

Assessment of pup production and the maternal investment strategies of the Australian sea lion *Neophoca cinerea* at Dangerous Reef in the 2006-07 breeding season



Photo: R Harcourt

Report to the Department for the Environment & Heritage, Wildlife Conservation Fund South Australia

Simon D Goldsworthy¹, Andrew Lowther², Peter D Shaughnessy³, Rebecca R McIntosh², Brad Page¹

¹South Australian Research and Development Institute (SARDI), 2 Hamra Avenue, West Beach SA 5024

²Zoology Department, La Trobe University, Bundoora, Victoria, 3086

³South Australian Museum, North Terrace, Adelaide, SA 5000



Assessment of pup production and maternal investment strategies of the Australian sea lion *Neophoca cinerea* at Dangerous Reef in the 2006-07 breeding season

SD Goldsworthy, A Lowther, PD Shaughnessy, RR McIntosh, B Page

South Australian Research and Development Institute

SARDI Aquatic Sciences

2 Hamra Avenue

West Beach SA 5024

Telephone: (08) 8207 5400

Facsimile: (08) 8207 5481

<http://www.sardi.sa.gov.au/>

Disclaimer

The authors warrant that they have taken all reasonable care in producing this report. The report has been through the SARDI Aquatic Sciences internal review process, and has been formally approved for release by the Chief Scientist. Although all reasonable efforts have been made to ensure quality, SARDI Aquatic Sciences does not warrant that the information in this report is free from errors or omissions. SARDI Aquatic Sciences does not accept any liability for the contents of this report or for any consequences arising from its use or any reliance placed upon it.

Copyright South Australian Department for the Environment and Heritage and South Australian Research and Development Institute 2007.

This work is copyright. Apart from any use as permitted under the Copyright Act 1968, no part may be reproduced by any process without prior written permission from the author.

Printed in Adelaide, November 2007

SARDI Aquatic Sciences Publication Number F2007/000929-1

SARDI Research Report Series No. 249

Authors: SD Goldsworthy, A Lowther, PD Shaughnessy, RR McIntosh, B Page

Reviewers: A Linnane and S Roberts

Approved by: T Ward

Signed:



Date: 8 November 2007

Circulation: Public Domain

TABLE OF CONTENTS

1 EXECUTIVE SUMMARY	2
2 INTRODUCTION	3
AIMS AND OBJECTIVES	5
3 PUP PRODUCTION ESTIMATES AT DANGEROUS REEF	6
INTRODUCTION	6
METHODS.....	8
Field site.....	8
Live and dead pup counts	9
Mark-recapture.....	9
Test for equal catchability.....	11
Trends in abundance	11
RESULTS.....	11
Pup counts.....	11
Mark-recapture estimates of pup numbers.....	12
Equal catchability.....	12
Pup mortality.....	12
Trends in abundance at Dangerous Reef.....	13
DISCUSSION	19
4 MATERNAL STRATEGIES OF AUSTRALIAN SEA LIONS AT DANGEROUS REEF ..	21
INTRODUCTION	21
METHODS.....	27
RESULTS.....	31
DISCUSSION	37
5 COMPARISON OF TRENDS IN ABUNDANCE AND MATERNAL STRATEGIES OF AUSTRALIAN SEA LIONS AT DANGEROUS REEF AND SEAL BAY	41
INTRODUCTION	41
METHODS.....	41
Population trends.....	41
Maternal strategies	41
RESULTS.....	42
Population trends.....	42
Maternal strategies.....	42
DISCUSSION	43
Population trends and maternal strategies.....	43
Population trends and fishery interactions	44
Conclusion	48
6 ACKNOWLEDGMENTS	49
7 REFERENCES.....	49

1 EXECUTIVE SUMMARY

Australian sea lion pup abundance was determined for the Dangerous Reef population during the 2006-07 breeding season. Using mark-recapture methods (including cumulative mortality), pup production was estimated to be 708 (95% CL 632-779). The exponential rate of increase in pup production from 1999 until 2006-07, based on maximum live-pup counts plus cumulative mortality and mark-recapture methods, ranged between 6.7-9.9% per breeding season, or 4.4-6.4% per year. This provides further evidence of strong positive growth in the population, which has been occurring since 2000.

A study to characterise the maternal strategies of Australian sea lions at Dangerous Reef was also undertaken. The parameters of maternal investment assessed included female mass, the duration of foraging trips and shore attendance bouts, the percentage time that females spent ashore, the birth mass and growth rates of pups to 100 days of age, and the lipid content of milk. These were compared to results from an earlier study undertaken at Seal Bay. No differences were detected in the mass of adult females, or the duration of foraging trips (~1.8 days) between sites. However, the duration of attendance bouts was significantly longer at Seal Bay (1.6 days vs. 0.9 days), and as a consequence, females at Seal Bay were ashore for a greater percentage of time (48% vs. 32%). Although the estimated birth mass of pups at Dangerous Reef was greater than that at Seal Bay, the growth rates of pups at Seal Bay were 27% higher than at Dangerous Reef. Consistent with this, the estimated milk-lipid content for females at Seal Bay was about 27% greater than that estimated for Dangerous Reef females. Based on these results, conditions for foraging and for raising pups would appear more optimal at Seal Bay than at Dangerous Reef, although there is uncertainty in this conclusion due to difference in the timing of the studies.

Available data suggest a marked difference in the respective population trends of the Australian sea lion populations at Dangerous Reef and Seal Bay. The Dangerous Reef population is currently increasing by about 5% per year, while Seal Bay population has been declining by about 1% per year, for at least 20 years. Comparison of the maternal strategies at each site are contrary to expectations based on the differing population trajectories, suggesting that differences in population trajectories are not related to differences in foraging conditions at each site. There is a growing consensus that the most likely cause for the lack of recovery in Australian sea lion populations is principally due to anthropogenic related mortality, especially from fishery bycatch. The recent pronounced increase in pup abundance at Dangerous Reef has occurred coincidentally with the cessation of shark fishing in Spencer Gulf in 2001. This provides circumstantial evidence that positive growth has followed a reduction in anthropogenic mortality for this population. In contrast, demersal gillnet fishing effort remains significant in waters adjacent to the Seal Bay population, and entanglement rates in monofilament gillnets and a declines in pup abundance suggests that mortality related to fishery bycatch may be significant in this population.

2 INTRODUCTION

The Australian sea lion (*Neophoca cinerea*) is Australia's only endemic and least numerous seal species. It is unique among pinnipeds because it is the only species that has a non-annual breeding cycle, which is temporally asynchronous across its range. They have the longest gestation period of any pinniped and a protracted breeding and lactation period. The evolutionary determinants of this unusual reproductive strategy remain enigmatic. These factors, including the species small population size (11,000 individuals), which is distributed over numerous, small colonies, make the Australian sea lion vulnerable to extinction (Goldsworthy and Page 2007). Recent population genetic studies have indicated little or no interchange of females among breeding colonies, even those separated by short distances (Campbell 2003). The important management implication is that each colony is a closed population. As such, the Australian sea lion poses significant conservation and management challenges. The species has recently been listed as 'vulnerable' under the threatened species category of the Commonwealth EPBC Act.

The population of Australian sea lions at Dangerous Reef is the largest for the species, consisting of approximately 1,600 individuals with a mean pup production of 375 pups (s.d. = 103, n= 11 seasons, Shaughnessy 2005). Pup production has been estimated at Dangerous Reef since 1994-95. Between 1994 and 1999 pup production was monitored by counting pups. Since 1999, pup production estimates have been improved by conducting mark-recaptures and monthly counts. Port Lincoln Department for the Environment (DEH) staff determine the onset of breeding by the presence of the first newborn pup at the colony. After this, monthly pup counts are undertaken to monitor pup production and pup mortality. At the peak of the pup production (usually 5 months after the first pup was born) the mark-recapture is conducted. The mark-recapture gives a more accurate estimate of pup production because it provides a confidence interval around the mean. Pup production is monitored until the maximum count is obtained and the subsequent count reflects dispersal of the pups, recognised as a drop in the total number of pups counted. This method has now been used for three breeding seasons at Dangerous Reef and is now being applied at Seal Bay Conservation Park (hereafter Seal Bay) and The Pages Islands. This method is proving to be a useful tool for detecting trends in sea lion populations.

Foraging data of Australian sea lions at Seal Bay and Dangerous Reef suggest that female foraging behaviour in breeding colonies may vary with differing local environments (Costa and Gales 2003, Goldsworthy et al. 2005, McKenzie et al. 2005). Such habitat heterogeneity and differing foraging strategies may lead to the evolution of alternative reproductive strategies (Boness 1991), which may be reflected in pup production and mortality. Given the differences in population trajectories of the Seal Bay and Dangerous Reef Australian sea lion populations (declining and increasing, respectively, Shaughnessy 2005, Shaughnessy et al. 2006), it is important to determine if these are related to differences in foraging conditions (provisioning strategies).

There are approximately 70 known breeding locations for Australian sea lions, most (40) of which occur in South Australia, where the species is most numerous (75% of pup production for the species). The species was subject to sealing in the late 18th and early 19th century, resulting in a reduction in population size, and extirpation of populations in Bass Strait (non-breeding) and many islands within their current range (Ling 1999). Despite the large number of breeding sites, the average number of pups born at each colony is low (44), with total pup production for the species during each breeding cycle estimated at only 2,861, and an estimated population size of about 11,000 seals (Goldsworthy et al. 2003). The Australian sea lion has not recovered since harvesting ceased, unlike the fur seal species throughout southern Australia.

Dangerous Reef (34° 49' S, 136° 13' E) is 35 km southeast of Port Lincoln and forms part of the Sir Joseph Banks Group Conservation Park. It comprises Main Reef with nearby East Reef and West Reef, which cover about 12 ha (Robinson et al. 1996). Sea lion pups have been counted at Dangerous Reef since 1994-95 with assistance of staff of National Parks and Wildlife SA (NPW SA), Department for Environment and Heritage. Before this time, counts were made opportunistically from 1975 by NPW SA staff and by John Ling and colleagues (Ling and Walker 1976, Dennis 1999). For the seventeen pupping seasons between 1975 and 1999, data from ten breeding seasons were collated by Dennis (1999). Overall, data are available from only 11 seasons, because counts were unreliable in some seasons (Shaughnessy 2005). Mark-recapture estimates began in July 1999.

Because we are uncertain about the accuracy of historic pup count data, developing a correction factor for these data is a priority. Unfortunately, given that mark-recapture surveys only commenced in 2002, confirmation of population trajectories may take some time. Mark-recapture provides the most appropriate method for censusing pup production. Comparisons of mark-recapture estimates of Australian sea lion pups with direct counts have been made in three seasons at Dangerous Reef and were all similar. The discrepancy between the direct counts and the mark-recapture estimates on each occasion result from the difficulty of sighting all pups in the colony. Pups asleep under rocks or behind rocks that can't be accessed are missed during direct counting.

Mark-recapture estimates provide better population estimates than direct counts, because the latter tends to miss pups that are hidden under bushes or behind rocks and pups that have dispersed away from the colony. This method is being applied to other large Australian sea lion colonies such as Seal Bay (McIntosh et al 2007) and The Pages Islands (reference). Due to the easy access and DEH management of Seal Bay as a tourist locality, this Australian sea lion population has supported the bulk of research for this species. It is important to conduct population demography and maternal investment projects at other breeding colonies, to explore differences in behaviour that may be due to adaptations to differing local environments and resources. Dangerous Reef provides a great opportunity for such as study because there is a historic data set on pup production (Shaughnessy 2005) and extensive foraging ecology work has been undertaken (Goldsworthy et al. 2005).

Aims and Objectives

The aims of this study were to:

1. Monitor the pup numbers at Dangerous Reef by conducting monthly pup counts
2. Monitor dead pup numbers during the monthly count
3. Estimate pup numbers using mark-recapture to obtain a more reliable estimate of pup production than direct counting
4. Gather empirical data on the maternal investment strategies of Australian sea lions at Dangerous Reef.
5. Compare the 2006 pup production data with data from previous breeding seasons at Dangerous Reef, and compare the pup production data and maternal strategy data with that from Seal Bay.

The report is divided into three main chapters. Chapter 3 involves estimates of pup production at Dangerous Reef, addressing the first three aims above. Chapter 4 focuses on a study of maternal strategies of Australian sea lions at Dangerous Reef, addressing aim four above. This work was undertaken as an Honours project by Mr Andrew Lowther through La Trobe University. His supervisors were Dr Simon Goldsworthy (SARDI) and Prof Neil Murray (Genetic Department, La Trobe University). Chapter 4 with the exception of some minor editorial changes and absent appendices is a reproduction of Lowther's Honours Thesis. Aim 5 is addressed in Chapter 5.

3 PUP PRODUCTION ESTIMATES AT DANGEROUS REEF

SD Goldsworthy, A Lowther, PD Shaughnessy, RR McIntosh and B Page

Introduction

The Australian sea lion (ASL), *Neophoca cinerea*, is one of five sea lion species in the world that form around one-third of species in the Otariidae family. Over recent decades there has been growing concern over the status of all five sea lion species. In the North Pacific Ocean, the Steller sea lion, *Eumetopias jubatus*, has been declared endangered in parts of its range and is considered threatened with extinction in other parts (Trites et al. 2007). Although the total population of California sea lions in California and Mexico is increasing (Caretta et al. 2004), the Mexican stock is in decline (Szteren et al. 2006). There have also been reductions in numbers of the Galapagos subspecies of the Californian sea lion, *Zalophus californianus wollebaeki* (Alava and Salazar 2006), and the Japanese subspecies, *Z. c. japonicus*, is possibly extinct (Mate 1982). Numbers of South American sea lions, *Otaria flavescens*, have reduced considerably in recent years (Crespo and Pedraza 1991, Reyes et al. 1999, Shiavini et al. 2004), especially in the Falkland Islands (Thompson et al. 2005), and numbers of New Zealand sea lions, *Phocarctos hookeri* (Lalas and Bradshaw 2003), and Australian sea lions (McKenzie et al. 2005) have not recovered from historic sealing, and form the smallest population of all sea lion species.

There are 73 known breeding locations for ASLs, 47 of which occur in South Australia (SA) where the species is most numerous (80% of pups counted), with the remainder (26 colonies) occurring in Western Australia (McKenzie et al. 2005). The species was subject to sealing in the late 18th, the 19th and early 20th centuries, resulting in a reduction in overall population size and extirpation of populations in Bass Strait and other localities within its current range. Total pup production for the entire species during each breeding cycle has been estimated at about 2,500 with an estimated overall population size based on a demographic model developed by Goldsworthy et al. (2003), of around 9,800 (McKenzie et al. 2005). A re-analysis of this demographic model, in conjunction with improved estimates of pup production for some sites, has increased estimates of the SA pup production to about 2,700 per breeding cycle and the size of the ASL population in SA to about 10,900 individuals (Goldsworthy and Page 2007). Based on pup production estimates of 709 for WA sites (Goldsworthy et al. 2003), the total pup production for the species is currently estimated at about 3400 per breeding cycle, with an estimated overall population estimate of around 14,000 (Goldsworthy, unpublished data). The life tables associated with the revised population model produced population estimates that were 4.08 times that of pup production (Goldsworthy and Page 2007), which is in line with expectation based on pinniped populations (Harwood and Prime 1978).

There are 38 ASL breeding sites in SA, when the criterion for classification as a breeding colony is set at ≥ 5 pups present per breeding cycle (Goldsworthy and Page 2007). Of these, only six (16%)

produce more than 100 pups, and these account for 67 % of the State's pup production. The largest population is Dangerous Reef in Southern Spencer Gulf (585 pups), followed by The Pages (577 pups) in Backstairs Passage between Kangaroo Island and mainland Australia (summarised in Goldsworthy and Page 2007). The next largest populations are Seal Bay (214 pups) on Kangaroo Island, West Waldegrave (157 pups) and Olive Islands (131 pups) off the west coast of the Eyre Peninsula, and Purdie Island (132 pups) in the Nuyts Archipelago (summarised in Goldsworthy and Page 2007). The median pup production for SA colonies is 25.5 per colony, with 60% of breeding sites producing fewer than 30 pups per season, 42 % fewer than 20 pups, and 13% fewer than 10 pups (Goldsworthy and Page 2007). These analyses do not take into account at least another 11 breeding sites (termed 'haul-out sites with occasional pupping'), where fewer than 5 pups have been recorded at some time (McKenzie et al. 2005).

Although the pre-harvested population size of the ASL is unknown, the overall population is still believed to be in recovery. Unlike populations of the Australian fur seal, *Arctocephalus pusillus doriferus* and New Zealand fur seal, *Arctocephalus forsteri*, which have been recovering rapidly throughout southern Australia, there is a general view that the overall population recovery of the Australian sea lion appears to be limited, and the reasons for this are unclear.

McKenzie et al. (2005) noted that the quality of data on pup production across the range of Australian sea lions was typically poor. Poor data are largely due to the species' protracted breeding season meaning that by the end of the pupping period, some pups may have died, dispersed or moulted, hence may go unrecognised (Shaughnessy et al. 2005). Because of this, researchers have tried to estimate the maximum numbers of pups present from single counts, timed when maximum pup numbers are expected in the colony, or from multiple point counts made throughout the breeding season in order to recognise the maximum. Where possible, the accumulated number of dead pups is added to these estimates. These methods are likely to result in underestimates of the true number of pups produced, but to what extent is poorly understood and is likely to vary among sub-populations. These issues, in conjunction with the absence of a realistic and representative population model, make it difficult to estimate the size of the Australian sea lion population accurately.

Further, reliable estimates of pup abundance are available for few ASL colonies, with time-series data available for even fewer. The methodologies to estimate pup numbers have advanced in recent years in conjunction with an understanding of the timing of breeding seasons at certain colonies. Despite these advances, the quality of time-series data is typically poor because early records were based on limited surveys. The high variability in pup numbers recorded between breeding seasons has made interpreting trends in population abundance difficult.

One of the longest time-series of data on Australian sea lion pup abundance is for the Dangerous Reef population. Sea lion pups have been counted at Dangerous Reef since 1996 with assistance of staff of National Parks and Wildlife SA (NPW SA), Department for the Environment and Heritage.

Before then, counts were made opportunistically from 1975 by NPW SA staff and by John Ling and colleagues of the South Australian Museum (Ling and Walker 1978; Dennis 2005).

For the seventeen pupping seasons between 1975 and 1999, ten data sets were collated by Dennis (2005). Analyses by Shaughnessy (in litt) have determined that only seven of these seasons provided reliable estimates (1975, 1976-77 and those for five seasons from 1990 to 1999), principally because the others were based on a single visit and most likely underestimated pup production. In all of these cases the observed maximum was less than half of the average pup numbers recorded in the colony (Shaughnessy in litt). Pup counts are also available for the four seasons from 2000-01 to 2005 (Shaughnessy and Dennis 2001, 2003; Shaughnessy 2004b; Shaughnessy in litt). Overall, pup production data are available from 11 prior-seasons. Mark-recapture estimates of live pup abundance around the peak of pupping are available for Dangerous Reef for three prior breeding seasons; 1999; 2003-04 and 2005 (Shaughnessy and Dennis 1999, Shaughnessy 2004, Shaughnessy in litt).

This study extends this data set to the 2006-07 breeding season by:

1. Monitoring the pup numbers at Dangerous Reef by conducting monthly pup counts,
2. Monitoring dead pup numbers during monthly counts,
3. Estimating pup numbers using mark-recapture techniques to obtain a reliable estimate of pup production.

Methods

Field site

Dangerous Reef (34.870 S, 136.2170 E) is 35 km south-east of Port Lincoln and forms part of the Sir Joseph Banks Group Conservation Park (Figure 1). It comprises Main Reef with nearby East Reef and West Reef. They cover about 12 ha in area (Robinson et al. 1996). Sea lion pups are born on Main Reef, and some of them move to the West Reef several weeks after birth. Dangerous Reef was accessed by charter vessel from Port Lincoln, Eyre Peninsula, South Australia, between 26 July 2006 and 5 February 2007. Nine trips to the island were made over this period, as part of the study undertaken by A. Lowther (see chapter 4).

During each visit to the island, sea lion pup numbers were surveyed by direct counting of live pups, surveying of dead pups and for three of the visits to the island by mark-recapture. Methodology for these approaches are detailed below.

