DEMOGRAPHY OF AUSTRALIAN FUR SEALS

(Arctocephalus pusillus doriferus)

BY

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**ABSTRACT**

The Australian fur seal *Arctocephalus pusillus doriferus* population has displayed a relatively slow rate of recovery since being hunted by commercial sealers during the early 19th century. Despite this, population abundance doubled in the past 2 – 3 decades, indicating that the population growth rate has recently increased. Yet, the factors influencing the population’s dynamics are poorly understood, primarily because basic demographic rates are unknown.

Female age, survival, fecundity, breeding and physiology were studied at Kanowna Island, Bass Strait, Australia, between 2003 – 2006 by conducting censuses and captures (n = 294). Mark-recapture estimates of pup production were used to validate direct pup counts, allowing a 9-year dataset to be used for calculation of the population growth rate (2.2% p.a.) and investigation of environmental influences on reproductive success. Annual pup production (x = 3108) was synchronous, with 90% of births occurring within 28 days of the median birth date of 23 November. Births occurred earlier in years when pup production and female body condition were high and these factors were correlated with local oceanographic indicators, suggesting that reproductive success is constrained by environmentally-mediated nutritional stress.

Pregnancy was assessed by blood plasma progesterone radioimmunoassay and the pupping status of the same females was observed during breeding season. Despite high mid-gestation pregnancy rates (x = 84%), the birth rate was lower than in other fur seals (x = 53%), suggesting that late-term abortion is common. Lactating females were less likely to pup, indicating that nutrition may be insufficient to support concurrent lactation and gestation.
Age and morphometric data were used to construct body growth, age structure and survivorship models. Adult female survival rates were similar to those of other fur seals ($x = 88.5\%$). A life table was constructed and its age-specific survival and fecundity rates used in a Leslie-matrix model to project the population growth rate (2.2% $p.a.$) and determine the relative influence of each parameter. The abundance of female non-pups was 6 times greater than that of female pups, which is approximately 50% higher than previous conversion factors used to extrapolate population abundance from pup censuses in Australian fur seals. However, if the non-pup sex ratios of other otariids are considered, the pup:population conversion factor is 4.5.

Compared to a study performed before the recent population increase, the modern population displays similar body growth and fecundity rates but higher survival rates. This suggests that recent population growth resulted from a relaxation of hunting and/or predation mortality rather than from increased food availability. The low population growth rate is attributed to a low birth rate associated with nutritional stress, yet despite this, body growth occurs rapidly. Such characteristics are typical of sea lions rather than fur seals, perhaps because Australian fur seals employ the typical sea lion strategy of using benthic foraging to exploit a continental shelf habitat. The effect of ecological niche on population dynamics in the Otariidae is discussed.
DECLARATION

This is to certify that

i. the thesis comprises only my original work towards the PhD except where indicated in the Preface,

ii. due acknowledgement has been made in the text to all other material used,

iii. the thesis is less than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices.

........................................

John Robert Gibbens
June 2009
This thesis comprises original work undertaken for my PhD qualification. It was conducted solely by myself except as detailed below. The core chapters have been submitted for publication in peer-reviewed journals but have not been submitted for any other qualification.

The majority of field work required for Chapter 2 was conducted by myself (85%) but is supplemented with the work of others. I performed 6 of 9 post-breeding direct pup counts with my supervisor performing the other 3. I also performed daily pup counts during 4 of 5 breeding seasons, with the other one performed by fellow PhD candidates Claire Wallis and Andrew Hoskins. Female body condition was assessed by myself in 3 of 5 years with John Arnould and Andrew Hoskins allowing data from their own studies to be used for the other 2. All other field work, data analysis and writing was performed by myself.

Dr John P.Y. Arnould is a co-author of the submitted chapters as he provided field assistance, resources, mentoring and editorial advice in his role as supervisor. The article based on Chapter 3 was also co-authored with Dr. Laura J. Parry who provided instruction in the plasma progesterone assay procedure, assistance in the interpretation of its results, and use of a laboratory.

All photographs were taken by myself during my field work.
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CHAPTER 1

INTRODUCTION

1.1 Population ecology

Population ecologists are concerned with questions about how and why populations change in abundance through time (population dynamics). Essentially, the proximate mechanisms of population dynamics are the demographic parameters of survival and fecundity rates (Sinclair et al. 2006). To determine what influences these rates, one must study an organism’s physiology (e.g. reproductive capability) and interactions with the environment (e.g. resource use, competition, predation) (Caughley 1980). Demography, therefore, links population dynamics with the organism and its environment.

Physiological characteristics arise through adaptation to an optimal life history strategy. At the extremes of the strategic spectrum are $r$- and $K$-selected organisms (MacArthur & Wilson 1967). In risky, unstable environments, $r$-strategists attempt to maximise their population growth rate ($r$) by producing a large quantity of offspring whenever possible. Consequently, parental investment in each offspring is low, resulting in low survival rates (e.g. insects and small mammals). Conversely, $K$-strategists are adapted to stable environments where population abundances are maintained close to the environmental carrying capacity ($K$). In these competitive environments, quality of offspring is more important than quantity, such that the few offspring that are produced receive a high degree of parental investment. Typically, $K$-selected species are large-bodied, have low reproductive rates and high survival rates (e.g. large mammals).
1.2 Population ecology in the Otariidae

The Pinnipedia superfamily (seals) is comprised of three families of large marine carnivores – Odobenidae (walrus), Phocidae (true seals) and Otariidae (eared seals) (Berta & Adam 2001). The Otariidae are distinguished from other pinnipeds by their pinnae (external ear flaps) and robust fore-limbs which confer terrestrial agility (Bonner 1994). The Otariidae are composed of the fur seal and sea lion sub-families which are distinguished in body size and type of insulating integument (Brunner 2003). Fur seals are smaller than sea lions (female mass range: 22 – 76 kg, compared with 80 - 273 kg) and are insulated by double-layered air-trapping fur (Gentry & Kooyman 1986, Bester 1987). In contrast, sea lions possess thinner, single-layered fur and are more reliant on blubber for thermal insulation (Costa & Gales 2003).

It has been suggested that these physiological differences are adaptive trade-offs optimising foraging efficiency in different ecological niches (Kooyman 1989). Fur seals generally forage near the surface of upwellings and oceanic frontal structures (epipelagic foraging) for patchy distributions of small, schooling prey (Gentry & Kooyman 1986). Conversely, most sea lions forage near the benthos of continental shelves (benthic foraging) for large, evenly distributed prey (Costa & Gales 2000, Costa & Gales 2003). Sea lions are better adapted for deep diving than fur seals as their larger body sizes mean they have greater oxygen stores and lower metabolic rates, allowing them to stay submerged for longer durations (Costa 1991). Furthermore, the fur seals’ insulating integument loses effectiveness with depth as trapped air is expressed by water pressure (Gentry et al. 1986). Although benthic diving is more energetically expensive than epipelagic diving, benthic foragers may use less energy searching for prey patches than epipelagic foragers (Costa & Gales 2000, Costa & Gales 2003). Many fur seal and sea lion populations are sympatric,
suggesting that divergent physiology is associated with ecological niche partitioning (Costa et al. 2006).

Associated with otariid phylogeny are patterns of population dynamics. These are readily compared because most populations were hunted to very low densities during the commercial sealing era of 1790 – 1850 (Bonner 1994). In the post-sealing era, most fur seal populations recovered at rates of 10 – 15% p.a. and attained population sizes in the order of $10^5 – 10^6$ (Wickens & York 1997). In contrast, most sea lion populations recovered more slowly, are currently stable or declining, and are an order of magnitude smaller than those of fur seals (Costa et al. 2006). The more rapid recovery of fur seal populations may be associated with the higher primary productivity typical of upwelling/frontal habitats compared to the continental shelves exploited by sea lions (Carr et al. 2006). However, differences in phylogeny and foraging mode efficiency have made this relationship unclear (Arnould & Costa 2006). Furthermore, demographic comparisons are problematic because although the large populations of epipelagic-foraging otariids are well studied (Wickens & York 1997), little information exists for benthic foraging ones.

1.3 Divergent population dynamics in *Arctocephalus pusillus*

The Australian fur seal *Arctocephalus pusillus doriferus* population is believed to have originated from the Cape fur seal *A. p. pusillus* population of southwestern Africa and migrated to Australia some 12,000 years ago towards the end of the last ice-age (Wynen et al. 2001, Demere et al. 2003). Subsequently, Australian fur seals became geographically isolated and the 2 populations are described as separate subspecies (Lento et al. 1997, Higdon et al. 2007).
Curiously, while the Cape fur seal forages epipelagically in an upwelling region (Kooyman & Gentry 1986), the Australian fur seal forages on the benthos of a continental shelf and is the only fur seal primarily dependent on such a niche (Arnould & Hindell 2001). The sympatric occurrence of an epipelagic-foraging otariid, the New Zealand fur seal *A. forsteri* (Arnould *et al.* 2000) suggests that Australian fur seals adapted their foraging mode in response to inter-specific competition, leading to resource partitioning (Page *et al.* 2005). New Zealand fur seals are also sympatric with a third Australian otariid population, that of the benthic foraging Australian sea lion *Neophoca cinerea*, which is now allopatric to Australian fur seals (Gales *et al.* 1994).

The two *A. pusillus* populations displayed starkly divergent population dynamics in the post-sealing era. The Cape fur seal population is believed to have fully recovered and stabilised at approximately 2 million individuals (Kirkman *et al.* 2007). In contrast, the Australian fur seal population numbers approximately 90,000 animals, <50% of its estimated pre-sealing abundance (Kirkwood *et al.* 2005). It has been suggested that the divergent dynamics of the two *A. pusillus* populations was caused by differences in habitat productivity (Warneke & Shaughnessy 1985). While Cape fur seals forage in one of the world’s most biologically productive upwelling systems (Koné *et al.* 2005), Australian fur seals exploit a relatively nutrient-poor continental shelf (Gibbs *et al.* 1986). However, Australian fur seals grow to a larger body size and at a faster rate than their African conspecifics, suggesting that the population may be constrained by factors other than nutrition (Arnould & Warneke 2002). Comparing demography in the two populations of *A. pusillus* could aid the understanding of relationships between niche type and population dynamics in the Otariidae while largely controlling for phylogeny. However, while vital rates have
been quantified in the Cape fur seal population (Butterworth et al. 1995, Odendaal et al. 2002), comparable data is lacking in the modern Australian fur seal population.

A second area of interest in the Australian fur seal population concerns its variable dynamics (Kirkwood et al. 2005). Pre-sealing population abundance was estimated from the cargo records of sealing ships at approximately 200,000 (Ling 2002), however, little is known of post-sealing abundance in the following century (Warneke & Shaughnessy 1985, Ling 1999). The first censuses, conducted by aerial survey in 1945, 1975 and 1986, observed no increases in abundance (Pearse 1979, Warneke 1988) and it was suggested that the population had stabilised at less than 25% of the pre-sealing level (Warneke & Shaughnessy 1985, Warneke 1988). Pup production estimates then doubled between 1986 and 2002 (Warneke 1988, Kirkwood et al. 2005), although the low accuracy of the aerial survey technique makes it difficult to ascertain whether this increase occurred over 2 or 3 decades (Seber 1982). Nonetheless, after several decades of relative stability, the population growth rate increased substantially for reasons unknown (Kirkwood et al. 2005).

1.4 Australian fur seal life history

Australian fur seals most commonly occur within Bass Strait (Kirkwood et al. 2005), a shallow (<80m) continental shelf zone between the Australian mainland and Tasmania (Gibbs 1992). Some individuals, mostly males, extend their range to the east and South Australian coasts (Page et al. 2005), however breeding colonies are restricted to 10 islands within Bass Strait (Fig. 1.1, Kirkwood et al. 2005). Foraging occurs primarily near the benthos and exclusively within the continental shelf (Arnoould & Hindell 2001, Arnoould & Kirkwood 2008). Females forage for 4 – 7 days on fish, cephalopods and crustaceans (Hume et al. 2004, Kirkwood et al. 2008),
before returning to their colony to rest and suckle young for 2 days (Arnould & Hindell 2001).

Like most otariids, Australian fur seals breed synchronously during summer (Warneke & Shaughnessy 1985, Boyd 1991). Males arrive at breeding colonies in October and compete for territories within which they maintain a harem of approximately 9 females (Warneke & Shaughnessy 1985). Most (90%) births occur within a 28 day period with a median birth date of 1 December (Warneke & Shaughnessy 1985). Pups remain dependent on milk until weaning in October (Arnould & Hindell 2001), although lactation extends into a second year for some young (Hume et al. 2001).

Existing demographic information is limited to a study performed in 1971-2 which indicated that Australian fur seals had very low survival rates relative to other fur seals (Arnould et al. 2003). Early- to mid-gestation pregnancy rates were similar to those of other fur seals but declined in late-gestation (Arnould et al. 2003). Logically, the recent population increases must have coincided with increased demographic rates and, therefore, the study of Arnould et al. (2003) may no longer be relevant to the current population. It does, however, provide baseline data with which current rates can be compared so that the causes of the recent population increase may be better ascertained.

The paucity of demographic information for Australian fur seals has lead to data from other fur seal populations being used to estimate their prey consumption and population abundance (Goldsworthy et al. 2003, Kirkwood et al. 2005). However, these other populations have displayed much greater growth rates than the Australian fur seal population and, accordingly, probably have higher birth and/or survival rates (Wickens & York 1997). The demography of stable populations of benthic-foraging
sea lions might be more similar to that of Australian fur seals but unfortunately, such information is scarce. Therefore, establishment of demographic rates in Australian fur seals is not only crucial to understanding their dynamics but may also assist in understanding the dynamics of sea lion populations, many of which are small, declining and of conservation significance (Reijnders et al. 1993, Costa et al. 2006).

1.5 Research objectives and study site

The general objectives of this study were to determine the influences on the population dynamics of Australian fur seals. In doing so, the project will enable comparisons of conspecific populations from habitats of differing productivity. The dynamics of interest are: 1) the relatively slow post-sealing era recovery and; 2) the recent increase that caused the population to double in the past 2 – 3 decades. Female reproductive performance is the limiting factor in the population growth of large polygynous mammals like seals (Caughley 1980). Therefore, the study aimed to 1) determine female age structure, age-specific fecundity and age-specific survivorship and 2) investigate environmental and physiological influences on demography.

The study was performed at Kanowna Island (39°10’ S 146°18’ E), located 4.5km south of Wilsons Promontory, Bass Strait, south-eastern Australia (Fig. 1.1). The island supports the 5th largest of the 10 known colonies of Australian fur seals and is central to their longitudinal range (Kirkwood et al. 2005). Most (>75%) of seals reside in 2 elevated areas of the island – “Main” and “East”, while the rest occur at lower densities around the island perimeter. Main and East areas are rocky amphitheatres occurring approximately 20 - 50m above sea level. On the northern summit of the island these areas meet in a flat area dominated by tussock grass (Poa sp.) where seals can be safely captured with minimal disturbance to non-target seals.
Most fieldwork was conducted from 2003 – 2005, although it is supplemented with work performed between 1997 – 2007.

Figure 1.1: Map of southeastern Australia with Australian fur seal breeding colonies (circles), including Kanowna Island (open circle). Australian fur seals generally remain within the continental shelf area of this map.
1.6 Thesis structure

The three core chapters of this thesis have been accepted by peer-reviewed journals for publication. Chapter 2 describes relationships between pup production, adult female body condition and the environment. Annual capture-mark-resight (CMR) and direct count (DC) estimates of pup production were conducted from 2003 – 2005. This validated the accuracy of DCs and allowed DCs conducted from 1997 – 2007 to be used in the investigation of trends and environmental relationships. Interannual variation in pup production, its timing, and adult female body condition were investigated by comparison with environmental indicators such as sea surface temperature, chlorophyll concentration, wind speed and the Southern Oscillation Index.

Chapter 3 examines reproduction by establishing age-specific rates of lactation, pregnancy, birth and late-term abortion. Results of a novel progesterone radio-immunoassay technique for pregnancy determination in Australian fur seals are presented. The influences of maternal size, mass, body condition, age and lactation status on pregnancy and birth rates are investigated.

