

**POPULATION DEMOGRAPHICS OF NEW ZEALAND FUR SEALS
(*ARCTOCEPHALUS FORSTERI*)**

Submitted by

Jane McKenzie, BSci (Hons)

A thesis submitted in total fulfilment
of the requirements for the degree of

Doctor of Philosophy

Sea Mammal Ecology Group
Zoology Department
School of Life Sciences
Faculty of Science, Technology and Engineering

La Trobe University
Bundoora, Victoria, 3086
Australia

July 2006

STATEMENT OF AUTHORSHIP

Except where reference is made in the text of the thesis, this thesis contains no material published elsewhere or extracted in whole or in part from a thesis submitted for the award of any other degree or diploma.

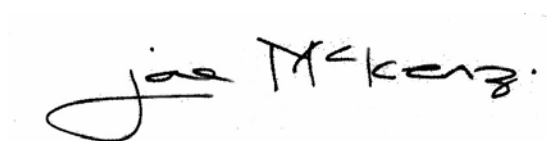
No other person's work has been used without due acknowledgement in the main text of the thesis.

The thesis has not been submitted for the award of any degree or diploma in any other tertiary institution.

This thesis is presented as a series of published or submitted papers. Although I did the significant aspects of analysis and interpretation of the results, the following people are co-authors of some of these papers because they assisted in the pursuit of the research or preparation of the thesis as described below:

B Page, A Morrissey, R McIntosh, SD Goldsworthy, A Baylis, N Calvert, M Berris, D Dowie, PD Shaughnessy, LJ Parry and many others assisted with field and laboratory work. SD Goldsworthy and MA Hindell supervised this project and received grants that funded part of this research. I offered coauthorship on papers to the people who helped considerably on this project.

All research procedures reported in the thesis were approved by the La Trobe University Animal Ethics Committee and the South Australian Department for Environment and Heritage Animal Ethics Committee.



.....
Jane McKenzie

24 July 2006

PUBLICATIONS

The following peer-reviewed papers resulted from work completed during candidature:

McKenzie, J., Parry, L.J., Page, B., and Goldsworthy, S.D. (2005) Estimation of pregnancy rates and reproductive failure in New Zealand fur seals (*Arctocephalus forsteri*). *Journal of Mammalogy*, 86, 1237-1246.

McKenzie, J., Page, B., Shaughnessy, P.D., and Hindell, M.A. (*in press*) Age and reproductive maturity of New Zealand fur seals (*Arctocephalus forsteri*), in southern Australia. *Journal of Mammalogy*.

McKenzie, J., Page, B., Goldsworthy, S.D., and Hindell, M.A. (*in press*) Growth strategies of New Zealand fur seals (*Arctocephalus forsteri*), in southern Australia. *Journal of Zoology (London)*.

McKenzie, J., Page, B., Goldsworthy, S.D., and Hindell, M.A. (*in review*). Behavioural responses of New Zealand fur seals (*Arctocephalus forsteri*) to darting and the effectiveness of midazolam and tiletamine-zolazepam for remote chemical immobilisation. *Marine Mammal Science*.

Page, B., McKenzie, J., McIntosh, R., Baylis, A.M.M., Morrissey, A., Calvert, N., Haase, T., Berris, M., Dowie, D., Shaughnessy, P.D., and Goldsworthy, S.D. (2004) Entanglement of Australian sea lions and New Zealand fur seals in lost fishing gear and other marine debris before and after Government and industry attempts to reduce the problem. *Marine Pollution Bulletin*, 49, 33-42.

Page, B., McKenzie, J., and Goldsworthy, S.D. (2005) Dietary resource partitioning among sympatric New Zealand and Australian fur seals. *Marine Ecology Progress Series*, 293, 283-302.

Page, B., McKenzie, J., Hindell, M.A., and Goldsworthy, S.D. (2005) Drift dives by male New Zealand fur seals (*Arctocephalus forsteri*). *Canadian Journal of Zoology*, 83: 293-300.

Page, B., McKenzie, J., and Goldsworthy, S.D. (2005) Inter-sexual differences in New Zealand fur seal diving behaviour. *Marine Ecology Progress Series*, 304, 249-264.

Baylis, A.M.M., Page, B., Peters, K., McIntosh, R., McKenzie, J., and Goldsworthy, S.D. (2005) The ontogeny of dive behaviour in New Zealand fur seal pups (*Arctocephalus forsteri*). *Canadian Journal of Zoology* 83, 1149-1161.

Page, B., McKenzie, J., Sumner, M.D., Coyne, M., and Goldsworthy, S.D. (2006) Spatial separation of foraging habitats among New Zealand fur seals. *Marine Ecology Progress Series*, 323, 263-279.



“They say around here that once a year, on Midsummer Night’s Eve, selkies who are seals the rest of the time come up out of the water and take the form of women. And if you find one of their discarded seal skins and take it home with you and hide it, then the selkie is bound to you until she finds her skin. And she may even love you a little, but she never stops looking for her skin. And she always finds it. It may take her a hundred years, but she finds it, and returns to the sea. Always.”

Sea Change – Susan Stern.

ABSTRACT

Assessment of trophic interactions between increasing populations of New Zealand fur seals (*Arctocephalus forsteri*) and fisheries in southern Australia is limited due to a lack of species specific demographic data and an understanding of the factors influencing population growth. To establish species specific demographic parameters a cross-sectional sample of New Zealand fur seal females (330) and males (100) were caught and individually-marked on Kangaroo Island, South Australia between 2000 and 2003. The seals were aged through examination of a postcanine tooth, which was removed from each animal to investigate age-specific life-history parameters. Annual formation of cementum layers was confirmed and accuracy in age estimation was determined by examination of teeth removed from individuals of known-age. Indirect methods of assessing reproductive maturity based on mammary teat characteristics indicated that females first gave birth between 4-8 years of age, with an average age at reproductive maturity of 5 years. Among reproductively mature females, age-specific reproductive rates increased rapidly between 4-7 years of age, reaching maximum rates of 70-81% between 8-13 years, and gradually decreased in older females. No females older than 22 years were recorded to pup. Age of first territory tenure in males ranged from 8-10 years. The oldest female and male were 25 and 19 years old, respectively. Post-weaning growth in females was monophasic, characterised by high growth rates in length and mass during the juvenile growth stage, followed by a gradual decline in growth rates after reproductive maturity. In contrast, growth in males was biphasic and displayed a secondary growth spurt in both length and mass, which coincided with sexual and social maturation, followed by a rapid decline in growth rates. Age-specific survival rates were high (0.823-0.953) among prime-age females (8-13 yrs of age) and declined in older females. Relative change in annual pup production was strongly correlated with reproductive rates of prime-age females and adult female survival between breeding seasons.

ACKNOWLEDGEMENTS

This project would not have been possible if it had not been for the dedication, enthusiasm and sheer strength of many people.

I thank Simon Goldsworthy and Mark Hindell for their tremendous enthusiasm, continuous encouragement, generous support and worldly advice throughout this project. Simon handed me a dream project and trusted me to run with it in the many directions I did, for that I will always be grateful and the skills I learned along the way will always be with me. Mark proved a tremendous pillar of strength in trying to get this project off the ground and taught me diplomacy. Peter Shaughnessy provided endless support and enthusiasm throughout this project and helped develop my skills in communication in both the scientific and political arena. Peter's tireless efforts to monitor pup production at the Cape Gantheaume year after year and past tagging efforts provided invaluable data for this project.

Sally Troy first introduced me to the Cape and the private lives of seals in 1992. Sue Robinson and Simon are to blame for reuniting me with my love for seals (and other things) and the wild, wicked and spectacular places they live. The crew in Hobart provided countless coffees, beers and words of understanding, advice and support in the early days in Tasmania. Rupe Woods provided veterinary advice and enormous encouragement and Stephen Aldous at the Pharmaceutical Department, University of Tasmania helped in preparation of drugs used in the field. David Middleton, Brian Walters and Rodger Martin are thanked for use of darting equipment during the initial daring trials.