Live and dead pup counts

The number of live pups was counted while slowly walking around the island, taking care not to disturb animals on the top of the island, to reduce the chance of double counting. After counting around the periphery of the island, the counters walked through the centre of the island to count the pups.

We recorded the number of pups that had died since the previous visit. To avoid double counting, dead pups were sprayed with paint or covered with rocks when they were counted. The number of dead pups was added to give the number of 'accumulated dead pups'. When that number was added to the number of live pups, it gave the best available estimate of pup production to that date.

Mark-recapture

Direct counts are known to underestimate total pup production, because they fail to count pups that are hidden from view (sightability bias) or absent from the colony (availability bias) at the time of the survey. The influence of these factors on estimates of pup numbers can be reduced to some degree by undertaking a mark-recapture procedure. Petersen estimate mark-recapture methods have been used to estimate pup production at fur seal colonies in Australia since 1988 (Shaughnessy et al. 1995a, Shaughnessy et al. 2002, Kirkwood et al. 2005), but have only been recently applied to estimating pup production in the Australian sea lion at Seal Bay, Dangerous Reef, Olive and North Page and South Page Islands (Goldsworthy et al. 2007, McIntosh et al. 2006a, Shaughnessy 2006).

A mark-recapture procedure was used to estimate the number of live pups on the Main Reef of Dangerous Reef in November 2006 (session 7 of the current study) and January and February 2007 (sessions 8 and 9). A total of 207 pups were tagged during two visits to Dangerous Reef in October and November 2007 (sessions 6 and 7). Pups were tagged in the trailing edge of each fore-flipper with individually numbered plastic tags (Dalton® Size 1 Supertags). During each field trip to Dangerous Reef, individual re-sight records were collected for marked individuals with the aid of binoculars. As noted above, a record of dead pups was obtained by placing rocks on top of carcasses to avoid repeat counting. Records of the total number of tagged, untagged and newly recorded dead pups were noted on each field trip.

Six recapture sessions were undertaken in November 2006, and in January and February 2007. Individual re-sights of tagged pups usually undertaken over a minimum of three days prior to recapture surveys, were used as the sample of 'marked' individuals in the population available for recapture. During recapture surveys, the individual identity of tagged pups was determined by reading tag numbers with binoculars. The number of untagged pups were also recorded and as were new dead pups that had not been marked.

Mark-recapture estimates of pup numbers (\hat{N}) were calculated using a variation of the Petersen method (formula attributed to D.G. Chapman by Seber 1982), with the formula

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

where M is the number of marked pups at risk of being sampled during recapture operations, n is the number of pups examined in the recapture sample, and m is the number of marked pups in the recapture sample.

The variance of this estimate is calculated as

$$\text{var}(\hat{N}) = \frac{(M + 1)(n + 1)(M - m)(n - m)}{(m + 1)^2 (m + 2)},$$

and the 95 % confidence limits calculated from

$$\hat{N} \pm (1.96 * \text{var}(\hat{N})^{0.5}).$$

Where several mark-recapture estimates (\hat{N}_j) are undertaken (one from each recapture session), they are combined by taking the mean (\hat{N}) using formulae from White and Garrott (1990, pp. 257 & 268):

$$\hat{N} = \sum_{j=1}^q \frac{\hat{N}_j}{q}$$

where q is the number of estimates for the colony (i.e., the number of recapture sessions). The variance of this estimate is calculated from

$$\text{var}(\hat{N}) = \frac{1}{q^2} \sum_{j=1}^q \text{var}(\hat{N}_j)$$

and its standard deviation as

$$sd = \text{var}(\hat{N})^{0.5}$$

The Petersen estimates yields an accurate result as long as a number of conditions are met. These include:

- the probability of capturing an individual is the same for all individuals in the population,
- no animal is born or immigrates into the study area between marking and recapturing,
- marked and un-marked individuals die or leave the area at the same rate, and
- no marks are lost (Caughley 1977).

Test for equal catchability

The key assumption of mark-recapture studies is that the probability of capture is the same for all individuals in the population. This was tested within the tagged population by examining the number of times that individual marked pups were resighted within each capture session. We used the Leslie's test for equal catchability, following methods detailed in Caughley (1977), and for each of the six capture sessions, examined the number of times known-to-be-alive individuals were resighted. We used the Leslie's test in favour of the zero truncated Poisson test because it enabled us to use data on zero recaptures, (animals known to be alive from subsequent recapture session, but not sighted). This could be achieved for all but the final recapture session. The assumption in Leslie's test is that if catchability is constant across all individuals, the recapture frequencies will form a binomial distribution. This assumption can be tested as a Chi-square with $(\sum f) - 1$ degrees of freedom, by comparing the observed variance to the expected binomial variance, where

$$\chi^2 = \frac{\sum fi^2 - \frac{(\sum fi)^2}{\sum f}}{\frac{\sum fi}{\sum f} - \frac{\sum n^2}{(\sum f)^2}},$$

and n is the number of individually tagged pups resighted during each recapture, i is the number of times individual pups were resighted during recapture sessions and f is the number of individual resighted i times (Caughley 1977).

Trends in abundance

The rate of change in pup numbers was calculated using linear regression of the natural logarithm of the mean estimate of pup numbers against year or breeding season (~1.5 years). The exponential rate of increase (r) is the slope of the regression line. An exponential rate of increase has been demonstrated for other seal species, for example the New Zealand fur seal on Kangaroo Island (Shaughnessy et al. 1995). It can be expressed as a percentage increase using the following formula

$$(e^r - 1) * 100.$$

Results

Pup counts

On the first visit to Dangerous Reef on 26 July 2006, 2 live and 1 dead pups were counted, indicating that the breeding season had commenced in mid-late July. On a survey undertaken on 1 February 2007, a total of 4 new-born pups, which were being mate-guarded by their mothers (0-10 days post-partum), were counted, indicating the breeding season was coming to a close. Therefore the duration of the breeding season for 2006/07 was about 7 months. Counts of live and dead pups surveyed at

Dangerous Reef during the 2006/07 pupping season are presented in Table 1 and Figure 2. The largest estimate of live pups was 495 on 15 January 2007. Accumulated dead pups to this date was 80, giving a maximum direct count of 575. This does not include the pups that were born beyond 15 January 2007.

Mark-recapture estimates of pup numbers

The mark-recapture estimates procedure utilised 207 tagged pups. Resights of these tagged pups over several days prior to recapture surveys were used to provide a pool of tagged pups for each recapture session. The number of tagged pups available to be resighted varied considerably between surveys (100-189, Table 3.2). Mark-recapture estimates increased from 436 (95%CL 416-455) in November 2006 (session 7), to 629 (95% CL 556-703) in January 2007 (session 8), and then declined to 497 (95% CL 430-543) in February 2007 (session 9) (Table 3.2). Adding accumulative dead pups to these values provided estimates of 503 (95% CL 4483-522), 709 (95% CL 636-783) and 585 pups (95% CL 518-631), respectively.

Comparisons of mark-recapture estimates with direct counts at Dangerous Reef have now been made four times (Table 3.3). Each time, the mark-recapture estimate was between 1.19 and 1.32 times the direct count of pups (95% confidence limits of comparisons range from 1.12 to 1.42). This indicates the comparison of mark-recapture estimates with direct counts of pups were similar in the four pupping seasons. The discrepancy between the direct counts and the mark-recapture estimates on each occasion results from the difficulty of sighting all pups in the colony. Some pups may not be viewed during counting because they are swimming in the shallows or obscured by rocks.

Equal catchability

Results from Leslie's test of equal catchability are presented in Table 3.4. Results from all three recapture sessions were non-significant, indicating that the assumption that the distribution of recaptures was binomial, and that of equal catchability of tagged pups is supported.

Pup mortality

For the 2006-07 pupping season at Dangerous Reef, 80 dead pups were recorded by 15 January when the estimated number of births reached a maximum of 575, giving an incidence of pup mortality 13.9% (Table 3.5).

For the last eight pupping seasons at Dangerous Reef (since 1996), the incidence of pup mortality has ranged from 14% to 45% (Table 3.5). It was high for pupping seasons that occurred predominantly in winter (30% in 1996, 42% in 1999, 45% in 2002 and 31% in 2005, with unweighted average 37%) and lower for pupping seasons that occurred predominantly in summer (15% in 1997-

98, 23% in 2000-01, 19% in 2003-04, and 14% in 2006-07 with unweighted average 18%). For this analysis, data for pupping seasons before 1996 have been omitted because insufficient attention had been directed at dead pups. A one-way ANOVA comparing the mortality rate between summer and winter breeding seasons, indicated that mortality rates (proportion of dead pups) were significantly higher in winter breeding seasons ($F_{1,6} = 25.896$, $P < 0.010$, arcsine transformed data). A two-way ANOVA examining the relationship between the total cumulative dead pups and year, with season (summer or winter breeding) as a factor determined that cumulative dead pups have been increasing significantly each breeding season since 1996 ($F_{1,4} = 29.456$, $P < 0.001$). Although season (summer/winter) alone was not a significant factor ($F_{1,4} = 3.849$, $P = 0.121$), the interaction between season and year was ($F_{1,4} = 9.301$, $P = 0.050$), indicating that the relationship between year and cumulative pup deaths was different between summer and winter seasons (Figure 3.2).

Trends in abundance at Dangerous Reef

Live and dead pup surveys

For the Dangerous Reef Australian sea lion population, estimates of pup numbers by direct counting are available for twelve pupping seasons from 1975 to 2006-07, and range from 248 to 585 with an average of 392 (sd = 114) (Table 3.5, Figure 3.2).

Because dead pups were not counted in the 1994-95 season, the number of live pups in that season has been adjusted to estimate the number of births (Table 3.4, Shaughnessy 2005).

Using the maximum live-pup counts and numbers of cumulative dead pups over these twelve breeding seasons (1975 to 2006-07) as an index of pup production, the number of pups born at Dangerous Reef has increased at an exponential rate of $r = 0.027$ or 2.7% per breeding season (~ 1.5 years) or $r = 0.018$ or 1.8% per year. The trend is significant for both season and year ($F_{1,10} = 7.439$, $P = 0.0213$, $R^2 = 0.427$).

Data from three pupping seasons are considerably smaller than the others: 262 pups in 1976-77, 260 in 1990 and 248 in 1997-98 (Figure 3.2). Each of these counts was made in the fourth month after pupping began, whereas maximum counts for all but one of the other seasons were made in the fifth month or later (Table 3.5). Counting that ended in the fourth month of a pupping season is likely to underestimate pup production considerably. The 1996 season had a large count, so it is assumed that its surveys was undertaken at least 5 months from the beginning of the breeding season. With data from the three low-count seasons are omitted from the trend analysis, nine seasons of data remain, for 1975, 1994-95, 1996, and for the six consecutive seasons from 1999, the rate of increase for these nine pupping seasons is $r = 0.021$ or 2.1% per breeding season or $r = 0.014$ or 1.4% per year. The trends is significant for both season and year ($F_{1,7} = 6.076$, $P < 0.050$, $R^2 = 0.465$).

Accurate pup count data have been collected since 1994-95, data for the 1997-98 season were incomplete because counts did not extend beyond the fourth month of the season. If that data point is

omitted and data for the other eight pupping seasons from 1994-95 are analysed, pups counts have increased at $r = 0.067$ or 6.9% per breeding season, equivalent to $r = 0.045$ or 4.6% per year. This is the best interpretation of these data and the trend is significant ($F_{1,6} = 43.443$, $P < 0.001$, $R^2 = 0.879$).

Mark-recapture surveys

Mark-recapture estimates for live pups plus cumulative dead pups to the time of survey, have been undertaken over four breeding seasons (1995 to 2006-07, Table 3.3). Trend data for the four seasons show an increase between seasons of $r = 0.094$ or 9.9% per season, which is equivalent to $r = 0.062$ or 6.5% increase per year (Figure 3.2). These trends are significant ($F_{1,3} = 19.121$, $P < 0.050$, $R^2 = 0.858$).

Table 3.1. Summary of details of Australian sea lion pup counts, tagging, cumulative mortalities and various direct count and mark-recapture abundance estimates during 9 visits (sessions) to Dangerous Reef between July 2006 and February 2007.

Session	1	2	3	4	5	6	7	8	9
Date	26-Jul	27-Aug	3-Sep	27-Sep	2-Oct	21-Oct	25-Nov	15-Jan	5-Feb
Cumulative tagged	-	-	-	-	-	50	207	207	207
Maximum untagged counted	2	23	42	89	103	111	142	127	98
Maximum count (live)	2	57	42	89	103	161	330	495	-
Cumulative dead (un-tagged)	1	1	6	18	23	27	62	74	81
Cumulative dead (tagged)	0	0	0				5	6	7
Total accumulative dead	1	1	6	18	23	27	67	80	88
Maximum count (live) + cumulative dead	3	58	48	107	126	188	397	575	-
Cum. tagged + dead + max untagged	3	24	48	107	126	188	411	408	386
Petersen Estimate (live)							436	629	497
Petersen Estimate Lower – Upper CL (No. recapture estimates)							416-455	560-707	430-543
							6	6	6
Petersen Estimate (live) + cumulative dead							503	709	585
Lower – Upper CL							(483-522)	(636-783)	(518-631)

Table 3.2. Details of Petersen mark-recapture procedures undertaken at Dangerous Reef between November 2006 and February 2007. M = number of marked pups in the population, n = the total number of pups sampled and m = the number of marked pups in each recapture sample. N = the estimated pup population size, sd = standard deviation and V = variance. % = the percentage of marked pups in each sample, CV = the coefficient of variation. The lower and upper 95% confidence limits (CL) of each estimate, respectively.

Date	Recapture No.	Marked M	Examined n	M-R m	N	sd	V	%	CV	95% CL	
										Lower	Upper
Session 7											
28-Nov	1	181	203	87	421	24	587	43%			
28-Nov	2	181	218	90	437	25	609	41%			
29-Nov	3	189	245	107	432	20	416	44%			
29-Nov	4	189	195	81	453	29	822	42%			
29-Nov	5	189	243	101	454	23	541	42%			
29-Nov	6	189	204	92	418	23	520	45%			
				Mean	436	10		43%	2.3%	416	455
Session 8											
11-Jan	1	145	170	43	566	61	3712	25%			
11-Jan	2	154	108	22	734	123	15106	20%			
11-Jan	3	162	145	44	528	55	3045	30%			
11-Jan	4	167	135	37	600	72	5169	27%			
12-Jan	5	169	160	37	719	89	7891	23%			
12-Jan	6	176	173	48	628	64	4105	28%			
				Mean	629	33		26%	5.9%	556	703
Session 9											
3-Feb	1	100	123	28	431	58	3395	23%			
3-Feb	2	114	125	31	452	58	3345	25%			
4-Feb	3	121	127	29	520	71	5046	23%			
4-Feb	4	133	126	33	500	63	3912	26%			
5-Feb	5	139	117	30	532	71	5094	26%			
5-Feb	6	144	86	22	547	88	7758	26%			
				Mean	497	28		25%	5.9%	430	543

Table 3.3. Summary of mark-recapture estimates of the abundance of Australian sea lion pups at Dangerous Reef over four breeding seasons, highlighting comparison between mark-recapture estimates and live pup counts. For the 2006/07 season comparisons between methods can be made for two of the three mark-recapture estimates.

Date	Max. direct count (inc. dead)	Direct count of pups	Mark-recapture estimate of pups	Comparison	95% confidence interval	No. month since pupping commence to		Source
						Max count	Mark-recapture estimate	
July 1999	383	240	285	1.19	1.12 to 1.25	4	4	Shaughnessy & Dennis (1999)
Jan 2004	499	333	423	1.27	1.21 to 1.31	5.5	5	Shaughnessy (2004)
July 2005	585	272	326	1.20	1.15 to 1.25	6	6	Shaughnessy (2005)
Nov 2006	397	330	436	1.32	1.26 to 1.38	4	4	This report
Jan 2007	575	495	629	1.27	1.12 to 1.42	6	6	This report

Table 3.4. Leslie's test for equal catchability across each recapture session at Dangerous Reef. n is the number of individually tagged pups resighted during each recapture, i is the number of times individual pups were resighted during recapture session and f is the number of individuals resighted i times. Chi-squared (χ^2) and degrees of freedom (df) values are also given. Non-significant (NS), probability (P) values indicate equal catchability.

Session No.	Recapture No.	n	n^2	i	f	$f \cdot i$	$f \cdot i^2$	χ^2	df	P
7	1	58	3364	0	53	0	0	0.016	187	NS
	2	57	3249	1	62	62	62			
	3	53	2809	2	45	90	180			
	4	78	6084	3	18	54	162			
	4			4	10	40	160			
	Σ	246	15506		188	246	564			
8	1	43	1849	0	36	0	0	0.043	152	NS
	2	21	441	1	53	53	53			
	3	32	1024	2	22	44	88			
	4	37	1369	3	22	66	198			
	5	37	1369	4	10	40	160			
	6	41	1681	5	10	50	250			
	6			6	0	0	0			
	Σ	211	7733		153	253	749			
9	1	28	784	0	22	0	0	0.041	99	NS
	2	28	784	1	39	39	39			
	3	26	676	2	21	42	84			
	4	23	529	3	12	36	108			
	5	23	529	4	5	20	80			
	6	13	169	5	0	0	0			
	6			6	1	6	36			
	Σ	141	3471		100	143	347			

Table 3.5. Estimated number of births of Australian sea lions at Dangerous Reef, South Australia for 11 pupping seasons between 1975 and 2005. Data are collated from Dennis (2005), Shaughnessy and Dennis (2001, 2003), Shaughnessy (2004), Shaughnessy (2005) and this report. The data for 1994-95 includes an adjustment to account for pup mortality because only live pups (295) were counted in that season (following Shaughnessy 2005).

Pupping season	Cumulative dead pups at max. live count ^a	Max. pup count ^b	Pup mortality (%)	Month of max. live count since pupping began	Max. cumulative dead pup
1975	73	356	20.5	5	73
1976-77	26	262	9.9	4	26
1990	55	260	21.2	4	55
1994-95	-	354 ^c	not estimated	6.5	
1996	110	363	30.3	-	110
1997-98	38	248	15.3	4	43
1999	161	383 ^d	42.0	4	165
2000-01	90	393	22.9	7	90
2002	190	426 ^e	44.6	6	190
2003-04	93	499 ^f	18.6	5	100
2005	182	585 ^g	31.1	5	274
2006-07	80	575 ^h	13.9	6	88

^a 'Cumulative dead pups' refers to the number of dead pups counted through to the maximum live pup count.

^b 'Max. pup count' refers to the maximum live pup count plus cumulative dead pups up until the date of the maximum live pup count.

^c Adjusted for pup mortality using: "Maximum pup count" x 1.19954, where 0.19954 is the un-weighted average proportion of dead pups in three summer pupping seasons, 1997-98, 2000-01 and 2003-04.

^d In addition, 23 newly-born pups were recorded on the last two visits; that number plus the previous estimate (of 383) leads to an estimate of pup numbers for the season of 406.

^e In addition, 29 newly-born pups were recorded on the last visit; that number plus the previous estimate (of 426) leads to an estimate of pup numbers for the season of 453.

^f In addition, 27 newly-born pups were recorded on the last visit; that number plus the previous estimate (of 499) leads to an estimate of pup numbers for the season of 526.

^g In addition, 32 newly-born pups were recorded on the last three visits; that number plus the previous estimate (of 585) leads to an estimate of pup numbers for the season of 617.

^h In addition, 4 newly-born pups were recorded on the last visit; that number plus the previous estimate (of 575) leads to pup count for the season of 579.