Chapter 4 models body growth and age structure using age-length, age-mass, age-frequency and age-specific fecundity data. Age-specific survival rates are derived from the age structure and a complete life table presented. Survival and fecundity parameters are used in a Leslie matrix model to project population growth and determine the relative influences of each demographic parameter. The age-structure model also quantifies the pup:non-pup ratio, thereby improving population abundance estimates.

The discussion chapter places the findings within a framework of otariid ecology, focusing on relationships between ecological niche and population
dynamics. Influences on the recent doubling of the Australian fur seal population are reviewed and suggestions for research and management are made in light of the new demographic information.

1.7 Literature cited


Kirkman, S., Oosthuizen, W., Meýer, M., Kotze, P., Roux, J. and Underhill, L. 2007. Making sense of censuses and dealing with missing data: trends in pup counts of


Group of Australian fur seal pups in the eastern breeding area, Kanowna Island, December 2005
CHAPTER 2

INTERANNUAL VARIATION IN PUP PRODUCTION AND THE TIMING OF BREEDING IN BENTHIC FORAGING AUSTRALIAN FUR SEALS

Abstract: Large interannual variations in reproductive success caused by fluctuations in oceanography and prey availability are common to many species of air breathing epipelagic predators. In contrast, little is known about variation in benthic foragers such as Australian fur seals (Arctocephalus pusillus doriferus). Between 1997-2007, pup production was assessed in 9 years, while the timing of breeding and adult female condition was assessed in 5 years at Kanowna Island in Bass Strait, southeastern Australia. Pup production was variable (mean = 1726 ± 42, range = 1386 – 2301) but without temporal trend, as was median birth date (mean = Nov 23 ± 1, range = Nov 21 – 25) and pupping synchrony (period of 90% births: mean = 28 ± 2 d, range = 23 – 31 d). Pup production was negatively correlated with median birth date and positively correlated with female condition, winter sea-surface temperature (SST) and zonal wind strength within Bass Strait. Pup production was also negatively correlated with SST in the previous summer within Bass Strait and in the eastern Great Australian Bight upwelling region. The results suggest that the reproductive success of Australian fur seals is influenced by oceanography but less so than in otariids foraging epipelagically in major upwellings. Despite spanning several El Niño events, no correlation between pup production and the Southern Oscillation Index was observed.

2.1 Introduction

Seasonal and interannual variations of the environment have strong influences on mammalian reproductive success (Bronson 1985). The adaptive advantage gained by animals breeding at the most favourable time of year has caused seasonal breeding to develop in most mammals (Ims 1990). Seasonal breeding phenology can be determined by several factors, some with interannual constancy (e.g. daylength) and others with interannual variability (e.g. climate, food availability) (Bertram et al. 2001). Therefore, interannual variation in the timing and success of seasonal breeding can reveal the impacts of climate and food availability on a population, thereby improving understanding of its dynamics (Frederiksen et al. 2004).

In most otariids, births occur in early summer to coincide with peak food availability for adults and optimal temperatures for pups (Boyd 1991). Oestrus and mating occur 4-12 days later (Atkinson 1997), allowing males to disperse until the next breeding season. The fertilized egg develops to blastocyst stage, then enters diapause until implantation and the beginning of active gestation approximately 4 months later (Boyd 1991). Timing of the reproductive cycle is primarily determined by the photoperiodic control of blastocyst implantation (Temte & Temte 1993) occurring close to the autumn equinox (Boyd 1991). However, females under nutritional stress may delay implantation, extend active gestation, and give birth later than usual as they gather the resources necessary for reproductive success (Boyd 1984, Boyd 1996, York & Scheffer 1997). When nutritional stress is too high, pregnant females may abort gestation, resulting in reproductive failure (Guinet et al. 1994, Guinet et al. 1998). Therefore, a population experiencing low food availability may demonstrate lower pup production and later births than normal (Duck 1990, Pitcher et al. 2001, Soto et al. 2004).
Air breathing marine predators forage in two main habitat types with differing levels of interannual variability (Kooyman 1989). The majority forage epipelagically within the mixing layer (<200 m depth) of upwellings and oceanic frontal systems (Arnould & Costa 2006). Although highly productive, prey distribution in these systems is typically patchy both temporally and spatially (Weimerskirch 2007). For example, El Niño Southern Oscillation (ENSO) events can reduce the activity of upwellings in the eastern South Pacific Ocean, dramatically reducing prey availability and causing mass mortality in epipelagic foraging otariids and seabirds (Glynn 1988, Trillmich & Ono 1991). Conversely, continental shelf areas are exploited by benthic (seafloor) foragers (Kooyman 1989), where reduced oceanographic activity results in a less productive but more stable habitat (Lalli & Parsons 1993). Although diving to the seafloor is energetically expensive (Costa 1991), it has been suggested that benthic foragers benefit from the spatial and temporal uniformity of prey found there (Gremillet et al. 2004, Arnould & Costa 2006). While numerous studies have investigated the responses of air breathing marine predators to interannual environmental fluctuations (e.g. those related to El Niño), these have largely focussed on epipelagic foragers in upwellings or frontal systems (Forcada et al. 2005, Weimerskirch 2007). In contrast, comparatively little is known of the oceanographic factors influencing populations of benthic foragers (Costa & Gales 2003, Gremillet et al. 2004), presumably because of the difficulty in detecting change in less variable benthic environments.

The Australian fur seal *Arctocephalus pusillus doriferus* is a temperate latitude species with breeding colonies found exclusively within Bass Strait (Kirkwood et al. 2005), a shallow (60-80 m) continental shelf zone of low primary productivity (Gibbs 1992) located between the Australian mainland and Tasmania. Foraging by lactating
females occurs exclusively within this shelf region and, unlike most other fur seals, is primarily benthic (Arnould & Hindell 2001, Arnould & Kirkwood 2008). In stark contrast, the conspecific Cape fur seal *A. p. pusillus* forages epipelagically in the productive upwellings of the Benguela current (Kooymann & Gentry 1986). Both species were severely over-exploited during the commercial sealing era of the 18th and 19th centuries (Bonner 1994) but have since been largely protected (Warneke 1975, Wickens & York 1997). The two subspecies have experienced divergent population recovery rates with Cape fur seals now considered to be the most numerous otariid (approximately 2 million individuals) despite extensive culling (Wickens & York 1997). Australian fur seal numbers have doubled in the past 3 decades to approximately 90,000 (Kirkwood *et al.* 2005), yet are still at <50% of their estimated pre-sealing level (Warneke & Shaughnessy 1985, Ling 1999). It has been suggested that this divergence in population recovery rates is due to the large differences in primary productivity of the marine environments the two subspecies occupy (Warneke & Shaughnessy 1985).

Although the Cape fur seal population has experienced rapid growth, it has also been subject to periods of dramatic reproductive failure and adult mortality linked to variation of the Benguela upwelling (Roux 1998). In contrast, it is not known to what degree environmental variability influences Australian fur seals. Furthermore, while the impacts of interannual variation on otariid populations have been extensively studied in the eastern Pacific Ocean (Glynn 1988, Trillmich & Ono 1991), there is comparably little information for populations in the western Pacific Ocean. The aims of this study, therefore, were to: 1) determine the degree of interannual variability in pup production and the timing of breeding in Australian fur seals; and 2) investigate the environmental factors which may influence these.
2.2 Methods

The study was conducted between 1997 - 2007 on Kanowna Island (39°10’ S 146°18’ E; Fig 1), northern Bass Strait, the site of a large colony of Australian fur seals with an annual pup production of approximately 3000 (Kirkwood et al. 2005). The colony is dispersed around the island but is concentrated in two elevated main breeding areas which produce >75% of pups.

2.2.1 Pup production and timing of breeding

As an index of annual pup production, direct counts were conducted for the whole island at the end of the pupping season (December 12-18) in each year with the exception of 1999 and 2001. In the two main breeding areas where pups tended to congregate in groups, observers used binoculars and tally counters to conduct triplicate counts from a distance of 10-30 m. In other areas where pups were more widely distributed, observers in groups of 2 or 3 walked through each area once, checking the terrain at close range (<10 m) for pups and performing their own count.

Previous studies have indicated that direct counts underestimate pup numbers and that this is colony specific due to topography (Kirkwood et al. 2005, Shaughnessy et al. 1995). Therefore, capture-mark-resight experiments (CMR) were performed to assess the reliability of using direct counts as a pup production index. Following the methods of Kirkwood et al. (2005), CMRs were conducted approximately 1 month after the direct counts of 2003 - 05, when territorial bulls have left the colony but pups are still land-bound and readily caught. A team of four people caught pups by hand and marked them by clipping a 70 mm diameter patch of black fur from the crown of the head with small hand shears, revealing light brown underfur visible at distance. Each pup was then released and the mark recorded by a scribe. Resights were
conducted 24-48 hours later to allow marked and unmarked pups to become randomly distributed (Kirkwood et al. 2005). Resights were conducted by the same method as the direct counts, with the marking status of each clearly visible pup noted. A modified Petersen estimate was used to calculate pup numbers (Kirkwood et al. 2005).

To determine the timing of breeding, pups in the two main breeding areas were counted daily during the 2003-07 breeding seasons. To avoid disturbance to seals, a single person observed from a single position in each area. Counts were conducted at the same time of day in each area, between 07:00-09:00 and 17:30-18:30 AEDT, so that the hottest part of the day when seals thermoregulate in the water was avoided. Binoculars and a tally counter were used to make triplicate counts of newborn black-coated pups, mature females and territorial bulls, which were then averaged. Non-territorial males and juveniles were not recorded, nor were adults in 2007.

Counts were intended to cover the period of 90% of births (26 days; Shaughnessy & Warneke 1987) centred on the published median birth date for Australian fur seals (1 December; Warneke unpublished data, cited in Warneke & Shaughnessy 1985). Unexpectedly, however, the peak pupping period occurred approximately 1 week earlier than this. In addition, logistical constraints prevented early access to the colony such that the start of pupping was not observed from 2003-2006. The 2007 count recorded the entire pupping season and indicated that the pupping rate conformed to an unskewed normal distribution. Consequently, assuming a similar distribution in all years (Duck 1990), curves were fitted to the daily pup counts according to the sigmoid method of Trites (1992), using a computer program (Microcal Origin 5.0, Microcal Software Inc., Northampton, USA). Median birth date
and birth synchrony (period of 90% births) were calculated from parameters of the sigmoid curve (Trites 1992). The daily female and territorial bull counts were approximated with second order polynomial and linear regressions, respectively and analysed using analysis of covariance (ANCOVA).

2.2.2 Female condition and environment
As part of concurrent studies occurring from 2003 - 07, adult females were selected at random from those able to be approached while causing minimal disturbance to other seals in the colony. The density and distribution of seals and the appropriate directions of approach change constantly due to weather variations and, therefore, the selection technique is unlikely to cause substantial bias. Females were captured using a modified hoop net (Fuhrman Diversified, Seabrook, Tex., USA) and an intramuscular dose of Midazolam (0.15 mg·kg⁻¹, Hypnovel®, Roche Products Pty Ltd., Dee Why, NSW, Australia) was administered to facilitate handling and induce gas anaesthesia (Isoflurane; Gales & Mattlin 1998). Seals were then transferred to a flat platform, weighed using a spring scale (200 ± 0.5 kg; Salter, Peterborough, UK), and measured with a tape measure (standard length ± 0.5 cm) while in ventral recumbancy. Because female body condition is known to vary throughout the year (Arnould & Warneke 2002), sampling was restricted to winter (June - August) which is the period of maximum lactational demand and when females undertake the longest foraging trips (Arnould & Hindell 1999, Arnould & Hindell 2001). Hence, females are presumed to be under maximum nutritional stress at this time. Individual female body condition was estimated using a body condition index (BCI) that has been correlated with blubber depth in Australian fur seals (Arnould & Warneke 2002). Mass was regressed against standard length using a power function, and each individual’s residual value
taken as its BCI (Arnould & Warneke 2002, Guinet et al. 1998). Mean BCI was calculated for each year to facilitate interannual comparison of female condition.

To investigate potential environmental effects on pup production, the timing of breeding and female condition, the following variables were analysed. The Southern Oscillation Index (SOI; Troup 1967) measures ENSO, which influences many of the oceanographic features of southern Australia (Middleton et al. 2007). Monthly means were obtained from the Bureau of Meteorology, Australia (http://www.bom.gov.au/climate/current/soihtm1.shtml). Monthly means for sea surface temperature (SST; indicative of different water masses), sea surface chlorophyll-a concentration (CHL-a; an index of primary productivity) and zonal (west to east) wind speed (the primary driver of water movement through Bass Strait, Sandery & Kämpf 2007) were obtained for the central Bass Strait region (39-41° S, 144-148° E, Fig 2.1), encompassing the main foraging zone of female Australian fur seals from Kanowna Island (Arnould & Hindell 2001, Arnould & Kirkwood 2008). Additionally, the SST of the eastern Great Australian Bight (eGAB; 38-39° S, 140-141° E, Fig 2.1) was investigated because this region has significant summer upwelling activity and is the primary source of Bass Strait water (Middleton & Bye 2007).

Data for SST were extracted from the Reynolds Optimally Interpolated dataset, a combination of AVHRR satellite and in situ data (Reynolds & Smith 1994), obtained using the online PO.DAAC Ocean ESIP Tool (http://poet.jpl.nasa.gov, NASA Jet Propulsion Laboratory, Pasadena, CA). Data for CHL-a was derived from the SEAWiFS satellite, obtained with the GES-DISC Interactive Online Visualization and Analysis Infrastructure (Giovanni; http://reason.gsfc.nasa.gov/Giovanni). As SEAWiFS data is only available from September 1997 onwards, analyses with CHL-a
Figure 2.1. Locations of study site, major water masses (arrows), continental shelf edge (black line representing 200m bathymetric contour) and regions for which environmental data were analysed (rectangles).
were only performed between 1998-2007. Zonal wind speed data were extracted from
the NCEP Reanalysis 2 dataset (http://www.cdc.noaa.gov, NOAA/OAR/ESRL PSD,
Boulder, Colorado, USA).

Annual means were derived from monthly means according to annual
reproductive period of Australian fur seals (1 December – 30 November; Warneke &
Shaughnessy 1985). Because SST oscillations lag atmospheric temperature
oscillations by approximately 1 month, seasonal means were calculated accordingly.
For example, summer was defined as occurring from January – March for
oceanographic variables (SST, CHL-a) and from December to February for
atmospheric variables (SOI, zonal wind speed). Annual and seasonal means of
environmental variables were then compared with biological variables (pup
production index, median birth date, pupping synchrony, female BCI). All data were
tested for normality using the Kolmogorov-Smirnov test. Data are presented as means
± 1 SE and results considered significant at the P < 0.05 level.

2.3 Results

2.3.1 Pup production and timing of breeding

For the 3 years in which they were conducted (2003 – 05), CMR estimates ranged
from 2936 – 3206 (x = 3108 ± 139). The numbers of pups marked in each year were
between 28 – 34 % of the CMR estimates, more than the 25% recommended by
Caughley (1980) to maximise accuracy of the method. The CMR estimates were
consistently higher than the direct counts by a factor of 1.75 ± 0.02 (Table 2.1).
Therefore, while direct counts do not accurately measure total pup production, they
provide a reliable index for analysing interannual variation. This pup production
index, obtained in 9 years between 1997 – 2007, ranged from 1386 - 2301 (x = 1726 ±
There was no consistent trend over this period \( (r^2 < 0.01, n = 9, P > 0.9) \). Using the 1.75 multiplier, this represents an estimated live pup total of 2426 – 4027 \( (x = 3021) \). Although dead pups were counted during direct counts and CMRs (range 156 – 365), these counts were considered inaccurate as there are many places for dead pups to become obscured at Kanowna Island. Previous studies on the species have assessed pup mortality to reach 15% by early January (Warneke 1975, Pemberton & Kirkwood 1994). Using this mortality estimate, total pup production from 1997 – 2007 is estimated as ranging from 2854 – 4738 \( (x = 3554) \).