My heartfelt thanks go to the many people who embraced life in the wilds of Cape Gantheaume, who lost weight, gained muscle mass, bruised knees and back sides, outwitted seals, took numerous great grabs, wore out countless pairs of boots, put up with tiger snakes, wicked weather and AM radio, and memorised (or tried to) every rock and location of countless seals over 3km of spectacular coast line, and especially those that rejoiced with every birth, bull fight or just an "awesome squid spew" they witnessed along the way. Special thanks go to Adam Morissey, Al Baylis, Norna Calvert, Bec McIntosh, Kristian Peters, and David Lamb who fine tuned their skills in catching seals and spotting tags and came back time and again to help. Adam provided a pillar of strength right from the beginning in many ways - the Cape Gantheaume Bar still stands

as testament of your efforts to bring laughter and enjoyment to the end of each hard working day. Al your love and enthusiasm for the Cape, seals, crapped-out 4 Wheel Drives, “lifers” and fishing efforts will always be appreciated. Bec reminded me of the value of laughter each day and kept us all on our toes. Norna your efforts over numerous summers took the weight off my shoulders and your kindness and company made summers a breeze. David your dedication to retrieving field note books from the bottom of cliffs has never been surpassed – next time I’ll show you the easy route down. Kristian thanks for all your hard work, kindness, endless enthusiasm and your mum’s recipe for steamed jam-tin cakes.

Many others provided field assistance and their efforts are greatly appreciated; Cath Sliwa, Stephanie Pfennigwerth, Annett Finger, Nina Trikojus, Derek Hamer , Cory Williams, Jess Elmer, Mike Sparg, Cam Ralph, Roan Plotz, Kathy Tsang, Kylie Russell, Rick Taylor, Mags Chambellant, Luke Einoder, Charles Littnan, Mel and Steve Berris, Jason Nichols, Sue, Simon, Mark, Tami Haase, Marty Haase, Glenys McIntosh, Fiona Bird, Peter Frappel, Simon and Jane Talbot, Jenny Kingston, Jen Palmer, Nathan Dowie, Tobie Cougsipetcos, Ilse Kiessling, Leah, Wendy Elsner, Rod Page, Dave Sutherland. Tami, Al and Roan also added to the resight and pup tagging efforts during their own times at the Cape.

Special thanks also go to Dave, Linda, Nathan and Lewis Dowie, Mel and Steve, Fiona Gill, Anthea Howard, and Jason for soft beds, hot showers, heart warming food and good company away from the Cape. I’m also grateful to Anthony Maguire, Dave and other National Parks staff who helped with field logistics and supported the project with great enthusiasm. Special thanks also go to the countless clippers and catchers that worked hard to keep the Kangaroo Island CSIRO pup mark-recapture program an ongoing event. Their efforts have made an invaluable contribution to many other research programs.

In assisting with training and development of ageing techniques special thank go to Kelly Robertson, Mike Goebel and Jessica Lipsky of the Southwest Fisheries Science Centre, La Jolla, California and Peter Boveng of the National Marine Mammal Laboratory, Seattle, WA , USA. Special thanks also to Julia and Mike Oswald and Kate Stafford for providing accommodation and hospitality during my stay in the states, and thanks to Brian Malone for use of the freezing microtome at La Trobe University. Laura Parry provided tremendous advice and encouragement in developing the progesterone

assays and guided a pure field biologist through the world of test tube science. Thanks to Kath Handasyde and Marilyn Renfree (University of Melbourne) for use of laboratory space and equipment, and welcoming me back to my old stomping grounds. Thanks also Andrew Siebel for his guidance in the lab.

This project was generously supported by: Sea World Research and Rescue Foundation, Holsworthy Wildlife Research Fund, South Australian Department for Environment, National Parks and Wildlife Council Wildlife Conservation Fund, Royal Zoological Society of NSW, Ethel Mary Read Research Grant, PADI Project AWARE Foundation, Roche Products Pty. Ltd. (donation of midazolam), Kangaroo Island Sealink, Arnotts Pty Ltd. (Thanks for the Tim Tams guys) and an Australian Postgraduate Award.

To the Bungalow landlords Fi and Andy and faithful watch dogs Oscar and Rudi, I'll always cherish your friendship, support, walks, "hups" and having somewhere to call home. My family are especially thanked for their continuous support, enthusiasm and understanding of my long absences. Mum your Christmas cakes are legendary and I'm sure they were the reason for people returning time again to spend Christmas at the Cape. Dad your contribution of the "bodge" made pulling teeth so much easier and will continue to further seal science for many more years. Finally, Brad what can I say - I couldn't have wished for a better companion to have shared so many adventures with to wild and wonderful places, and the privilege of getting to know a little about the creatures that inhabit such places. Your strength, support, understanding, enthusiasm and love helped me follow my dreams and kept me on track. Thanks.

TABLE OF CONTENTS

STATEMENT OF AUTHORSHIP	II
PUBLICATIONS	III
ABSTRACT	VI
ACKNOWLEDGEMENTS	VII
LIST OF FIGURES.....	XIV
LIST OF TABLES	XVIII
CHAPTER 1. GENERAL INTRODUCTION.....	1
ORGANISATION AND STRUCTURE OF THIS THESIS	2
GENERAL BACKGROUND	3
STUDY AIMS AND OBJECTIVES	6
STUDY POPULATION AND STUDY SITE.....	8
SUMMARY OF THE LIFE HISTORY OF NEW ZEALAND FUR SEALS	11
CHAPTER 2. BEHAVIOURAL RESPONSES OF NEW ZEALAND FUR SEALS (<i>ARCTOCEPHALUS FORSTERI</i>) TO DARTING AND THE EFFECTIVENESS OF MIDAZOLAM AND TILETAMINE-ZOLAZEPAM FOR REMOTE CHEMICAL IMMOBILISATION	13
INTRODUCTION	14
MATERIALS AND METHODS	17
Behavioural trial	17
Midazolam immobilisation.....	17
Tiletamine-zolazepam immobilisation.....	19
Data analysis	21
RESULTS	22
Initial behavioural response to darting	22
Midazolam trial.....	25
Tiletamine-zolazepam.....	25
Body condition index.....	29
Multiple darts	29
Behaviour of drugged seals in the water	29
Adverse effects and mortality	31
DISCUSSION	32

Risk of drugged animals entering the water and drowning.....	32
Midazolam	34
Tiletamine-zolazepam immobilisation.....	34
Conclusion and recommendations	37
CHAPTER 3. ESTIMATION OF PREGNANCY RATES AND REPRODUCTIVE FAILURE IN NEW ZEALAND FUR SEALS (<i>ARCTOCEPHALUS FORSTERI</i>)	39
INTRODUCTION	40
MATERIALS AND METHODS	43
Population and study area	43
Animal capture and sample collection	43
Reproductive cycle	43
Reproductive classifications	46
Radioimmunoassays	46
Assay procedure.....	47
Validation of the radioimmunoassay.....	47
Statistical analyses	48
RESULTS	48
Validation of progesterone assay	48
Progesterone profile over early active gestation.....	49
Pregnancy rates.....	51
Reproductive failure.....	52
Previous reproductive history	52
DISCUSSION	52
Progesterone profile	52
Potential error and biases in pregnancy testing.....	54
Pregnancy rates.....	55
Timing and extent of reproductive failure.....	56
Factors affecting reproductive failure.....	58
CHAPTER 4. AGE AND REPRODUCTIVE MATURITY OF NEW ZEALAND FUR SEALS (<i>ARCTOCEPHALUS FORSTERI</i>) IN SOUTHERN AUSTRALIA.....	60
INTRODUCTION	61
MATERIALS AND METHODS	64
Study population.....	64
Animal capture and data collection.....	64

Tooth preparation	65
Age estimation	66
Reproductive maturity and status	67
Data Analysis	68
RESULTS	70
Validation and accuracy of aging technique	70
Validation and accuracy of mammary teat classification	70
Age-specific maturity and reproductive rates in females	71
Age-specific territory tenure in males	73
Longevity and size at reproductive maturity	74
DISCUSSION	77
Age determination.....	77
Longevity	78
Age and size at reproductive maturity	79
 CHAPTER 5. INTER-SEXUAL DIFFERENCES IN THE GROWTH OF NEW ZEALAND FUR SEALS (<i>ARCTOCEPHALUS FORSTERI</i>) IN SOUTHERN AUSTRALIA	 82
INTRODUCTION	83
MATERIALS AND METHODS	85
Study population	85
Animal capture and data collection.....	86
Data analysis	87
RESULTS	88
Season of capture and age distribution	88
Growth	89
Allometric relationships between mass, length and girth.....	96
DISCUSSION	97
Potential sources of bias.....	97
Sexual differences in growth.....	99
Growth after reproductive maturity	102
Growth and foraging ecology.....	103
Comparisons between populations.....	104
Summary	107