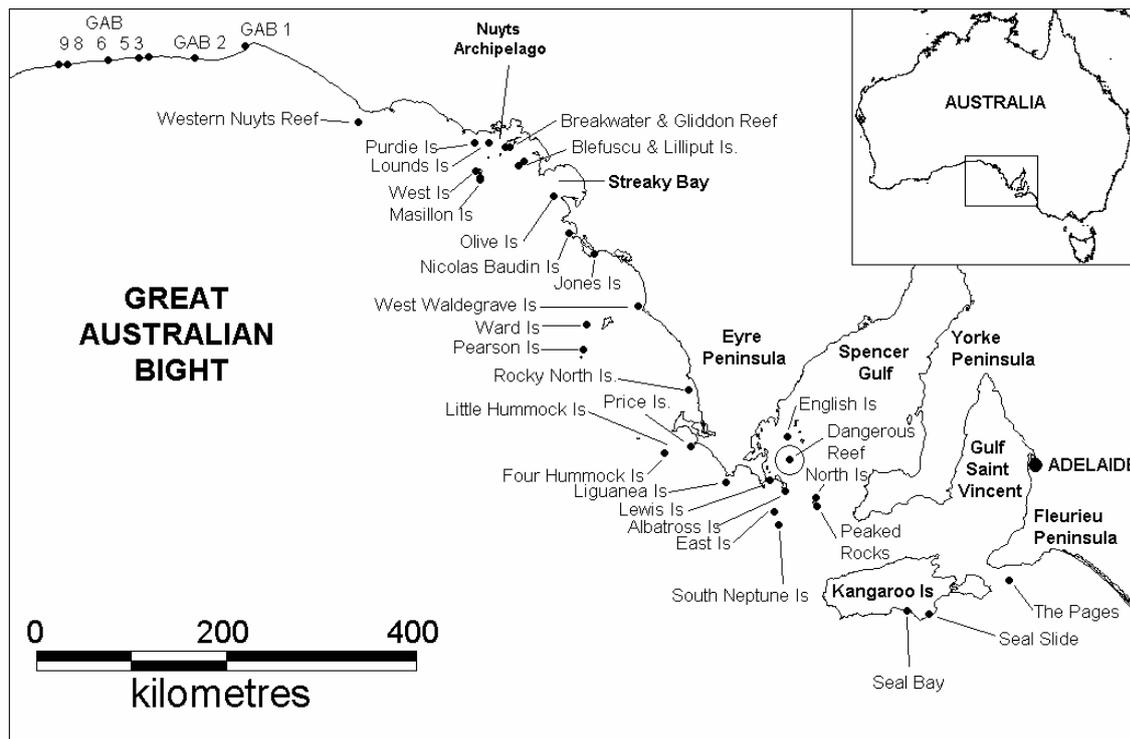


Figure 3.1. Location of Dangerous Reef in southern Spencer Gulf, relative to other Australian colonies in South Australia.

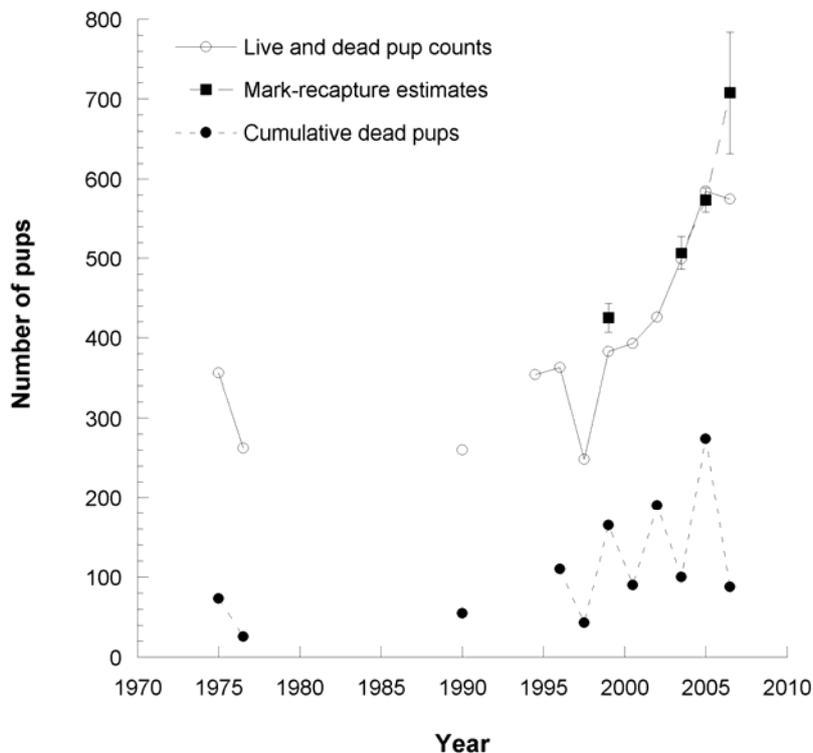


Figure 3.2. Trends in the abundance of Australian sea lion pups at Dangerous Reef, based upon maximum live and cumulative dead pup counts, mark-recapture estimates (inclusive of cumulative dead pups) and total cumulative dead pups counted for 12 breeding season between 1975 and 2006-07. Error bars around mark-recapture estimates are \pm 95% CL.

Discussion

Australian sea lion pup abundance estimates for the 2006-07 breeding season at Dangerous Reef provide additional evidence that pup production is increasing. Although the maximum live-pup count with cumulative deaths is slightly lower than the count for the 2005 season (575 vs. 585, respectively), the mark-recapture estimate inclusive of cumulative dead pups has produced the largest minimum estimate of pup production for the population (mean 709, 95% CL 636-783). Because this estimate was undertaken on 15 January 2007, about a month prior to the end of the breeding season, it does not include pups born between the mark-recapture survey and the end of the breeding season. Importantly, a mark-recapture estimate undertaken about 20 days following the 15 January survey produced an estimate that was 0.79 of the maximum estimate, indicating fewer pups were present on the island at that time. A decline in the number of pups following the peak is likely to be due to dispersal and mortality of pups.

There have been numerous observations that dispersal to nearby haul-out sites occur in some pups before the pupping season is completed. Movements of pups from Dangerous Reef to English Island were suspected in August and September 2002 (Shaughnessy et al. 2005a) and in July 2005 (approximately 5 months into the breeding season), some pups seen at English Island had been marked at Dangerous Reef as part of the mark-recapture procedure (D. Hamer, pers. comm.). Most recently, a tagged mother-pup pair from Dangerous Reef were sighted at English Island (6 February 07), the pup was known-aged and had managed to swim 20km to English Island when only four-months old (A. Lowther, pers. comm.). These observations suggest that even young pups have the capacity to travel to nearby haul-out sites and spend periods at sea, but the extent of this behaviour is poorly understood. In addition to dispersal, greater mobility as pups age means that their sightability within the colony is likely to diminish because they spend more time in the water. This was found to be the likely cause for low colony counts of live and cumulative dead pups in a recent Australian sea lion survey at Olive Island. Live plus cumulative dead counts at Olive Island peaked on the third survey to the island, but mark-recapture estimates of live pups increased until the fifth survey (Goldsworthy et al. 2007).

An increase in cumulative pup mortality as the breeding season progresses contributes to underestimation of total pup numbers at the end of the breeding season, especially if daily death rates exceed birth rates. Generally, dead pups are more difficult to see than live pups and may be overlooked during surveys. Dead pups may disappear before being counted because: 1) high tides and storm-driven waves may wash them away; 2) older sea lions trample them into the ground, and 3) avian scavengers gradually remove them.

A recent study developed a new approach from improving estimates of pup production for large Australian sea lion colonies, using mark-recapture methods in conjunction with Cormack-Jolly-Seber (CJS) models (Goldsworthy et al. 2007). This method requires individual tagging of pups in conjunction with resight histories to estimate mortality and dispersal rates of pups. This is important in

accounting for the assumptions of the mark-recapture procedure. CJS methods were trialled at Olive Island during the 2006 breeding season and produced pup production estimates that were greater than those based on direct counting and on the Petersen mark-recapture method. Pup mortality during the study period was estimated to range from 15-52 individuals. Because recovered mortalities numbered 34 in total, ground surveys may have underestimated pup mortality by up to 35%. There was no evidence for permanent emigration in the Olive Island study, suggesting that the most important source of error in mark-recapture procedures there were due to unaccounted mortality. The best estimate of pup production for the 2006 season at Olive Island based on CJS methods was 205 (range 193-256). This was 1.37 times the estimate based on direct counting methods (150 pups), but was similar to the result (1.03 times larger) obtained from the Petersen mark-recapture estimate (mean 197, range 191-203). However, an adjusted Petersen estimate (adding the mortality range 34-52) produced essentially the same estimate as the CJS approach (206, range 191-223) (Goldsworthy et al. 2007). Individual resight histories from pups tagged at Dangerous Reef will be used to estimate mortality and dispersal. Results will be important in providing confidence around the present methodology, and most important in providing critical insight to improving future surveys.

A pattern of alternating levels of pup mortality between winter and summer breeding seasons is apparent at Dangerous Reef. The levels average 37% in winter and 18% in summer. A difference in pup mortality between a winter and a summer pupping season was also observed by Gales et al. (1992) at islands in the Jurien Bay region on the west coast of Western Australia. They reported high pup mortality in the first five months of a breeding season that included the 1989 winter, averaging 24% over the three islands. Pup mortality rates were considerably lower (7%) in the preceding pupping season, which occurred during the summer. The difference in mortality rates between seasons was thought to have been related to timing of the sea lions' pupping seasons in winter and in summer, but the cause for differences between summer and winter seasons is unclear. The cumulative number of mortalities appear to be increasing across breeding seasons at Dangerous Reef, but based on our analyses these appear to mirror the increase in pup production. That is, the number of mortalities is increasing but not the rate (percentage) of mortality.

The most important finding of this survey at Dangerous Reef is continuing evidence for a sustained increase in pup abundance since at least 1999. This is supported both from count data and mark-recapture methods. Best estimates for the rate of increase (using count data and mark-recapture estimates as minima and maxima, respectively) range between 6.7-9.9% per breeding season, or 4.6-6.54% per year. Dangerous Reef is the only known Australian sea lion population that is presently increasing in size. Given the extreme depletion that is apparent for most other breeding sites (60% produce < 30 pups per season, Goldsworthy and Page 2007), continuation of monitoring at Dangerous Reef in conjunction with investigations into the cause(s) for population increase, will be critical in understanding the causes for declines in some populations, and managing the recovery of the species in general. Some of these issues are discussed in Chapter 5.

4 MATERNAL STRATEGIES OF AUSTRALIAN SEA LIONS AT DANGEROUS REEF

A Lowther

Introduction

Maternal strategies and selection

Parental care and the provisioning of offspring (pre- and post- partum) are the most energetically costly aspects of reproduction (Oftedal 1984, Gittleman et al. 1988, Boness and Bowen 1996).

Parental care in mammals occurs in three forms (biparental, uniparental female and communal) and is associated with the mating systems of different species (Clutton-Brock 1991). Biparental care is most common in monogamous species. Communal care is seen in species that exhibit social structure such as the primates where parents receive assistance in rearing and provisioning from other individuals. Many mammals are polygynous with uniparental female care (maternal care) being the most common reproductive strategy (Clutton-Brock 1991).

For sexually dimorphic mammals that have a polygynous breeding system, differences in the variance in reproductive success between males and females can be substantial (Clutton-Brock 1988). Females often operate at the limit of metabolic expenditure when feeding young and as a result the female's ability to find food and convert it to milk may constrain the number of offspring she can rear (Clutton-Brock 1991). Reproductive success in males requires large body size in order to compete with other males for matings (Weckerley 1998, Kruuk et al. 1999). Species such as the red deer (*Cervus elaphus*) and the northern elephant seal (*Mirounga angustirostris*) emphasise the competitive requirements of mating with the majority being performed by a small minority of males who have competed successfully (Clutton-Brock 1988, Le Boeuf et al. 1989).

The theory of Maynard Smith (1980) suggests that if one sex has a greater variance in reproductive success then parents should preferentially invest in favour of that sex to maximise fitness.

Differential investment theory in sexually dimorphic polygynous mammals predicts that mothers invest more in male offspring because they are often the sex with the greatest variance in reproductive success (Trivers 1972, Trivers and Willard 1973, Clutton-Brock et al. 1984). In many species male offspring are larger at birth and at the completion of parental investment suggesting they incur a greater cost to parents compared to female offspring (Le Boeuf et al. 1989, Lunn et al. 1993).

In contrast to the theory of differential investment, the theory of equal investment (Fisher 1930, Shaw and Mohler 1953, Charnov 1982) predicts that offspring sex is under genetic control and an equal amount of investment is imparted to males and females. Fisher (1930) suggested that if one sex was more costly to raise then parents would maximise their fitness by producing a greater number of offspring of the cheaper sex. The resulting bias in sex ratio would be ecologically unstable.

Many sexually dimorphic mammal species have a 1:1 sex ratio at the completion of parental investment (Clutton-Brock 1988, Hewison and Gaillard 1999) which according to equal investment theory indicates no difference in the cost of rearing male or female offspring. The sex-specific manner in which offspring metabolise invested energy (males produce more lean muscle mass, which weighs more for the same volume of fat) may explain the occurrence of preweaning mass differences in some species (Le Boeuf et al. 1989, Byers and Moodie 1990, Pelabon et al. 1995). Phenotypic traits associated with maternal care and provisioning strategies are expected to be under strong selection pressure (Arnold and Duvall 1994). As phenotypes are a product of genetic and environmental interaction, maternal strategies are likely to be influenced by ecological pressures and phylogenetic constraints. Measuring the ultimate effects of maternal care requires data on individual fitness (Clutton-Brock 1988). Generation length is considerable in some species and proximate measures of investment (maternal milk energy, lactation duration and nursing patterns) and proximate effects (offspring birth mass, length, growth rates and survival) may be more appropriate (Gentry et al. 1986, Byers and Moodie 1990, Pelabon et al. 1995).

Pinnipeds and maternal strategies

The Pinnipedia are a sexually dimorphic and polygynous order of the Mammalia. Pinnipeds represent a group amenable to the study of maternal care strategies as pups are completely reliant on maternal milk for nutrition (Trillmich 1996). Pinnipeds are faced with a unique set of selection pressures due to the spatial separation of onshore birthing grounds and at-sea foraging habitat (Gentry 2000). Three maternal care strategies have historically characterised each family of the Pinnipedia (Boness and Bowen 1996). These maternal strategies are aquatic nursing (walrus), fasting (earless seals) and foraging cycle (eared seals) (Boness and Bowen 1996). Walrus (*Odobenus rosmarus*) inhabit the Arctic and breed on ice flows during the Boreal winter (Kastelein 2002). As birthing sites are unpredictable and unstable, calves have adapted to enter the water shortly after birth and accompany their mothers on foraging trips to sea (Boness and Bowen 1996). Females are able to nurse calves during foraging trips and provide maternal care for up to three years although exclusive reliance on milk may only last up to five months (Fay 1982). This behaviour is more akin to terrestrial mammals with offspring care and maternal foraging not being spatially or temporally separated (Wells et al. 1999).

Earless seals (Phocidae) inhabit all major oceans except the Indian Ocean (Hammill 2002). Phocid seals are referred to as capital breeders as prior to birthing females store energy in the form of blubber and use this stored capital to provide offspring with nutrition whilst maintaining maternal metabolic function (Boyd 2000). Female phocids fast on land or ice for the duration of the lactation period, returning to sea to forage only after pups have weaned (Boness and Bowen 1996).

The eared seals (Otariidae) are generally smaller than phocids and are found in subpolar, temperate and tropical regions (Gentry 2000). Female otariids are referred to as income breeders who supplement the energetic demands of lactation with foraging trips to sea (Boness and Bowen 1996, Boyd 2000).

There are exceptions to these generalised maternal strategy hypotheses; the Harbour seal (*Phoca vitulina*) is a small phocid (females are approximately 80kg, similar to otariids) documented as displaying a foraging cycle strategy particularly in the latter stages of lactation when body stores are depleted (Boness et al. 1994). There is anecdotal evidence of one other small phocid (the ringed seal *Phoca hispida*) demonstrating similar foraging cycle tendencies (Boness et al. 1994). Boyd (2000) suggested that maternal body size was influential in determining maternal strategy. Logistic regression of mass, age and body length on reproductive events within two capital breeding phocid and one income breeding otariid species produced interesting results. In the capital breeding phocid seals, body mass accounted for 55% of the variance in pregnancy rates. However for the income-breeding otariid seals, body length was most important (Boyd 2000). As body length is positively correlated with age (McLaren 1993, Rosas et al. 1993, Winship et al. 2001) the findings suggest a positive relationship between successful reproductive events and age in otariid females.

Sex allocation, equal investment or differential utilisation of maternal resources

Evidence for differential maternal investment favouring male offspring (Trivers 1972, Trivers and Willard 1973, Maynard Smith 1980) and equal investment between both offspring sexes (Fisher 1930, Shaw and Mohler 1953, Charnov 1982) has been found in relation to pinnipeds. Research of the southern elephant seal (*Mirounga leonina*) exhibited no sex-biased difference in absolute maternal investment as predicted by equal investment theory, but larger mothers tended to produce male pups (Wilkinson and Aarde 2001) which could be interpreted as support for Maynard Smith (1980). Similar research on northern elephant seals (*M. angustirostris*) also showed no preferential investment in male offspring, supporting Fisher (1930) (Kretzmann et al. 1993).

Several otariid species display patterns of maternal investment that appear to support differential investment theory. Male pups of New Zealand fur seals (*Arctocephalus forsteri*) are born heavier and grow faster than female pups, with mothers of sons spending longer at sea foraging (Chilvers et al. 1995, Lea and Hindell 1997, Goldsworthy 2006). California sea lion (*Zalophus californianus*) male pups are born heavier, receive more maternal milk, display faster growth rates and wean heavier than female pups though mothers with sons did not forage for longer (Ono and Boness 1996). The Galapagos fur seal (*A. galapagoensis*) has a sex ratio at birth of 1.06 with male pups growing faster and weaning at a younger age than female pups (Trillmich 1986).

Recent studies have suggested that the intersexual differences in pup weaning masses and growth rates may be a result of pups utilising equal levels of maternal investment in different ways. The intersexual differences in growth rates of Antarctic fur seal (*A. gazella*) pups resulted from male and female pups having different body compositions and metabolic rates (Arnould et al. 1996, Guinet et al. 1999, Guinet and Georges 2000). Cape fur seal (*A. pusillus pusillus*) pups display intersexual differences in body mass despite equal consumption rates of milk, due to male pups having lower body-lipid levels and metabolic rates than female pups (Gamel et al. 2004). Similar explanations have

been suggested for intersexual growth parameter differences in Australian and New Zealand fur seal pups (Arnould and Hindell 2002, Goldsworthy 2006).

There is no clear evidence in support of a single maternal investment theory amongst pinnipeds with current research focussing on the issues of differential investment as opposed to differential utilisation of equal investment by male and female pups (Guinet and Georges 2000, McMahon et al. 2000, Kirkman et al. 2002, Goldsworthy 2006).

The Otariidae

All otariid seals exhibit a similar pattern of maternal care characterised by extended lactation periods punctuated by regular foraging trips to sea (Boness and Bowen 1996, Gentry 2000). Masses of pups at birth and weaning as a function of maternal mass are similar across the family (Gentry et al. 1986, Schulz and Bowen 2005). Critical differences between species are related to the age at weaning, which is defined as the greatest change in the rate of parental investment over time signifying the decrease in offspring reliance on maternal resources (Martin 1984).

Lactation length (weaning age) varies between four months and three years in otariid seals (Costa 1991b). Otariids that inhabit higher latitudes are faced with seasonal and highly predictable prey resource promoting short lactation periods. At lower latitudes, otariids face less seasonal and more unpredictable prey resource (Gentry et al. 1986) which induces strong selective pressure on the length of lactation and thus age at weaning. The physiological and behavioural development of pups is also associated with lactation length. Antarctic fur seal pups have moulted their lanugo pelage, shed milk teeth and are morphologically and physiologically prepared for nutritional independence when they wean at four months (Lunn et al. 1993, Guinet et al. 1999). Pups of temperate latitude species such as the Australian fur seal require an additional five months of maternal dependence to reach a similar stage of development at weaning (Arnould and Hindell 2002, Arnould et al. 2003), whereas Galapagos fur seals take between 1-3 years to wean their young (Trillmich 1986). Most species of otariid occur in temperate latitudes, and for these species both lactation length and the duration of foraging trips can vary both within and between species. Northern fur seals (*Callorhinus ursinus*) and Galapagos fur seals display intraspecific variation in lactation length dependent on the availability of prey, suggesting that intra-specific differences are due to local environmental variation as opposed to genetically fixed traits (Gentry and Holt 1986, Trillmich 1995).