Sigmoid curves accurately modelled the daily pup counts in the main breeding areas from 2003-07 \( (r^2 > 0.85, n > 19, P < 0.001 \) in all cases, Fig 2.3a). The upper asymptotes of the fitted curves were lower (by a factor of 1.63 ± 0.02) but correlated with the pup production index (Spearman \( \rho = 0.1, n = 5, P < 0.002 \)), indicating that counts in the main breeding areas were indicative of total colony numbers. Median birth date in all years was 23 Nov ± 1 d, with an interannual range of 4 d (21 – 25 Nov). The period within which 90% of births occurred (pupping synchrony) ranged from 23 – 31 d, and on average was 28 ± 2 d (Table 2.1). Median birth date was negatively correlated with the pup production index (Spearman \( \rho = -1, n = 5, P < 0.002 \)). Pupping synchrony, however, was not significantly correlated with pup production or median birth date (Spearman \( \rho = 0.50, n = 5, P = 0.39 \) in both cases).

During the breeding seasons of 2003-06, the increase and decrease in adult female numbers was best described by 2nd-order polynomials \( (r^2 > 0.82, P < 0.001 \) in all cases, Fig 2.3b). Females reached 50% of their peak numbers 2 - 4 days before the median birth date \( (r^2 = 0.90, n = 4, P = 0.05, \) Fig 2.3b), and peak numbers were reached 9 - 10 days after the median pupping date \( (r^2 = 0.94, n = 4, P < 0.05; \) Table 2.1), indicating that the timing of female arrival was correlated with the timing of
<table>
<thead>
<tr>
<th>Year</th>
<th>Median Birth Date (Nov)</th>
<th>90% Births Period (days)</th>
<th>CMR Pups Marked</th>
<th>CMR Estimate ± SE</th>
<th>CMR / Direct Count</th>
<th>Female Winter BCI ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td>24</td>
<td>31</td>
<td>916</td>
<td>2936 ± 58</td>
<td>1.77</td>
<td>-0.16 ± 0.98</td>
</tr>
<tr>
<td>2004</td>
<td>21</td>
<td>26</td>
<td>894</td>
<td>3206 ± 99</td>
<td>1.71</td>
<td>0.86 ± 0.78</td>
</tr>
<tr>
<td>2005</td>
<td>22</td>
<td>23</td>
<td>1086</td>
<td>3205 ± 77</td>
<td>1.79</td>
<td>-1.32 ± 0.76</td>
</tr>
<tr>
<td>2006</td>
<td>25</td>
<td>30</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>-4.13 ± 2.09</td>
</tr>
<tr>
<td>2007</td>
<td>24</td>
<td>31</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>-2.91 ± 1.45</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td></td>
<td>23 ± 1</td>
<td>28 ± 2</td>
<td>965</td>
<td>3108 ± 139</td>
<td>1.75 ± 0.02</td>
</tr>
</tbody>
</table>

Table 2.1. Timing of breeding, CMR results and female winter BCI, Kanowna Island 2003 - 07. * indicates no CMR performed.
Figure 2.2. Pup production index at Kanowna Island, 1997-2007, with bars indicating standard error. * indicates no direct count performed.
birth. ANCOVA modelling indicated that there were statistically significant
differences between the fitted quadratic curves for the four years ($F = 21.42$, df = 9,
94, $P < 0.001$), and pairwise comparisons indicated that all fitted curves were
statistically significant from each other ($P < 0.001$ in all cases). Pairwise comparisons
of the peaks of the curves showed that the 2006 peak was significantly lower than in
2003 ($t = 3.48$, d.f. = 94, $P < 0.001$), 2004 ($t = 3.00$, d.f. = 94, $P = 0.003$) and 2005 ($t
= 2.90$, d.f. = 94, $P = 0.005$). The peaks in 2003-05 were not significantly different to
each other ($P > 0.5$ in all cases, Fig. 2.3b).

From 2003-06, bulls had already established territories before daily counts
began, so the timing of territory establishment or how it varied between years can not
be determined. The number of territorial bulls increased linearly as the breeding
season progressed ($r^2 \geq 0.2$, $P < 0.02$ in all cases, Fig. 2.3c). The rate of increase
differed between years (ANCOVA: $F = 5.1$, d.f. = 3, $P = 0.003$), and post-hoc
pairwise comparisons indicated that the 2004 rate was lower than in 2003 ($t = 2.77$,
d.f. = 98, $P = 0.007$), 2005 ($t = 2.01$, d.f. = 98, $P = 0.047$) and 2006 ($t = 2.22$, d.f. =
98, $P = 0.029$), but other years were not significantly different ($P > 0.5$ in all cases).
In all years combined, there was a significant rate of increase (ANCOVA: $F = 85.64$,
d.f. = 1, $P < 0.001$) of 1.42 territories per day. The mean number of established
territories differed between years (ANCOVA: $F = 22.82$, d.f. = 3, $P < 0.001$). Least
squares means were calculated and post-hoc comparisons indicated that on the mean
date of all daily counts (November 30), territory number differed between all years ($t
> 5.4$, d.f. = 98, $P < 0.001$) except between 2003 and 2005, where the difference
approached significance ($t = 1.98$, d.f. = 98, $P = 0.051$).

In 2003-06, the lowest pup production occurred in 2006. This coincided with a
substantially lower peak number of females (1404) than in the other study years
Figure 2.3. Daily counts of a) pups 2003-07, b) adult females 2003-06, and c) territorial bulls 2003-06 in main breeding areas, Kanowna Island.
(1554 – 1587). There were also markedly fewer territorial males in the colony in 2006 (187) compared with other years (212 – 228).

2.3.2 Female condition and environment

The morphometrics of all adult females captured in 1997 – 2008 were used to create a mass/length power function regression \( (r^2 = 0.72, n = 383, P < 0.0001) \), the residuals from which constituted an individual’s BCI. Interannual comparisons of mean BCI were only made between similar seasons to account for seasonal variation (Arnould & Warneke 2002). Furthermore, not all years had enough females captured for statistical analysis. Therefore, the sample was restricted to females measured during the winters (Jun – Aug) of 2003 – 07, as sampling had been most common in those periods \( (n = 228, \text{Table 1}) \). During 2003 – 07, the mean winter BCI of adult females was correlated with the pup production index (Spearman \( \rho = 0.90, n = 5, P = 0.04 \)) and negatively correlated with median birth date (Spearman \( \rho = -0.90, n = 5, P = 0.04 \)).

Biological variables (pup production index, median birth date, synchrony and female BCI) were not correlated with any means of the SOI and CHL-a. There were also no correlations with annual means of SST or zonal wind speed \( (P > 0.05 \text{ in all cases}) \). However, relationships were found with summer and winter SST, and winter zonal wind speed. The pup production index was negatively correlated with Bass Strait summer SST in 9 years \( (r^2 = 0.47, n = 9, P < 0.05; \text{Fig 2.4a}) \), and a similar, yet stronger correlation was found with eGAB summer SST \( (r^2 = 0.66, n = 9, P = 0.01; \text{Fig 2.4b}) \). Summer eGAB SST was also negatively correlated with female BCI during 2003 - 07 (Spearman \( \rho = -0.98, n = 5, P = 0.002 \)).

The pup production index was also correlated with winter Bass Strait SST \( (r^2 = 0.46, n = 9, P < 0.05) \). However, unlike the negative correlation found in summer,
Figure 2.4. Correlations of the pup production index (n = 9) with summer SST in Bass Strait (a) and the eGAB (b), 1997 – 2007.
Figure 2.5. Correlations of the pup production index (n = 9) with winter Bass Strait SST (a) and zonal wind speed (b), 1997 – 2007.
the relationship in winter was positive (Fig 2.5a). A stronger relationship existed between the pup production index and winter Bass Strait zonal wind speed ($r^2 = 0.68$, $n = 9$, $P < 0.01$; Fig 2.5b). Female BCI was also correlated with winter Bass Strait zonal wind speed (Spearman $\rho = 0.90$, $n = 5$, $P = 0.04$).

**2.4 Discussion**

2.4.1 Pup production and timing of breeding

The overall median birth date reported in the present study (November 23) was 8 days earlier than previously reported for Australian fur seals at the nearby Seal Rocks colony (125 km away, 38°30'S, 145°10'E) in the 1970s (Warneke & Shaughnessy 1985). While latitude can influence birth date across a species’ range (Temte 1985), the 1° difference between the colonies is unlikely to cause such a large difference in birth date (Temte 1993). The current Kanowna Island population is known to have a younger female age structure than that of Seal Rocks in the 1970s (Chapter 4, Arnould *et al.* 2003), and, because younger females in long-lactating fur seals, such as the conspecific *A. p. pusillus*, are known to pup earlier than older females (Rand 1955, Georges & Guinet 2000), this change in age structure could potentially affect the median birth date. A median birth date of November 26 was reported in southern Bass Strait in 1990 (Pemberton & Kirkwood 1994), which is consistent with the hypothesis that earlier births coincide with a trend towards younger age classes in a growing population.

Breeding seasons with high pup production coincided with an early pupping period and occurred after winters when female condition was high. This is consistent with studies showing that females in good condition implant earlier (Boyd 1984), have a shorter gestation time (Boyd 1996) and have a greater chance of reproductive
success than those in poor condition (Boyd 1991, Lunn & Boyd 1993, Guinet et al. 1998, Pitcher et al. 1998). Accordingly, a negative relationship between pup production and median birth date is expected and has been observed in several other species of otariids (Duck 1990, Majluf 1992, Soto 2004). Direct comparisons with these studies, however, are problematic due to them being conducted over different time periods and levels of environmental variation. Nonetheless, some general comparisons can be made. Pup production in the lowest year of the present study was 40% less than in the highest year, and median birth date varied by 4 days. These figures contrast markedly with those of otariids foraging in eastern boundary current upwellings. For example, El Niño-related reductions in prey availability have resulted in 100% pup mortality and adult starvation in several species of otariids (Trillmich & Ono 1991). In Southern sea lions *Otaria flavescens*, median birth date, correlated with fish biomass, varied by 16 days over a 6 year period, and pup mortality of 100% occurred after the 1997-98 El Niño event (Soto et al. 2004). Similarly, variations in the Benguela upwelling have caused mass mortalities in adult Cape fur seals and their pups (Roux 1998). The smaller amount of interannual variation observed in the present study suggests that prey availability on the Bass Strait continental shelf is more temporally stable than in eastern boundary current upwelling systems.

Few females were present at the colony when daily counts began, as many undertake long post-weaning foraging trips at this time (Arnould & Hindell 2001). The timing of the increase in female numbers was related to the median birth date and consistent with studies indicating that female otariids return to the colony 1.5 – 2 days pre-partum. (Higgins & Gass 1993, Lunn & Boyd 1993). Female numbers did not begin declining until 9 days after the median birth date, which corresponds with the period of perinatal attendance observed in Australian fur seals (8.4 d; Arnould &
Female patterns of attendance at the colony, therefore, appear determined by pupping date, and, hence, are ultimately the result of interannual variation of the environment.

Bulls had already established territories when daily counts began and therefore it can not be determined if the timing of male arrival and territory establishment varies interannually. A gradual increase in territory number was observed over the pupping period, similar to that observed in other species (Duck 1990, Gales & Fletcher 1999, Goldsworthy & Shaughnessy 1994). This is likely due to the abandonment of territories by experienced bulls late in the season, allowing numerous novices to establish smaller territories (Duck 1990). It is not known why the rate of territory increase was lower in 2004 than in other years.

Numbers of females were substantially lower in 2006 than 2003-05. The number of territorial males was also anomalously low in 2006, most likely the result of reduced female availability. However, a “bachelor area” with several hundred non-territorial males observed between the breeding areas in 2003-05 was absent in 2006 (Gibbens, unpublished data), suggesting that many males avoided Kanowna Island during the 2006 breeding season. In that year, the winter condition of females was lower than in 2003-05 and therefore, it is likely that environmental conditions in 2006 caused some adults to have visited other colonies or non-breeding haulouts.

2.4.2 Environmental relationships

Unfortunately, data on prey availability were not available for comparison with the present study. Therefore, environmental data were analysed as proxies to investigate the oceanographic and climatic processes likely to influence prey availability. Most notable were the relationships between 9 years of pup production data and summer
SSTs in Bass Strait and the eGAB; and winter Bass Strait SST and zonal wind speed. Together, these may provide some insight into how the complex oceanography of Bass Strait affects Australian fur seals.

Three water masses of differing temperature and primary productivity advect onto the Bass Strait shelf, so that SST and CHL-a analysis can provide an estimate of the activity of each (Sandery & Kämpf 2007). Contributing the most water is the warm South Australian Current (SAC), a coastal current flowing east from the eGAB into Bass Strait (Fig 1) (Sandery & Kämpf 2007). Active year-round, the SAC is driven by prevailing westerly winds that reach maximum strength in winter (Cirano & Middleton 2004, Sandery & Kämpf 2007). During the winter months, the subtropical convergence (STC) moves northward into Bass Strait, allowing cold, nutrient-rich Subantarctic Surface Water (SASW) to enter from the southwest and mix with the SAC (Prince 2001, Sandery & Kämpf 2005). In summer, the STC returns south of Bass Strait and the very warm, nutrient poor East Australia Current (EAC) extends south to the eastern edge of the Strait (Sandery & Kämpf 2007). However, SASW remains present at depth (Prince 2001) and upwells at the shelf edges of Bass Strait (Evans & Middleton 1998) and particularly, the eGAB (Kämpf et al. 2004, McClatchie et al. 2006). Australia’s most productive upwellings occur during summer at the Bonney coast, immediately west of Bass Strait (Fig 2.1). The pelagic productivity of this northern boundary current system is comparable to the lower end of the range of productivity observed in eastern boundary current systems (Ward et al. 2006).

While it might be expected that pup production would be higher after winters with low SST and high CHL-a caused by an anomalously greater presence of cool, nutrient rich SASW in Bass Strait, this was not the case. In fact, pup production was
correlated with high winter Bass Strait SST and zonal wind speed, both related to SAC activity (Sandery & Kämpf 2007). Warm winter Bass Strait SST anomalies have been correlated with fish stocks (Jenkins & King 2006) and, together with westerly winds, with reproductive success in little penguins *Eudyptula minor* (Mickelson *et al.* 1992). Conversely, pup production was correlated with low summer SSTs in Bass Strait and, particularly, in the eGAB, which can result from upwelling of cool SASW (McClatchie *et al.* 2006). From these correlations it appears that pup production is related to summer upwelling activity and winter SAC activity.

Dietary analysis of Australian fur seals indicates that a constant presence of benthic prey species is supplemented by a variable presence of pelagic species (Gales *et al.* 1993, Gales & Pemberton 1994, Hume *et al.* 2004, Kirkwood *et al.* 2008). The presence of pelagic species in the diet is interesting, considering that Australian fur seals are considered exclusively benthic foragers (Arnould & Kirkwood 2008). Pelagic productivity of nearby upwellings may advect onto the Bass Strait shelf, then occupy benthic habitats (Malatesta & Auster 1999) and become vulnerable to diving predators as vertical migration is constrained (Perissinotto & McQuaid 1992, Tremblay & Cherel 2000, Takahashi *et al.* 2003). It is therefore plausible that interannual variations in summer upwelling and winter SAC activity are the important oceanographic processes determining prey availability for Australian fur seals. However, further evidence is required to reinforce the correlations found by the present study.

Extremes of the El Niño Southern Oscillation are known to cause spectacular population crashes (Trillmich & Ono 1991, McMahon & Burton 2005, Forcada *et al.* 2005), or, sometimes, population increases (Sydeman & Allen 1999) of marine predators. The present study, however, did not reveal any such responses. The years
of highest and lowest pup production, observed in 2002 and 2006, respectively, did not correspond to ENSO events. Similarly, the very strong 1997 El Niño that caused mass mortality is the eastern Pacific (Soto et al. 2004) did not correspond with anomalous pup production in Bass Strait. In the southeastern Australian marine region, winter El Niño conditions can weaken the SAC and enhance upwelling activity the following summer but summer El Niños are believed to have little impact (Middleton et al. 2007, Middleton & Bye 2007). Seasonal analysis of the SOI did not reveal any correlations with pup production in this study, however a longer time series of data may be required to determine what effects, if any, large-scale climate oscillations have on Australian fur seals.