CHAPTER 6. POPULATION DYNAMICS OF NEW ZEALAND FUR SEALS IN SOUTH AUSTRALIA: GENERAL PATTERNS AND VARIATION IN VITAL RATES ...	108
INTRODUCTION	109
MATERIALS AND METHODS	112
Population and animals studied.....	112
Reproduction	113
Survival	115
Tag loss	117
Population age structure.....	118
Life table analysis	118
RESULTS	120
Parturition period	120
Annual and age-specific reproductive rates.....	121
Early pup mortality (0-30 days).....	123
Annual and age-specific survival rates of breeding age females.....	125
Relationships between vital rates and pup production	128
Adult female age structure.....	129
Life table analysis	131
DISCUSSION	134
Age-specific reproductive patterns in New Zealand fur seals.....	134
Age-specific survival patterns in New Zealand fur seals	136
Pup survival	137
Adult survival	138
Recruitment (juvenile survival).....	139
Variation in adult reproductive and survival rates in relation to pup production...	140
REFERENCES.....	144

LIST OF FIGURES

CHAPTER 1. GENERAL INTRODUCTION

- Fig. 1. Location of Cape Gantheaume in relation to Kangaroo Island and the surrounding mainland. 10
- Fig. 2. Colony location at Cape Gantheaume and census sectors boundaries referred to in this study and used for mark-recapture estimates of pup abundance (Goldsworthy and Shaughnessy 1994; Shaughnessy et al.1995). The Beach Sector referred to by Shaughnessy (2006) is abbreviated as BS. 10

CHAPTER 2. BEHAVIOURAL RESPONSES OF NEW ZEALAND FUR SEALS TO DARTING AND THE EFFECTIVENESS OF MIDAZOLAM AND TILETAMINE-ZOLAZEPAM FOR REMOTE CHEMICAL IMMOBILISATION

- Fig. 1. Percent of initial responses to darting displayed by adult female New Zealand fur seals in relation to (a) the dart delivery system used (cross bow or dart gun) and (b) the presence of absence of a pup. Numbers above each bar indicate number of individuals. 24
- Fig. 2. Percent of initial responses to darting by New Zealand fur seals in relation to sex. Data are combined results from the behavioural trial and subsequent darting events using tiletamine-zolazepam. Numbers above bars indicate number of individuals. 26
- Fig. 3. The relationship between initial dose and maximal level of immobilisation reached for (a) male ($n = 54$) and (b) female ($n = 20$) New Zealand fur seals and the influence of relative body condition. Positive BCI indicates animals are in relatively good condition compared to those with negative BCI. Mean doses for each level of immobilisation are for all animals combined and include additional males for which BCI values were unavailable. 28

CHAPTER 3. ESTIMATION OF PREGNANCY RATES AND REPRODUCTIVE FAILURE IN NEW ZEALAND FUR SEALS

- Fig. 1. Reproductive cycle of the New Zealand fur seal at Cape Gantheaume, Kangaroo Island, South Australia, indicating the estimated number of days since parturition at which ovulation, implantation and the following birth occur. Blood samples were taken May-August. 44

- Fig. 2. Serum progesterone concentration at each gestational stage, over days prepartum of female New Zealand fur seals that did not subsequently give birth (○, $n = 75$) compared to females that did (●, $n = 81$), shown as mean \pm SE. Differences in progesterone concentrations between the two groups appears to occur by 29 June. 50
- Fig. 3. Variation in reproductive outcome of female New Zealand fur seals sampled. Percentage of full term pregnancies (black bars) compared to failed pregnancies in mid to late active gestation (diagonal lines in bars) and missed pregnancies (light grey bars). Numbers of females in each category are indicated for each year. 51

CHAPTER 4. AGE AND REPRODUCTIVE MATURITY OF NEW ZEALAND FUR SEALS IN SOUTHERN AUSTRALIA

- Fig. 1. The proportion of female New Zealand fur seals estimated to have given birth at least once (reproductively mature, solid circles) and the average reproductive rate (open circles) as a function of age. Proportions mature are based on data pooled between 2000 and 2003 ($n = 331$). Reproductive rates are for tag-resight data pooled between 2001 and 2003 ($n = 528$). Numbers on graph are sample sizes and data for females 19-25 years of age are pooled. 72
- Fig. 2. Age-specific proportion of territorial male New Zealand fur seals based on tag-resight data pooled between 2001 and 2003 ($n = 102$). Numbers above the graph are sample sizes and data for males 16-19 years of age are pooled. 74
- Fig. 3. The relationship between reproductive maturity, standard body length (in non-breeding season) and age (in previous breeding season), in female New Zealand fur seals (1-10 yrs). Open circles indicate mature individuals and closed circles indicate immature individuals (based on mammary teat status). Solid lines indicate the body length of the smallest mature (lower line) and largest immature females (upper line), and the dashed line indicates the estimated average age at first birth. 76
- Fig. 4. The relationship between observed territorial status, body length (in non-breeding season) and age (in following breeding-season) in male New Zealand fur seals. Open circles indicate males that were observed to hold territories ($n = 21$) in the summer following capture and closed circles indicate males that were non-territorial ($n = 24$). The solid line indicates the minimum body length of males that attempted to hold territories and the dashed line indicates the estimated average age at reproductive maturity. Body length was not available for 8-year-old territorial males sampled. 77

CHAPTER 5. INTER-SEXUAL DIFFERENCES IN THE GROWTH OF NEW ZEALAND FUR SEALS (*ARCTOCEPHALUS FORSTERI*) IN SOUTHERN AUSTRALIA

- Fig. 1. Age-frequency distribution of female ($n = 326$) and male ($n = 88$) New Zealand fur seals sampled at Cape Gantheaume between 2000 and 2003 that were used for development of growth models in this study. 89
- Fig. 2. Standard length growth curves (solid lines) and age-specific growth rates (dashed lines) for (a) female and (b) male New Zealand fur seals at Cape Gantheaume. Fitted growth curves are Gompertz for females and a two-component logistic model for males (see Table 2 for parameter estimates). Solid circles indicate females ($n = 322$) and males ($n = 86$) measured in this study and the open circle indicates mean curvilinear length at birth (0 days) from Mattlin (1978a). 91
- Fig. 3. Body mass growth curves (solid lines) and age-specific growth rates (dashed lines) for (a) female and (b) male New Zealand fur seals at Cape Gantheaume. Fitted growth curves are Gompertz for females and a two-component logistic model for males (see Table 2 for parameter estimates). Solid circles indicate females ($n = 320$) and males ($n = 87$) measured in this study and the open circle indicates mean mass at birth (0 days) from Goldsworthy (2006). 92
- Fig. 4. Comparison of growth in standard length of female New Zealand fur seals from Kangaroo Island, South Australia (solid line \pm 95% confidence interval) and New Zealand (dashed line). For comparison, growth curves are calculated using the Gompertz growth function, where t equals age at last breeding season, following Dickie and Dawson (2003). 107

CHAPTER 6. POPULATION DYNAMICS OF NEW ZEALAND FUR SEALS IN SOUTH AUSTRALIA: GENERAL PATTERNS AND VARIATION IN VITAL RATES

- Fig. 1. Estimated number of New Zealand fur seal pups born at Cape Gantheaume, based on mark-recapture at the end of the breeding season (calculated from data in Shaughnessy 2006). Trendlines are based on exponential rate of growth from 1988-1989 to 2005-2006 (solid line) and from 1988-1989 to 1999-2000 (dashed line). 113
- Fig. 2. Annual variation in the reproductive rates of young (5-7 yrs), prime-age (8-13 yrs) and older (14-25 yr) New Zealand fur seal females monitored at Cape

Gantheaume. Numbers of resident adult females sampled each year were;

2000-2001 = 68, 2001-2001 = 162, 2002-2003 = 187, and 2003-2004 = 169.... 122

Fig. 3. Age specific reproductive rates for New Zealand fur seals at Cape Gantheaume, pooled over three years (2001-2003). Data for females 19-25 years of age are pooled. Sample sizes are shown at the top of the graph. The regression equation is $y = 0.00915 + 0.137x - 0.00613x^2$ 122

Fig. 4. Relationships between relative change in pup production and variation in vital rates of mature age New Zealand fur seal females at Cape Gantheaume, 2000-2003. Relative change in pup production was calculated based on pup abundance at the end of the breeding season as calculated by Shaughnessy (2006), adjusted for early pup mortality (this study). Survival rates correspond to the periods between breeding seasons. 129

Fig. 5. Pooled age distribution of mature female New Zealand fur seals sampled over three breeding season at Cape Gantheaume, 2000-2001 to 2002-2003 ($n = 244$). Shading indicates the three major life-stages of breeding age females: recently mature young females (black bars), prime-age females (hatched) and senescent older female (white). 131

Fig. 6. Survival (l_x) curve for female New Zealand fur seals at Cape Gantheaume, 2000-2003, based on maximum likelihood fit of a modified Siler model to survival data for mature age animals (4-25 yrs). Closed circles indicate estimates derived from measured survival rates and open circles indicate values based on estimated survival rates (see text). 132