When pups are young and small they have a limited ability to fast and this places restrictions on the duration of maternal foraging trips (Oftedal et al. 1987). It is expected that such restrictions select for breeding locations in close proximity to reliable sources of prey (Gentry 2000). As the distance to foraging grounds and the predictability and abundance of prey resources can vary considerably from location to location, these factors appear to be the most critical in shaping the differences in maternal strategy both within and between species (Gentry et al. 1986, Lunn et al. 1993, Boness and Bowen 1996). This includes the duration of lactation required to raise pups to weaning, and the way females

partition the duration and frequency of foraging trips between nursing bouts ashore. Subantarctic fur seals (*A. tropicalis*) at Amsterdam Island spend up to 23 days foraging and four days nursing whilst conspecifics at Macquarie Island forage for only three days and nurse for two days (Goldsworthy 1999, Guinet and Georges 2000).

Significant intra-specific differences in maternal strategies related to environmental variation indicate a degree of phenotypic plasticity amongst temperate-latitude otariids (Gentry and Holt 1986, Boness 1991, Francis et al. 1998, Goldsworthy 1999). There is a finite limit to plasticity exemplified by the effects of El Nino events. South American fur seal (*A. australis*) mothers extended foraging trip duration outside its normal range during the 1983 El Nino leading to mass starvations of pups (Trillmich et al. 1991). El Nino conditions reduce food availability requiring females to extend foraging trips (Heath et al. 1991, Trillmich et al. 1991). The maternal strategies of this species, although able to accommodate significant environmental variation, break down during El Nino conditions when investment is terminated to ensure maternal survival. Similarly California sea lion mothers cannot increase the energy delivered to pups to fully compensate for extended fasting periods during El Nino (Heath et al. 1991). With regards to milk energy (fat) and pup fasting, milk fat levels are positively correlated to the duration of foraging trips across the otariid group (Arnold and Trillmich 1985, Trillmich and Lechner 1986, Costa 1991a, Arnould and Boyd 1995). This may provide a mechanism to compensate pups for prolonged fasting (Scheiner 1993).

Current research on maternal strategies of lactating otariid seals is focussed on relationships with oceanographic features (Bradshaw et al. 2000, Guinet et al. 2001, Ream et al. 2005).

The Southern Ocean is subdivided into several distinct regions delineated by strong frontal zones (Pakhomov and McQuaid 1996). The subpolar front, subantarctic front and subtropical front are located where the colder high latitude waters meet the warmer subantarctic and tropical waters. Frontal zones are characterized by areas of strong horizontal gradients in temperature and salinity (Moore et al. 1999). The intensification of frontal zones during the Austral spring creates upwellings that intermix cold and warm water around topographical features, leading to an increase in primary productivity and biomass (Laubscher et al. 1993, Pakhomov and McQuaid 1996). Data indicates that maternal strategies are principally influenced by the proximity to foraging grounds (Goldsworthy 1999, Georges and Guinet 2000) and seasonal availability and abundance of prey species (Trillmich 1995, Goldsworthy 2006). Within these broader constraints the extent to which mothers invest resources in individual offspring is also influenced by maternal experience (age), mass and possibly pup sex (Gentry et al. 1986, Costa 1991b, Boyd 2000).

The Australian sea lion, *Neophoca cinerea*

One seal that is stimulating research interest is Australia's only endemic otariid, the Australian sea lion (*Neophoca cinerea*) as it represents an outlier in the behavioural range of temperate latitude otariids. Listed in 2005 as 'Threatened' under the *Environmental Protection and Biodiversity Conservation Act* (1999) the species current and historical status remains unclear as Australian sea lion numbers are not thought to have recovered since seal harvesting ceased, unlike other seal species in the same

region (New Zealand and Australian fur seals) (McKenzie et al. 2005). The Australian sea lion has an unusual gestation period of 17.6 months (Higgins and Gass 1993) resulting in the timing of birth in alternate breeding seasons occurring about one month earlier. Embryonic diapause is similar in length to that of other otariids (~4-5 months) meaning the Australian sea lion has the longest post-implantation period recorded of any pinniped (~13-14 months) (Gales et al. 1997).

Breeding colonies are asynchronous in the time of pup birthing and mating with females remaining at the same colony for their entire reproductive lives (Campbell 2003). This life history pattern contrasts that of geographically sympatric fur seal species (New Zealand and Australian fur seals) and all other otariids that share annual and highly synchronous breeding seasons (Trillmich et al. 1991, Shaughnessy et al. 1995, Ochoa-Acuña et al. 1998, Goldsworthy 1999, Arnould and Hindell 2001). Breeding seasons of other temperate latitude otariids appear closely linked to the seasonal increases in prey availability linked with the subantarctic and subpolar fronts in the Southern Ocean. Why Australian sea lions display such a unique breeding cycle remains unclear though localised cold-water upwellings along the coast of southern Australia may have an influence (Costa and Gales 2002, Fowler et al. 2006).

The foraging behaviour of otariids tends to reflect their physiology (Costa et al. 2004). The Australian sea lion is thought to be well adapted to a benthic foraging strategy with large body size for deep diving and insulating blubber that does not change in buoyancy characteristics with depth (as opposed to air-trapping under-fur in fur seals) (Costa and Gales 2002). Some suggest that Australian sea lions have maternal strategies adapted to an aseasonal environment characterized by low primary productivity reflected in short foraging trips more commonly observed in tropical otariids (Costa and Gales 2002). One of the longest lactation cycles recorded for an otariid suggests that the maternal strategies of Australian sea lions are adapted to buffer offspring against unpredictable aseasonal prey resource and provide more time for pups to develop foraging skills prior to independence (Gentry et al. 1986, Higgins and Gass 1993).

Asynchronous breeding is thought to be reinforced by regional adaptations to localised foraging conditions in conjunction with limited migration (McKenzie et al. 2005). As such there may be considerable differences in some maternal strategies among populations that relate to localised adaptations. Only one other study has been conducted into maternal care and provisioning of Australian sea lions. Observational data of maternal attendance patterns and pup growth rates were collected from birth to three months from 1987 to 1990 at Kangaroo Island (Kretzmann et al. 1991, Higgins 1993, Higgins and Gass 1993). Significant intra-population variation in foraging trip duration was observed. Foraging trip and nursing bout duration remained constant throughout the initial three months of lactation. Lactating Australian sea lions displayed no differences in the time spent foraging, nursing or the proportion of time spent ashore with regards to pup sex. Milk-lipid levels were unrelated to maternal mass, length, foraging trip duration or pup sex. There were no intersexual differences in pup birth masses or growth rates, with the latter being linear for the first 150 days.

Aims

The principle aim of this study was to describe the general pattern of maternal care in Australian sea lions during the early stages of lactation, determine whether the unusual life-history of the species has resulted in any departure from the typical otariid model and speculate how Australian sea lion maternal strategies reflect the exploitation of foraging habitat. To achieve this, the study sought to examine:

- How females allocate time ashore to nurse their pup between foraging trips to sea.
- How the patterning of foraging and nursing changes throughout lactation.
- Whether maternal size, milk-lipid content and maternal attendance behaviour influences the size and growth of pups.
- Whether pup sex influences provisioning of maternal resources in line with the theory of differential investment.
- How lunar and diurnal influences on foraging strategy relate to known foraging behaviour and habitat.

Methods

Study site

Dangerous Reef (34°50'S 136°15'E) measures 600m east-west and 200m north-south and is situated in the southern Spencer Gulf 18 nautical miles east of Port Lincoln in South Australia (Figure 4.1) .

Access and sampling regime

Six trips of five to 11 days duration were made with all fieldwork conducted between 28 August 2006 and 14 February 2007. Animal capture and sampling procedures were approved by the La Trobe University Animal Ethics Committee (AEC06/24(BG)/V1) and the South Australian Department for Environment and Heritage (Permit #A24684).

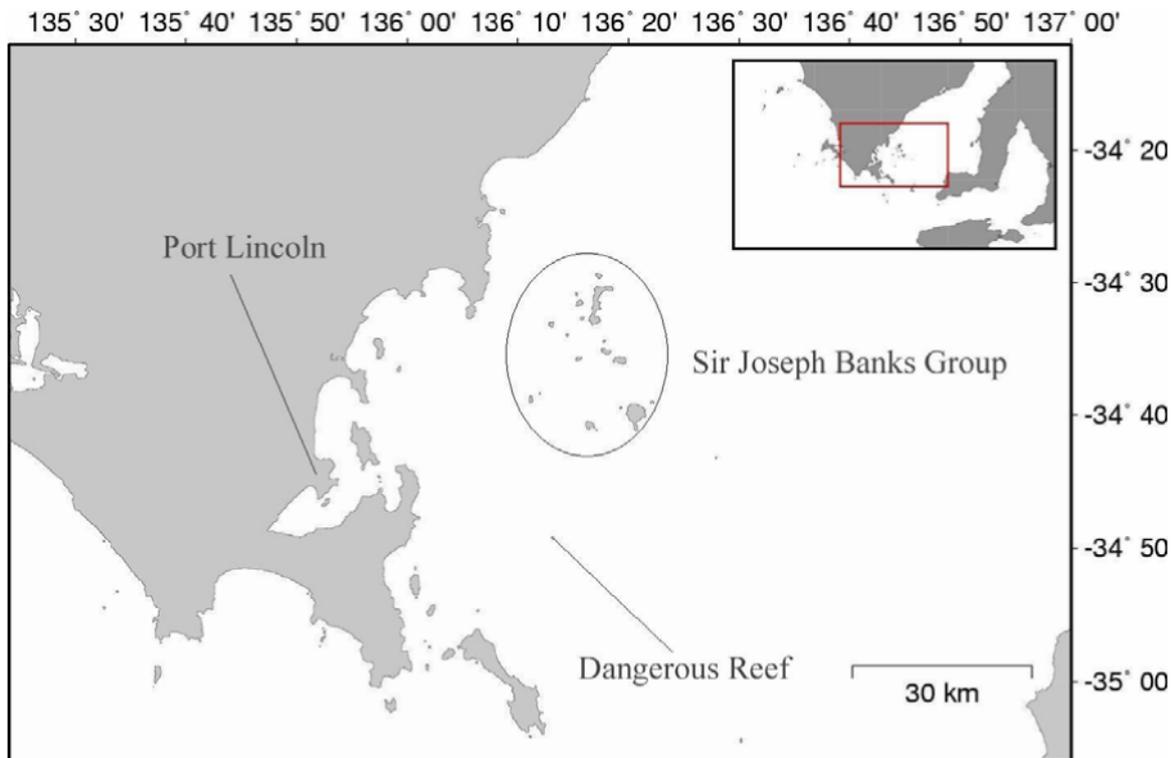


Figure 4.1. Map of study site in relation to Spencer Gulf, South Australia.

Known-age pup data collection

Dates of birth for 36 pups were determined as the observed date of birth ($n=10$), the date when fresh placenta was observed ($n=14$) or as midnight of the previous day if a new birth occurred between sunset and sunrise ($n=12$). Peri-natal attendance of females prevented the capture and marking of some pups ($n=16$) so their mothers were marked with Nyanzol-D dye (J. Belmar Inc., Andover, Massachusetts, USA). As mothers only give birth to one pup (Gentry 2000), this facilitated identification of known-age pups so they could be captured and marked on subsequent field trips.

The known-age pups were captured and marked with a unique number on the pelage across the pelvic girdle using bleach (Clairol[®], Bristol-Myers Squibb Ltd, West Ryde, N.S.W, Australia). Sex, standard length (straight-line length from tip-of-nose to tip-of-tail, to nearest 0.5cm) and axillary girth (exhaled, nearest 0.5cm) of each pup were recorded. The mass of pups were measured using a 25 x 0.1kg spring balance (Salter Weigh-Tronix, Blackburn, Victoria, Australia.). On completion pups were released back to the area of capture and observed until mother and pup were reunited.

When possible, know-age pups were recaptured at monthly intervals and measured. Numbered plastic tags (Dalton porcine Supertag[®], Dalton Supplies Ltd, U.K.) were also fitted to the trailing edge of each foreflipper to facilitate identification because bleach marks faded as pups aged.

Maternal attendance, female body condition and milk collection

Thirteen adult female Australian sea lions whose pups had been sampled were used for gathering maternal attendance data. Females were captured, restrained and anaesthetised using isoflurane (5% induction, 3% maintenance) (Veterinary Companies of Australia, Artarmon, New South Wales) delivered through a portable anaesthesia machine. Capillary refill, breathing rate and tactile response were used to monitor animals during each procedure. Animals were observed until they regained mobility and coordination. Once females had recovered, they were reunited with their pups. After anaesthetic induction the animal was secured on a hammock and suspended from a 100 x 0.5kg spring balance (Salter Weigh-Tronix, Blackburn, Victoria, Australia.). Standard length and axillary girth measurements were taken as for pups.

An activated 20g two-stage VHF radio transmitter (150-151Mhz) (Sirtrack Ltd, Havelock North, New Zealand) with a unique pulsing frequency (Appendix I) was attached to each animal either to the pelage distal to the midpoint on the back using two-part Araldite[®] 2014 epoxy resin (n=9) or to the trailing edge of the right foreflipper of each animal (n=4). Animals were tagged using numbered plastic tags (Dalton porcine Supertag[®], Dalton Supplies Ltd, U.K.) on the trailing edge of the foreflipper. An intramuscular injection of Oxytocin (0.7ml, 10 UI mL⁻¹, Syntocin-Sandoz) was given five minutes prior to collecting milk samples. Two 5ml vials of milk were collected per animal by manual expression of the teat, and stored in 5ml Eppendorf tubes. Milk could not be expressed from three females (ID# 562, 566 and 574). All samples were frozen at -20°C until analysed.

VHF data collection

Presence or absence of mothers at the colony was monitored using a DCC II scanning receiver (Model 2000B receiver, range 150-151 MHz, Advanced Telemetry Systems Inc., Isanti, Minnesota 55040, U.S.A.) connected to a programmable data logger (Model 5040, Advanced Telemetry Systems Inc.). Frequencies were monitored sequentially every 60 seconds and pulses from each transmitter were recorded between 10 October 2006 and 31 January 2007. The logging array was assembled and tested at the study site on 28 August 2006. All transmitters were activated and carried around the extremities of the reef whilst signal strength was checked via the logging array prior to deployment on animals. Raw data were downloaded during each trip to Dangerous Reef.

Laboratory analysis

Individual milk samples were thawed for four hours and emptied onto separate petridishes and weighed (300-HG scales max=3 10g d=0.001g) then placed into an oven at 60°C for 48hours (Department of Genetics, La Trobe University, Bundoora). On completion, the dishes and dried content were reweighed. Dried mass was subtracted from wet mass to estimate water content (nearest 0.01g), and expressed as a percentage.

Statistical analyses

Statistical tests were performed using R Software (R Core Development Team 2006). Normal distribution and homogeneity of variance were checked using Shapiro-Wilks and Levene's tests respectively. Unless otherwise stated, data are presented as mean \pm Standard Error and results were considered significant at $p < 0.05$.

To quantify foraging trip and attendance bout durations, VHF pulse recordings of less than five pulses per minute were disregarded as background noise (transmission drift, radio interference from passing vessels etc). Foraging trips of less than five hours ($n=5$ across the entire dataset) were assumed to represent females either in areas obstructing VHF signal (e.g. thermoregulating in pools of water) or swimming close onshore and were not included in analyses. Proportions of total time spent ashore for each adult were arcsine transformed prior to analysis.

Australian sea lions grow in length throughout most of their lives with female length reaching an asymptote at approximately 13 years (McIntosh unpub). Residuals from the linear regression of adult female Australian sea lion mass on length were used to create a body condition index (BCI) independent of length (Trites 1991). Proportion of time spent ashore, mean foraging trip and attendance bout duration were tested against maternal BCI, length and mass in a series of single factor ANOVA. Kruskal-Wallis rank sum testing was used when data were not normally distributed.

Intersexual differences in maternal provisioning and changes in foraging cycle were examined as a function of pup age. Australian sea lions lactate for 17.6 months (Higgins and Gass 1993), however telemetric and observational data available after 90 days post partum suggested attendance cycle patterns were distorted by the movement of pups away from the colony as they grew older (two 100-day old pups were seen on a mark-recapture visit to English Island 30km away). For each female, durations of foraging trips and nursing bouts were grouped into 30, 60 and 90 days after pup birth. Foraging trips or attendance bouts that spanned a 30 day block were placed into the block in which the female arrived (foraging trip) or departed (attendance bout).

The use of repeated-measures ANOVA to determine the significance of individual changes in maternal attendance through lactation was made untenable due to missing blocks of data (caused by failure of transmitters at different times throughout sampling). As such, data were analysed by ANOVA with sequential Bonferroni adjustment of p -values after the method of Goldsworthy (1999). Kruskal-Wallis rank sum testing was used in place of ANOVA when data were not normally distributed.

There is considerable evidence supporting a highly significant relationship between milk water content and gross energy (lipid) content among many otariid species including Australian sea lions (Trillmich and Lechner 1986, Kretzmann et al. 1991, Gales et al. 1996, Goldsworthy and Crowley 1999) ($r^2 > 0.90$ in all cases studied). As such, milk-lipid levels were estimated in this study by converting measures of milk-water content to milk-lipid using the regression equation developed for Australian sea lions by Kretzmann et al. (1991) (% wet weight (Milk-lipid) = $91.365 - 1.054 \times$ (%wet weight Milk

Water), $r^2=0.95$). Mean % milk-lipid showed a bimodal distribution and arcsine transformation was unsuccessful in normalising data. Lipid content was graphed against female length, mass, body condition, foraging trip length, attendance bout length, proportion of time spent ashore and pup age to observe any relationships. Plots were separated into high-value and low-value cells for each parameter using median values and counts were made for each cell. Pearson's chi square tests with Yates continuity correction for small sample size were used to test for significant relationships between milk-lipid levels and adult mass, length, body condition, foraging trip length, nursing bout duration and pup age. Intersexual differences in the levels of milk-lipid fed to pups were examined using Student's t-test.

Not all pups were available for recapture on each sampling visit. Pup growth rates, birth masses and masses at 90 days were estimated from the linear regression of individual pup masses which consisted of three or more sampling points. Type I error rates were extremely unlikely given the considerable literature supporting linear pup growth during the early stages of lactation (Guinet et al. 1999, Guinet and Georges 2000, Arnould and Hindell 2002, Goldsworthy 2006). Regressions showed high r^2 values and as only slope and intercept values were required p-values were adjusted upwards to 0.12 (Quinn and Keough 2004). Estimated pup birth mass, growth rates and mass at 90 days were tested for intersexual differences by Student's t-tests.

Individual and multiple linear regression modelling of pup growth with maternal characteristics (length, mass, BCI, milk-lipid content, foraging trip duration, attendance bout duration and proportion of time spent on shore) were conducted to identify which variables best explained variance in estimated pup birth masses, growth rates and masses at 90 days. Sample size was a limiting factor so to gauge which multivariate model provided best explanatory power Bayesian estimation of the parameters and an iterative model averaging approach was used. In most cases, statistical analyses used followed those described by Quinn and Keough (2004).

Results

Maternal attendance

Telemetric data over 102 consecutive days was collected for ten lactating Australian sea lions. Three units failed on attachment or shortly after and as such the duration of longitudinal data sets among females varied (range 23-102 days, mean = 93.9 days \pm 13.36 days SE). An average of 20.4 (range 9-40, $n=10$) foraging trips and 18.8 (range 4-39, $n=10$) attendance bouts were recorded for each female. Foraging trips lasted 1.91 days (\pm 0.23 days SE) between attendance bouts of 0.83 days (\pm 0.13 days SE). Across all attendance data, female Australian sea lions spent approximately 33% of their time on land (mean time ashore / total time = 0.32, \pm 0.03 SE). Individual mean foraging and attendance bouts are summarised at Table 4.1.

Proportion of time spent ashore, foraging trip or attendance bout duration did not change over the lactation period sampled when all data were pooled (Kruskal $\chi^2 = 1.79$, d.f = 2, $p > 0.05$ in all cases) (Figure 4.2a). There were no differences in the duration of foraging trips (ANOVA $F_{2,22} = 1.9$, $P > 0.05$ Bonferroni Adjusted p-value) or attendance bouts (Kruskal $\chi^2 = 1.79$, d.f=2, $p > 0.05$) for mothers with sons or daughters throughout the study period. However, mothers with sons spent a significantly greater proportion of total time ashore (33.9%) compared with daughters (23.2%) (Figure 4.2b) over the study period (ANOVA $F_{2,22} = 3.86$, $p < 0.05$ Bonferroni Adjusted p-value) although this result was not significant during the first 30 days of lactation (Student's t-test, $t = 0.77$, d.f=7, $p > 0.05$).