2.5 Literature Cited


Australian fur seal female with suckling pup, Kanowna Island, May 2006
CHAPTER 3

INFLUENCES ON FECUNDITY IN AUSTRALIAN FUR SEALS

Abstract: Recovery of the Australian fur seal (*Arctocephalus pusillus doriferus*) population has been slower than that of other fur seals, perhaps due to nutritional constraints on fecundity. However, the population doubled in recent decades, suggesting that reproductive rates may have changed. In this study, pregnancy and birth rates were estimated and the influences of maternal age, size, condition and lactation status investigated over three consecutive breeding seasons (2003-05). Mid-gestation pregnancy rate, estimated from plasma progesterone concentrations, was 84 ± 3%, and was negatively influenced only by age (*P* < 0.001). Birth rate, estimated from observations of females with new-born pups during the breeding season, was 53 ± 3%, and was negatively influenced by lactation status (*P* = 0.035). The difference between pregnancy and birth rates suggests that a high degree of late-gestation abortion occurs, especially in younger females. Lactation status was not influenced by any variables and the high rate (86 ± 2%) suggests that many juveniles are suckled beyond the normal weaning period. Although relationships between reproductive rates and body condition were not found, the results are consistent with a nutritional stress hypothesis. The recent increase in population growth is not due to increased fecundity, which remains low compared to other otariids. Paradoxically, high pregnancy rates were observed in young females (3 years), suggesting that rapid maturity is adaptive for benthic foragers.

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3.1 Introduction

Fecundity and survival control the dynamics of populations (Caughley 1980) and, in most mammals, these parameters are influenced by the balance between energy intake and expenditure (Bronson 1985). Survival requires individuals to gather sufficient energy to support growth and metabolism, whereas fecundity requires females to gather additional resources for the support of gestation and lactation (Widdowson 1981). Accordingly, large mothers, or those with substantial energy reserves, can more readily devote energy towards reproduction than small mothers, or those in poor condition (Bronson 1985). Because females require a period of growth to reach reproductive size and then eventually senesce, fecundity is also age-dependent (Clutton-Brock 1988). Reproducing when nutritionally stressed poses risks to a female’s survival and, therefore, is usually avoided by mechanisms of infertility, abortion of gestation or abandonment of suckling offspring (Bronson 1989). These mechanisms, operating within environmental and life history constraints, form adaptive reproductive strategies (Clutton-Brock 1988).

In the Family Otariidae (fur seals and sea lions), reproduction is characterized by the production of a single offspring during a synchronised annual breeding season (Atkinson 1997). Reproductive synchrony is maintained by post-partum mating and a period of embryonic diapause between fertilization and active gestation (Boyd 1991b). In high-latitude species, pups are suckled for the duration of embryonic diapause and are weaned as active gestation begins (Boyd 1991b). In contrast, temperate-latitude species suckle pups for most of the year, and weaning occurs less than 2 months prior to the birth of the next pup (Boyd 1991b). Thus, lactation and gestation occur concurrently, and the energetic demands of the two processes are additive. Furthermore, females continually return to a central place (the breeding
colony) to suckle pups, which limits foraging range. Temperate-latitude otariid reproduction is therefore energetically expensive relative to that of other pinnipeds (Costa 1993). A consequence of the annual breeding cycle is that resource availability during the most energetically expensive phase of reproduction, the third trimester of gestation (Trites 1991), is impossible to predict at fertilization, some 10-12 months earlier. To maximize fitness within an unpredictable environment, otariid fertility rates are initially close to 100% and reproductive failures may occur later in the cycle as energy demands mount (Guinet et al. 1998; McKenzie et al. 2005; Pitcher et al. 1998).

The Australian fur seal Arctocephalus pusillus doriferus is a temperate latitude species breeding in Bass Strait (Kirkwood et al. 2005), a continental shelf area of low primary productivity between the Australian mainland and Tasmania (Gibbs 1992). Both the Australian fur seal and the conspecific Cape fur seal A. p. pusillus were severely over-exploited during the commercial sealing era (Bonner 1994) but have since been largely protected (Warneke 1975; Wickens & York 1997). The Cape fur seal population forages in the nutrient rich upwellings of the Benguela current and recovered rapidly to a size of approximately 2 million individuals (Wickens & York 1997). In contrast, recovery of the Australian fur seal population has been slower, and now numbers approximately 90,000 individuals (Kirkwood et al. 2005). It has been suggested that the divergent recovery rates and population sizes are the result of differing energy availability and subsequent influences on fecundity (Warneke & Shaughnessy 1985). Australian fur seals produce fewer pups in years when the mean body condition of adult females is low (Chapter 2) and have the lowest mass-specific rate of growth among pups of any otariid ( Arnould & Hindell 2002). Hence, while there is some evidence of nutritional constraint on fecundity, actual reproductive rates
and the maternal characteristics that influence them are unknown. Therefore, this study aimed to determine pregnancy and birth rates in Australian fur seals, and investigated the influences of maternal age, body size, body condition and lactation status on these rates.

3.2 Methods
The study was conducted between 2003-5 at Kanowna Island (39°10’ S 146°18’ E), northern Bass Strait, the site of an Australian fur seal colony with annual pup production of approximately 3550 (Chapter 2). The colony is dispersed around the island but is concentrated in two elevated main breeding areas comprising >75% of the population. Captures were conducted in the main breeding areas from winter to mid-spring (23 June – 7 October). All methods pertaining to live animal use were approved by ethics committees at the University of Melbourne and Deakin University.

Adult females were selected at random from those able to be approached while causing minimal disturbance to other seals in the colony. The density and distribution of seals and the appropriate directions of approach change constantly due to weather variations and, therefore, the selection technique is unlikely to cause substantial bias. Individuals were captured using a modified hoop net (Fuhrman Diversified, Seabrook, USA) and given an intramuscular dose of Midazolam (0.15mg/kg; Hypnovel®; Roche Products Pty Ltd., Dee Why, Australia) to reduce stress and induce gas anaesthesia (Isoflurane; Gales & Mattlin 1998). Seals were transferred to a flat platform on their ventral surface, weighed using a spring scale (200 ± 0.5 kg; Salter, Peterborough, UK), and measured (± 0.5 cm) for standard length (STL) and axillary girth, (AXG) using a metal tape measure (Bonner & Laws 1993). Individually numbered plastic tags (Super Tags, Dalton I.D. Systems Ltd, Henley-on-Thames, UK) were placed in
the trailing edge of both fore-flippers and large numbers were bleached into the dorsal fur using commercial hair bleach. The presence of a pup was noted before capture, and females not observed with a pup were checked for lactation status by manual expression of the teats after oxytocin injection (0.5–1.0 mL, 10 UI mL\(^{-1}\), Heriot Agvet, Rowville, Victoria) to stimulate milk release. A blood sample was drawn into a heparinised syringe from a small vein in the rear flipper, centrifuged, and the plasma fraction separated and stored at -20º C until analysis in the laboratory for pregnancy determination. After injection of local anaesthetic in the gum (10 mg lignocaine hydrochloride; Xylocaine: AustraZeneca Pty. Ltd., North Ryde, New South Wales, Australia), dental elevators were used to extract a first postcanine tooth from the lower jaw, which was stored in 70% ethanol until analysis for aging.

During the breeding seasons, marked seals in the main breeding areas of the island were observed on 4 occasions each day between the hours of 0800 – 1800 EDT and on other areas of the island once daily between 1000 – 1400 EDT. Observations were conducted between November 15 – December 15 in each year, a period approximately 1 week later than that within which 90% of pups are born (Nov 9 – Dec 7, Chapter 2). This period was optimal for resighting marked females with their new-born or yearling pups suckling or resting alongside. Although pups born prior to November 15 could have died before observation, these would have been few in number and unlikely to be a major source of bias. Only observations of females at rest were recorded because females moving through the colony often do not have their young with them (J. Gibbens, personal observation). It was possible, however, that the offspring of some of the females were obscured or absent during observation. Therefore, to reduce error and bias, pupping status was estimated only for those females for which at least 2 consistent resights were recorded (i.e. observed \(\geq\) twice
with young or ≥ twice alone). Additionally, resights were required to occur ≥ 2 days apart so that they were likely to have been separated by a maternal foraging trip and, therefore, represent discrete attendance events (Arnould and Hindell 2001). Females not meeting these criteria were assigned unknown pupping status.

3.2.2 Pregnancy estimation

Pregnancy status was determined by measuring plasma progesterone concentrations. High progesterone concentrations occur in pregnant females, and at around the timing of implantation, also occur in non-pregnant females, a condition termed “pseudopregnancy” (Boyd 1991a, 1991b; Guinet et al. 1998; McKenzie et al. 2005). Therefore, pregnancy status cannot be determined until progesterone concentrations diverge, which occurs 1.5 months post-implantation in New Zealand fur seals A. forsteri (McKenzie et al. 2005). The timing of implantation has not been determined in Australian fur seals, but in Cape fur seals and other congenerics it occurs 3 – 5 months post-fertilization (Atkinson 1997; Bester 1995; Boyd 1991b). Fertilization occurs approximately 7 days post-partum (Arnould & Hindell 2001; Boyd 1991b) and, therefore, implantation should take place between mid-February and mid-May. In the present study, sampling began 1.3 months after the end of this period (Fig. 1), so only a very small proportion of samples may have come from pseudopregnant females. Because there is no existing information on plasma progesterone concentrations in pregnant and non-pregnant Australian fur seals, pregnancy status was estimated based on individuals having a “high” or “low” concentration. The threshold between these states was chosen based on the distribution of progesterone concentrations in conjunction with breeding season observations of marked females with new-born pups (n = 55) that were assumed to have been pregnant when captured.
Progesterone concentrations were measured using coated-tube radioimmunoassay kits (Spectria, Progesterone RIA, Orion Diagnostica, Espoo, Finland) as described by McKenzie et al. (2005) for New Zealand fur seals. The organic component of each sample of plasma was extracted with ethyl acetate then resuspended in water to achieve a 1:4 dilution. A 50 µl aliquot of diluted extract was added to duplicate polyclonal (rabbit) progesterone antibody-coated assay kit tubes with 500 µl of $^{125}$I-progesterone and incubated for 2 hours at room temperature before measurement. To provide samples of known high and low progesterone concentrations for each assay run (quality control high and low), samples were used from a female known to have pupped, and a juvenile male, respectively. The interassay coefficient of variation was 10.2% (n = 7 assays), and the intraassay coefficient of variation was 7.5%.

3.2.3 Age determination

Extracted teeth were rinsed in flowing water for $\geq$6 hours to remove ethanol, then immersed in a hydrochloric acid decalcifying agent (RDO, Apex Engineering Products Corporation, Illinois, USA) until flexible to the touch (8-24 hours). Decalcified teeth were rinsed in deionised water for $\geq$6 hours, embedded in a mounting compound, then $\geq$6 sections of 25µm thickness were cut on a microtome at -10°C. After staining with haemotoxylin and fixing with 5% ammonia solution, the 6 sections with best definition were mounted on glass slides using a mounting compound (DPX) and glass coverslip. Sections were viewed with transmitted light on a stereo microscope (4x – 10x) with a rotatable polarising filter. Each pair of alternating dark and light bands in the tooth cementum indicate one year of growth in the species (Arnould et al. 2003) and were counted to determine age at the
individual’s previous birthday (median birth date November 23; Chapter 2). Five blind readings were made for each tooth and the median value used as the final age. A single person performed all readings to reduce inter-reader variability and because accuracy increases with reader experience (McCann 1993).

3.2.4 Definition of variables and statistical analyses

Body size was defined as standard length (STL). Body condition was estimated by regressing mass against body size with a power function, and using the residuals as an index of body condition (BCI). This type of BCI has been shown to correlate with sternal blubber depth in Australian fur seals (Arnould and Warneke 2002). Measures of body mass for pregnant female seals were corrected by subtracting the estimated mass of the foetus and placenta. Foetal mass was estimated from capture date using foetal growth curves derived from a previous study \( n = 67; \) Arnould & Warneke 2002), with placental mass assumed to be 10% of fetal mass (Boyd & McCann 1989).

The likelihoods of being classified as pregnant, lactating, resighted, and (for those that were resighted) having pupped, were each modelled using binary logistic regression (Afifi et al. 2004). Capture date, age, STL, BCI, pregnancy status and lactation status were used as explanatory variables, except pregnancy status was not included in the pupping model. Mass was not included in any models due to its strong correlations with age \( r = 0.71 \) and STL \( r = 0.86; \) Afifi et al. 2004) and because exploratory analysis indicated that it was not a significant predictor of any status. A backwards stepwise elimination method was used, where all variables were entered in the first step of the model and the least significant variable eliminated from the next step (if \( P > 0.1 \)). Results are presented for each variable included in the final step.
Figure 3.1. Plasma progesterone concentration (ng·ml⁻¹) at sampling date for female Australian fur seals later observed with pups (closed circles) and of uncertain pregnancy status (open circles). The pregnancy classification threshold is indicated by the dotted line. Approximate phases of the reproductive cycle are indicated by arrows.
Analyses were performed with statistical software SPSS 16.0 (SPSS, Chicago, USA) and means are presented ± 1 SE.

3.3 Results

The mean age of captured females was 7.9 ± 0.3 years (range: 3 – 20 years, n = 207), and 75% of females were aged ≤ 10 years. Mean female STL was 153.3 ± 0.6 cm (range: 131.0 – 174.0 cm) and body mass was 77.5 ± 0.9 kg (range: 45.0 – 110.5 kg). Growth in length follows a von Bertalanffy function with 95% of asymptotic length attained at 5 years of age (Arnould & Warneke 2002), however the present study only measured adults of ≥ 3 years. This portion of the age-length relationship could be approximated with linear regression ($r^2 = 0.43$, d.f. = 206, $P < 0.0001$). Age was also weakly correlated with the BCI (linear regression: $r^2 = 0.03$, d.f. = 206, $P = 0.0174$). Hence, body size and condition tend to increase over a female’s lifetime. Most females were lactating (86 ± 2%) and lactation rates did not vary interannually (Table 3.1). Logistic regression modelling indicated that none of the explanatory variables could predict lactation status (Table 3.2).

The distribution of progesterone concentrations (Fig. 3.1) was analysed by allocating each value to a 1 ng•ml$^{-1}$ class and analysing class frequencies. The highest frequencies of occurrence were in the 0-1 ng•ml$^{-1}$ and 12-13 ng•ml$^{-1}$ classes, suggesting that these represented non-pregnant and pregnant females, respectively. The lowest frequency of occurrence was in the 5-6 ng•ml$^{-1}$ class, and the lowest progesterone concentration for a female observed with a pup in a subsequent breeding season (and, therefore, pregnant when sampled) was 3.1 ng•ml$^{-1}$. The threshold value used to classify females as either pregnant or non-pregnant was therefore set at 3.1 ng•ml$^{-1}$. Females classified as non-pregnant (≤ 3.0 ng•ml$^{-1}$) had a mean progesterone
<table>
<thead>
<tr>
<th>Year</th>
<th>Lactation rate, (n)</th>
<th>Pregnancy rate, (n)</th>
<th>Pupping rate, (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td>88% (58)</td>
<td>85% (58)</td>
<td>48% (23)</td>
</tr>
<tr>
<td>2004</td>
<td>82% (67)</td>
<td>85% (67)</td>
<td>64% (36)</td>
</tr>
<tr>
<td>2005</td>
<td>85% (82)</td>
<td>81% (82)</td>
<td>46% (35)</td>
</tr>
</tbody>
</table>

Table 3.1. Annual reproductive rates with sample sizes in parentheses, and results of $\chi^2$ tests for interannual variation ($d.f. = 2$ in all cases).
concentration of $0.99 \pm 0.1 \text{ ng}\cdot\text{ml}^{-1}$ ($n = 34$), while females classified as pregnant ($\geq 3.1 \text{ ng}\cdot\text{ml}^{-1}$) had a mean of $15.15 \pm 0.6 \text{ ng}\cdot\text{ml}^{-1}$ ($n = 173$). Some of the variation in the progesterone concentrations of pregnant-classified females could be explained by negative correlations with age (linear regression: $r^2 = 0.06$, $d.f. = 172$, $P = 0.0009$) and sampling date (linear regression: $r^2 = 0.05$, $d.f. = 172$, $P = 0.0049$). Overall, $84 \pm 3\%$ of females were estimated to be pregnant, and there was no interannual variation in pregnancy rate (Table 3.1). Logistic regression modelling indicated that age was the only variable that predicted pregnancy, and that younger females were more likely to be pregnant than older ones (Table 3.2). Age-specific pregnancy rates (Fig. 3.2) were higher in ages 3 – 10 than for ages 11 – 16+ years (Mann-Whitney: $U = 48$, $n_1 = 8$, $n_2 = 6$, $P = 0.0007$).