LIST OF TABLES

CHAPTER 2. BEHAVIOURAL RESPONSES OF NEW ZEALAND FUR SEALS TO DARTING AND THE EFFECTIVENESS OF MIDAZOLAM AND TILETAMINE-ZOLAZEPAM FOR REMOTE CHEMICAL IMMOBILISATION

Table 1. Initial response of target seals and others within a 10m radius.....	18
Table 2. Level and degree of immobilisation (adapted from Boyd et al. 1990).	19
Table 3. Level of immobilisation reached for female New Zealand fur seals following a single dose of midazolam (mean \pm SD). Data are for animals of known mass.....	25
Table 4. Level of immobilisation reached following an initial dose (mean \pm SD) of tiletamine-zolazepam for female and male New Zealand fur seals. Data are for animals of known mass and exclude animals that escaped immediately following darting.	27

CHAPTER 3. ESTIMATION OF PREGNANCY RATES AND REPRODUCTIVE FAILURE IN NEW ZEALAND FUR SEALS

Table 1. Number of individual adult New Zealand fur seals sampled during each gestational stage of 26 days duration and the number that subsequently gave birth (“pupped”) and those that did not (“no pup”).	45
--	----

CHAPTER 5. INTER-SEXUAL DIFFERENCES IN THE GROWTH OF NEW ZEALAND FUR SEALS (ARCTOCEPHALUS FORSTERI) IN SOUTHERN AUSTRALIA

Table 1. Growth models used to fit size (S_t) at age (t) data for New Zealand fur seals. S_{∞} is the predicted asymptotic size, k determines the rate of approach to the asymptote (growth rate parameter), and t_0 is the hypothetical age at which growth is zero, but should be interpreted with caution (McLaren 1993).	88
Table 2. Parameter estimates (\pm SE) for growth models fitted to New Zealand fur seal size-at-age data from Cape Gantheaume. See Table 1 for model and parameter details. Sample size for female length, 322; female mass, 320; male length, 86; and male mass, 87.....	93
Table 3. Predicted standard length and body mass of New Zealand fur seals in southern Australia. Standard length and mass for animals ≥ 1.5 years calculated using Gompertz growth models for females and two-component logistic models for males (Table 2). Estimated size at birth (0 days old) are observed mean sizes from	

Mattlin (1978a) Open Bay Is., New Zealand (*) and Goldsworthy (2006) Cape Gantheaume 1988 (**). Maximum ages are based on tag-resight data for the population studied (Chapters 4 & 6; McKenzie et al. in press b).	95
Table 4. Allometric regression of non-breeding season body mass on standard length, axillary girth, and volume for New Zealand fur seals (≥ 1.5 years) from Kangaroo Island, South Australia.	96
Table 5. Reported mean standard lengths (\pm SD and 95% confidence interval) for New Zealand fur seals from Australia and New Zealand. Approximate values estimated from published graphs are indicated by *. Age range of animals sampled at Kangaroo Island have been adjusted to assist comparison (i.e. females > 22 years and males > 12 years have not been included).	106

CHAPTER 6. POPULATION DYNAMICS OF NEW ZEALAND FUR SEALS IN SOUTH AUSTRALIA: GENERAL PATTERNS AND VARIATION IN VITAL RATES

Table 1. Parturition period for New Zealand fur seals at Cape Gantheaume for 2000 to 2003 calculated for tagged females and total population based on daily pup counts during the breeding season. Values are \pm SD (sample size).	120
Table 2. Age-specific proportions reproductively mature for New Zealand fur seals at Cape Gantheaume (Chapter 4; McKenzie et al. in press b) and reproductive rates of mature females pooled over three years (this study) at Cape Gantheaume. SE is standard error and n is sample size. Predicted values from the fitted curves (see text).	123
Table 3. Pup mortality for New Zealand fur seals at Cape Gantheaume. Sample sizes of pups monitored are in parentheses.	124
Table 4. Results of model selection using program MARK and resight data for tagged resident adult female New Zealand fur seals at Cape Gantheaume, 2000 to 2003. Models are ranked according to their Akaike weights (AICc W). Values are Akaike's Information Criterion (AICc), difference in AICc (Δ AICc) between models and number of parameters (No. Par.).	126
Table 5. Annual survival rates of mature New Zealand fur seal females at Cape Gantheaume based on resight data of tagged animals between the 2000-2001 and 2003-2004 breeding seasons. S_{xc} are survival rates corrected for tag loss, S_x are uncorrected survival estimates, SE are standard errors, CI are confidence intervals and n is sample size.	127
Table 6. Age-specific annual survival rates (S_x) of adult female New Zealand fur seals at Cape Gantheaume using return rates. S_{xc} are survival rates corrected for tag	

loss, S_x are uncorrected survival estimates, SE are standard errors, CI are confidence intervals and n is sample size.....	128
Table 7. Age structure of adult female New Zealand fur seals resighted at Cape Gantheaume in the first breeding season following their initial capture. Sample sizes n are indicated in parentheses.....	130
Table 8. Parameter estimates for the modified Siler model fitted to New Zealand fur seal survival data for mature age animals (4-25 yrs).	132
Table 9. Life table for female New Zealand fur seals based on maximum likelihood fit of a modified Siler model to population parameters for ages 4-25 yrs, measured between 2000 and 2003. Survival to age 1yr is estimated survival to weaning at 8-11 months and is likely to be positively biased. Survival to age 4yrs and annual survival rates for ages 4 and 5 are estimated based on reported rates for subantarctic fur seals (Beauplet et al. 2005).....	133

CHAPTER 1. GENERAL INTRODUCTION



ORGANISATION AND STRUCTURE OF THIS THESIS

This thesis is arranged as a series of five papers, which are either published or awaiting publication. The five chapters are self-contained and consequently, some material is duplicated, because they overlap in content. The abstracts, acknowledgements and references have been combined in an attempt to reduce the amount of duplication. The figure and table numbers refer only to the chapter in which they are contained.

The general introduction (Chapter 1) outlines the context of this study and the need to quantify key demographic parameters for the New Zealand fur seal, and provides a brief background into the known life history of the species and the population studied. Chapter 2 assesses the effectiveness of a cross bow and a dart gun to deliver sedative and anaesthetic drugs to adult male and female New Zealand fur seals, which has been submitted for publication in *Marine Mammal Science*. Chapter 3 examines differences in progesterone concentrations at different stages of gestation and the use of progesterone concentrations to estimate pregnancy rates and patterns of reproductive failure. This chapter was published in the *Journal of Mammalogy* in December 2005. Chapter 4 validates the use of growth layer groups in postcanine teeth for aging female and male New Zealand fur seals, and outlines inter-sexual differences in their age at reproductive maturity, and relationship with morphology. This chapter has been accepted for publication in the *Journal of Mammalogy*. Chapter 5 compares the post-weaning growth rates of male and female New Zealand fur seals, and has been accepted for publication in the *Journal of Zoology* (London). The final chapter (Chapter 6) presents age-specific reproductive and survival rates of adult females and mortality of pups, and assesses the influence of annual variation in vital rates on short-term changes in pup abundance. It brings together the results of the previous chapters and discusses the influence of life-history parameters of growth and maturity on age-specific reproduction and survival. This chapter also draws on the life history of other pinniped species to speculate on age-specific parameters for which data are lacking in the New Zealand fur seal and highlights areas of further research that would build on our understanding of the population dynamics of this species. This chapter is currently being prepared for submission to an appropriate journal.

GENERAL BACKGROUND

The New Zealand fur seal (*Arctocephalus forsteri*) is a temperate latitude species that breeds on offshore islands along the southern coastline of Australia from Western Australia to Tasmania, and on the coastline and offshore islands of New Zealand and its subantarctic islands (Shaughnessy et al. 1994; Harcourt 2001; Goldsworthy et al. 2003). Although populations throughout this region were greatly reduced by unregulated harvesting in the late 18th and early 19th centuries (Ling 1999), the species has been recovering and recolonising its former range, particularly in recent decades, and is now the most abundant fur seal species in the Australian-New Zealand region (Harcourt 2001; Goldsworthy et al. 2003). A recent estimate of the overall population in Australia is around 57,400 animals (Goldsworthy et al. 2003). In New Zealand the size of the total population has been suggested to be around 100,000 animals (Taylor et al. 1995). However, reliable measures of pup production are not available for a large number of colonies throughout New Zealand (Harcourt 2001). Populations in Australia are rapidly increasing and it has been suggested that they may treble over the next 15-30 years (Goldsworthy et al. 2003). Pup production at several colonies indicate high rates of increase (16-19% per annum, Shaughnessy et al. 1995), similar to those observed in other otariid species in the southern hemisphere, which were legally protected following extensive exploitation in the 19th and 20th centuries (Roux 1987; Harwood and Rohani 1996; Wickens and York 1997). Similar rates of population increase have also been reported for this species in New Zealand (Lalas and Harcourt 1995; Taylor et al. 1995; reviewed in Harcourt 2001) where several populations were hunted to local extinction by Polynesians prior to European exploitation (Smith 1989).