To examine whether patterns of foraging or nursing affected maternal body condition, mass on length regression residuals for adult females sampled ($r^2 = 0.8$, $F_{1,11} = 47.5$, $p < 0.001$) were used as a body condition index (BCI) (Table 4.2). Maternal time spent at sea, ashore and the proportion of total time spent ashore had no significant influence on body size or condition ($F_{1,8} = 1.27$, $p > 0.29$ in all cases).

Milk-lipid content

The estimated milk-lipid levels during the first two months of lactation of individual females was 21.0% ($\pm 1.18\%$ S.E) (Table 4.2) and did not vary with pup age, foraging trip length, shore attendance duration or proportion of total time spent ashore (Pearson's $\chi^2 = 0.63$, $p > 0.05$ in all cases) (Figure 4.5). Mothers of sons did not produce significantly different levels of milk-lipid to mothers of daughters ($t = 0.23$, d.f=8, $p < 0.05$). The length of females was negatively related to their milk-lipid content (Pearson's $\chi^2 = 4.23$, d.f = 1, $p < 0.05$), with shorter females having higher lipid levels than longer females. Similarly, lighter females had higher milk-lipid levels compared to heavier females (Pearson's $\chi^2 = 3.6$, d.f = 1, $p = 0.06$) but these relationships did not extend to estimates of maternal body condition (Pearson's $\chi^2 = 0.39$, d.f = 1, $p > 0.05$) (Figure 4.5) suggesting that milk composition is primarily influenced by the size and not the condition of females.

Pup Growth

A total of 36 pups were measured between 27 August 2006 and 31 January 2007, with a maximum sampling age of 168 days (Appendix V). Birth mass (male $n = 13$, female $n = 5$) estimated from the y-intercept ranged from 7.6-10.7kg with a mean of 9.1kg (± 0.3 kg SE). Growth rates (male $n = 13$, female $n = 5$) varied from 0.50- 0.11kg day⁻¹ with a mean of 0.09kg day⁻¹ (± 0.01 kg day⁻¹ SE) (Table 4.3).

There were no significant differences between the estimated masses at birth, masses at 90 days (mean male=17.4kg ± 0.8 kg SE; mean female=16.2kg ± 0.7 kg SE) or estimated growth rates of male and female pups (Student's t-test, $t < 1.25$, d.f=16, $p > 0.05$ in all cases). *Post hoc* assessment revealed low statistical power (29%) to detect intersexual differences in pup growth parameters with a larger sample size (male $n = 55$, female $n = 55$) required to increase power to 80%. Estimated birth masses, masses at 90 days and growth rates were unrelated to maternal length ($F_{[1,7]} < 1.41$, $p > 0.27$ in all cases) though approached significance with maternal mass (mass at 90 days $F_{[1,7]} = 4.51$, $p = 0.07$; growth rates $F_{1,7} = 4.15$, $p = 0.08$).

Generalised linear modelling procedures were used to examine the importance of maternal parameters (length, mass, BCI, milk-lipid content, foraging trip duration, attendance bout duration and proportion of time spent ashore), both individually and interactively, in enhancing the estimated mass of pups at birth and 90 days, and their growth rates. Individual linear modelling of maternal parameters and estimated pup birth masses, growth rates and masses at 90 days resulted in a positive relationship between proportion of time spent ashore by mothers (P) and estimated pup growth rates ($r^2 = 0.56$, $F_{1,6} = 7.58$, $p < 0.05$). The regression equation was:

$$\text{Pup growth rate (kg day}^{-1}\text{)} = 0.14 P - 0.04$$

No other single maternal parameter contributed significantly to estimating growth rates or masses at 90 days ($F_{[1,6]} < 4.14$, $p > 0.05$ in all cases). No single maternal parameter significantly predicted estimated birth mass ($F_{[1,6]} < 0.56$, $p > 0.05$ in all cases). The relationship of proportion of time spent ashore and estimated pup growth was strengthened only when maternal length (L) was considered ($r^2 = 0.70$) though evidence was weak (Bayesian posterior probability $B_{pp} = 60.6\%$). The regression equation was:

$$\text{Pup growth (kg day}^{-1}\text{)} = 0.164 P + 0.001 L \text{ (cm)} - 0.19'$$

Modelling of the same maternal variables provided weak supporting evidence for estimated pup mass at 90 days ($r^2 = 0.56$, $B_{pp} = 55.9\%$). The regression equation was:

$$\text{'Pup mass at 90 days (kg)} = 14.65 P + 0.18 L \text{ (cm)} - 17.77'$$

No combination of maternal parameters significantly predicted estimated birth mass ($B_{pp} < 50\%$ in all cases). Predicted pup growth rates and masses at 90 days fitted well with observed data (growth rate: $F_{[1,6]} = 14.13$, $p < 0.01$; mass at 90 days: $F_{[1,6]} = 7.59$, $p < 0.05$) ($r^2 = 0.70$ and 0.56 respectively) (Figure 4.6) suggesting that maternal length (age) and the proportion of time spent ashore positively influence pup growth rates and mass at 90 days.

Table 4.1. Summary of foraging and attendance bout duration for individual lactating Australian sea lions in days. Numbers of events in parentheses. Standard Errors shown.

Female ID	Mean duration (days) Foraging \pm SE				Prop time		
	Attendance				\pm SE	ashore	\pm SE
564	1.98	(27)	0.18	1.08 (26)	0.14	0.38	0.03
562	2.28	(31)	0.14	0.39 (26)	0.05	0.18	0.02
566	2.32	(18)	0.13	1.29 (17)	0.12	0.34	0.02
561	1.89		0.15	1.00 (20)	0.14	0.36	0.03
553	1.22	(40)	0.08	0.02 (39)	0.09	0.33	0.03
574	2.16	(9)	0.54	0.57 (7)	0.12	0.27	0.05
560	1.18	(15)	0.19	1.09 (14)	0.26	0.56	0.05
559	2.28		0.15	1.09 (21)	0.58	0.34	0.02
572	1.95	(15)	0.21	0.46 (14)	0.06	0.23	0.03
581	1.86	(6)	0.55	0.56 (4)	0.31	0.18	0.04
\bar{x}	1.91		0.23	0.83	0.13	0.32	0.03

Table 4.2. Maternal body length, body condition index and milk-lipid levels for lactating Australian sea lions at Dangerous Reef. '-' indicate milk samples not obtained.

Female ID	Length (cm)	BCI (residuals)	Lipid levels (%)	\pm SE
573	167	6.13	14.5	0.84
566	146	4.54	-	-
572	150	4.39	24.8	4.57
561	156	2.92	16.7	0.82
574	161	2.11	-	-
559	158	1.09	14.7	0.43
553	155	0.08	28.2	1.49
560	159	-0.57	11.8	0.63
564	143	-0.97	26.1	0.39
563	156	-1.08	26.3	1.39
562	157	-2.24	-	-
558	170	-7.35	13.8	0.15
581	146	-9.04	33.3	1.06
\bar{X}	155.7		21.0	1.18

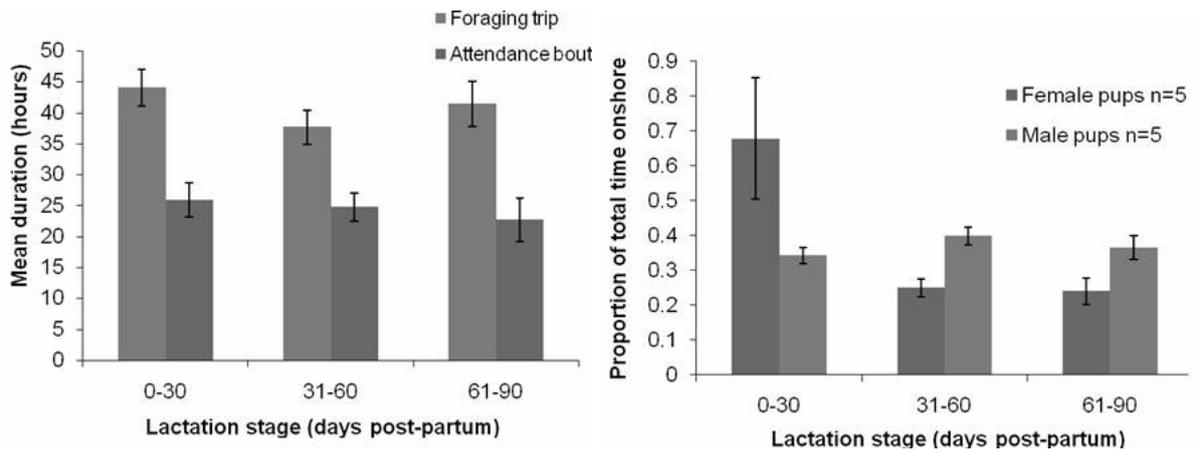


Figure 4.2. Telemetry data grouped by stage of lactation for mean foraging and attendance bout duration (left) and proportion of time spent ashore by mothers with respect to pup sex (right). Standard Error bars shown. There were no significant changes in foraging cycle through lactation, though mothers of male pups showed a propensity to remain ashore for a greater proportion of time than those with female pups after 30 days post-partum.

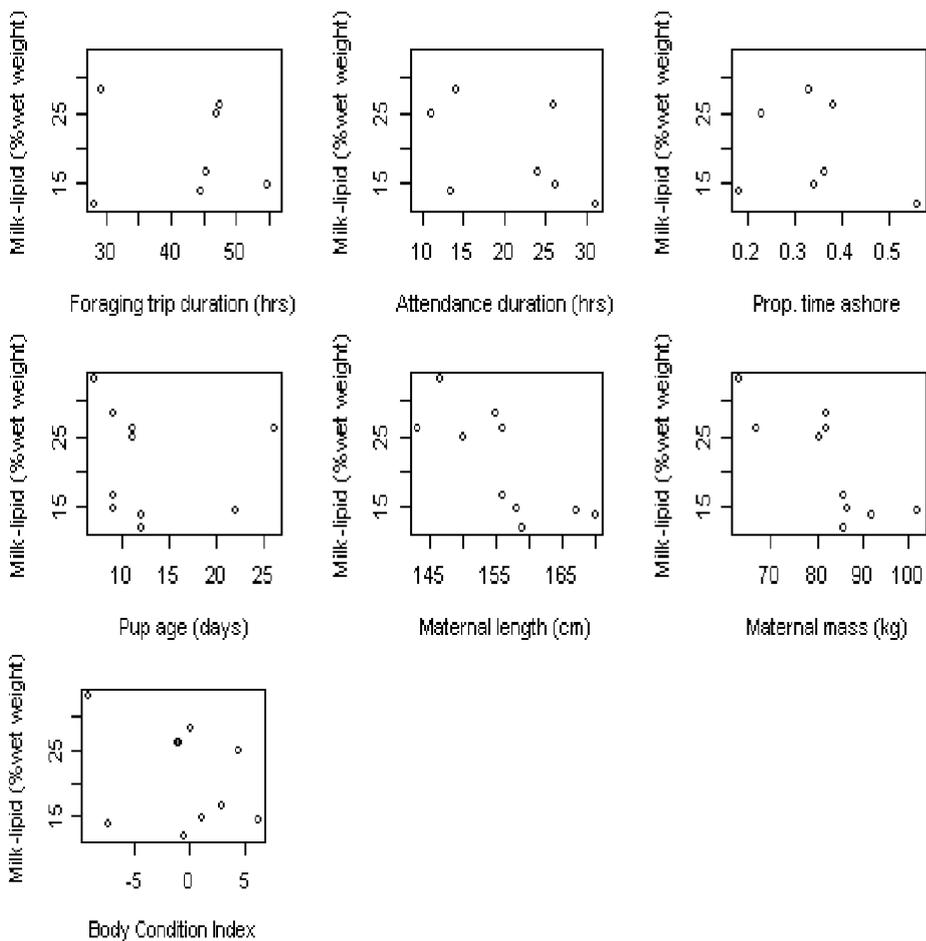


Figure 4.5. Plots of estimated milk-lipid levels among female Australian sea lions against pup age at time of sampling, mean foraging trip length, shore attendance duration, proportion of total time spent ashore, adult female mass, length and body condition. Milk-lipid levels were negatively related to maternal length and mass only.

Table 4.3. Summary of linear regressions of mass on age for 18 individual pups with three or more sampling points.

Pup ID#	Sex	y-intercept	Slope	r ²	p
2	M	9.8	0.100	1.00	0.01
3	F	8.6	0.103	0.98	0.08
5	M	10.7	0.099	1.00	<0.001
8	M	9.9	0.061	0.97	0.11
9	M	10.1	0.106	1.00	<0.001
10	M	10.7	0.119	0.97	0.11
11	M	8.5	0.064	1.00	<0.001
12	M	9.5	0.110	0.97	0.11
19	F	8.1	0.089	0.99	<0.001
22	F	9.3	0.050	0.99	0.05
23	M	10.2	0.109	1.00	0.01
26	M	9.4	0.110	0.99	0.06
28	M	7.8	0.075	0.98	0.01
30	M	7.6	0.105	0.99	0.01
31	M	6.3	0.059	1.00	0.02
32	F	8.9	0.090	0.98	0.10
34	F	8.8	0.080	0.97	0.11
35	M	8.7	0.076	0.99	0.01

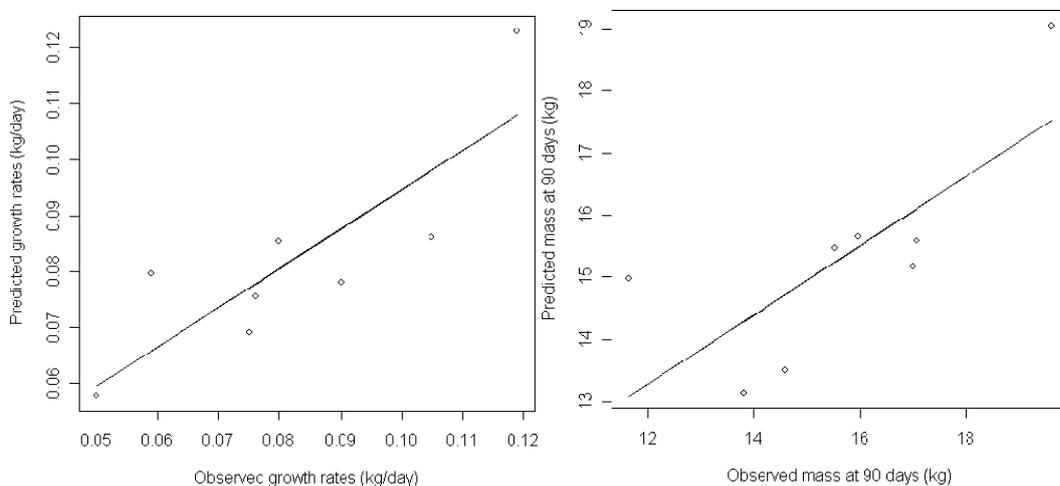


Figure 4.6. Plots of (a) estimated pup growth rates and (b) mass at 90 days against predicted values generated by GLM modelling of maternal length and proportion of time spent ashore. Maternal length and the proportion of time spent ashore positively influence pup growth rates and masses at 90 days.

Discussion

Maternal investment theory

This study detected no intersexual differences in estimated birth masses, growth rates or masses at 90 days of Australian sea lion pups. This is consistent with the findings of a previous study on Australian sea lions at Kangaroo Island that also failed to detect intersexual differences in estimated pup growth parameters (Higgins 1993). Although intersexual differences in pup birth mass and growth are commonly reported in other otariid species (Trillmich 1986, Cappozzo et al. 1991, Chilvers et al. 1995, Ono and Boness 1996, Arnould and Hindell 2002), occasionally they are not (Higgins and Gass 1993, Lunn and Arnould 1997, Goldsworthy 2006). This study is consistent with the latter.

For Australian sea lions to express sex-biased maternal investment it would be expected that faster growing, heavier male pups may require greater maternal foraging effort (reflecting their extra energy requirements for additional investment) resulting in a smaller proportion of time to nurse with mothers and would receive either a greater quantity of milk or milk of a higher fat content than female pups (Trivers 1972, Trivers and Willard 1973, Maynard Smith 1980). If pups express intersexual differences in the utilization of maternal resource, it is expected that faster growing, heavier male pups would receive the same amount of maternal investment as female pups.

The conditions under which intersexual growth differences are expressed in otariids pups, and whether similarities or differences in mass and growth rates reflect differences in maternal allocations or differential utilization of maternal resources by pups remains keenly debated. In a comprehensive review of maternal investment data for Antarctic fur seals Lunn and Arnould (1997) detected no intersexual differences in pup growth, suckling behavior or mass at weaning and no differences in maternal investment. This is contradicted by a later study which showed Antarctic fur seal male pups grew faster than females, whilst fasting females lost weight at a greater rate than males for the same levels of maternal investment indicating intersexual differences in metabolism (Guinet et al. 1999). Australian fur seal female pups invest more in body fat reserves whilst males invest energy in depositing lean muscle leading to male pups weighing more than females for the same amount of maternal investment (Arnould and Hindell 2002).

Intersexual growth differences in Californian sea lion pups recorded during favourable foraging conditions (Ono and Boness 1996) were not detected when prey availability decreased during El Niño (Ono et al. 1987). New Zealand fur seal pups displayed intersexual differences in growth at Maatsuyker Island (Tasmania) and Cape Foulwind (New Zealand) but not at Kangaroo Island (Chilvers et al. 1995, Lea and Hindell 1997, Goldsworthy 2006). This suggests local environmental variation affects maternal foraging efficiency (such as availability of suitable prey) and may determine whether intersexual growth differences are observed or not (Goldsworthy 1992, Trillmich 1996). Increasing the duration of foraging trips as lactation progresses has been observed in many otariids and may result from increased energy demands of pups and gestation as well as a seasonal

reduction in prey abundance (Goldsworthy 1995, Ochoa-Acu-a et al. 1998, Goldsworthy 1999, Goldsworthy and Crowley 1999, Guinet and Georges 2000, Arnould and Hindell 2001, Goldsworthy 2006). Whether increasing foraging trip duration is related to intersexual differences in maternal expenditure on male and female pups remains unclear. New Zealand fur seal mothers with sons spend longer at sea foraging than mothers with daughters (Goldsworthy 2006). This trend has been recorded in Antarctic fur seals at Heard Island (Goldsworthy 1995) but not at South Georgia (Lunn and Arnould 1997). Lactating Australian sea lions spent approximately two days at sea foraging and 0.83 days ashore with significant variation between females at Dangerous Reef (range 0.5 – 4.7 days) with no variation throughout the first 90 days of lactation or with respect to pup sex. The breeding colony at Kangaroo Island displayed similar tendencies across the first three months of winter and summer breeding cycles (Higgins and Gass 1993). This study suggests that *N. cinerea* does not express differential investment in the form of elongated foraging trips by mothers with sons in accordance with the theory of Maynard Smith (1980), and does not appear to experience a decrease in foraging efficiency due to seasonal variation in prey abundance.

Longer (possibly older) females spent a significantly greater proportion of time ashore resulting in faster growing, heavier pups of both sexes. Maternal experience is likely to influence pup growth in two ways 1) by increasing foraging efficiency therefore reducing metabolic costs incurred through feeding (Bowen et al. 2001a) and 2) by optimising foraging and attendance durations to meet maternal energy budgets and limit the fasting requirements of pups (Lunn et al. 1993). Older Harbour seal (*Phoca vitulina*) mothers wean pups significantly faster than younger mothers (Bowen et al. 2001b) and subantarctic fur seal pup growth is positively related to maternal foraging efficiency and age (Lunn et al. 1993, Guinet and Georges 2000).

The influence of maternal experience on offspring birth masses and growth rates may also translate into increased post-weaning survival. Northern fur seal 2nd year and southern elephant seal 1st year survival rates were significantly higher for heavier pups at birth and weaning respectively (Baker and Fowler 1993, McMahan et al. 2000). The maternal experience of older Australian sea lion mothers may be responsible for producing faster growing, heavier pups and these pups may have higher survival rates than those pups of younger mothers. As a consequence male pups of older Australian sea lions may have a fitness benefit over those male pups of younger mothers.