Of the 207 adult females that were captured, 68 were not resighted during the following breeding season, 85 were resighted once, and 94 were resighted $\geq$ twice. Our analyses indicated that females resighted $\geq$ twice were younger (mean difference = 1.6 years), had a higher pregnancy rate (by 17%), and tended to have later capture dates than other females (Table 3.2). Fifty-three percent ($\pm 3\%$) of the females that were resighted $\geq$ twice were determined to have given birth that year. Twenty-seven adult females (29%) were observed with yearling pups and of these, 11 attended to both yearling and new-born pups. Adult female seals resighted with new-born pups were less likely to have been lactating the previous winter than females without new-born pups (Table 3.2). Although age was significantly associated with pregnancy status, age did not influence the likelihood of pupping. In addition, age-specific birth rates (Fig. 3.2) were not correlated with age (linear regression, weighted to sample size: $r^2 = 0.087$, $d.f. = 1$, $P = 0.357$). Estimated age-specific abortion rates (pregnancy minus birth rate) were significantly higher in females aged 3 – 10 years than in those
<table>
<thead>
<tr>
<th>Model</th>
<th>Explanatory Variables</th>
<th>n</th>
<th>$\chi^2$</th>
<th>df</th>
<th>P</th>
<th>Exp(B)</th>
<th>(95% C.I.)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lactation</td>
<td>None</td>
<td>207</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pregnancy</td>
<td>Age</td>
<td>207</td>
<td>33.074</td>
<td>1</td>
<td>&lt;0.001</td>
<td>0.729</td>
<td>(0.646 – 0.823)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Resighting</td>
<td>Overall model</td>
<td>207</td>
<td>22.281</td>
<td>3</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Date</td>
<td>207</td>
<td>6.488</td>
<td>1</td>
<td>0.011</td>
<td>1.015</td>
<td>(1.003 – 1.026)</td>
</tr>
<tr>
<td></td>
<td>Pregnancy</td>
<td>207</td>
<td>4.719</td>
<td>1</td>
<td>0.030</td>
<td>2.859</td>
<td>(1.108 – 7.375)</td>
</tr>
<tr>
<td></td>
<td>Age</td>
<td>207</td>
<td>4.305</td>
<td>1</td>
<td>0.038</td>
<td>0.907</td>
<td>(0.828 – 0.995)</td>
</tr>
<tr>
<td>Pupping</td>
<td>Lactation</td>
<td>94</td>
<td>4.447</td>
<td>1</td>
<td>0.035</td>
<td>0.217</td>
<td>(0.044 – 1.065)</td>
</tr>
</tbody>
</table>

Table 3.2. Binary logistic regression models of lactation, pregnancy, resighting, and pupping likelihoods. *values <1 indicate a negative effect.
Table 3.3. Female characteristics according to incidence of resighting during breeding season. † indicates a significant difference between groups (see Table 2).

<table>
<thead>
<tr>
<th>Resighting Status</th>
<th>n</th>
<th>Pregnancy Rate</th>
<th>n</th>
<th>Pupping Rate</th>
<th>Age (Mean ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>≥ 2 Resights</td>
<td>94</td>
<td>93%†</td>
<td>50</td>
<td>53.2%</td>
<td>7.1 ± 0.3†</td>
</tr>
<tr>
<td>≤ 1 Resight</td>
<td>113</td>
<td>76%†</td>
<td>-</td>
<td>-</td>
<td>8.6 ± 0.4†</td>
</tr>
<tr>
<td>All females</td>
<td>207</td>
<td>84%</td>
<td>-</td>
<td>-</td>
<td>7.9 ± 0.3</td>
</tr>
</tbody>
</table>
Figure 3.2. Age-specific pregnancy rates (circles) and birth rates (diamonds), with sample sizes shown on the axes. Regression equation: Pregnancy rate = \(-0.38\times\text{age}^2 + 2.88\times\text{age} + 89.3, r^2 = 0.96, d.f. = 2, 13, P < 0.001\).
aged 11 – 15 years (Mann-Whitney: $U = 31, n_1 = 8, n_2 = 5, P = 0.008$). Assuming a 1:1 sex ratio at birth (Wickens & York 1997), the estimated fecundity rate (live female offspring per adult female per year: Caughley 1980) is 0.266.

3.4 Discussion

In the present study, a substantial difference was observed between mid-gestation pregnancy rates and birth rates, suggesting that many pregnant Australian fur seals do not carry their foetus to full term. Mid-gestation pregnancy status was influenced by age but not by the energetic correlates of size, condition or lactation status. Surprisingly, age had little influence on birth status. However, differences between age-specific pregnancy and birth rates indicated that older pregnant females are more likely to complete gestation than younger ones. Furthermore, pupping status was influenced by lactation status, suggesting that the cost of provisioning existing young reduces the ability of pregnant females to carry their foetus to term.

3.4.1 Pregnancy rate & influences

Pregnancy likelihood did not decrease with time, suggesting that few abortions occurred during the sampling period. Although some otariid studies have observed declining pregnancy rates between early and late gestation (Arnould et al. 2003; McKenzie et al. 2005; Pitcher et al. 1998), the sampling period of the present study was relatively brief and limited to mid-gestation. Constant pregnancy likelihood also suggests that the positive bias potentially caused by pseudopregnancy was low, as rates of pseudopregnancy decline rapidly in the post-implantation period (Guinet et al. 1998, McKenzie et al. 2005).
Bias may also exist if the threshold concentration of progesterone in plasma for distinguishing between pregnant and non-pregnant females (set at 3.1 ng•ml$^{-1}$ based on our results) was incorrect. Because progesterone concentrations were influenced by age and sampling date, a single threshold value may not accurately indicate pregnancy status for all females. Females with progesterone concentrations slightly below the threshold (e.g. 1.0 – 3.0 ng•ml$^{-1}$, $n = 10$, 5% of sample) or slightly above it (e.g. 3.2 – 5.0 ng•ml$^{-1}$, $n = 7$, 3% of sample) could, therefore, be incorrectly classified. Nevertheless, the estimated pregnancy rate observed in our study (84%) was comparable to those recorded for the conspecific Cape fur seal (78 – 79%, Butterworth et al. 1995; Guinet et al. 1998) and other congenerics for which there are data (71 – 86%, McKenzie et al. 2005; Wickens & York 1997).

The logistic regression model of pregnancy likelihood was not influenced by body size, condition or lactation status, suggesting that energetic factors were not critical to maintaining pregnancy during mid-gestation. This contrasts with Cape fur seals, in which early to mid-gestation pregnancy likelihood was influenced by body condition (Guinet et al. 1998). However, seasonal fluctuations in body condition, presumably related to variation in availability of food, follow different patterns in the 2 subspecies. The body condition of Cape fur seals reaches a minimum during early to mid-gestation and then improves as the breeding season approaches (Guinet et al. 1998). In contrast, the body condition of Australian fur seals is maximal during winter (when females in the present study were sampled) and decreases as breeding is approached, reaching a minimum during the third trimester (Arnould & Warneke 2002), when fetal growth is greatest (Trites 1992). Therefore, pregnancy in Australian fur seals may only become condition-dependent during late-gestation, as has been reported for Steller sea lions (Eumetopias jubatus, Pitcher et al. 1998).
Pregnancy was strongly age-dependent and followed the typical mammalian pattern of being higher in younger females than older ones (Bronson 1989; Wickens & York 1997). Most (88%) 3-year-olds were pregnant, and 59% were lactating, indicating they first attained pregnancy at age 2. It is possible that the pregnancy rates of younger females were positively biased because only those of adult appearance were selected for capture. Hence, smaller females, which are less likely to be sexually mature (Laws 1956), may have been avoided. Furthermore, inferring pregnancy status from lactation status may induce a positive bias (Bester 1995). The 3-year-old pregnancy rate is, however, similar to that previously reported for the species by a study not subject to these biases; where all age classes were randomly sampled and their reproductive tracts inspected directly (Arnould et al. 2003). Although rates of sexual maturity in the younger age classes were not quantified, the high pregnancy rates suggest that Australian fur seals attain sexual maturity earlier than Cape and most other fur seals, which attain it between 4 – 6 years (Butterworth et al. 1995, Wickens & York 1997, Dabin et al. 2004, McKenzie 2007). Similarly divergent rates of body growth have been reported in the fur seals, indicating that Australian fur seals grow and reach maturity relatively rapidly (Arnould & Warneke 2002). While rapid maturity can indicate that resources are plentiful (Bengtson & Laws 1985; Pistorius et al. 2001), the low birth rate observed in the present study and the nutrient-poor nature of the environment (Gibbs 1992) suggests that this was unlikely.

Rapid maturity may instead be adaptive to the ecological niche. In benthic foraging otariids (those that spend most foraging effort near the substrate of continental shelves), the benthos may be inaccessible to juveniles whose small bodies lack sufficient oxygen storage capability for sustained diving (Costa & Gales 2003, Pitcher et al. 2005, Fowler et al. 2006). The Australian fur seal is the only
predominantly benthic foraging fur seal species, a trait characteristic of sea lions, and pups are unable to match the dive durations of adults (Arnould & Hindell 2001, Arnould & Costa 2006, Spence-Bailey et al. 2007). Consequently, pups may not gain nutritional independence until growing to a relatively large size. Rapid growth in a nutrient-poor environment may be achieved via a relatively high degree of maternal investment provided via extended lactation. Australian fur seals often provision pups beyond the 10 month period typical of temperate-latitude otariids (Boyd 1991b, Hume et al. 2001) and in the present study, 29% of females were resighted with yearling pups (i.e. approx. 1 year old). Furthermore, the mid-gestation lactation rate was some 33% higher than the pupping rate, suggesting that provisioning may continue well into a second year. While extended lactation is sometimes seen in fur seals in response to occasional nutritional stress (Gentry & Kooyman 1986), it has been reported as routine in benthic foraging otariids such as Steller sea lions (Pitcher et al. 1998) and Australian sea lions (Neophoca cinerea, Higgins & Gass 1993).

3.4.2 Birth rate & influences

In the present study, 53% of females resighted ≥ twice were observed with newborn pups during the breeding season. However, these females had a 17% higher mid-gestation pregnancy rate than those observed once or not at all, suggesting that the actual birth rate could be lower. Conversely, pups that die or are abandoned soon after birth may not be observed with their mothers, negatively biasing the birth rate. These two potential sources of bias would be conflicting and, therefore, unlikely to greatly influence the results.

Despite a low birth rate, a common sign of nutritional stress in many mammal populations (Bronson 1985), the likelihood of pupping was not influenced by body
condition. Mass, however, was measured during mid-gestation and may not reflect late-gestation mass when energetic demand is greatest and body condition is minimal (Arnould & Warneke 2002). Spontaneous abortions may occur in females unable to maintain sufficient body condition during late-gestation and, hence, energy income (foraging) at that time may be more important than energy capital (lipid reserves) accumulated previously (Boyd 2000). In a concurrent study performed from 2003-07, the mean body condition of adult females during winter was correlated with pup production, earlier breeding, and oceanographic variables, indicating that reproductive success was indeed influenced by environmentally-mediated body condition (Chapter 2). Therefore, to determine the influence of condition on fecundity, mass needs to be measured close to parturition.

Lactating females were less likely to pup than non-lactating ones, suggesting that the demands of provisioning a pup may limit resources available to the foetus. Lactating otariids may produce smaller pups and have a lower late-gestation pregnancy rate than non-lactating mothers (Lima & Paez 1995, Pitcher et al. 1998). In light of their relatively rapid growth and maturity (this paper, Arnould & Warneke 2002) and limited foraging ability of juveniles (Spence-Bailey et al. 2007), it may be adaptive for Australian fur seals and other benthic foragers to continue provisioning juveniles until they are large enough to forage independently, perhaps at the expense of successful gestation.

The 31% difference between rates of pregnancy and rates of pupping suggests that a substantial amount of abortion of gestation occurred during the study. Because the likelihood of pregnancy did not decline with sampling date, failures probably occurred after the sampling period by late-gestation abortion, still-births or abandonment of pups at birth. Aborted foetuses are commonly observed in Australian
fur seal colonies, particularly during the energetically-expensive third trimester (J. Gibbens, personal observation). Similar rates of spontaneous abortion have been reported in New Zealand fur seals (35%, McKenzie et al. 2005) and Steller sea lions (40%, Pitcher et al. 1998), suggesting that pregnancy rates may not be reliable indicators of fecundity in otariid seals, except when sampling occurs very close to parturition.

Interestingly, abortion was more common to younger seals. Although birth rates were similar across all age classes, higher pregnancy rates were observed in younger seals (3 – 10 years; 92%) than older seals (11+ years; 57%), suggesting that reproduction in younger seals is regulated by late-term abortion. In contrast, most older seals pregnant when captured in mid-gestation were later resighted with a pup. Fertilization rates are typically high in otariids (Guinet et al. 1998, Lunn & Boyd 1993, McKenzie et al. 2005) presumably because resource availability at the time of maximum energy demand is largely unpredictable (Boyd 1991b). Boyd (1991b) suggested that nutritionally stressed pinnipeds avoid reproductive costs by failing to implant after diapause, thereby completely avoiding gestation. However, late-gestation abortion has been proposed as a more common strategy in temperate-latitude otariids (McKenzie et al. 2005, Pitcher et al. 1998). In the present study, the latter strategy was evident among younger females, while older ones may be more prone to reproductive failure at the time of fertilization, implantation, or early gestation.

3.4.3 Demographic implications
The birth rate estimated by the present study was substantially lower than birth rates in rapidly increasing populations of New Zealand fur seals (67–70%, Goldsworthy &
Shaughnessy 1994, McKenzie 2006), subantarctic fur seals (A. tropicalis, 79–84%, Hes & Roux 1983, Bester 1995) and Antarctic fur seals (A. gazella, 68%, Lunn et al. 1994, Wickens & York 1997). The birth rate from our study was similar to those reported in steady or declining populations of Australian sea lions (birth rate: 71% per 17.6 mo = 48% p.a, Higgins & Gass 1993) and Steller sea lions (late-gestation pregnancy rate: 55%, Pitcher et al. 1998). Although some fur seals have demonstrated very low birth rates during years of anomalous food availability (e.g. McKenzie et al. 2005), we do not believe this occurred during the present study as pup production from 2003 – 5 was close to the mean of censuses conducted from 1997 – 2007 at Kanowna Island (Chapter 2). Therefore, the fecundity of Australian fur seals is likely to be consistently low and be a proximate factor limiting the recovery rate of the population following the cessation of commercial sealing in the 1830s (Kirkwood et al. 2005, Ling 1999). During the past 2-3 decades, however, this population has doubled in size (Kirkwood et al. 2005). Because fecundity has not changed greatly during this period (1971-2 late-gestation pregnancy rate: 55%, Arnould et al. 2003), it is unlikely that resource availability for pregnant females has altered. Therefore, the population may not have reached density dependence and may continue to grow in the near future.

3.5 Literature Cited


Female Australian fur seals, Kanowna Island, June 2005
CHAPTER 4

AGE-SPECIFIC GROWTH, SURVIVAL AND POPULATION DYNAMICS OF FEMALE AUSTRALIAN FUR SEALS

Abstract: Post-sealing population recovery rates of fur seals and sea lions have differed markedly, perhaps due to habitat type. Australian fur seals *Arctocephalus pusillus doriferus* employ a benthic foraging mode similar to sea lions, and have exhibited similarly slow population recovery. Nonetheless, the population doubled in recent decades, suggesting a recent change in demographic rates. In the present study, the frequency and size of known age females (*n* = 297) were used to create body growth and survivorship models. These were compared with models obtained in the 1970s before the recent population increase. Body growth, which is relatively rapid in comparison to other fur seal species, remains unchanged since the 1970s, suggesting that density-dependent effects are absent despite the population increases. Adult survival rates (weighted mean: 0.885) have increased greatly since the 1970s and are the likely mechanism of the recent increases. Total population abundance was estimated to be 4.5 times that of pups. Australian fur seals display high survivorship, rapid body growth, low fecundity and low population growth rates, characteristics typical of benthic foraging sea lions rather than other fur seals.