As in other parts of the world, increasing fur seal populations in Australia are perceived to be competing with commercial fisheries (Butterworth 1992; Wickens et al. 1992; Goldsworthy et al. 2003). With the development of more intense fishing practices, increased global demand for fisheries production and over-exploitation of some local fish stocks, concern among conservation and fisheries managers with respect to seal-fisheries interactions and their potential impact on recovering seal populations and declining fish stocks has become an issue of considerable concern and debate (Shaughnessy 1995; Goldsworthy et al. 2003; Shaughnessy et al. 2003; National Seal Strategy Group 2005). In southern Australia, New Zealand fur seals interact at an operational level (e.g., incidental catch and entanglements in debris) with most major

fisheries, including trawl, long-line, drop-line, purse-seine, gill net, pot and marine finfish aquaculture (reviewed in Shaughnessy et al. 2003; Page et al. 2004; National Seal Strategy Group 2005). However, quantitative and independent data on the extent of interactions is limited (Shaughnessy et al. 2003; National Seal Strategy Group 2005). Even less is known of the significance of trophic interactions between seals and commercial fisheries (Goldsworthy et al. 2003). New Zealand fur seals in southern Australia are generalist predators which target a number of pelagic and benthic fish and cephalopod species including commercial species such as Western school whiting (*Sillago bassensis*), Jack Mackerel (*Trachurus declivis*), Gould's squid (*Nototodarus gouldi*) and Southern Ocean arrow squid (*N. filippovae*) (reviewed in Goldsworthy et al. 2003; Page et al. 2005b), indicating considerable potential for overlap in prey consumption between seal populations and local fisheries.

In a recent attempt to assess the extent of trophic interactions between growing populations of pinnipeds and fisheries in southern Australia, Goldsworthy et al. (2003) developed a number of trophic-dynamic models based on age-structured population and bio-energetic models of the three species of otariid seals (fur seals and sea lions) that occur in southern Australia: the Australian (*Arctocephalus pusillus doriferus*) and New Zealand fur seal and the Australian sea lion (*Neophoca cinerea*). Based on current estimates of pup production for all three species, they estimated that nationally, total consumption by seals was about 2.5 times that of fisheries catch and about 5 times that of the fisheries catch in Australia's south-eastern region alone. Estimates of a 7.5 to 15-fold increase in seal consumption of the current fishery catch in south-eastern Australia if seal populations were to return to pre-European numbers sent shock waves through the fishing industry (McDougall 2006). However, as the authors emphasised, the outcomes of the models should be interpreted with caution as many of the parameters used were based on limited data and assumptions about the population dynamics of pinnipeds and marine ecosystems in Australia.

Concern by the commercial fishing industry of the impact of increasing New Zealand fur seal populations is not a recent development. In New Zealand, due to pressure from the commercial fishing industry just over six thousand New Zealand fur seals were culled in 1946 in southern parts of the South Island and in the vicinity of Stewart Island (Sorensen 1969). Many of the earlier studies on diet and biology of the species were prompted by the desire to collect relevant data that could dispel the controversy over impacts of seals on fish stocks and that would assist in the management and

conservation of the species should the need ever arise (Street 1964; Mattlin 1978a; Taylor et al. 1995). A number of studies have been conducted on the diet and foraging behaviour of New Zealand fur seals (Harcourt et al. 1995; Lake 1997; Mattlin et al. 1998; Fea et al. 1999; Harcourt 2001; Harcourt et al. 2002; Page et al. 2005a, 2005b) and more recently on inter-sexual differences in foraging spatial distribution (Page et al. 2006). Throughout Australia and New Zealand considerable effort has been directed towards identifying population distributions and monitoring trends in pup production as an index of population growth (reviewed by Harcourt 2001; Goldsworthy et al. 2003), and in identifying habitat preferences and patterns in the re-colonisation process (Ryan et al. 1997; Bradshaw et al. 2000a, 2002). However, despite a considerable number of studies undertaken on the general biology of this species since the 1960s (reviewed in: Crawley and Wilson 1976; Crawley 1990; Harcourt 2001), key aspects of the species' biology are still poorly understood. Quantitative data on age-specific survival and reproductive rates required for modelling population growth are sparse, as well as data on age-specific growth and mass, which are required for modelling food consumption. Consequently, local and regional population and biomass estimates for the species have been largely based on life-history patterns and values measured for other fur seal species (Crawley and Brown 1971; Taylor 1982; Taylor et al. 1995; Goldsworthy et al. 2003).

Unlike other abundant otariid species such as the northern (*Callorhinus ursinus*), South American (*Arctocephalus australis*), and South African (*Arctocephalus pusillus pusillus*) fur seals, extensive known-age samples of harvested or culled samples have not been available for examination of age-specific demographic parameters in the New Zealand fur seal. The greatest advancement in establishing age-specific reproductive and growth parameters in recent times came from the examination by Dickie and Dawson (2003) of New Zealand fur seals incidentally caught during fisheries operations off the coast of New Zealand in 1996. Although the number of samples available was limited (57 females and 64 males), Dickie and Dawson's (2003) work presented valuable information on both growth and reproduction in the New Zealand fur seal.

Few studies have attempted to examine the factors influencing the population dynamics of New Zealand fur seals, perhaps in part due to the species' common status and lack of acute conservation or management issues. The lack of demographic data is also likely to relate to the practical difficulties of monitoring wild populations of large long-lived animals that spend a considerable proportion of their lives dispersed at sea

(Harwood and Rohani 1996). Long-term mark-recapture studies of New Zealand fur seals based on animals marked as pups have been limited due to the time and logistics required to monitor animals that inhabit often remote and relatively inaccessible offshore islands. Long-term information gained from tagging pups is also limited, due to issues of high tag loss and tag wear, which are largely a result of the rocky substrates on which New Zealand fur seals haul-out (Bradshaw et al. 2000b). Permanent methods of marking such as freeze- and hot-iron branding have been trialled with variable success (Troy et al. 1997; Goldsworthy unpublished data). New Zealand fur seals are also typically flighty when they smell or see humans, making capture of adult animals difficult and dangerous, particularly when capturing large males and working on rocky coastlines. Although territory males stand their ground when approached by humans during the breeding season (Troy et al. 1997), they readily flee at other times of the year. Although chemical immobilisation by dart is an established method used to facilitate the capture and restraint of many otariid and phocid seals, extensive drug or darting trials have not been conducted on New Zealand fur seals (reviewed in: Gales 1989; Erickson and Bester 1993; Lynch et al. 1999). In addition, darting of free-ranging seals is still considered high risk, due to the risk of drugged animals escaping to the sea and drowning (David et al. 1988).

STUDY AIMS AND OBJECTIVES

The primary objective of this study was to establish species specific estimates of fecundity, survival and growth for the New Zealand fur seal and, by adding to existing population and biological data available for this species, provide sound and realistic parameter values on which population and biomass models can be based. The study largely focuses on adult females, but where data collected were sufficient, life-history parameters for other female age groups and for males were examined. Inter-sexual comparisons for several demographic parameters aid in highlighting differences in the life history of male and female New Zealand fur seals, and in interpreting factors influencing the population dynamics of the species. Although largely based on cross-sectional data, and therefore likely to incorporate some level of error due to issues of random sampling and sample size, longitudinal data has also been incorporated where possible, and measures of confidence and variances provided. The study is also limited in that it focuses on one population over a relatively short time period (4 yrs). The demographic parameters presented therefore pertain to a particular population and point in time and may not be indicative of longer-term trends in the

population or of other populations. However, the life-history patterns presented and variation in rates measured are likely to reflect the dynamics of other populations.

A secondary objective of this study was to develop and improve on existing methods employed in studying the population dynamics of pinnipeds, such as methods of live capture, aging and assessment of reproductive status. It is hoped that such methods will assist in future research into the population biology of New Zealand fur seals and other pinnipeds.