Pup growth and milk-lipid levels

In general, lipid levels at Dangerous Reef were similar to those found during the same stage of lactation at Kangaroo Island (21% and 24% respectively). Australian sea lion lipid levels are similar to Southern sea lions (32%) and Californian sea lions (26%) which spend a longer proportion of time ashore throughout lactation delivering a greater volume of milk to larger and faster growing pups irrespective of pup sex and maternal body size (Ono et al. 1987, Thompson et al. 1998). Milk-lipid levels of Australian sea lions are considerably lower than subantarctic fur seals (43%), Antarctic fur seals (42%) and nearby Australian fur seals (42%) which spend proportionately less time with pups by

extending foraging trips through lactation, with longer females producing higher milk-lipid levels (Goldsworthy and Crowley 1999, Arnould and Hindell 2002).

Many otariid species decrease milk fat levels during the onset of foetal gestation possibly due to the partitioning of maternal resources, but this may be due to either seasonal variation in prey abundance experienced in late-lactation or as part of the weaning process (Arnould and Hindell 1999, Goldsworthy and Crowley 1999, Georges et al. 2001). Australian fur seals increase milk fat levels from 42% to a peak of 50% at the beginning of the Austral winter when pups are seven months old. Milk fat levels in this species then decrease through winter to 45% when pups wean at nine months (Arnould and Hindell 1999). Throughout lactation, the milk-lipid content of Antarctic fur seals has been shown to increase in response to increasing foraging trip duration, from 32% following birth to 44% at weaning (Goldsworthy and Crowley 1999). Antarctic and Northern fur seals are unique among otariids in that the period of placental gestation does not overlap with the lactation period (Lunn and Arnould 1997).

Similar to other studies that have examined milk-lipid levels in otariids, this study detected no difference in the milk-lipid levels fed to male and female pups, nor a significant relationship between milk-lipid levels and the duration of maternal foraging trips. This is consistent with studies on the milk content of Australian sea lions at Kangaroo Island (Kretzmann et al. 1991). However, contrary to the study at Kangaroo Island, larger female Australian sea lions at Dangerous Reef produced lower milk-lipid levels than shorter females. Post-implantation gestation commences at five months when energy demands are increasing in association with the onset of foraging ontogeny (Fowler et al. 2006). Older northern elephant seal mothers impart more maternal energy to gestation (resulting in the production of heavier pups at birth) and create a greater amount of milk than younger mothers for the same amount of maternal energy invested (Crocker et al. 2001). It is possible that longer (presumably older) Australian sea lions invest more energy in gestation and produce more milk (with a lower energy content) which can be delivered to pups during the proportionally longer nursing bouts relative to shorter (younger) females.

From 30 to 90 days after birth Australian sea lion mothers of all body sizes spent proportionally more time ashore with male pups at Dangerous Reef. Given the lack of intersexual differences in pup growth parameters throughout the study period, the increased proportion of time spent ashore with male pups may represent an increase in maternal investment to compensate for slower acquisition and processing of milk by male pups. Conversely the greater proportion of time spent ashore may indicate an increase in maternal foraging efficiency enabling more time to be allocated to rest (with a subsequent reduction in maternal metabolic expenditure) between foraging trips. Investigating milk-intake efficiency of male and female Australian sea lion pups by measuring the dilution of pup body water (labelled using hydrogen isotopes – see Costa 1987) with maternal milk water throughout a nursing bout would clarify this.

No data is available for late-lactation foraging trip durations or pup growth rates making it impossible to determine if Australian sea lions partition maternal energy resources between lactation and gestation and whether maternal experience influences how energy is delivered to pups. The serial sampling of milk from a broad range of adult female Australian sea lion body sizes throughout lactation and the relationship of milk-lipid levels to foraging trip duration would be required to examine these questions.

Conclusions

Results from this study suggest adult female Australian sea lions allocate similar resources to their male and female offspring, despite mothers with sons spending a greater proportion to time ashore. These results were supported by the lack of intersexual differences in 1) milk-lipid values, 2) estimated pup birth mass, 3) estimated growth rates and 4) estimated mass at 90 days and do not support differential investment theory (Trivers 1972, Trivers and Willard 1973, Maynard Smith 1980). Longer (older) mothers may increase their fitness by weaning larger pups with greater post-weaning survival probabilities and presumably reproductive fitness. If so, then maternal experience may be more important in determining the level of investment received by each pup rather than the sex of the pup itself. Given the measures used in this study, the theory of equal investment proposed by Fisher (1930) was not rejected. However given that this study focused on the early stages of lactation, when females are more likely to be able to meet the energetic requirements of their pups, it cannot discount the possibility of differential investment becoming evident later in lactation. Additional resource would be required to address this question.

Aseasonal variation in foraging trip duration through the first three months of lactation combined with relatively low energy-dense milk in Australian sea lions indicate that suitable localized foraging habitat can be found close to breeding colonies. Localised habitat appears to be exploited for both benthic and pelagic prey. A prolonged lactation period gives pups more time to gain experience in foraging for patchily distributed cryptic prey prior to weaning.

The typical otariid model of breeding and lactation being closely tied to seasonal abundance and availability of prey is not apparent in the maternal strategies of Australian sea lions. The unique life-history of Australian sea lions seems to be adapted to a low-energy lifestyle characterized by prolonged lactation and low milk-lipid levels, in contrast to other sympatrically breeding otariid species. The maternal strategies of this species seem to be unaffected by seasonal variation unlike other temperate otariids and this may be due in part to the influences of coastal cold-water upwellings on localized primary productivity.

5 COMPARISON OF TRENDS IN ABUNDANCE AND MATERNAL STRATEGIES OF AUSTRALIAN SEA LIONS AT DANGEROUS REEF AND SEAL BAY

SD Goldsworthy, A Lowther, PD Shaughnessy, and B Page

Introduction

Dangerous Reef and Seal Bay are the largest and third or fourth largest Australian sea lion populations, respectively, depending on whether The Pages population is considered a single colony or two (Goldsworthy and Page 2007). Dangerous Reef is located in the relatively shallow and warm sheltered waters of southern Spencer Gulf, whereas Seal Bay is located on the south coast of Kangaroo Island where sea lions forage over deeper, colder and more exposed continental shelf (Fowler 2005, Fowler et al. 2006). Leslie Higgins undertook the most comprehensive analysis of the maternal strategies of the species at Seal Bay in the late 1980s. She investigated the duration of foraging trips and shore attendance bouts, milk composition and pup growth rates (Higgins 1990, Kretzmann et al. 1991, Higgins and Gass 1993). Until the study by Lowther (2007, Chapter 4) on the maternal strategies of Australian sea lions at Dangerous Reef, the study of Higgins at Seal Bay provided the only data on maternal strategies of the species. The aim of this chapter is to determine whether differences in the relative trends in pup production between the Dangerous Reef and Seal Bay populations are correlated with differences in the maternal strategies of females at each location. That is, can differences between the population trajectories of each colony be accounted for by difference in the capacity of females to meet the energy demands of raising pups during lactation.

Methods

Population trends

Data on the status and trends in abundance of the Dangerous Reef Australian sea lion population are derived from summary data and analyses presented in this report (Chapter 3). Data on the status and trends in abundance of the Seal Bay population were derived from count data reviewed and analysed by Shaughnessy et al. (2006), and surveys by McIntosh et al. (2006), and McIntosh (2007).

Maternal strategies

Data on the maternal strategies of Australian sea lions at Dangerous Reef were based on data presented in this report (Chapter 4) or in Lowther (2007). Comparable data for Seal Bay were derived from Higgins (1990), Kretzmann et al. (1991), and Higgins and Gass (1993). Raw data on maternal mass, attendance behaviour (foraging trips and shore bout durations) from telemetrically monitored females and pup growth rates were derived from Higgins (1990). Pup growth data presented in Higgins (1990) were used where they were comparable to that provided by Lowther (2007, Chapter 4,

growth data extending to about 100 days). Statistical comparison of Dangerous Reef and Seal Bay data were undertaken using Students t-tests. Proportional data were arcsine transformed prior to ANOVA.

Results

Population trends

Dangerous Reef

The best estimate of pup production for the 2006-07 season is 709 (95% CL 636-783) (Chapter 3). The exponential rate of increase in pup production from 1999 until 2006-07, based on maximum live pup counts plus cumulative mortality, and mark-recapture methods ranges between 6.7-9.9% per breeding season, or 4.6-6.5% per year (Chapter 3, Figure 5.1).

Seal Bay

Based on mark recapture estimates of live pup abundance at Seal Bay conducted over the last three breeding season, pup numbers were 230 (95% CL 203-257) in 2002-03, 288 (95% CL 203-229) in 2004 and 203 (95% CL 162-245) for the 2005-06 season (McIntosh et al. 2006, McIntosh 2007). Based on maximum live-pup counts between 1985 and 2002-03, the exponential rate of decline in pup production is 1.14% per breeding season or 0.77% per year (Shaughnessy et al. 2006). This represents a 12.6% decline between the 1985 and 2002-03 (Shaughnessy et al. 2006).

Maternal strategies

Comparisons of seven key components of maternal strategies which were measured at Dangerous Reef and Seal Bay, are presented in Table 5.1. The components include female mass, the duration of foraging trips and shore attendance bouts, the percentage time that females spend ashore, the birth mass and growth rates of pups over the first 100 days, and the estimated milk lipid content.

There was no difference in the mass of adult females, or the duration of foraging trips (~1.8 days) between sites. The duration of attendance bouts were significantly longer at Seal Bay (1.6 days vs. 0.9 days Dangerous Reef), and as a consequence females at Seal Bay were ashore for a significantly greater percentage of time (48% vs. 32% Dangerous Reef) (Table 5.1). Although the estimated birth mass of pups at Dangerous Reef were greater than those at Seal Bay, the growth rates of pups at Seal Bay were significantly greater than those observed at Dangerous Reef, to the point that the average mass of pups at Seal Bay would be greater than those at Dangerous Reef from 40 days onwards. By 100 days the average difference in mass would be about 2kg (average pup mass 18kg for Dangerous Reef compared to 20 kg for Seal Bay). Finally, the estimated milk lipid content for females at Seal Bay was significantly greater than that estimated at Dangerous Reef (about 27% milk lipid difference, Table 5.1). However, it must be noted that milk lipid content at Dangerous Reef was estimated from milk water content whereas a regression equation was developed for estimating milk lipid from milk water content from Seal Bay (Kretzmann et al. 1991).

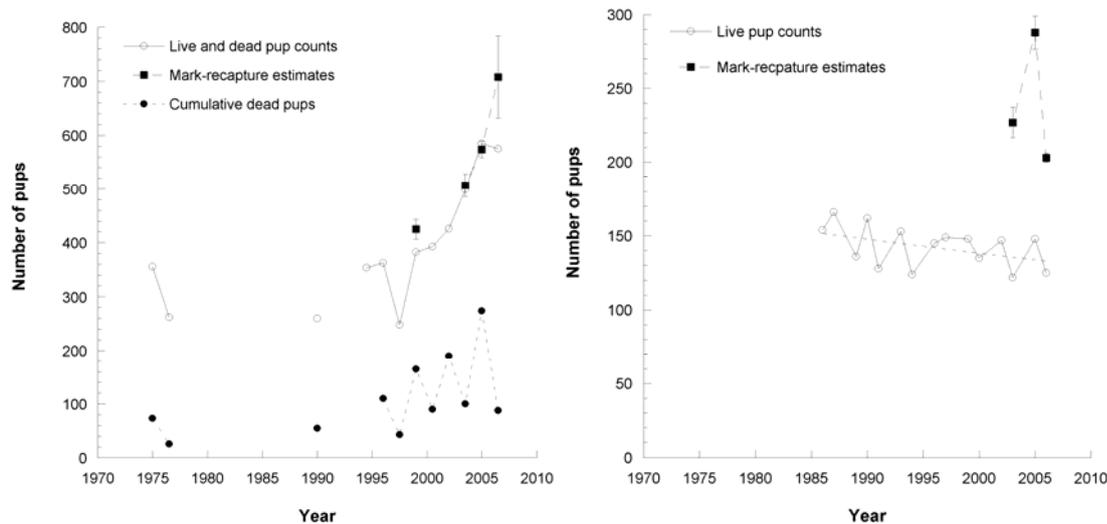


Figure 5.1. Trends in the abundance of pup numbers at Dangerous Reef (1975 to 2006-07)(left) and Seal Bay (1985 to 2005-06, right). Dangerous Reef data from those compiled in this report. Seal Bay data from Shaughnessy et al. (2006), McIntosh et al. (2006) and McIntosh (2007).

Table 5.1. Comparison of the mean (sd, n) values of key maternal strategy factors between Dangerous Reef and Seal Bay Australian sea lions. Data from Dangerous Reef derived from Lowther (2007, this report) for the 2006-07 breeding season. Data from Seal Bay were primarily derived from Higgins (1990), Kretzmann et al. (1991), and Higgins and Gass (1993). Statistical comparisons from Student's t-tests. Proportional data were arcsine transformed prior to analysis.

Maternal Strategy Factor	Dangerous Reef	Seal Bay	Probability
Adult female mass (kg)	81.6 (10.4, 10)	79.8 (9.7, 15)	NS
Foraging trip duration (hrs)	46.0 (8.2, 10)	43.7 (10.2, 7)	NS
Shore bout duration (hrs)	22.3 (9.3, 10)	39.0 (4.8, 7)	P < 0.001
Percentage time ashore (%)	32.1 (10.9, 10)	47.6 (6.1, 7)	P = 0.004
Estimated birth mass (kg)	9.1 (1.1, 18)	7.8 (0.9, 18)	P = 0.001
Growth rate to 100d (kg/d)	0.089 (0.021, 18)	0.122 (0.012, 18)	P < 0.001
Estimated milk lipid (%)	21.0 (7.5, 10)	28.9 (6.5, 15)	P = 0.010

Discussion

Population trends and maternal strategies

Pup production data indicate marked differences in the population trends of Australian sea lion population at Dangerous Reef and Seal Bay. Dangerous Reef pup production has been increasing since 2000; in contrast, Seal Bay pup production has been declining by about 1% per year since at least the early 1980s (Shaughnessy et al. 2006).

Comparison of key parameters of maternal investment strategies of Australian sea lions at Dangerous Reef and Seal Bay indicate that females are of similar size, and despite the marked differences in the near colony marine environments (shallow gulf vs. deeper shelf waters), the foraging trip durations at each site were similar (~1.8 days). The duration of attendance bouts ashore were longer at Seal Bay, and as such females spent a greater proportion of time ashore there. The growth rates of pups at Seal Bay were about 27% greater than those at Dangerous Reef. These

differences may relate directly to the greater time available for pups to nurse at Seal Bay, and the great lipid concentration of their mother's milk.

Although comparison between sites is confounded in part by that large time difference between when the studies were undertaken at each site (about 17 years), and the uncertainty in the data for each site, they are the only data that are available. Assuming that the data are representative for each site, these differences cannot be explained by differences in the maternal strategies at each site. In fact the data available would suggest that conditions for foraging are better for females at Seal Bay compared to Dangerous Reef, principally because females at Seal Bay spend less time at sea and can grow pups at a higher rate compared to Dangerous Reef females. The conditions for foraging and lactation at each site are contrary to expectations, based on the population trajectories.

Population trends and fishery interactions

McKenzie et al. (2005) undertook an assessment of the factors that could be impeding the growth of Australian sea lion populations. They concluded, based on data available at the time, that bottom-up factors (food limiting), either natural (climate change, competition) or anthropogenic (fisheries removal) were unlikely to be significant in the regulation of Australian sea lion populations. They identified the most likely factors as those being of an anthropogenic and top-down (mortality driven) origin. Three factors fell into these categories: direct killing, pollutants and toxins, and fishery bycatch and entanglement. There was no evidence that either direct killing or pollution and toxins were significant factors regulating the growth of Australian sea lion populations. There was, however, evidence that fishery bycatch and entanglement could be a significant contributing mortality factor, at least in parts of the Australian sea lion's range.

More recently, Goldsworthy and Page (2007) provided a detailed appraisal of the risks posed by fisheries interactions with the Australian sea lion population in South Australia. They examined the implication of interactions between Australian populations and the South Australian southern rock lobster and demersal gillnet sector of the Commonwealth managed Southern and Eastern Scale and Shark Fishery (SESSF). Bycatch from the gillnet SESSF was most likely to provide the greatest risk to Australian sea lions, because of the almost complete spatial overlap in fishing effort with sea lion foraging effort and because it is a year-round fishery with relatively high fishing effort, which can potentially target all sea lion age-classes. Impact from the southern rock lobster fishery was likely to be less because there was less overlap in fishing effort with sea lion foraging effort as fishing is restricted to seven months of the year (November-May in the northern zone rock lobster fishery), and bycatch is likely to be restricted to pups and juvenile seals (Goldsworthy and Page 2007). However, the potential additive and interactive impacts posed by combined bycatch in these fisheries could be significant (Goldsworthy and Page 2007). They noted that the apparent depletion (ie. very low pup production) of a large number of sea lion subpopulations may be indicative of widespread subpopulation declines, and that the potential that such declines may be ongoing and attributable to fishery bycatch.

The risk posed from bycatch in the demersal gillnet SESSF to the Seal Bay and Dangerous Reef Australian sea lion populations differs due to differences in the level of fishing effort that occurs near both populations (Goldsworthy and Page 2007). Figure 5.2 indicates the Marine Fishing Areas (MFAs) for which historical fishery effort data are available, and the relative size of MFAs adjacent to Dangerous Reef and Seal Bay. Based on satellite tracking studies undertaken Dangerous Reef (Goldsworthy et al. unpublished data) and at Seal Bay (Fowler et al. 2006), the principal MFAs are 129 and 132 for Dangerous Reef, and 149 for Seal Bay (Figure 5.2).

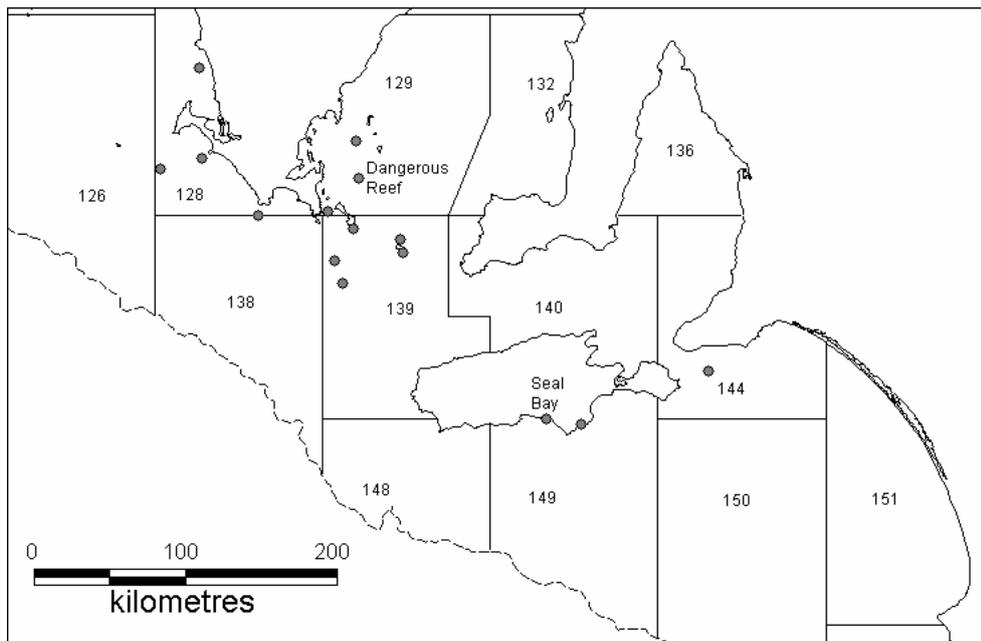


Figure 5.2. Gill-net sector SESSF Marine Fishing Areas (MFAs) near to the Dangerous Reef and Seal Bay Australian sea lion populations. Other sea lion populations in the region are marked by grey circles. The 200m isobath that indicates the edge of the continental shelf is indicated by a dashed-line.