4.1 Introduction

During the commercial sealing era of 1790 – 1850, many populations of otariids were hunted to very low numbers (Bonner 1994). Since then, the recovery rates of fur seal and sea lion populations have differed markedly (Costa et al. 2006). It has recently been suggested that these divergent population dynamics are in fact associated with habitat type rather than phylogeny (Arnould & Costa 2006). Epipelagic foragers (most fur seals) exploit the upper portion of upwellings and frontal structures which are typically rich in nutrients and their populations recovered rapidly to large sizes. In contrast, benthic foragers (most sea lions) hunt near the benthos of continental shelves which are typically of lower productivity. Their populations are an order of magnitude smaller and most are stable or declining (Arnould & Costa 2006, Costa et al. 2006).

Australian fur seals *Arctocephalus pusillus doriferus* are one of the few exceptions to this pattern and are the only fur seal species known to use benthic foraging exclusively (Arnould & Hindell 2001, Arnould & Kirkwood 2008). Their status as conspecific to epipelagic foraging Cape fur seals *A. p. pusillus*, from which they separated some 12,000 years ago (Wynen et al. 2001, Deméré et al. 2003), makes them an ideal candidate in which to investigate the effects of habitat type on population dynamics while controlling for phylogeny.

The Cape fur seal population forages in the nutrient-rich Benguela upwelling off southwestern Africa (Kooyman & Gentry 1986) and recovered rapidly to a size of approximately 2 million individuals (Butterworth et al. 1995). In contrast, the Australian fur seal population exploits the nutrient-poor continental shelf of Bass Strait (Gibbs 1992, Arnould & Hindell 2001, Arnould & Kirkwood 2008) and recovered relatively slowly to approximately 100,000 animals (Kirkwood et al. 2005). Curiously, half of the abundance of the Australian fur seal population was attained in
the last 2 decades (Kirkwood et al. 2005). Prior to this, no growth had been observed from 1945 – 1986 and the population was thought to have stabilised at a quarter of its estimated pre-sealing size (Pearse 1979, Warneke & Shaughnessy 1985, Warneke 1988). The population’s recovery is presumably constrained by its reproductive rate, which is the lowest observed in fur seals and is similar to rates recorded in sea lions (Chapter 3). Yet, the current reproductive rate is similar to that reported in the 1970s, such that the recent doubling in population abundance can not be attributed to increased fecundity (Arnould et al. 2003).

The recent population increases have been inferred from trends in pup production because unquantifiable numbers of adults and juveniles spend time at sea during which they are invisible to counters (Berkson & DeMaster 1985). Pup production has also been used to estimate population abundance, however this is dependent on the ratio of pups to non-pups in the population (Wickens & Shelton 1992), which has not been quantified in Australian fur seals. Previously, ratios derived from other pinniped species (e.g. Harwood & Prime 1978) have been used (Pemberton & Kirkwood 1994, Shaughnessy et al. 2002, Pemberton & Gales 2004, Kirkwood et al. 2005). However, the ratio is influenced by the fecundity rate, and because fecundity is relatively low in Australian fur seals, the ratios of other species may result in inaccurate abundance estimates (Wickens & Shelton 1992, Chapter 3).

The Australian fur seal population now represents the largest marine predator biomass in the Bass Strait ecosystem, raising concerns about increased rates of conflict with the local commercial fishing industry (Pemberton & Shaughnessy 1993, Goldsworthy et al. 2003). However, the current lack of demographic information hinders understanding of its dynamics, abundance and management requirements. Demographic information obtained for other fur seals is extensive (Wickens & York
1997) but may not be appropriate for modelling the dynamics of benthic foraging populations. Demographic information for benthic foraging species is scarce and largely limited to the Steller sea lion *Eumetopias jubatus* (Holmes & York 2003, Eberhardt *et al.* 2005). To better understand the Australian fur seal population and the effects of a benthic foraging mode on population dynamics, there is a need for the basic parameters of survival and body growth rates to be determined. Therefore, the aims of this study were to i) determine female age structure, ii) derive a survivorship model from the age structure, iii) model female body growth, iv) compare the models with ones obtained prior to the recent population increase, and v) investigate the abundance and dynamics of the Australian fur seal population.

4.2 Methods

The study was conducted between 2003 – 05 at Kanowna Island (39°10’ S 146°18’ E), northern Bass Strait, the site of an Australian fur seal colony with annual pup production of approximately 3550 and median birth date of November 23 (Chapter 2). Breeding occurs all around the island but is concentrated in two main areas comprising >75% of the colony (J. Gibbens *unpublished data*). Captures of juvenile and adult females (≥1 year old) were conducted in the main breeding areas from March – October, with 84% of captures occurring in winter (June – August). Female pups (<1 year) were captured from January – May.

Adult females were selected at random from those able to be approached while causing minimal disturbance to other seals in the colony. The density and distribution of seals and the appropriate directions of approach change constantly due to weather variations and, therefore, the selection technique is unlikely to cause substantial bias. Individuals were captured using a modified hoop net (Fuhrman Diversified, Seabrook, USA) and given an intramuscular dose of Midazolam (0.15mg/kg; Hypnovel®; Roche
Products Pty Ltd., Dee Why, Australia) to reduce stress and induce gas anaesthesia (Isoflurane; Gales & Mattlin 1998). Seals were transferred to a flat platform in the prone position, weighed using a spring scale (200 ± 0.5 kg; Salter, Peterborough, UK), and measured for straight-line length (STDL) and axillary girth (AXG) using a metal tape measure (Bonner & Laws 1993). To enable comparison of the prone STDL measurements with earlier records in which length was measured with animals supine (Arnould & Warneke 2002), a subsample of adults (n = 50) were measured in both positions. Individually numbered plastic tags (Super Tags, Dalton I.D. Systems Ltd., Henley-on-Thames, UK) were placed in the trailing edges of both fore-flippers. After injection of local anaesthetic (10 mg lignocaine hydrochloride; Xylocaine: AustraZeneca Pty. Ltd., North Ryde, Australia) in the gum, dental elevators were used to extract a first postcanine tooth from the lower jaw, which was stored in 70% ethanol until analysis.

Pups and yearlings (age classes 0 and 1 year) were targeted separately to adults because they tend to form distinct aggregations. They were selected at random, caught by hand or hoop net and sedated with a low dose of Midazolam (0.15mg/kg I.M.). This allowed measurement of STDL and AXG with a tape measure, and of mass with a spring scale (50 ± 0.1 kg; Salter, Peterborough, UK). Tooth samples were not needed because the sizes of pups and yearlings are distinct.

4.2.1 Ageing

Extracted teeth were rinsed in flowing water for ≥6 hours to remove ethanol, then immersed in a hydrochloric acid decalcifying agent (RDO; Apex Engineering Products Corporation, Illinois, USA) until flexible to the touch (8 – 24 hours). Decalcified teeth were rinsed in deionised water for ≥6 hours, embedded in a
mounting compound, then ≥6 sections of 25µm thickness were cut on a freezing microtome at -10°C. After staining with haemotoxylin and fixing with 5% ammonia solution, the 6 sections with best definition were mounted on glass slides using a mounting compound (DPX; Sigma-Aldrich Pty. Ltd., Sydney, Australia) and glass coverslip. Sections were viewed with transmitted light on a stereo microscope at 4 – 10x magnification with a rotatable polarising filter. Pairs of dark and light bands in the tooth cementum each indicate one year of growth in the species (Oosthuizen 1997, Arnould et al. 2003) and were counted to determine age at the previous birthday. Five blind readings were made for each tooth and the median value used as the final age. A single person performed all readings to reduce inter-reader variability and because accuracy increases with reader experience (McCann 1993).

4.2.2 Statistical analyses

For age-specific growth analyses, ages were calculated to one decimal place by estimating the period between the animal’s capture and its previous birthday. All seals were assigned a birth date of November 23 as 90% of births at the study site occur within 14 days of this date (Chapter 2). Growth in STDL (cm) and mass (kg) were modelled using the von Bertalanffy function (von Bertalanffy 1938), which was found to best describe body growth in a 1970s sample of female Australian fur seals (Arnould & Warneke 2002).

Adult ages (n3-20) from the 3 years of captures were pooled, grouped into discrete annual age classes, and used to construct an age structure. Frequencies of pups and yearlings were not used because they were captured in a separate sampling regime. Instead, expected pup frequency (N0) was estimated as \( \sum n_x \cdot B_x \), where \( B_x \) represents female birth rate (Barlow & Boveng 1991). Birth rates were estimated in a
concurrent study from observations of marked females and their attendant offspring (Chapter 3). Although mid-gestation pregnancy rates of these females were age-dependent, their birth rates were not. Therefore, a single birth rate was used for adults (3+ years) in the present study (0.532) which, assuming a 1:1 sex ratio at birth, is a female birth rate of 0.266 (Table 2).

Because \( n_3 \) was possibly under-represented, it was treated as missing and initially estimated as \( N_3 = 2n_4 - n_5 \). The age structure was then fitted with Siler’s 5 parameter competing risk mortality model (Siler 1979) scaled to longevity, which was estimated as the 99th percentile of \( n_{3-20} \) (Barlow & Boveng 1991). The frequencies of \( N_0 \) and \( N_3 \) were then re-estimated and the fitting repeated until these values did not change between iterations (Barlow & Boveng 1991). The pup to population abundance conversion factor was estimated from the model as \((\sum N_x / N_0)\).

Survivorship at age \( x \) (\( l_x \)) was derived by scaling the modelled age distribution to pup frequency (\( N_x / N_0 \)) and then adjusting for population growth by multiplying by the correction factor \( e^{rx} \), where \( r \) is the exponential growth rate and \( e \) is the base of natural logs (Caughley 1980, Sinclair et al. 2006). The exponential growth rate was estimated from pup production censuses (Berkson & DeMaster 1985) at the study site from 1997 – 2005 (Chapter 2), and calculated as:

\[
\hat{r} = \frac{\sum Ct - (\sum C) (\sum t)/c}{\sum t^2 - (\sum t)^2/c}
\]

where \( C \) is the natural log of the count, \( t \) is time in years and \( c \) is the number of counts (Caughley 1980). This trend was assumed to have been constant during the lifetime of all sampled females.
Population projections were made using the Leslie matrix model:

\[ N_{t+1} = AN_t \]

where \( N_t \) is a vector describing the female age structure at time \( t \) and \( A \) is a population-projection matrix parameterized for a birth-pulse population with post-breeding census (Caswell 1989). The observed and estimated frequencies \( n_{4.20} \) and \( N_0 \) were used as the initial age distribution. Matrix fecundity rates were calculated as the product of survival and female birth rates \( (P \cdot B_x) \). Eigenvalues and elasticities were calculated using the PopTools plugin for Microsoft Excel (Hood 2008). Growth and survivorship models were fitted using least-squares nonlinear regression in SPSS (SPSS 16.0, Chicago, USA), which provided model parameters with bootstrapped estimates of standard error.

4.3 Results

4.3.1 Growth

A total of 294 females were captured, encompassing an age range of 1 month – 20.6 years. Of these, 54 were classified as pups and juveniles (0 < 3 years) and 240 as adults (≥ 3 years, \( x = 7.83 \) years).

Standard length of females ranged from 67.5 – 174.0 cm and its age-specific increase was accurately modelled by the von Bertalanffy function \( (r^2 = 0.945, d.f. = 293, P < 0.001, \text{Fig. 4.1a}) \). Females reached 87% and 95% of asymptotic length at 3.6 and 6.3 years, respectively (Table 4.1). Mass (range = 7.8 – 110.5 kg) increased at a slower rate than STDL (Fig 4.1b), with 95% of asymptotic mass being obtained at 9.8 years \( (r^2 = 0.899, d.f. = 293, P < 0.001) \). Adult mass (3+ years) ranged from 45.5 – 110.5 kg \( (x = 78.2 \pm 0.81) \). Mass was correlated with STDL \( (r^2 = 0.98, n = 293, \)
Figure 4.1. Age-length (a) and age-mass (b) data for female Australian fur seals with fitted von Bertalanffy growth functions.
Table 4.1. Parameter estimates for von Bertalanffy growth functions, where \( K \) = growth constant, \( t_0 \) = hypothetical time at which length or mass = 0.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>n</th>
<th>Asymptote ± SE</th>
<th>K ± SE</th>
<th>( t_0 ) ± SE</th>
<th>Age at 95% of asymptote</th>
<th>( r^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length</td>
<td>295</td>
<td>160.02 ± 0.696</td>
<td>0.372 ± 0.016</td>
<td>-1.654 ± 0.084</td>
<td>6.3 years</td>
<td>0.945</td>
</tr>
<tr>
<td>Mass</td>
<td>293</td>
<td>87.97 ± 1.169</td>
<td>0.343 ± 0.016</td>
<td>-2.104 ± 0.124</td>
<td>9.8 years</td>
<td>0.899</td>
</tr>
</tbody>
</table>
$P < 0.0001$) and AXG ($r^2 = 0.95$, $n = 293$, $P < 0.0001$) according to power regressions. Measurements of STDL taken in the prone position were shorter than those taken in the supine position by $1.2 \pm 0.3\%$, $t = 3.973$, $d.f. = 49$, $P < 0.0002$).

4.3.2 Survivorship and population dynamics

Longevity was calculated as 17 years, and the survivorship model scaled accordingly. The survivorship model was a good fit to the observed adult age frequencies ($n_{4-20}$) and estimated pup frequency ($N_0$) ($r^2 = 0.983$, $d.f. = 13$, $P < 0.001$, Fig 2). Model parameters ($\pm$ SE), using the notation of Barlow & Boveng (1991), were: $a_1$: 7.562 $\pm$ 2.047, $a_2$: -0.473 $\pm$ 0.485, $a_3$: 0.186 $\pm$ 0.337, $b_1$: 6.925 $\pm$ 3.497, $b_3$: 4.374 $\pm$ 1.162. The relative abundance of all age classes compared to that of pups ($\sum N_i / N_0$) was 6.02.

Using the direct pup count data from Chapter 2 ($n = 7$), pup production at the study site increased at 2.2% p.a. ($r = 0.022$) between 1997 - 2005. The modelled age distribution was scaled to pup abundance and adjusted for this trend, resulting in the annual age-specific survivorship and survival rates ($P_x$) presented in the life table (Table 4.2). The mean adult ($\geq$ 3 years) survival rate, weighted to $N_x$, was 0.885.

The Leslie matrix model projected a stable population growth rate ($r \pm 0.001$) within 2 years. The dominant eigenvalue of 1.0221 suggests that the population will grow at 2.2% p.a. ($r = 0.022$). Elasticity analysis indicated that $r$ is more sensitive to changes in survival rates than fecundity rates (Fig 4.3). Adult survival rates were up to 6.9 times more influential to $r$ than fecundity rates.