The specific aims of this study were therefore to:

1. estimate average pregnancy rates in adult females and examine interannual variations in the timing and extent of reproductive failure;
2. estimate the average age at reproductive maturity in females and first territory tenure in males and examine the influence of age and size on maturation rates;
3. estimate maximum longevity of female and male New Zealand fur seals;
4. establish age-specific reproductive and survival patterns in adult females and estimate annual variation in reproductive and survival rates;
5. estimate mean annual mortality rates in pups and examine variation among years;
6. assess the influence of annual variation in vital rates on short-term changes in pup production;
7. estimate the age structure of the adult female population;
8. develop a life table for New Zealand fur seals based on available data to facilitate future population growth models;
9. establish age and sex-specific patterns of post-weaning growth and
10. present age-specific mass and length tables to facilitate the development of future biomass and consumption models.

To assist in achieving these aims the following methods were developed and/or validated for the New Zealand fur seal:

1. An effective and safe method of remote chemical immobilisation of free-ranging seals.
2. The use of progesterone concentrations to estimate pregnancy rates and determine reproductive failure in live animals.
3. The accuracy of using growth layer groups in the structure of teeth for aging New Zealand fur seals.
4. The use of mammary teat characteristics in classifying live females as reproductively immature or mature.

STUDY POPULATION AND STUDY SITE

This study was conducted at the second largest and one of the most accessible New Zealand fur seal breeding colonies in Australia. The study colony, located on Kangaroo Island at Cape Gantheaume (36°04'S, 137°28'E), accounts for about 15% of annual pup production in Australia (Goldsworthy et al. 2003). Pup production at Cape Gantheaume has been monitored over successive summers since 1988-1989 using mark-recapture techniques and direct counts (Shaughnessy et al. 1995), providing the most robust and long-term data series of annual pup production for this species. In 2000, the population was estimated at around 9,100 individuals based on pup numbers (Goldsworthy et al. 2003), with an average annual growth rate of about 16% since 1989 (Shaughnessy 2000). Annual pup abundance at Cape Gantheaume and other colonies on Kangaroo Island fluctuated between 2001-2003, but has since continued to increase at an average rate of 12.5% (Shaughnessy 2006).

The colony at Cape Gantheaume is located on the southernmost point of Kangaroo Island and currently extends north-east along the coast for approximately 0.5 km and to the north-east of the Cape for 2 km. Animals haul-out and breed on narrow irregular rocky platforms and boulder fields interspersed with small rock pools (Goldsworthy and Shaughnessy 1994). Within the colony breeding areas are interspersed with haul-out areas which are occupied throughout the breeding and non-breeding periods. Animals are easily observed from the cliffs and slopes above the colony (15-30 m), using binoculars and spotting scopes. Since monitoring of pup numbers began the colony has been divided into separate “sectors” (Fig. 2) to simplify mark-recapture procedures and enable trends in abundance and expansion to be compared between parts of the

colony (Goldsworthy and Shaughnessy 1994; Shaughnessy et al. 1995). As the population has been expanding animals have moved into vacant areas both within and adjacent to sectors. This study incorporated the entire colony at Cape Gantheaume. During this study other breeding and haul-out sites on Kangaroo Island were also monitored for movement of tagged animals. However, monitoring of other sites was largely opportunistic due to time and logistical constraints.



Fig. 1. Location of Cape Gantheaume in relation to Kangaroo Island and the surrounding mainland.

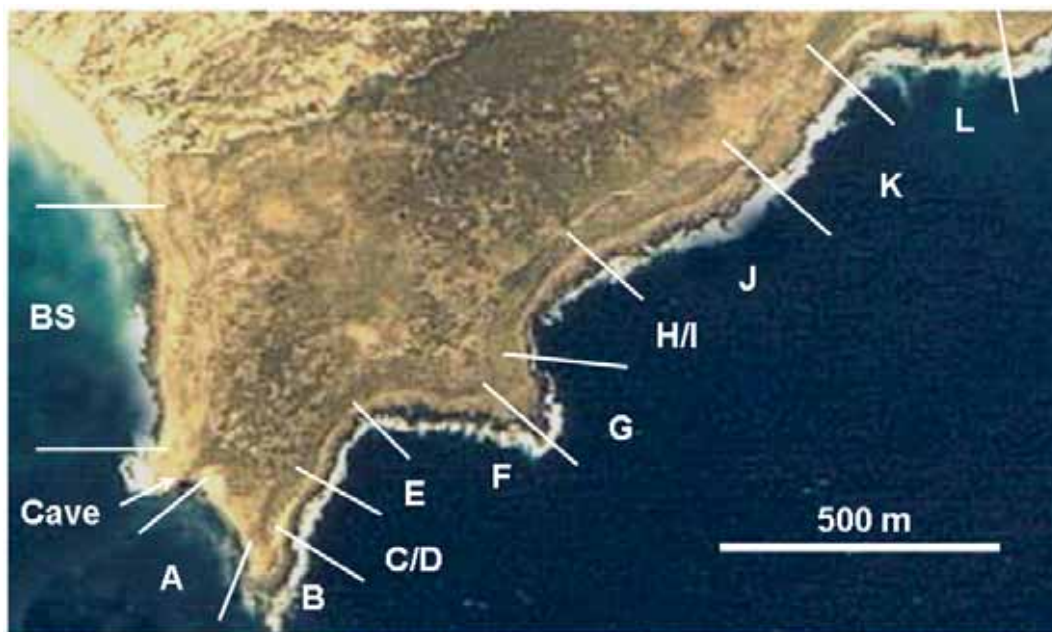


Fig. 2. Colony location at Cape Gantheaume and census sectors boundaries referred to in this study and used for mark-recapture estimates of pup abundance (Goldsworthy and Shaughnessy 1994; Shaughnessy et al.1995). The Beach Sector referred to by Shaughnessy (2006) is abbreviated as BS.

SUMMARY OF THE LIFE HISTORY OF NEW ZEALAND FUR SEALS

New Zealand fur seals give birth and mate between late November and late January with median pupping in mid to late December (Miller 1975b; Mattlin 1981; Goldsworthy and Shaughnessy 1994; Lalas and Harcourt 1995). Females give birth to a single pup and mate about 7 days later (Miller 1975b; Goldsworthy and Shaughnessy 1994). During the perinatal period females remain onshore for between 6-18 days before departing on their first foraging trip since hauling out to pup, although females may undertake very short trips of several hours during longer perinatal periods (McNab and Crawley 1975; Miller 1975b; Mattlin 1987; Crawley 1990; Goldsworthy and Shaughnessy 1994; Harcourt 2001). Like other fur seals, females regularly alternate between time ashore suckling their pups and foraging at sea to replenish milk and energy reserves (Stirling 1971; Miller 1975b; Bonner 1984; Gentry and Kooyman 1986; Harcourt et al. 1995; Lea and Hindell 1997; Mattlin et al. 1998; Haase 2005; Goldsworthy 2006). Females and pups return to the birth site or in close proximity to it throughout the lactation period (McNab and Crawley 1975). Females only tolerate their own pup and fostering appears to be rare (Miller 1971; McNab and Crawley 1975; Haase 2005). Pups are weaned between 8-11 months of age (Crawley 1975; Mattlin 1981; Haase 2005; Goldsworthy 2006), which is similar in length to other temperate fur seal species (Wickens and York 1997). Although pups are totally dependant on their mothers to provide milk over most of the lactation period (Gentry and Kooyman 1986), pups start to display independent foraging behaviour as early as 5-6 months of age (Baylis et al. 2005).

Females are present in the colony throughout the year with lowest numbers ashore in the two months immediately prior to the start of the breeding season (Stirling 1971; Miller 1975b; Goldsworthy and Shaughnessy 1994). Adult males may hold breeding territories for up to 63 days, during which time they fast (Miller 1975b; Troy 1997). Individual males may hold breeding territories for several seasons, while others never mate (Troy 1997). Juvenile and sub-adult males return to the breeding colony or adjacent haul-out areas during the breeding season and all three age classes, juveniles, sub-adults and adult males are present in variable numbers during the non-breeding season (Stirling 1971; Miller 1975b; Goldsworthy and Shaughnessy 1994). At some colonies adult males have been observed to display non-breeding season territoriality over the winter months (Troy 1997).

Data on age-specific patterns and rates of reproduction are limited. Sexual maturity is thought to occur between 4-6 years of age in females and between 5-9 years in males, based on gross examination of reproductive tracts (Mattlin 1978a; Dickie and Dawson 2003). Females are thought to first give birth as early as 5 yrs based on pregnancy data (Mattlin 1978a; Dickie and Dawson 2003) and males have been observed to first attempt to hold territories as young as 8 years (Troy 1997), although most are thought to delay first territory tenure until about 10 yrs (Mattlin 1978a). Dickie and Dawson (2003) reported an average pregnancy rate of 69% following examination of 51 reproductive tracts and Goldsworthy and Shaughnessy (1994) estimated an average reproductive (birth) rate of 67% based on observations of 30 marked females over three breeding seasons. Published estimates of survival are largely limited to the pre-weaning period (Miller 1974; Mattlin 1978b; Lalas and Harcourt 1995; Shaughnessy et al. 1995; Bradshaw et al. 2003). Troy et al. (1999) presented a minimum mean annual survival estimate for adult males (aged 7-15 yrs) of 0.76 based on 19 animals followed over 4-5 years. There are currently no published estimates for juvenile or adult female survival for this species. Reported maximum known ages are 22 for females and 15 years for males (Mattlin 1978a; Troy et al. 1999; Dickie and Dawson 2003).