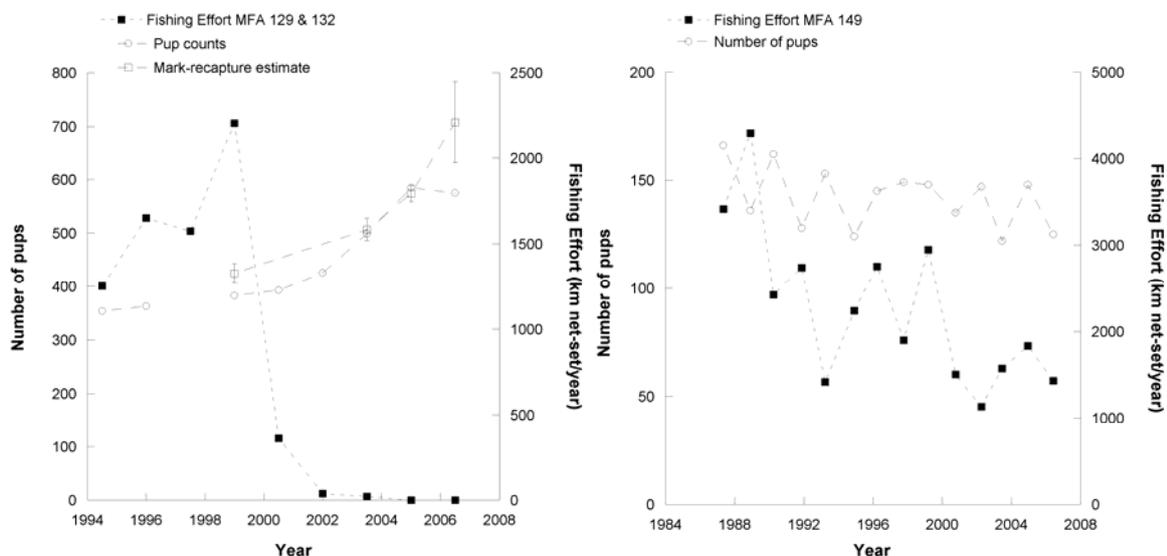


Figure 5.3. Trends in the abundance of pup numbers at Dangerous Reef (1994-95 to 2006-07) (left) and Seal Bay (1985 to 2005-06, right). Seal Bay data from those compiled in this report, those from Seal Bay are from Shaughnessy et al. (2006), McIntosh et al. (2006) and McIntosh (2007). Fishing effort data derived from Goldsworthy et al. (2007).

Figure 5.3 presents data on the levels of fishing effort in adjacent MFAs to the Dangerous Reef and Seal Bay populations, relative to measures of pup abundance at each site. For Dangerous Reef, demersal gillnet fisheries were excluded from fishing in Spencer Gulf in 2000. Throughout the 1980s and 1990s the average level of fishing effort in MFAs 129 and 132 was 1,709 km net-set/year (range 711 to 3,200) (Goldsworthy et al. 2007). Since restrictions on school and gummy shark fishing were introduced into Gulf waters in 2001 (see below), the level of fishing effort reduced to zero in 2005 and 2006 (Figure 5.3). A clear observation from the Dangerous Reef population is that the major period of increase in pup production coincides with the period during which gillnet fishing effort reduced substantially in response to the closures enacted in 2000 (Figure 5.3). Fishing effort in MFAs 129 and 132 significantly declined between 1994-05 and 2006-07 ($F_{1,8} = 11.806$, $P = 0.011$, $R^2 = 0.575$, Figure 5.3). Further, there was a significant negative relationship between fishing effort and pup abundance at Dangerous Reef over this period ($F_{1,8} = 6.462$, $P < 0.050$, $R^2 = 0.438$, excluding 1997-98 season).

The cessation of demersal gillnet fishing in Spencer Gulf (and other internal waters in South Australia) came about through independent changes in the management of two fisheries at about the same time (2001). The Offshore Constitutional Settlement (OCS) arrangement transferred the State management of school and gummy shark in coastal waters (extending from 3 nautical miles offshore, excluding internal waters in bays and inlets) to the Commonwealth Australian Fisheries Management Authority (AFMA) (SA Government Gazette, 22 March 2001, pp.1060-1061), while the State introduced bycatch limits on school and gummy shark in the SA Marine Scale Fishery within its waters (SA Government Gazette, 2 May 2001, pp. 1703).

Trends in fishing effort in MFA 149 (adjacent to Seal Bay) are presented in Figure 5.3, relative to pup abundance data for the Seal Bay Australian sea lion population. Throughout the 1980s and 1990s, the average fishing effort in MFA 149 was 1,972 km net-set per year (range 110-4,620 km) (Goldsworthy et al. 2007, Figure 5.3). Between 1986 and 2004, the level of fishing effort declined significantly in MFA 149 ($F_{1,13} = 12.828$, $P < 0.010$, $R^2 = 0.476$), and since 2000, has averaged about 1,500 km net-set per year. However, there was no significant relationship between the level of fishing effort in MFA 149 and pup abundance ($F_{1,13} = 0.452$, $P > 0.05$, $R^2 = 0.036$, Figure 5.3).

The above analyses suggest that differences in the population trajectories of Dangerous Reef and Seal Bay may be explained by differences in the levels of interactions between seals and demersal gillnet fisheries. For Dangerous Reef, the marked increase in pup production since 2001 coincides with the cessation of shark fishing in the region. Although fishing effort has been declining in the vicinity of Seal Bay while the population maintains a steady rate of decline, the level of fishing effort is still relatively high, almost as high as it was in southern Spencer Gulf prior to 2001. Although it is possible that these results may be coincidental, there is evidence for ongoing interactions between Australian sea lions from Seal Bay and demersal gillnet fisheries. Page et al. (2004) reported 19 individual Australian sea lions entangled in monofilament gillnet at Seal Bay (Kangaroo Island) over a 15-year period, averaging about 1.3 entangled seals/year. Because most of this population is

monitored daily by SA Department for the Environment and Heritage (DEH) staff, it provides a unique opportunity to monitor the nature and extent of entanglement in fishing gear (Page et al. 2004).

It is impossible to estimate what proportion of the population are entangled in demersal gillnets, and what fraction of these free themselves and reach shore entangled in gillnet material. Fowler (1987) and Fowler et al. (1990) undertook a study of entanglement in northern fur seals (*Callorhinus ursinus*), and determined that entangled seals were less likely to be observed on land because, a) an unknown number drown during or shortly after entanglement; b) entangled seals will be encountered less often on shore because of their lower survival, and c) entangled seals spend longer periods at sea foraging because of the additional drag of entangling material. Fowler et al. (1990) suggested that because of these factors, entanglement-related mortality of juvenile northern fur seals was 35 times that of onshore entanglement rates (ie. entangled seals ashore represent 2.9% of all animals entangled).

Based on subpopulation derived fishery interaction probabilities, Goldsworthy and Page (2007) estimated that about 11.4% of Australian sea lion bycatch in the demersal gillnet fishery would be from individual seals of the Seal Bay population. Given this the 1.3 entangled seals ashore/year would imply an annual SA bycatch of 23 seals, if entangled seals ashore represent 50% of all those entangled, 114 seals (if entangled seals ashore represent 10% of all those entangled), 227 seals (if entangled seals ashore represent 5% of all those entangled), and 376 seals (if entangled seals ashore represent about 3% of all those entangled), as in the study of Fowler et al. (1990). If entangled seals ashore represent between 1-10% of all ASL that become entangled, then annual bycatch rates for SA and adjacent waters could number between 100-300+ seals/year.

Goldsworthy and Page (2007) developed population viability analyses for all SA Australian sea lion populations. They developed PVAs for populations that were stable, declining ($r = -0.01$, equivalent to current rate at Seal Bay) and increasing ($r=0.05$, equivalent to rate of increase at Dangerous Reef). Using the declining population model, which is based on the Seal Bay population, 2.7 female bycatch mortalities per year would tip the population to *Endangered* and *Critical* status, and 10 female bycatch mortalities per year would drive the population to quasi-extinction (<10 females) within about 60 years. Based on Goldsworthy and Page's (2007) calculations, *Endangered* and *Critical* status would be achieved if the current entanglement rates (1.3 seals per year) represented 28% of all animals that get entangled, and quasi-extinct within 60 years if they represent only 7.6% of all entanglements. These values are greater than the estimated values of 2.9% estimated by Fowler et al. (1990).

There is a large amount of uncertainty with respect to determining the risk from fishery bycatch for Seal Bay and other populations. Studies such as Goldsworthy and Page (2007), Page et al (2003) and Fowler et al. (1990), that have 1) undertaken risk assessments based on PVAs, 2) compared the spatial distribution of fishing effort and seal foraging effort in order to calculate interaction and bycatch probabilities, 3) estimated the numbers of animals that survive entanglement and reach the shore,

and 4) the scale of entanglement among populations, provide some basis to evaluate the potential magnitude of risks. However, the absolute magnitude and significance of these interactions will not be able to be assessed until independent fishery observer programs are established.

SARDI is currently leading a program that is funded by the Fisheries Research and Development Corporation (FRDC) and the Australian Government Department of Environment and Water Resources, SA DEH and the fishing industry. This program will develop mitigation strategies to reduce the impacts from bycatch in demersal gillnet and rock lobster fisheries in South Australia. This includes an independent observer program, which commenced in 2006, in conjunction with the Australian Fisheries Management Authority (AFMA) observer program and voluntary industry reporting. Improving data sets on the spatial distribution of fishing effort will come from satellite linked vessel monitoring systems (VMS), which were introduced in July 2007. Additional seal satellite tracking will be undertaken to improve models of spatial distribution of foraging effort. These data will be pooled and analysed to develop spatial tools to assist developing options for spatial management of fishing effort with respect to demersal gillnet fisheries, and seal exclusion/pot-protection devices to eliminate seal bycatch in the rock lobster fishery.

Conclusion

Based on the data available on the maternal strategies of Australian sea lions at Seal Bay and Dangerous Reef, conditions for foraging and for raising pups would appear more optimal at Seal Bay than at Dangerous Reef. Females at Seal Bay spent 15% more time ashore, and the growth rates of their pups were 27% higher than those at Dangerous Reef. Although we could not determine if these differences were due to seasonal and/or temporal difference, they are contrary to expectations based on the differing population trajectories at each site (ie. Seal Bay is declining, Dangerous Reef is increasing). Results suggest that differences in population trajectories are not related to differences in the foraging conditions at each site. There is a growing consensus that the most likely cause for the lack of recovery in Australian sea lion populations are due to anthropogenic related mortality, especially from fishery bycatch. The recent increase in pup production at Dangerous Reef provides circumstantial evidence that positive growth has followed a reduction in anthropogenic mortality for the population. In contrast, demersal gillnet fishing effort remains significant adjacent to the Seal Bay population, and entanglement rates in monofilament gillnets and a continuing decline in pup abundance suggests that mortality related to fishery bycatch may be significant in this population.

6 ACKNOWLEDGMENTS

Transport to Dangerous Reef was provided in the MEKALI-K with Tony Jones and skippered by Adam Kemp of 'Protec Marine' at Port Lincoln. The work was conducted under an animal ethics permit from SA Department for the Environment and Heritage and the PIRSA Animal Ethics Committee. We thank Kate Lloyd and Peter Canty (SA Department for the Environment and Heritage) for provision of SA DEH Permits. We thank Derek Hamer for his assistance, and Adrian Linnane, Shane Roberts and Tim Ward for their critical feedback.

7 REFERENCES

- Alava, J.J., and Salazar, S. (2006) Status and Conservation of Otariids in Ecuador and the Galápagos Islands. pp 495-519. In 'Sea Lions of the World'. (Eds A. W. Trites, S. K. Atkinson, D. P. DeMaster, L. W. Fritz, T. S. Gelatt, L. D. Rea and K. M. Wynne). Alaska Sea Grant College Program, University of Alaska: Fairbanks, Alaska.
- Arnold, S. J. and D. Duvall. 1994. Animal mating systems: a synthesis based on selection theory. *American Naturalist* 143:317-348.
- Arnold, W. and F. Trillmich. 1985. Time budget in Galapagos fur seal pups: The influence of the mothers presence and absence on pup activity and play. *Behaviour* 92:302-321.
- Arnould, J. P. Y. and I. L. Boyd. 1995. Inter- and intra-annual variation in the milk composition in Antarctic fur seals (*Arctocephalus gazella*). *Physiological Zoology* 68:1164-1180.
- Arnould, J. P. Y. and M. A. Hindell. 1999. The composition of Australian fur seal (*Arctocephalus pusillus doriferus*) milk throughout lactation. *Physiological and Biochemical Zoology* 72:605-612.
- Arnould, J. P. Y. and M. A. Hindell. 2001. Dive behaviour, foraging locations, and maternal-attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*). *Canadian Journal of Zoology* 79:35 - 48.
- Arnould, J. P. Y. and M. A. Hindell. 2002. Milk composition, body composition and preweaning growth rates of Australian fur seal (*Arctocephalus pusillus doriferus*) pups. *Physiological and Biochemical Zoology* 72:605-612.
- Arnould JPY, Boyd IL and Speakman JR. 1996. The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. *Journal of Zoology* 239: 769-782
- Arnould, J. P. Y., S. P. Luque, C. Guinet, D. P. Costa, J. Kingston and S. A. Shaffer. 2003. The comparative energetics and growth strategies of sympatric Antarctic and subantarctic fur seal pups at Iles des Crozet. *Journal of Experimental Biology* 206:4497-4506.
- Baker, J. D. and C. W. Fowler. 1993. Pup weight and survival of northern fur seals *Callorhinus ursinus*. *Journal of Zoology* 227:231-238.
- Boness, D. J. 1991. Determinants of mating systems in the Otariidae (Pinnipedia). Pages 1-36 in D. Renouf, editor. *The Behaviour of Pinnipeds*. Chapman & Hall, London.

- Boness, D. J. and W. D. Bowen. 1996. The evolution of maternal care in pinnipeds. *Bioscience* 46:645 - 654.
- Boness, D. J. W. D. Bowen and O. T. Oftedal. 1994. Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. *Behavioural Ecology and Sociobiology* 34:95-104.
- Bowen, T. M., S. J. Iverson, D. J. Boness and O. T. Oftedal. 2001a. Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. *Functional Ecology* 15:325-334.
- Bowen, W. D., S. L. Ellis, S. J. Iverson and D. J. Boness. 2001b. Maternal effects on offspring growth rate and weaning mass in harbour seals. *Canadian Journal of Zoology* 79:1088-1101.
- Boyd, I. L. 2000. State-dependent fertility in pinnipeds: contrasting capital and income breeders. *Journal of Functional Ecology* 14:623 - 630.
- Bradshaw, C. J. A., L. S. Davis, C. Lalas and R. G. Harcourt. 2000. Geographic and temporal variation in the condition of pups of the New Zealand fur seal (*Arctocephalus forsteri*): evidence for density dependence and differences in the marine environment. *Journal of Zoology* 252:41-51.
- Byers, J. A. and J. M. Moodie. 1990. Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. *Behavioural Ecology and Sociobiology* 26:157 - 164.
- Campbell, R. A. 2003. Demography and genetic population structure of the Australian sea lion (*Neophoca cinerea*). Unpublished PhD Thesis. Department of Zoology. University of Western Australia, Perth.
- Cappozzo, H. L., C. Campagna and J. Monserrat. 1991. Sexual dimorphism in new born Southern sea lions. *Marine Mammal Science* 7:3-85.
- Carretta, J.V., K.A. Forney, M.M. Muto, J. Barlow, J. Baker, and M. Lowry. (2004) U.S. Pacific marine mammal stock assessments. pp 5-11. NOAA-TM-NMFS-SWFSC-358 Tech. Memo. 295 pp.
- Caughley G (1977) Analysis of vertebrate populations. John Wiley & Sons. 234 pp.
- Charnov, E. L. 1982. The theory of sex allocation. Princeton University Press, Princeton, New Jersey.
- Chilvers, B. L., K.-J. Wilson and G. J. Hickling. 1995. Suckling behaviours and growth rates of New Zealand fur seals, *Arctocephalus forsteri*, at Cape Foulwind, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 22:263-270.
- Clutton-Brock, T. H. 1988. Reproductive Success - Studies of individual variation in contrasting breeding systems. The University of Chicago Press, Chicago.
- Clutton-Brock, T. H. 1991. The Evolution of Parental Care - monographs in behaviour and ecology. Princeton University Press, Princeton, New Jersey.
- Clutton-Brock, T. H., S. D. Albon and F. E. Guinness. 1984. Maternal dominance, breeding success and birth sex ratios in red deer. *Nature* 308:358-360.
- Costa, D. P. 1991a. Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. *American Zoologist* 31:111-130.

- Costa, D. P. 1991b. Reproductive and foraging energetics of pinnipeds: implications for life history patterns. Pages 300-338 in D. Renouf, editor. *The Behaviour of pinnipeds*. Chapman & Hall, London.
- Costa, D. P. and N. J. Gales. 2002. Energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecological Monographs* 73:27-43.
- Costa, D. P. and Gales, N. J. (2003). Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecological Monographs* 73: 27-43.
- Costa, D. P., C. E. Kuhn, M. J. Weise, S. A. Shaffer and J. P. Y. Arnould. 2004. When does physiology limit the foraging behaviour of freely diving marine mammals ? *International Congress Series* 1275:359-366.
- Crespo, E.A., and Pedraza, S.N. (1991) Estado actual y tendencia de la poblacion de lobos marinos de un pelo (*Otaria flavescens*) en el litoral norpatagonico (Spanish). *Ecologia Austral* 1: 87-95.
- Crocker, D. E., J. D. Williams, D. P. Costa and B. J. Le Boeuf. 2001. Maternal traits and reproductive effort in northern elephant seals. *Ecology* 82:3541-3555.
- Dennis, T.E. 1999. Australian sea lion survey, and historical record, for South Australia. Report to the Department of the Environment, Heritage and Aboriginal Affairs, Wildlife Conservation Fund, South Australia
- Dennis, T. E. (2005). Australian sea lion survey (and historical) records for South Australia. Report to the Wildlife Conservation Fund, Department for Environment and Heritage, South Australia.
- Fay, F. H. 1982. Ecology and biology of the Pacific Walrus *Odobenus rosmarus divergens Illiger*. North American fauna no.74: U.S Fish and Wildlife Service, Washington D.C.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Oxford University Press, Oxford.
- Fowler CW. 1987. Marine debris and northern fur seals: a case study. *Marine Pollution Bulletin* 68: 326-335
- Fowler CW, Merrick R and Baker JD. 1990. Studies of the population level effects of entanglement on northern fur seals. In: Shomura RS, Godfrey ML (eds) *Proceedings of the second international conference on marine debris*, 2-7 April 1989, Honolulu, Hawaii. p 453-474. US Department of Commerce, NOAA Tech Memo, NMFS, NOAA-TM-NMFS-SWFSC-154
- Fowler, S.L. (2005) Ontogeny of diving in the Australian sea lion. PhD Thesis. University of California, Santa Cruz.
- Fowler, S. L., D. P. Costa, J. P. Y. Arnould, N. J. Gales and C. E. Kuhn. 2006. Ontogeny of diving behaviour in the Australian sea lion: trials of adolescence in a late bloomer. *Journal of Animal Ecology* 75:358-367.
- Francis, J., D. J. Boness and H. Ochoa-Acuña. 1998. A protracted foraging and attendance cycle in female Juan Fernandez fur seals. *Marine Mammal Science* 14:552-574.
- Gales, N. J., D. P. Costa and M. B. Kretzmann. 1996. Proximate composition of Australian sea lion milk throughout the entire supra-annual lactation period. *Australian Journal of Zoology* 44:651-657.
- Gales, N. J., Shaughnessy, P. D. and Dennis, T. E. 1994. Distribution, abundance and breeding cycle of the Australian sea lion, *Neophoca cinerea* (Mammalia: Pinnipedia). *Journal of Zoology* 234:353-370.