4.4 Discussion

Age-size and age-frequency data were accurately modelled with non-linear functions, allowing analysis of age-specific body growth, survivorship, relative pup abundance
Figure 4.2. Age structure of female Australian fur seals, 2003-5. Observed frequencies of adults ($n_{3,20} = 239$) and estimated pup frequency ($N_0$) shown by columns. Modelled frequencies represented by line. $n_3$ excluded from model due to underrepresentation.
<table>
<thead>
<tr>
<th>Age</th>
<th>Observed Frequency</th>
<th>Modelled Frequency</th>
<th>Survivorship ( \left( \frac{N_x}{N_0} \cdot e^{0.022x} \right) )</th>
<th>Survival Rate</th>
<th>Female Birth Rate(^{‡})</th>
<th>Fecundity</th>
<th>( P_x \cdot B_x )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>-</td>
<td>66.0(^{‡})</td>
<td>1.000</td>
<td>0.720</td>
<td>0</td>
<td>0</td>
<td>0.000</td>
</tr>
<tr>
<td>1</td>
<td>-</td>
<td>46.5</td>
<td>0.720</td>
<td>0.811</td>
<td>0</td>
<td>0</td>
<td>0.000</td>
</tr>
<tr>
<td>2</td>
<td>-</td>
<td>36.9</td>
<td>0.584</td>
<td>0.876</td>
<td>0</td>
<td>0</td>
<td>0.000</td>
</tr>
<tr>
<td>3</td>
<td>20(^{\ast})</td>
<td>31.6</td>
<td>0.512</td>
<td>0.919</td>
<td>0.266</td>
<td>0.255</td>
<td>0.000</td>
</tr>
<tr>
<td>4</td>
<td>29</td>
<td>28.4</td>
<td>0.470</td>
<td>0.945</td>
<td>0.266</td>
<td>0.264</td>
<td>0.251</td>
</tr>
<tr>
<td>5</td>
<td>27</td>
<td>26.3</td>
<td>0.444</td>
<td>0.958</td>
<td>0.266</td>
<td>0.263</td>
<td>0.255</td>
</tr>
<tr>
<td>6</td>
<td>25</td>
<td>24.6</td>
<td>0.425</td>
<td>0.960</td>
<td>0.266</td>
<td>0.263</td>
<td>0.255</td>
</tr>
<tr>
<td>7</td>
<td>24</td>
<td>23.1</td>
<td>0.409</td>
<td>0.954</td>
<td>0.266</td>
<td>0.262</td>
<td>0.254</td>
</tr>
<tr>
<td>8</td>
<td>17</td>
<td>21.6</td>
<td>0.390</td>
<td>0.940</td>
<td>0.266</td>
<td>0.261</td>
<td>0.250</td>
</tr>
<tr>
<td>9</td>
<td>23</td>
<td>19.9</td>
<td>0.366</td>
<td>0.918</td>
<td>0.266</td>
<td>0.260</td>
<td>0.244</td>
</tr>
<tr>
<td>10</td>
<td>15</td>
<td>17.8</td>
<td>0.336</td>
<td>0.887</td>
<td>0.266</td>
<td>0.257</td>
<td>0.236</td>
</tr>
<tr>
<td>11</td>
<td>20</td>
<td>15.5</td>
<td>0.298</td>
<td>0.847</td>
<td>0.266</td>
<td>0.254</td>
<td>0.225</td>
</tr>
<tr>
<td>12</td>
<td>13</td>
<td>12.8</td>
<td>0.253</td>
<td>0.797</td>
<td>0.266</td>
<td>0.250</td>
<td>0.212</td>
</tr>
<tr>
<td>13</td>
<td>8</td>
<td>10.0</td>
<td>0.201</td>
<td>0.737</td>
<td>0.266</td>
<td>0.246</td>
<td>0.196</td>
</tr>
<tr>
<td>14</td>
<td>5</td>
<td>7.2</td>
<td>0.148</td>
<td>0.664</td>
<td>0.266</td>
<td>0.242</td>
<td>0.177</td>
</tr>
<tr>
<td>15</td>
<td>7</td>
<td>4.7</td>
<td>0.099</td>
<td>0.581</td>
<td>0.266</td>
<td>0.240</td>
<td>0.155</td>
</tr>
<tr>
<td>16</td>
<td>3</td>
<td>2.7</td>
<td>0.057</td>
<td>0.489</td>
<td>0.266</td>
<td>0.234</td>
<td>0.130</td>
</tr>
<tr>
<td>17</td>
<td>1</td>
<td>1.3</td>
<td>0.028</td>
<td>0.390</td>
<td>0.266</td>
<td>0.232</td>
<td>0.104</td>
</tr>
<tr>
<td>18</td>
<td>0</td>
<td>0.5</td>
<td>0.011</td>
<td>0.292</td>
<td>0.266</td>
<td>0.229</td>
<td>0.078</td>
</tr>
<tr>
<td>19</td>
<td>1</td>
<td>0.1</td>
<td>0.003</td>
<td>0.201</td>
<td>0.266</td>
<td>0.227</td>
<td>0.053</td>
</tr>
<tr>
<td>20</td>
<td>1</td>
<td>0.0</td>
<td>0.001</td>
<td>0.000</td>
<td>0.266</td>
<td>0.226</td>
<td>0.000</td>
</tr>
</tbody>
</table>

Table 4.2. Life table for female Australian fur seals \(^{†}\)Excluded from model.  
\(^{\dagger}\)Estimated as \( \sum N_x \cdot B_x \). \(^{‡}\)From Chapter 3.
Figure 4.3. Elasticities of matrix survival rates (circles) and fecundity rates (squares), indicating their relative influence to the population growth rate.
and population dynamics. Several biases may exist in this data. For example, errors in age readings are possible, particularly by underestimation of older samples (≥9 years, Oosthuizen 1997, Arnould & Warneke 2002). As known-age tooth samples were unavailable for the present study, this potential bias in unquantified. However, a previous study found blind readings of known-age Australian fur seal teeth to be largely accurate (Arnould & Warneke 2002). Secondly, samples taken at breeding colonies can be unrepresentative of the population if non-breeding animals are absent. Yet many of the adults captured for the present study were resighted during the breeding season without pups (47%, Chapter 3) and, therefore, the sample was not limited to breeding females. Lastly, only females of adult appearance were selected in the adult capture procedure such that small, immature 3-year-olds may have been under-sampled. The length, mass and fecundity estimates for that age class, although potentially positively biased, were similar to those reported in a study that collected Australian fur seals at random (Arnould & Warneke 2002, Arnould et al. 2003, Chapter 3) and, therefore, are unlikely to greatly bias the model outputs.

4.4.1 Growth

Comparison of mass and length measurements (accounting for prone-supine differences) with those recorded at the nearby Seal Rocks colony (125 km away) in 1971-2 (Arnould & Warneke 2002) showed all growth model parameters to be statistically indistinguishable (t tests, $P > 0.08$ in all cases, Fig 4.4). This suggests that despite the doubling in population abundance that has occurred since the 1970s (Kirkwood et al. 2005), intra-specific competition has not increased sufficiently to limit food availability and individual growth (Fowler 1990). Therefore, there is no evidence of carrying capacity being attained.
Figure 4.4. Comparison of age-specific growth models of length (a) and mass (b) for Australian fur seals in 2003-5 (solid lines) and 1971-2 (dotted lines: Arnould & Warneke 2002).
As first observed in the 1970s population, Australian fur seals have a higher asymptotic mass and length than other fur seals, confirming their status as the largest-bodied species (Warneke & Shaughnessy 1985, Wickens & York 1997, Arnould & Warneke 2002). Benthic foraging otariids are thought to attain larger body sizes because it confers a greater aerobic dive limit, allowing deeper, longer dives (Costa et al. 2004). This has been suggested as the reason for sea lions being generally larger-bodied than fur seals (Arnould & Costa 2006). Australian fur seals are the only fur seal species known to employ an exclusively benthic foraging mode (Arnould & Hindell 2001) which may have selected for increased body size since migration from the Benguela upwelling region some 12,000 years ago (Wynen et al. 2001).

Female growth rates were relatively rapid, with 87% of asymptotic length attained at age 3, which coincides with their age of sexual maturity (2 – 3 years, Chapter 3) and, therefore, with the observation of Laws (1956) that puberty is attained at this length. Similarly, Steller sea lions attain sexual maturity and 87% of asymptotic length at 3 years (Winship et al. 2001) while fur seals grow more slowly, usually attaining maturity and comparable lengths at 4 – 6 years (Butterworth et al. 1995, Wickens & York 1997, Dabin et al. 2004, McKenzie et al. 2007a, b). Given that the shelf habitats of benthic foragers are generally less nutrient-rich than the upwellings and oceanic fronts exploited by epipelagic foragers (Lalli & Parsons 1993), it may seem unexpected that benthic foragers grow more rapidly. However, reaching the benthos is difficult for juvenile benthic foragers due to the restrictions of body size (Pitcher et al. 2005, Fowler et al. 2006, Richmond et al. 2006, Spence-Bailey et al. 2007). Rapid growth may therefore be adaptive by minimising the period of sub-optimal foraging efficiency encountered between weaning and maturity (Arendt 1997). The relatively long suckling period common to Australian fur seals
and sea lions may act to further minimise this period and increase juvenile growth rates (Pitcher et al. 1998, Hume et al. 2001).

4.4.2 Survivorship

The matrix model projected the same population growth rate as calculated from recent pup production estimates, suggesting that the model parameters were realistic (Seber 1982). Inter-specific comparisons of survival rates are difficult due to age-specific variations and the variety of methods used to derive them, however adult otariids generally display high survival rates. Adult survival rates reported in the present study were similar to those reported in Cape fur seals (Butterworth et al. 1995), northern fur seals Callorhinus ursinus (Barlow & Boveng 1991), New Zealand fur seals Arctocephalus forsteri (McKenzie 2006), South American fur seals Arctocephalus australis (Lima & Paez 1997), Antarctic fur seals Arctocephalus gazella (Boyd et al. 1995) and Steller sea lions (Calkins & Pitcher 1982). Therefore, while benthic foraging otariids may encounter lower nutrient availability than epipelagic foragers, this does not appear to substantially lower adult survival rates. Juvenile survival rates in the present study were relatively high, however these were not measured directly and should be treated cautiously. Survival rates declined rapidly in age classes > 10 years and a similar age-specific decline in pregnancy rates (but not birth rates) was observed in a concurrent study, perhaps indicative of senescence (Chapter 3).

High survival rates have not always been observed in Australian fur seals. A 1970s study reported an adult female age structure with relatively low frequencies in the middle age classes (5 – 11 years, Fig 4.5, Arnould et al. 2003). Survival rates were substantially lower than those of the present study (weighted adult mean: 0.498, compared with 0.885) and a rapid population decline of 8 – 24% p.a. was projected.
Figure 4.5. Comparison of observed adult female age frequencies of Australian fur seals at (a) Kanowna Island, 2003 – 5 (n = 239) and (b) Seal Rocks, 1971 – 2 (n = 156: Arnould et al. 2003).
(Arnould et al. 2003). The matrix elasticities of the present study (Fig 4.3) indicate that the population growth rate is up to 7 times more sensitive to changes in adult survival rates than fecundity rates, which is a general feature of fur seals and other large mammals (Wickens & York 1997, Oli & Dobson 2003). Therefore, the 0.387 increase in mean annual survival rates over the last 3 decades is the likely mechanism of the observed doubling in population abundance. In the same period, body growth and fecundity rates remained unchanged, suggesting that increased survivorship has resulted from the relaxation of an exogenous source of mortality rather than increased resource availability (Arnould & Warneke 2002, Arnould et al. 2003, Chapters 3, 4).

It has previously been suggested that fishers routinely culled seals because they were perceived as competitors and that this was particularly intense during the 1960s (Arnould et al. 2003). Australian seals were not protected from hunting until 1975 (Shaughnessy 1999). Until 1983, fishers in Victorian waters (northern Bass Strait) could legally shoot “nuisance seals” interfering with fishing operations, and anecdotal evidence suggests this was common (R.M. Warneke unpublished data). At least 8% of tagged juveniles retrieved as carcases during the 1970s had gunshot wounds (Warneke 1975). Introduction of protective legislation therefore coincides with increased survival and population growth.

4.4.3 Population abundance

The survivorship model indicated that total female abundance was 6.0 times greater than that of female pups. This is a greater difference than the 3.5 – 4.5 range estimated for grey seals (*Halichoerus grypus*, Harwood & Prime 1978) and frequently used as a conversion factor in both sexes of Australian fur seals (Pemberton & Kirkwood 1994, Shaughnessy et al. 2002, Pemberton & Gales 2004, Kirkwood et al.)
2005). It is also higher than the 3.95 factor estimated by scaling the demographic rates of female northern, Antarctic and South American fur seals to the maximum observed ages of male and female Australian fur seals (Goldsworthy et al. 2003). The conversion factor is influenced by the fecundity rate used to estimate $N_0$ (Wickens & Shelton 1992), which was estimated as 0.45 by Harwood & Prime (1978) and 0.39 by Goldsworthy et al. (2003: calculated from Barlow & Boveng 1991 and Lima & Paez 1997). These are higher fecundity rates than used in the present study (0.266) and accordingly, pups were estimated to comprise a smaller proportion of the female Australian fur seal population.

However, a conversion factor of 6.0 may not be suitable for the whole population because breeding male otariids experience additional mortality risks (e.g. fighting and fasting) and, consequently, have substantially lower survivorship than females (Butterworth et al. 1995, Wickens & York 1997). Reports of male survivorship are scarce, but in Steller sea lions and northern fur seals, female:male sex ratios in the non-pup component of the population were estimated as 2.13:1 and 2.77, respectively (Lander 1981, Calkins & Pitcher 1982, Trites & Larkin 1996). Applying the mean of these ratios to the survivorship model of the present study results in a pup:population conversion factor of 4.5. In the absence of survivorship data in male Australian fur seals, this factor is suggested for converting pup production to a population abundance estimate. The factor is comparable to ones previously used for the Australian fur seal population (Harwood & Prime 1978, Goldsworthy et al. 2003), which, although based on inappropriately high fecundity, ignored the potential for a highly female-biased sex ratio in non-pups.
4.4.4 Population dynamics

Stable population growth was projected rapidly (in 2 years) by the matrix model although this could be somewhat overestimated due to modeled values for \( N_{1,3} \) being used in the initial age structure. Nonetheless, the projection infers a largely stable adult age structure as would result from a period of constant survival and fecundity and survival rates (Caughley 1980). Survival rates were adjusted for the trend at the study site from 1997 – 2005 as information prior to this was unavailable. Slightly higher trends were observed at some colonies in the 1990s (Shaughnessy et al. 2002, Kirkwood et al. 2005) and if this was the case at the study site, the survival rates of older age classes (8+ years) could be negatively biased.

The similar survival rates of adult otariids suggests that fecundity is the characteristic distinguishing rapidly- and slowly-recovering populations. In benthic foraging Steller sea lions, late-gestation pregnancy rates of 0.63 – 0.55 have been recorded (Pitcher et al. 1998), similar to the late-gestation and birth rates of 0.55 and 0.53, respectively, recorded in Australian fur seals (Arnould et al. 2003, Chapter 3) and the 0.48 birth rate recorded in Australian sea lions (when converted to an annual rate; Higgins & Gass 1993). These rates are lower than birth rates recorded in epipelagic foraging New Zealand fur seals (0.699, McKenzie 2006), Antarctic fur seals (0.68, Lunn et al. 1994, Wickens & York 1997) and subantarctic fur seals *Arctocephalus tropicalis* (0.84, Hes & Roux 1983), suggesting that epipelagic foragers achieve higher rates of birth and, consequently, population growth.

Accordingly, Australian fur seals are unlikely to recover at the rates of 10 – 15% p.a. reported in other fur seals (Wickens & York 1997).

Species-wide pup censuses conducted in 2002 and 2007 observed a similar trend to that obtained by the present study (2.0% p.a.; R. Kirkwood personal
communication 2009). Using this growth rate, a 4.5 pup:population conversion factor and the 2007 pup production estimate of 21,882 (R. Kirkwood personal communication 2009), the estimated pre-sealing population size of 200,000 (Ling 2002) is projected to be reached in 2043. However, growth generally slows as a population becomes density dependent (Sinclair et al. 2006) and, furthermore, the current environmental carrying capacity is unknown. The commercial fishing industry may have lowered carrying capacity by altering trophic dynamics since the pre-sealing era (Goldsworthy et al. 2003). However, fishing has caused concurrent declines in predator populations, particularly that of the great white shark *Carcharodon carcharias* (Malcolm et al. 2001), and their roles in regulating the prehistoric seal population are unknown. Furthermore, a sympatric population of New Zealand fur seals is currently recovering at up to 11% p.a. and recolonising Bass Strait, which could introduce competition for prey and breeding sites (Arnoold et al. 2000, McKenzie 2006).

The prey, body condition and pup production of Australian fur seals are influenced by local oceanography (Kirkwood et al. 2008, Chapter 2), however it is difficult to predict how this may affect future population dynamics (Harley et al. 2006). Local oceanography is linked to the Southern Oscillation (Middleton & Bye 2007) and extremes of the oscillation (El Niño / La Niña events) may increase in strength and frequency with climate change (Trenberth & Hoar 1997). However, while El Niño is associated with catastrophic prey depletion and reproductive failure for many epipelagic foragers (Trillmich & Ono 1991), no such association has been found in Australian fur seals (Kirkwood et al. 2008, Chapter 2). Unless an oceanic regime shift occurs, like that implicated in the decline of the Steller sea lion population (Trites & Donnelly 2003), the near-future population dynamics of
Australian fur seals may be more influenced by interactions with humans than by environmental change.