Adult New Zealand fur seals display pronounced male-biased sexual size dimorphism (Miller 1975a), with territory males recorded to weigh up to 160kg (Troy et al. 1999) and females up to 69kg (Schulman 1996 in Wickens and York 1997). Birth mass varies considerably among locations and years, with mean mass ranging from about 4-6 kg in males and from 3-5 kg in females (Lea and Hindell 1997; Goldsworthy 2006). Although there are several studies on sex differences in pup growth for New Zealand fur seals (Crawley 1975; Mattlin 1981; Chilvers et al. 1995; Lea and Hindell 1997; Haase 2005; Goldsworthy 2006), age-specific data on the size and growth of older animals is limited. Several studies have presented morphological measurements of small numbers of adult males (Miller 1975a; Mattlin 1978a; Troy et al. 1999; Harcourt 2001) and females (Miller 1975a; Mattlin 1978a; Schulman 1996 in Wickens and York 1997; Goldsworthy 2006), but few have gathered sufficient samples of known-aged animals to allow for the modelling of sex-specific growth patterns. Troy et al. (1999) examined the relationship between age and size of adult males at the beginning of the breeding season but were limited by the narrow range of ages sampled. Dickie and Dawson (2003) presented growth models for females aged 1-22 years and some age-specific morphology data for males.

**CHAPTER 2. BEHAVIOURAL RESPONSES OF NEW ZEALAND FUR SEALS
(*ARCTOCEPHALUS FORSTERI*) TO DARTING AND THE EFFECTIVENESS OF
MIDAZOLAM AND TILETAMINE-ZOLAZEPAM FOR REMOTE CHEMICAL
IMMOBILISATION**



INTRODUCTION

Chemical immobilisation by dart is an established method used to facilitate the capture and restraint of otariid and phocid seals, particularly when working with large, dangerous or timid animals (see reviews by Gales 1989; Erickson and Bester 1993; Lynch et al. 1999). Injecting drugs remotely allows sedatives or anaesthetic agents to act with little arousal of the target animal, reduces disturbance of surrounding animals and lowers the level of stress and risk involved in physical capture and restraint (Lynch et al. 1999). Knowledge of species-specific drug responses and the selection of appropriate equipment and drug combinations have greatly reduced many of the side effects of chemical immobilisation reported in earlier studies, such as apnoea, thermoregulatory disturbance and overdose (e.g., Trillmich and Wiesner 1979; David et al. 1988; Mitchell and Burton 1991). The use of drug antagonists and respiratory stimulants to reduce the level and period of anaesthesia (e.g., Parry et al. 1981; Baker et al. 1988; Woods et al. 1995, 1996; Higgins et al. 2002), have also improved the safety of chemical restraint.

Despite the advances made in improving the safety of chemical immobilisation, remote injection of free-ranging seals is still considered high risk in comparison to hand injection of drugs following physical capture. Because the typical induction time for most immobilising agents delivered intramuscularly is 5-30 min (Erickson and Bester 1993), darted animals may escape to the water (e.g., David et al. 1988) and drown. Numerous authors (e.g., Lynch et al. 1999; Baker et al. 1990; Heath et al. 1996; Higgins et al. 2002) have stressed the importance of assessing and minimising this risk by developing an understanding of a species' response to darting and by careful selection of target animals. However, detailed reports of the behavioural reactions of seals to darting are scarce and few studies have reported on the fate of drugged seals that have entered the water.

The likelihood of a darted seal escaping to the water may depend on a number of factors, such as the flight response of a species or sex, time of year (e.g., breeding or non-breeding season), the physiological or behavioural state of an animal (e.g., resting or alert, ill or injured), experience of field personnel, the type of dart delivery systems and the type of drug used. Higgins et al. (2002) suggested that low impact dart systems were least likely to cause leopard seals (*Hydrurga leptonyx*) to flee. Similarly, Trillmich and Wiesner (1979) reported little response from Galapagos sea lions (*Zalophus*

californianus wolfebaeki) darted using a blowpipe (low impact), but of eight Galapagos fur seals (*Arctocephalus galapagoensis*) darted using the same system, two escaped to the sea (Trillmich 1983). In contrast, David et al. (1988) noted that adult male South African fur seals (*Arctocephalus pusillus pusillus*) were frequently frightened by the impact of the dart fired from a rifle (high impact) and several partially immobilised animals were netted at the water's edge or escaped to the sea.

The risk of a drugged animal drowning may depend on the drug used, dose administered and the animal's physiological state. Several drugs and drug combinations have been used for the remote immobilisation of pinnipeds with varying success (Gales 1989; Erickson and Bester 1993; Lynch et al. 1999).

Tiletamine-zolazepam (TZ) combinations have been used intramuscularly to facilitate immobilisation and restraint in a number of phocid and otariid species, both as a sole anaesthetic agent (Loughlin and Spraker 1989; Baker et al. 1990; Boyd et al. 1990; Phelan and Green 1992; Griffiths et al. 1993; Dabin et al. 2002; Higgins et al. 2002; Wheatley et al. 2006) and in combination with inhalation anaesthesia (Heath et al. 1996). Although the dose-response of otariids to TZ has been reported to be variable, induction and recovery following intramuscular injection are reported to be smoother, and with fewer side effects compared to other routinely used anaesthetic drugs such as ketamine (Stirling and Sjare 1988; Boyd et al. 1990; Dabin et al. 2002). However, respiratory depression has frequently been reported, particularly at higher dose rates (e.g., Loughlin and Spraker 1989; Boyd et al. 1990; Heath et al. 1996; Dabin et al. 2002) and the effects of TZ can only be partially reversed by the benzodiazepine antagonist flumazenil (Karesh et al. 1997 cited in Lynch et al. 1999; Higgins et al. 2002; Walzer and Huber 2002). Tiletamine-zolazepam has an advantage of being injected in small volumes, a rapid onset (~10 min) and a relatively wide safety margin, making it suitable for delivery by dart (Baker et al. 1990; Boyd et al. 1990). However, the use of TZ for darting free-range seal species is still considered risky because of its strong sedative effect and potential loss of essential body functions should drugged animals enter the water.

The benzodiazepine midazolam delivered intramuscularly, has been reported to produce light to moderate sedation in some seal species (Lynch et al. 1999).

Midazolam has been used alone (e.g., Lynch et al. 1999; Gales and Mattlin 1998; Bodley et al. 2005; Gales et al. 2005) and in combination with injectable anaesthetics (e.g., Woods et al. 1994; Higgins et al. 2002; Tahmindjis et al. 2003; Spelman 2004) to

sedate/anaesthetise seals. Midazolam has a wide safety margin and although slow acting (~ 30 min) the effect of midazolam can be reversed with flumazenil (Lynch et al. 1999; Tahmindjis et al. 2003). The main advantage of the use of midazolam in remote immobilisation of seals is that its relatively mild and transient sedative effect should allow animals to maintain sufficient coordination to swim and breathe should they enter the water.

The New Zealand fur seal (*Arctocephalus forsteri*) is typically flighty when it smells or sees humans and it inhabits rocky coastlines, making capture by hand held net difficult and dangerous. The average mass of adult females is 43 kg (Chapter 5; McKenzie et al. in press a) and adult males may weigh more than 160 kg during the breeding season (Troy et al. 1999). Although territory males stand their ground when approached by humans during the breeding season (Troy et al. 1997) they readily flee at other times of the year. Adult males cannot be captured and restrained manually without serious risk of injury.

During the course of demographic and foraging ecology studies on this species, over 500 animals were captured and anaesthetised to obtain body morphometrics and biological samples (blood, milk, postcanine tooth), apply identification marks (tags, bleach) and attach and remove instruments (satellite trackers, time depth recorders) (Page et al. 2005a; McKenzie et al. 2005a). Animals were also captured to remove marine debris (Page et al. 2004). Remote chemical immobilisation was used in situations where manual capture was risky (e.g., capture of adult males or capture on dangerous terrain) or when animals were exceptionally flighty (e.g., seals entangled in marine debris). Remote immobilisation was also used to reduce capture stress in animals used in satellite tracking and diving studies, because we believed it reduced adverse effects of capture on subsequent foraging behaviour and wariness on recapture. I evaluated the safety and efficiency of remotely immobilising animals with midazolam and tiletamine-zolazepam hydrochloride. Due to the flighty nature of this species two low-impact darting systems (a cross-bow and gas powered dart gun) were tested before being used to administer drugs, to assess the behavioural response of animals to darting and evaluate the likelihood of seals escaping to the water.