- Gales, N. J., P. Williamson, L. V. Higgins, M. A. Blackberry and I. James. 1997. Evidence for a prolonged postimplantation period in the Australian sea lion (*Neophoca cinerea*). *Journal of Reproduction and Fertility* 111:159-163.
- Gales, N.J., Costa, D.P. (1997) The Australian sea lion, a review of an unusual life history. In: Hindell, M., Kemper, C. (eds.). *Marine mammal research in the Southern Hemisphere, Vol. 1 Status, ecology and medicine*. Surrey Beatty and Sons, Chipping Norton. pp. 78-87.
- Gales, N. J. & Cheal, A. J. (1992) Estimating diet composition of the Australian sea-lion (*Neophoca cinerea*) from scat analysis: An unreliable technique. *Wildlife Research*, 19, 447-456.
- Gales, N. J., D. P. Costa and M. B. Kretzmann. 1996. Proximate composition of Australian sea lion milk throughout the entire supra-annual lactation period. *Australian Journal of Zoology* 44:651-657.
- Gamel, C. M., R. W. Davis, J. H. M. David and M. A. Meyer. 2004. Reproductive energetics and female attendance patterns of Cape fur seals (*Arctocephalus pusillus pusillus*) during early lactation. *The American Midland Naturalist* 153: 152-170.
- Gentry, R. L. 2000. Eared Seals (Otariidae). Pages 348-352 in W. F. Perrin, Wursig, B. and Thewissen, J. G. M. , editor. *Encyclopedia of Marine Mammals*. Academic Press, San Diego.
- Gentry, R. L., D. P. Costa, J. P. Croxall, J. H. M. David, R. W. Davis, G. L. M. Kooyman, P., T. S. McCann and F. Trillmich. 1986. Synthesis and conclusions. Pages 220-264 in R. L. Gentry and G. L. Kooyman, editors. *Fur Seals: Maternal Strategies on Land and at Sea*. Princeton University Press, Princeton.
- Gentry, R. L. and J. R. Holt. 1986. Attendance behaviour of northern fur seals. Pages 41-60 in R. L. Gentry and G. L. Kooyman, editors. *Fur seals: Maternal Strategies on Land and at Sea*. Princeton University Press, Princeton.
- Georges, J. -Y. and C. Guinet. 2000. Maternal care in the subantarctic fur seal on Amsterdam Island. *Ecology* 81:295-308.
- Georges, J.-Y., Y. Tremblay and C. Guinet. 2000. Seasonal diving behaviour in lactating fur seals on Amsterdam Island. *Polar Biology* 23: 59-69
- Gittleman, J. L. and S. D. Thompson. 1988. Energy allocation in mammalian reproduction. *American Zoologist* 28:863 - 875.
- Goldsworthy, S. 1995. Differential expenditure of maternal resources in Antarctic fur seals, *Arctocephalus gazella*, at Heard Island southern Indian Ocean. *Behavioral Ecology* 6:218-228.
- Goldsworthy, S. D. 1992. *Maternal care in three species of southern fur seal (Arctocephalus spp.)*. Monash University, Melbourne, Victoria.
- Goldsworthy, S. D. 1999. Maternal attendance behaviour of sympatrically breeding Antarctic and subantarctic fur seals, *Arctocephalus spp.*, at Macquarie Island. *Polar Biology* 21:3 16 - 325.
- Goldsworthy, S. D. 2006. Maternal strategies of the New Zealand fur seal: evidence for interannual variability in provisioning and pup growth strategies. *Australian Journal of Zoology* 54:31-44.
- Goldsworthy, S. D., and H. M. Crowley. 1999. The composition of the milk of Antarctic (*Arctocephalus gazella*) and subantarctic (*A. tropicalis*) fur seals at Macquarie Island. *Australian Journal of Zoology* 47:593-603.

- Goldsworthy SD and Page B (2007) A risk-assessment approach to evaluating the significance of seal bycatch in two Australian fisheries. *Biological conservation* 139: 269-285
- Goldsworthy SD, Bulman C, He X, Larcombe J, and Littnan C (2003) Trophic interactions between marine mammals and Australian fisheries: an ecosystem approach. In: Gales N, Hindell M, and Kirkwood R. (eds) *Marine Mammals and Humans: Fisheries, tourism and management*. CSIRO Publications. pp 65-99
- Goldsworthy SD, Shaughnessy PD, Page B, Hamer D, Peters K, and McIntosh R (2005) PIRSA Aquaculture/FRDC - Innovative solutions for Aquaculture planning and management: addressing seal interactions in the finfish aquaculture industry. Milestone Progress Report to the Fisheries Research Development Corporation. FRDC project number 2004/201. 97pp.
- Goldsworthy SD, Hamer and Page B. Assessment of the implications of interactions between fur seals and sea lions and the southern rock lobster and gillnet sector of the Southern and Eastern Scalefish and Shark Fishery (SESSF) in South Australia. Final Report to the Fisheries Research and Development Corporation. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, 164 pp. SARDI Publication no. F2007/000711-1.
- Guinet, C., L. Dubroca, M. A. Lea, S. Goldsworthy, Y. Cherel, G. Duhamel, F. Bonadonna and J.-P. Donnay. 2001. Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Marine Ecology Progress Series* 219:251-264.
- Guinet, C. and J.-Y. Georges. 2000. Growth in pups of the subantarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island. *Journal of Zoology* 251:289- 296.
- Guinet, C., S. D. Goldsworthy and S. Robinson. 1999. Sex differences in mass loss rate and growth efficiency in Antarctic fur seals (*Arctocephalus gazella*) pups at Macquarie Island. *Behavioral Ecology and Sociobiology* 46:157-163.
- Hammill, M. O. 2002. Earless Seals - Phocidae. Page 352 in W. F. Perrin, B. Wursig, and J. G. M. Thewissen, editors. *Encyclopedia of Marine Mammals*. Academic Press, San Diego, United States.
- Heath, C. B., Ono, K. A., D.J. Boness and J.M. Francis. 1991. The influence of El Nino on female attendance patterns in California sea lion. F. Trillmich, editor. *Pinnipeds and El Nino: Responses to Environmental Stress*. Springer Verlag, Berlin.
- Harwood J, and Prime JH (1978) Some factors affecting the size of British grey seal populations. *Journal of Applied Ecology* 15:401-11.
- Hewison, A. J. M. and J.-M. Gaillard. 1999. Successful sons or advantaged daughters ? The Trivers-Willard model and sex-biased maternal investment in ungulates. *Trends in Ecology and Evolution* 14:229 - 234.
- Higgins, L.V. (1990). Reproductive behavior and maternal investment of Australian sea lions. PhD Thesis, University of California, Santa Cruz. 126 pp.
- Higgins, L. V. 1993. The nonannual, non seasonal breeding cycle of the Australian sea lion, *Neophoca cinerea*. *Journal of Mammalogy* 74:270-274.

- Higgins, L. V. and L. Gass. 1993. Birth to weaning: parturition, duration of lactation, and attendance cycles of Australian sea lions (*Neophoca cinerea*). *Canadian Journal of Zoology* 71:2047 - 2055.
- Kastelein, R. A. 2002. Walrus - *Odobenus rosmarus*. Page 1294 in W. F. Perrin, B. Wursig, and J. G. M. Thewissen, editors. *Encyclopedia of Marine Mammals*. Academic Press, San Diego, United States.
- Kirkman, S. P., M. N. Bester, G. J. G. Hofmeyr, P. A. Pistorius and A. B. Makhado. 2002. Pup growth and maternal attendance patterns in subantarctic fur seals. *African Zoology* 37:13 - 19.
- Kirkwood, R., Gales, R., Terauds, A., Arnould, J. P. Y., Pemberton, D., Shaughnessy, P. D., Mitchell, A. T., and Gibbens, J. (2005) Pup production and population trends of the Australian fur seal (*Arctocephalus pusillus doriferus*). *Marine Mammal Science* 21: 260-282.
- Kretzmann, M. B., D. P. Costa and B. J. L. Boeuf. 1993. Maternal energy investment in elephant seal pups: evidence for sexual equality? *The American Naturalist* 141 :466 - 480.
- Kruuk, L. E. B., T. H. Clutton-Brock, K. E. Rose and F. E. Guinness. 1999. Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proceedings of the Royal Society B: Biological Sciences* 266:1655.
- Lalas, C. and Bradshaw, C.J.A. (2003) Expectations for population growth at new breeding locations for the vulnerable New Zealand sea lion (*Phocarctos hookeri*) using a simulation model. *Biological Conservation* 114: 67-78.
- Laubscher, R. K., R. Perissinotto and C. D. McQuaid. 1993. Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biology* 13:471-481.
- Le Boeuf, B. J., R. Condit and J. Reiter. 1989. Parental investment and the secondary sex ratio in northern elephant seals. *Behavioural Ecology and Sociobiology* 25:109 - 117.
- Lea, M.-A. and M. A. Hindell. 1997. Pup growth and maternal care in New Zealand fur seals, *Arctocephalus forsteri*, at Maatsuyker Island, Tasmania. *Wildlife Research* 24:307-318.
- Ling, J.K. (1999) Exploitation of fur seals and sea lions from Australian, New Zealand and adjacent subantarctic islands during the eighteenth, nineteenth and twentieth centuries. *Australian Zoologist*, 31: 323-350.
- Ling, J. K. and Walker, G. E. (1976). Seal studies in South Australia: progress report for the year 1975. *South Australian Naturalist* 50, 59-68, 72.
- Ling, J. K., and Walker, G. E. (1978). An 18-month breeding cycle in the Australian sea lion? *Search* 9, 464-465.
- Lowther, A.D. 2007. Maternal strategies of the Australian sea lion *Neophoca cinerea* at Dangerous Reef. Honours Thesis. La Trobe University.
- Lunn, N. J. and J. P. Y. Arnould. 1997. Maternal investment in Antarctic fur seals: evidence for equality in the sexes. *Behavioural Ecology and Sociobiology* 40:351 - 362.
- Lunn, N. J., I. L. Boyd, T. Barton and J. P. Croxall. 1993. Factors affecting the growth rate and mass at weaning of Antarctic fur seals at Bird Island, South Georgia. *Journal of Mammalogy* 74:908-919.
- Martin, P. 1984. The meaning of weaning. *Journal of Animal Behaviour* 32:1257- 1259.
- Mate, B.R. (1982) History and present status of the California sea lion, *Zalophus californianus*. *FAO Fisheries Series* 4: 303-9.

- Maynard Smith, J. 1980. A new theory of sexual investment. *Behavioural Ecology and Sociobiology* 7:247-251.
- McIntosh, R.R. 2007. Chapter 7 - Growth in body size of the Australian sea lion (*Neophoca cinerea*). Unpublished PhD thesis. Department of Zoology, La Trobe University, Bundoora Victoria.
- McIntosh, R. R., Shaughnessy, P. D. and Goldsworthy, S. D. and Kennedy, C. (2006). Developing appropriate monitoring strategies for the declining Australian sea lion population at Seal Bay. Report to the Wildlife Conservation Fund, Department for Environment and Heritage, South Australia.
- McKenzie, J., S.D. Goldsworthy, P.D. Shaughnessy and R.R. McIntosh. 2005. Understanding the impediments to the growth of Australian sea lion populations. SARDI Aquatic Sciences Division. Department of Environment and Heritage - Migratory and Marine Species Section
- McLaren, I. A. 1993. Growth in pinnipeds. *Biological Reviews of the Cambridge Philosophical Society* 68:1-79.
- McMahon, C. R., H. R. Burton and M. N. Bester. 2000. Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science* 12:149-152.
- Moore, J. K., M. R. Abbott and J. G. Richmann. 1999. Location and dynamics of the Antarctic Polar Front from satellite sea surface temperature data. *Journal of Geophysical Research* 104:3059-3073.
- Ochoa-Acuña, H., J. M. Francis and D. J. Boness. 1998. Interannual variation in birth mass and postnatal growth rate of Juan Fernandez fur seals. *Canadian Journal of Zoology* 76:978-983.
- Oftedal, O. T. 1984. Milk composition, milk yield and energy output at peak lactation; a comparative review. *Symposium of the Zoological Society of London* 51:33 - 85.
- Oftedal, O. T., D. J. Boness and R. A. Tedman. 1987. The behaviour, physiology and anatomy of lactation in the Pinnipedia. *Current Mammalogy* 1:175-245.
- Ono, K. A. and D. J. Boness. 1996. Sexual dimorphism in sea lion pups: differential maternal investment, or sex-specific differences in energy allocation? *Behavioural and Ecological Sociobiology* 38:31-41.
- Ono, K. A., D. J. Boness and O. T. Oftedal. 1987. The effect of a natural environmental disturbance on maternal investment and pup behaviour in the Californian sea lion. *Behavioural Ecology and Sociobiology* 21:109-118.
- Page, B., J. McKenzie, M. D. Sumner, M. Coyne and S. D. Goldsworthy. 2006. Spatial separation of foraging habitats amongst New Zealand fur seals. *Marine Ecology Progress Series* 323:263-279.
- Pakhomov, E. A. and C. D. McQuaid. 1996. Distribution of surface plankton and seabirds across the Southern Ocean. *Polar Biology* 16:27 1-286.
- Pelabon, C., J.-M. Gailard, A. Loison and C. Portier. 1995. Is sex-biased maternal care limited by total maternal expenditure in polygynous ungulates? *Behavioural Ecology and Sociobiology* 37:311 - 319.
- Quinn, G. P. and M. J. Keough. 2004. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- R Core Development Team. 2006. R: A language and environment for statistical computing. Vienna, Austria.

- Ream, R. L., J. T. Sterling and T. R. Loughlin. 2005. Oceanographic features related to northern fur seal migratory movements. *Deep-Sea Research II* 52:823-843.
- Reyes, L.M., Crespo, E.A., and Szapkievich, V. (1999) Distribution and population size of the southern sea lion (*Otaria flavescens*) in central and southern Chubut, Patagonia, Argentina. *Marine Mammal Science* 15: 478–493.
- Robinson, A.C., Canty, P., Mooney, T. & Ruddock, P., 1996. South Australia's offshore islands. Australian Heritage Commission, Canberra.
- Rosas, F. C. W., M. Haimovici and M. C. Pinedo. 1993. Age and growth of the South American sea lion *Otaria flavescens* (Shaw 1800), in southern Brazil. *Journal of Mammalogy* 74:141-147.
- Scheiner, S. M. 1993. Genetics and the evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* 24:35-68.
- Schulz, T. M. and W. D. Bowen. 2005. The evolution of lactation strategies in pinnipeds: a phylogenetic analysis. *Ecological Monographs* 75:159 - 177.
- Seber, GAF (1982). *The Estimation of Animal Abundance and Related Parameters*. MacMillan, New York.
- Shaughnessy, P. (2004a). Australian sea lions at Nuyts Reef on the west coast of Eyre Peninsula, South Australia. Progress Report to (Commonwealth) Department of the Environment and Heritage, 6 pp.
- Shaughnessy, P. (2004b). Population assessment of New Zealand fur seals and Australian sea lions in some South Australian breeding colonies and haul-out sites, 2003-2004. Report to Department for Environment and Heritage (South Australia). 49 + ix pp.
- Shaughnessy, P. (2005). Population assessment of New Zealand fur seals and Australian sea lions at some colonies in South Australia, 2004-05. Report to Department for Environment and Heritage (South Australia). 48 + xi pp, December 2005.
- Shaughnessy, P. and Dennis, T. (1999). Seal research in South Australia, 1998/1999: abundance of New Zealand fur seal pups on Kangaroo Island and Australian sea lion pups on Dangerous Reef. Report to South Australian National Parks and Wildlife, Department of Environment, Heritage and Aboriginal Affairs, October 1999, 39 pp.
- Shaughnessy, P. and Dennis, T. (2001). Research on New Zealand fur seals and Australian sea lions in South Australia, 2000-2001. Report to National Parks and Wildlife South Australia, Department for Environment and Heritage. 44 pp.
- Shaughnessy, P. and Dennis, T. 2003. Population assessment of New Zealand fur seals and Australian sea lions in some South Australian colonies, 2002-2003. Report to Department for Environment and Heritage. 46 pp.
- Shaughnessy P D, Goldsworthy S D, and Libke JA (1995a) Changes in the abundance of New Zealand fur seals *Arctocephalus forsteri* on Kangaroo Island, South Australia. *Wildlife Research* 22:201-15 .
- Shaughnessy PD, Kirkwood R, and Warneke RM (2002) Australian fur seals, *Arctocephalus pusillus doriferus*: pup numbers at Lady Julia Percy Island, Victoria, and a synthesis of the species population status. *Wildlife Research* 29: 185-192.

- Shaughnessy, P. D., Dennis, T. E. and Seager, P. G. (2005). Status of Australian sea lions, *Neophoca cinerea*, and New Zealand fur seals, *Arctocephalus forsteri*, on Eyre Peninsula and the far west coast of South Australia. *Wildlife Research* 32: 85-101.
- Shaughnessy, P. D., McIntosh, R. R., Goldsworthy, S. D., Dennis, T. E. and Berris, M. (2006). Trends in abundance of Australian sea lions, *Neophoca cinerea*, at Seal Bay, Kangaroo Island, South Australia. In 'Sea Lions of the World'. (Eds A. W. Trites, S. K. Atkinson, D. P. DeMaster, L. W. Fritz, T. S. Gelatt, L. D. Rea and K. M. Wynne). pp 325-351. (Alaska Sea Grant College Program, University of Alaska: Fairbanks, Alaska).
- Shaughnessy, P. D., Dennis, T.E., Dowie D., McKenzie, J. and McIntosh, R. (in prep.) Status of small colonies of the Australian sea lions, *Neophoca cinerea*, on Kangaroo Island, South Australia. *Australian Mammalogy*
- Shaughnessy, P. (in litt). Sea lions of Nicolas Baudin Island. In 'South Australia's Chain of Bays', compiled by Grant Hobson, Friends of Sceale Bay.
- Shaw, R. F. and J. D. Mohler. 1953. The selective significance of the sex ratio. *The American Naturalist* 87:337-342.
- Shiavini, A.C.M., Crespo, E.A., and Szapkievich, V. (2004) Status of the population of South American sea lion (*Otaria flavescens* Shaw, 1800) in southern Argentina. *Mammalian Biology* 69: 108-118
- Szteren, D., Auriolles, D., and Gerber, L.R. (2006) Population Status and Trends of the California Sea Lion (*Zalophus californianus californianus*) in the Gulf of California, Mexico. In 'Sea Lions of the World'. (Eds A. W. Trites, S. K. Atkinson, D. P. DeMaster, L. W. Fritz, T. S. Gelatt, L. D. Rea and K. M. Wynne). Alaska Sea Grant College Program, University of Alaska: Fairbanks, Alaska.
- Thompson, D., C.D. Duck, B.J McConnell and J. Garrett. 1998. Foraging behaviour and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. *Journal of Zoology* 246:135-146.
- Trillmich, F. 1986. Maternal investment and sex allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. *Behavioural Ecology and Sociobiology* 19:157 - 164.
- Thompson, D., Strange, I., Riddy, M. and Duck CD. (2005) The size and status of the population of southern sea lions *Otaria flavescens* in the Falkland Islands. *Biological Conservation* 121:357-367.
- Trillmich, F., G.L. Kooyman and P. Majluf. 1991. Attendance and diving behaviour of South American fur seals during El Nino in 1983. Pages 153-167 F. Trillmich, editor. Pinnipeds and El Nino: Responses to Environmental Stress. Springer-Verlag, Berlin.
- Trillmich, F. 1995. Attendance behaviour of Galapagos fur seals. Pages 169-185 in R. L. Gentry and G. L. Kooyman, editors. Fur seals: Maternal Strategies on Land and at Sea. Princeton University Press, Princeton.
- Trillmich, F. 1996. Parental investment in pinnipeds. *Advances in the Study of Behavior* 25:533-577.
- Trillmich, F. and E. Lechner. 1986. Milk of the Galapagos fur seal and sea lion, with a comparison of the milk of eared seals (Otariidae). *Journal of Zoology* 209:271-277.
- Trites, A. W. 1991. Fetal growth of northern fur seals: life-history strategy and sources of variation. *Canadian Journal of Zoology* 69:2608-2617.

- Trites, A.W., Miller, A.J., Maschner, H.D.G. et al. (2007) Bottom-up forcing and the decline of Steller sea lions (*Eumetopias jubatus*) in Alaska: assessing the ocean climate hypothesis. *Fisheries Oceanography*. 16: 46-67.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 135-179 in B. Campbell, editor. *Sexual selection and the descent of man*. Aldine Publications, Chicago II.
- Trivers, R. L. and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90 - 92.
- Weckerley, F. W. 1998. Sexual size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy* 79:33-52.
- Wells, R. S., D. J. Boness and G. B. Rathburn. 1999. Behavior. Pages 324-422 in J. E. White, G. C., and Garrott, R. A. (1990). 'Analysis of Wildlife Radio-tracking Data'. (Academic Press: San Diego).
- Wilkinson, I. S. and R. J. van Aarde. 2001. Investment in sons and daughters by southern elephant seals, *Mirounga leonina*, at Marion Island. *Marine Mammal Science* 17:873 - 887.
- Winship, A.J., A.W. Trites and D.G Calkins. 2001. Growth in body size of the Steller sea lion (*Eumetopias jubatus*). *Journal of Mammalogy* 82: 500-519.