding season. If all cows of breeding age are included, then the estimated total population becomes about 3650 individuals. If surplus bulls are added to this estimate, then the total number of pups and reproductively mature adults which use the rookery at some time during the breeding season is about 3700 individuals (Chapter 8).

(23) Based on known and speculative data, the New Zealand fur seal population within the New Zealand region has an intrinsic growth rate of about 2 percent per annum. For the growth rate to increase substantially, one or more of the following three conditions must occur: the age of first breeding in females must decrease, immature and in particular, first year survival must increase, or the overall pregnancy rate must increase (Chapter 8 and 9).

(24) A number of topics for future research on the New Zealand fur seal are apparent. They are:

a) A study into the cause of death in pups. Dead pups could be collected from the rookery and detailed autopsies and pathological studies performed. It probably would be possible to obtain a permit to collect live pups in order to collect baseline data, such as a tissue reference collection.

b) Thermoregulation. A study of behavioural and physiological thermoregulation would make a valuable contribution, not only to our knowledge of the New Zealand fur seal, but to fur seals in general.

c) Mother and pup behaviour. Studies have been made on mother/pup behaviour from birth until a few weeks after birth, but our knowledge of mother/pup interactions, feeding cycles, suckling periods and general behaviour up until weaning is slight.

d) Tagging. A tagging or marking programme should be developed, so that known-aged animals may be present on the rookery during future studies. Various types of tags should be tested, though freeze-branding probably has the greatest potential as a permanent, safe and reliable marking technique.

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APPENDIX A

NOMENCLATURE OF PINNIPEDS

The nomenclature used throughout the text is as follows[1]:

Carnivora	
Odobenidae	
Odobenus rosmarus	Walrus
Otariidae	
Otariinae	
Phocarctos hookeri	New Zealand sea lion
Otaria flavescens	South American sea lion
Zalophus californianus	California sea lion
Neophoca cinerea	Australian sea lion
Eumetopias jubatus	Steller sea lion
Arctocephalinae	
Callorhinus ursinus	Northern fur seal
Arctocephalus pusillus	Cape fur seal
A. p. doriferus	Tasmanian fur seal
A. gazella	Kerguelen fur seal
A. forsteri	New Zealand fur seal
A. tropicalis	Amsterdam Island fur seal
A. australis	South American fur seal
A. galapagoensis	Galapagos fur seal
A. philippi	Juan Fernandez fur seal
A. townsendi	Guadalupe fur seal

APPENDIX A continued

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[1] Based on:

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APPENDIX A continued

Phocidae	
Phocinae	
Phoca vitulina	Harbour seal
P. largha	Larga seal
P. hispida	Ringed seal
P. sibirica	Baikal seal
P. caspica	Caspian seal
P. groenlandica	Harp seal
P. fasciata	Ribbon seal
Halichoerus grypus	Grey seal
Erignathus barbatus	Bearded seal
Cystophorinae	
Cystophora cristata	Hooded seal
Mirounga leonina	Southern elephant seal
M. angustirostris	Northern elephant seal
Monachinae	
Monachus monachus	Mediterranean monk seal
M. schauinslandi	Hawaiian monk seal
Lobodon carcinophagus	Crabeater seal
Ommatophoca rossii	Ross seal
Hydrurga leptonyx	Leopard seal
Leptonychotes weddelli	Weddell seal

APPENDIX B

COLLECTION DATA

Data for specimens collected at Taumaka, Open Bay Islands (Z001-Z016, DT01, 1, 2, 4) and for specimens held at the National Museum, Wellington (DM733, DM1443-DM1448). Weights are given in kilograms and linear measurements are given in millimetres unless otherwise stated.

	Specimen number				
	Z001	Z002	Z003	Z004	Z005
Sex	male	male	male	male	male
Date collected	27.X.74	28.X.74	30.X.74	3.XI.74	5.XI.74
Collection site	Taumaka	Taumaka	Taumaka	Taumaka	Taumaka
Age (in years)	10	11	14	9	10
Weight	62.3	49.5	125.0	77.7	83.6
Standard length	1420	1403	1540	1545	1610
Curvilinear length	1530	1471	1615	1610	1675
Anterior length of left foreflipper	390	453	409	465	475
Anterior length of left hindflipper	328	332	283	340	345
Blubber thickness	35	36	44	20	25
Axillary girth	1000	1062	1425	1120	1120

	Specimen number				
	Z006	Z007	Z008	Z009	Z010
Sex	male	male	female	male	female
Date collected	7.XI.74	10.XI.74	12.XI.74	7.I.75	28.I.75
Collection site	Taumaka	Taumaka	Taumaka	Taumaka	Taumaka
Age (in years)	7	12	5	10	7
Weight	70.9	150.9	30.6	114.8	36.0
Standard length	1520	1730	1180	1625	1125
Curvilinear length	1590	1785	1225	1810	1230
Anterior length of left foreflipper	425	445	340	440	335
Anterior length of left hindflipper	305	310	245	325	240
Blubber thickness	23	55	20	40	15
Axillary girth	1100	1355	765	1215	790

APPENDIX B continued

APPENDIX B continued

	Specimen number				
	Z011	Z012	Z013	Z014	Z015
Sex	female	female	female	male	female
Date collected	30.I.75	31.I.75	6.VIII.75	29.X.75	31.X.75
Collection site	Taumaka	Taumaka	Taumaka	Taumaka	Taumaka
Age (in years)	4	8	12+	9	4
Weight	30.6	32.0	49.2	95.9	31.0
Standard length	1220	1185	1270	1670	1150
Curvilinear length	1325	1255	1335	1750	1220
Anterior length of left foreflipper	360	310	375	480	380
Anterior length of left hindflipper	270	225	285	355	225
Blubber thickness	10	15	35	25	20
Axillary girth	680	765	880	1125	840

	Specimen number				
	Z016	DT01	1	2	4
Sex	male	male	male	male	male
Date collected	10.XI.75	8.II.76	2.II.77	31.I.77	12.XII.76
Collection site	Taumaka	Taumaka	Taumaka	Taumaka	Taumaka
Age (in years)	10	10+	10	15	14+
Weight	154.1				
Standard length	1750				
Curvilinear length	1930	These four specimens were found dead, of unknown causes, and were badly decomposed.			
Anterior length of left foreflipper	420				
Anterior length of left hindflipper	350				
Blubber thickness	40				
Axillary girth	1430				

APPENDIX B continued

APPENDIX B continued

	Specimen number				
	DM733	DM1443	DM1444	DM1445	DM1446
Sex	male	male	male	male	male
Date collected	15.XII.47	8.I.62	8.I.62	8.I.62	8.I.62
Collection site	Breaksea Sound	Cape Saunders	Cape Saunders	Cape Saunders	Cape Saunders
Age (in years)	8	13+	7	7	12
Length (in inches)	53	66	54	59	67

	Specimen number	
	DM1447	DM1448
Sex	male	male
Date collected	14.XII.61	14.XII.61
Collection site	Cape Saunders	Cape Saunders
Age (in years)	4	8
Length (in inches)	51	55