In summary, Australian fur seals display rapid body growth, low fecundity and low population recovery rates. These characteristics resemble those of benthic foraging sea lions and contrast with the slower body growth, higher fecundity and higher population recovery rates observed in epipelagic foraging fur seals. Additional studies of benthic foraging sea lions would be useful for understanding the effects of habitat type on population dynamics, and the population model in the present study could be improved with information on juvenile and male survivorship in Australian fur seals.

4.5 Literature cited


CHAPTER 5

GENERAL DISCUSSION

5.1 Introduction

The objective of this thesis was to quantify the demographic parameters of female Australian fur seals so that influences on population dynamics could be investigated. The dynamics of interest were 1) the relatively slow population recovery rate in comparison to other fur seals; and 2) the recent increase in the population growth rate, causing abundance to double in the past 2 - 3 decades. In the previous chapters the demographic parameters of age-specific survivorship and fecundity were determined and used to model population growth. The influences of maternal characteristics and oceanography on fecundity were described, establishing links between population dynamics and the environment. The female age structure was modelled, improving estimates of abundance extrapolated from pup production. Observations of rapid body growth and sexual maturity suggested that a selective pressure for large body size exists from a young age. The aims of this chapter are to 1) synthesise these findings by placing the results within an ecological framework for the Otariidae; 2) describe recent habitat changes to account for any influences on population dynamics that were potentially overlooked and; 3) use the findings to suggest management and research priorities for the Australian fur seal population.

5.2 Effects of ecological niche on otariid population dynamics

A correlation between habitat productivity and population dynamics is one of the most basic ecological relationships (Dodson et al. 1998). Under a moderate degree of nutritional stress, animals will forego reproduction to preserve their own survival
(Widdowson 1981, Bronson 1985) and under severe stress they may die (Trillmich et al. 1991, Calkins et al. 1998, Roux 1998). The large difference in abundance of the two A. pusillus populations has been suggested to result from differences in habitat productivity (Warneke & Shaughnessy 1985), however anthropogenic mortality made the relationship unclear until now (Warneke 1975, Arnould et al. 2003a, Chapter 4).

Chapter 3 reported fecundity to be approximately two thirds that of Cape and most other fur seals (Wickens & York 1997, Odendaal et al. 2002). The reproductive cycle was characterised by a relatively high rate of late-gestation abortion and reduced pupping success in lactating females (Chapter 3). Interannual variation in the timing of breeding was correlated with pup production and body condition, suggesting that in years of lower food availability, reproductive success is lower and gestation may be extended (Boyd 1996, Chapter 2). Therefore, there is now substantial evidence that the relatively low recovery rate of the Australian fur seal population is caused by a relatively high degree of nutritional stress.

The information gained by the present study conforms to a framework of population ecology recently proposed for the Otariidae (Arnould & Costa 2006). It was originally thought that phylogenetic differences restricted otariids to a particular foraging mode and ecological niche (Gentry et al. 1986). Sea lions can dive deeper and longer than fur seals because of their larger body size and an integument that is unaffected by pressure, which presumably are adaptations for exploiting a continental shelf niche (Costa 1991). Such characteristics are not needed by fur seals foraging near the surface. However, there are two species that do not follow this pattern: the California sea lion Zalophus californius forages epipelagically in an upwelling and displays the high fecundity, population growth and abundance typical of fur seals (Melin 2002, Costa et al. 2006). Conversely, Australian fur seals forage on the
benthos of a continental shelf and display the low fecundity, low population growth
and abundance typical of sea lions (Arnould & Hindell 2001, Chapter 3, 4). These
exceptions suggest that niche type has a greater influence on otariid population
dynamics than phylogeny (Arnould & Costa 2006).

The present study contributes to the scarce literature on demography in
benthic foraging otariids and contributes to the framework of Arnould & Costa (2006)
by suggesting that body growth rates vary according to the foraging requirements of
the niche, rather than its productivity (Chapter 4). Typically, animals experiencing
nutritional stress display reduced body sizes and growth rates (Arendt 1997). For
example, variation in the body sizes of Steller sea lions and northern fur seals has
been correlated with prey availability (Fowler 1990, Calkins et al. 1998). Australian
fur seals, however, attain larger sizes than other fur seals and grow at more rapid
rates, which lead Arnould & Warneke (2002) to suggest that nutrient availability may
not be limiting population growth. However, the present study made the potentially
contradictory observations of rapid body growth and nutritional stress within a single
sample of females (Chapters 2, 3, 4). It was suggested that rapid growth enhances the
survival of juvenile otariids exploiting continental shelf niches because smaller
animals lack the oxygen stores necessary for reaching the benthos (Chapters 3, 4,
2007). If a selective pressure for rapid growth exists, how is it achieved within a
nutrient-poor environment? The results of the present study suggest that the energy
required for rapid growth may be provided by a relatively high degree of maternal
investment.

The lactation period of most temperate-latitude otariids, including Australian
fur seals, is approximately 10 months (Boyd 1991, Arnould & Hindell 2001).
However, some species have been reported to extend lactation in response to nutritional stress, suggesting that the lactation period has a degree of plasticity. For example, female South American *Arctocephalus australis* and Galapagos fur seals *A. galapagoensis* feed pups for longer during years when El Niño events cause the collapse of normal prey stocks (Gentry & Kooyman 1986). Yet, extended lactation has been reported as routine rather than occasional in benthic foraging otariids such as Australian fur seals, Australian sea lions and Steller sea lions (Pitcher & Calkins 1981, Higgins 1993, Hume *et al.* 2001). The results of the present study corroborate those reports: 53% of adult females were observed to have pupped in breeding season, yet 86% were observed to be lactating in winter, some 7 – 9 months later (Chapter 3). This suggests that 33% (86 – 53%) of adult females were suckling young aged at least 1.5 years old. If this is the case, and only 53% of females pup each year, then most infants (62%) receive milk for at least 1.5 years. The routine extended provisioning of Australian fur seal juveniles could theoretically allow them to grow more rapidly than they would if weaned at 10 months.

Rapid juvenile growth, facilitated through extended lactation, may incur reproductive costs. Females lactating during mid-gestation (and hence, provisioning an offspring) were less likely to give birth to a new pup in the following breeding season (Chapter 3), suggesting that lactation limits energy available to the foetus (Lima & Paez 1995). Extended lactation may, therefore, be associated with a lower birth rate in the population. According to evolutionary theory, such a strategy is adaptive if it increases total reproductive output, for example, recruitment to the adult population. There is little benefit in annual pup production if each pup has poor chances of survival when weaned after 10 months. Instead, it may be adaptive to produce fewer pups so that investment in each one can be extended.
This characteristic may be another reason why benthic foraging populations have recovered at slower rates than epipelagic foraging ones. Nutrient availability in benthic niches is relatively low and foraging there requires greater energy expenditure than in epipelagic niches (Arnould & Costa 2006). Furthermore, the inaccessibility of the benthos for juveniles may mean that they require greater maternal support, which may impose an additional constraint on fecundity. Indeed, the low birth rate and high lactation rate suggests that Australian fur seals may tend towards a biennial reproductive cycle. However, the high pregnancy rate indicates that reproduction is attempted in most years and, therefore, energy is often lost in failed attempts (Chapter 3). The apparently lower abortion rate in females aged older than 10 years suggests that they are more reproductively efficient (Chapter 3). This may constitute a selective pressure, as reproduction can incur risks to survival and cause females reproducing annually to die younger than those reproducing less frequently (Boyd et al. 1995, Beauplet et al. 2006). Such a pressure is a plausible explanation for the extended reproductive cycle of Australian sea lions, the only pinniped to breed non-annually. The per annum fecundity of the two species is similar, but by attempting reproduction less frequently, Australian sea lions attain a birth rate of 71% (Higgins & Gass 1993). This is presumably a more energy efficient strategy than that of Australian fur seals and also allows pups to be suckled for at least 1.5 years without the pup – yearling competition often observed in females with two offspring (J. Gibbens, personal observation). Australian fur seals are relatively recent immigrants, having migrated from productive African waters only 12,000 years ago. In contrast, Australian sea lions are believed to have existed for millions of years and, therefore, have had longer to adapt to the nutrient-poor Australian continental shelf environment (Wynen 2001, Arnason 2006).
In summary, benthic foraging otariids exhibit greater $K$-selection than epipelagic foragers. The niche is more stable (Chapter 2), fecundity is lower (Chapter 3), parental investment is higher (Chapter 3), body size is larger (Chapter 4), and the population growth rate is lower (Chapter 4). The ability for trait divergence to occur within a single species, *A. pusillus*, suggests that otariid demography is influenced by the ecological niche to a greater extent than the phylogenetic differences of the group.

5.3 Other factors influencing recent population dynamics

Changes to prey availability, fisheries interactions and predation could have contributed to the recent population increases of Australian fur seals. However, a lack of sufficient data prevented these aspects being comprehensively analysed in the preceding chapters. Chapters 3 and 4 reported that the body growth and fecundity rates of Australian fur seals have not increased since 1971-2 (Arnould & Warneke 2002, Arnould *et al.* 2003a), suggesting that prey availability has not changed. However, because Australian fur seals grow rapidly despite evidence of nutritional stress, body growth may be a poor indicator of nutrient availability (Chapters 2, 4). Furthermore, the birth rate in 1971-2 was estimated from the late-gestation pregnancy status of a small sample of females ($n = 28$) which may be insufficient to detect minor differences with the present study (Arnould *et al.* 2003a). The extreme mortality experienced by the 1970s population and attributed to hunting could have masked mortality from predation or fisheries interactions (Chapter 4, Arnould *et al.* 2003a). Therefore, some general observations on these factors are reviewed below.

Otariid prey availability can be affected by oceanographic regime changes and these have previously been linked to their population dynamics (Francis & Hare 1994, Pitcher *et al.* 1998, Weimerskirch *et al.* 2003). In Bass Strait, however, primary
productivity has remained largely unchanged in recent decades. Direct sampling in central Bass Strait conducted from 1979 – 81 found chlorophyll concentrations ranging from 0.2 – 0.5 mg·m$^{-3}$ (Gibbs et al. 1986). This is a similar range to that found in the satellite data analysed in Chapter 2 (0.3 – 0.6 mg·m$^{-3}$). The small discrepancy between these ranges may reflect different sampling techniques (Carr et al. 2006) and, therefore, the recent increase in the Australian fur seal population can not be attributed to increased nutrient input to the trophic web.

Commercial fishing activity can affect seals indirectly (prey competition) and directly (bycatch and entanglement mortality) (Pemberton et al. 1992, Shaughnessy et al. 2003). The principal fishery in Australian fur seal habitat is the South East Fishery (SEF), comprising trawl, gillnet and squid jig operations (Grieve & Richardson 2001). Fishing effort has generally increased throughout the 20th century and been associated with a decrease in fish stocks (Grieve & Richardson 2001, Klaer 2001, Larcombe et al. 2001). Comprehensive recording of fishing activity began in the 1980s and activity has increased since then (Grieve & Richardson 2001). For example, trawl effort increased from 84,013 – 102,781 hours p.a. between 1986 – 1998 (Grieve & Richardson 2001) and the Australian fur seal population increased substantially during this period (Kirkwood et al. 2005). Therefore, the Australian fur seal population increase can not be attributed to reductions in anthropogenic prey competition, bycatch and entanglement, as increases in fishing activity suggest that the opposite has occurred.

Increased fishing activity has, however, coincided with large declines in predator populations. Several species of shark, including the great white shark *Carcharodon carcharias* prey on otariids in Australian waters (Bruce et al. 2005, Kirkwood & Dickie 2005, Shaughnessy 2006) and shark bite wounds are regularly
observed on females at the study colony (Gibbens *unpublished data*). The Australian population of great white sharks is estimated to have declined by 60 – 95% between 1962 – 1998 (Pepperell 1992, Presser & Allen 1995, Malcolm *et al.* 2001) which coincides with an increase in Australian fur seal abundance. The removal of predatory sharks by fishing activity has been previously been reported to cause increases in prey populations (Myers *et al.* 2007). Predator removal therefore remains a possible but unquantified factor contributing to the recent population increase of Australian fur seals.

5.4 Research priorities

A key motivation for modelling the abundance of pinniped populations is to estimate their prey consumption for the purposes of fisheries management (*e.g.* Goldsworthy *et al.* 2003). Pinniped abundance estimates are generally derived from pup production estimates and age structure models because older individuals may be at sea and uncountable (Wickens & Shelton 1992). Chapter 4 modelled the female component of the population, potentially improving estimates of Australian fur seal abundance. However, the male component was not modelled, and in the 2 species in which it has been, adult male abundance was approximately half that of females (Lander 1981, Calkins & Pitcher 1982). The potentially large sex ratio bias in adult age classes, combined with substantial sexual size dimorphism (Arnould & Warneke 2002) suggests that the determination of male survivorship is crucial to abundance and consumption models.

Unlike estimates of abundance, estimates of population growth can be inferred directly from pup production trends without the need for an age-structure model (Berkson & DeMaster 1985). Censuses of Australian fur seal pups are currently
performed with capture-mark-resight experiments (CMR) every 5 years (Kirkwood et al. 2005, unpublished data). In the present study, interannual variation in pup production was found to be much greater than the trend (Chapters 2, 4) and consequently, the current 5-yearly census regime has limited power to detect a trend within the stochastic “noise” of interannual variation. Trend detection could be improved by conducting censuses annually (Seber 1982), however the logistical complexity of CMRs prevents this. Direct counts (DCs) underestimate CMRs substantially but predictably, such that they can be used as a pup production index (Chapter 2). Because DCs require approximately 5 times less logistical effort than CMRs (Chapter 2, Gibbens unpublished data), they could be performed annually without increased cost compared to the current 5-yearly CMR regime. Underestimation of pups is of minor importance until male survivorship has been quantified and accurate population abundance estimates are possible.

5.5 Management priorities
Apart from Australian fur seals, no other populations of benthic foraging otariids are increasing and several are declining and listed as vulnerable (Reijnders et al. 1993, Costa et al. 2006). Understanding the management requirements of these and other K-selected marine organisms is increasingly important as global climate change and the expanding human population increasingly affect the marine environment. In light of the demographic information gained by the present study, the most effective management strategies are briefly outlined.

Australian fur seals experience high rates of entanglement in marine debris (e.g. fishing nets) relative to other otariid populations (Pemberton et al. 1992, Shaughnessy et al. 2003, Kirkwood unpublished data). Entanglements predominantly
affect juveniles and are often lethal (Pemberton et al. 1992, Shaughnessy et al. 2003, Gibbens unpublished data) which is significant because juvenile survival is the primary demographic factor influencing Australian fur seal population dynamics (Chapter 4). Indeed, entanglement has been implicated in the population declines of several pinniped species (Fowler 1987).

Seals are also subject to drowning in fishing nets (bycatch) which has contributed to the declines of at least 7 pinniped species worldwide (Reijnders et al. 1993). In blue grenadier component of the SEF, approximately 500 Australian fur seals (approximately 0.4% of the population: Chapter 4) are drowned annually (Hamer & Goldsworthy 2006, Tilzey et al. 2006) which represents a significant contribution to the mortality rate. In this case most were males (94%, Tilzey et al. 2006), which would have little effect on population dynamics. However, juveniles are known to drown in craypots (Warneke 1975), and rates of female bycatch in other areas of the fishery are unknown (Arnould et al. 2003b).

There are anecdotal reports of fishers performing illegal culls at breeding colonies and haul-outs. Up to 100 shots were fired during an incident at the study site during 2006, causing the mortality of a substantial number of females (A. Hoskins, personal communication) and multiple shooting events are recorded in the media (J. Gibbens, personal observation). This source of mortality was believed to limited population growth in the 1970s and has an unquantified effect today (Arnould et al. 2003a). The Australian fur seal population has low potential for population growth due to the nutrient-poor nature of the habitat, making it sensitive to small increases in mortality (Chapters 2, 3, 4). Mitigation of entanglement, bycatch and illegal culling are potential methods for ensuring the continued existence of the population.
5.6 Literature cited


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