MATERIALS AND METHODS

Behavioural trial

The behavioural trial was conducted during the non-breeding season in winter 2000, at a large breeding colony situated at Cape Gantheaume (36°04' S, 137°28' E), on Kangaroo Island. Thirty adult females were darted with sterile water using a cross bow (Wildvet™, Lilydale, Australia) and a CO²-powered dart gun (Tranquil Arms Company, Melbourne, Australia). The cross bow fired a modified arrow (Wildvet™) approximately 30 cm long, which incorporated an air pressured syringe (1 cc) with an unbarbed 1.5 inch needle. The dart gun fired powder-charged darts (Tranquilarms Company., Melbourne, Australia), approximately 9 cm long (1 cc), with unbarbed 1.5 inch needles. A second brand of darts was used in subsequent captures (see below). Females were selected using the following criteria: (1) lying down, (2) no less than 5 m from the sea with (3) other seals present within a 10 m radius. Darting range of the cross bow was set at 25 ± 2 m, and at 8-22 m for the gas powered dart gun. Distance between the darter and target animal was determined by a range finder (Opti-Meter® 620, New York, USA).

The initial response of each target animal and the overall response of animals within a 10 m radius were classified and recorded as outlined in Table 1. Any changes in behaviour and movement (direction and distance) were then recorded for each target animal over the next 30 min. For each darting event the following were also recorded: presence or absence of a pup with target female, injection site, initial distance of darted animal from the sea and distance travelled following darting.

Midazolam immobilisation

After the behavioural trial, 22 adult females were darted with midazolam (Roche Products Pty. Ltd., Sydney, New South Wales) using the gas powered dart gun. Midazolam was supplied in crystalline form and reconstituted at 20 mg/ml in the laboratory prior to the trial. Each dart was filled with a standard volume of drug (1 ml) and dose rates were calculated following capture of animals. The response of these animals to darting was also recorded. Seals that appeared adequately immobilised were captured after 30 min using a hoop-net. Level of immobilisation on approach and capture was classified (Table 2) using a system adapted from Boyd et al. (1990).

Table 1. Initial response of target seals and others within a 10m radius.

Response	Definition	Intensity
Darted seal		
No reaction	Seal remained in original position, with little or no change in behaviour.	Low
Alert	Seal sat up in an alert posture and moved no more than 1m.	
Short flight	Seal immediately moved 1-5 m before settling in a sitting or lying position.	Moderate
Long flight	Seal immediately took flight and moved > 5 m from original location, but remained ashore.	Severe
Escape	Seal immediately took flight and entered the water.	
Surrounding seals		
No reaction	All seals remained in their original locations, displaying little or no response.	Low
Alert	Several seals immediately sat up in an alert posture and moved no more than 1m.	
Startled	Several seals immediately moved >5m before settling.	Moderate
Escape	Several seals immediately took flight and entered the water.	Severe

Table 2. Level and degree of immobilisation (adapted from Boyd et al. 1990).

Level	Response	Degree
0	No signs of the drug having had an effect.	
1	Some signs of uncoordinated movement but otherwise normal behaviour.	} Partial
2	Head down and unwilling to move, but still capable of locomotion when approached.	
3	Incapable of locomotion or substantial movement when approached and handled, but head movement possible.	Moderate
4	Completely immobile with regular breathing and response to needle stimulation.	} Complete
5	Completely immobile with irregular breathing, little or no response to needle stimulation but with corneal reflex	
6	Dead	

Tiletamine-zolazepam immobilisation

Due to the relatively light level of immobilisation induced by midazolam (see below) and the increased wariness of seals on recapture, a 1:1 mixture of tiletamine-zolazepam (Zoletil 100[®], Virbac Australia Pty. Ltd., Peakhurst, New South Wales) was used from winter 2001. An initial dose of 45 mg TZ for adult females and 100 mg for adult males was trialled and adjusted with experience and visual assessment of weight or previously recorded mass. The aim was to moderately immobilise seals (Level 3), allowing capture and restraint by net with minimal stress, but not to fully anaesthetise seals. Tiletamine-zolazepam was administered into the rump or shoulder when possible. The same make of gas powered dart gun as used in the midazolam and behavioural trial was used to fire 0.5 cc (female) and 1.0 cc (male) powder charged darts with 0.5 inch (female) and 1 inch (male) unbarbed needles (Pneu-Dart[®], Pennsylvania, USA). All females reported in the present study were lactating adults (> 5 yrs of age) and males were sub-adult or adults (> 8 yrs of age).

Following darting, seals' respiration depth (i.e. shallow or deep) and rate, level of coordination and tear secretion were monitored. Seals that appeared to be immobilised were approached and captured by hoop-net and immediately checked for reflexes and respiration. If an animal was still alert after 10 min, a second and in some cases third dart was fired. Animals showing some sign of uncoordination were given a supplementary doses of 25% of the original dose and those showing no sign of drug effect were given 100%. When a darted animal entered the water, the animal was observed using binoculars and followed until it either came ashore or resumed normal swimming behaviour.

Seals that required a greater level of anaesthesia or a longer period of immobilisation (> 15 min) were administered inhalation anaesthesia (Isoflurane[®] 0.5-5%; VCS, Artarmon, New South Wales) delivered from a closed circuit, low flow anaesthetic machine modified for use in the field, with an in-circuit vaporizer and soda lime CO₂ absorption unit (Komesaroff Small Animal Anaesthetic Machine, Medical Developments Australia, Melbourne, Victoria). In two cases where animals were not adequately immobilised remotely, a low doses of TZ was given intramuscularly (IM) following capture to assist in handling and placement of the gas mask. Sedated animals were weighed using a spring balance (50 kg \pm 0.1 kg or 200 kg \pm 1.0 kg; Salter, Melbourne, Victoria) and their dorsal standard length and axillary girth measured to the nearest centimetre with a tape measure. Each seal was individually marked using uniquely numbered flipper tags (Supertags[®], Dalton, Woolgoolga, New South Wales) and/or bleach marks (Clairol[®] Born Blonde 3).

Following capture, animals were continuously monitored for physical signs of level of anaesthesia and stress, including respiratory depth and rate, muscle tone in flippers and jaw, gum colour and capillary refill, palpebral reflex, eye position, iris appearance, and response to pain stimulus (e.g., pinching of the flippers). Capture during hot weather and during the middle of the day was avoided. If required, animals were kept cool by pouring water over their flippers and body. In the event of prolonged apnoea (greater than 1 min and no response to physical stimulus), hypoxia or respiratory and cardiac arrest the benzodiazepine antagonist flumazenil (Anexate[®], Roche Products Pty Ltd; 0.5 mg/5 ml), respiratory stimulant doxapram (Dopram-V[®], Hoechst Roussell; 20mg/ml), cardiac stimulant adrenaline (1:10 000; 0.1 mg/1 ml), and endotracheal tubes (10 and 14 mm diameter) were available. Following release all animals were monitored from a distance until they regained full coordination. Recovery times (time

between end of inhalation anaesthesia and animal sitting upright or lying but moving head freely) ranged from 2-55 min depending on the drug used, dose rate, period of inhalation anaesthesia and procedures undertaken. Detailed analysis of factors effecting recovery times is not included in the present study. Censuses of the study area were conducted every 3-4 days during the capture period, in order to record the location, reproductive status and condition of each animal captured. All research procedures were approved by the Animal Ethics Committees at La Trobe University and the South Australian Department for Environment and Heritage.

Data analysis

Because the initial behavioural response to darting was not affected by the solution injected, data from animals darted with water and midazolam (and later TZ) were pooled for analysis. Analysis of the movement and behaviour of females in the 30 min following darting was restricted to animals darted with water. Differences in the frequency of response categories in relation to dart delivery system, presence of a pup and sex of the target animal were investigated using 2-tailed Chi-square goodness of fit tests and Fisher's exact test (2-tailed). Responses were ranked according to intensity: 'no reaction' and 'alert' were pooled and ranked as low level responses, 'short flight' as a moderate response, and 'long flight' and "escape" were pooled and ranked as severe responses. Because 'short flights' were considered of lower risk in term of animals entering the water compared to 'long flights', low and moderate responses were pooled for some analyses.

The relationship between dose rate and level of immobilisation was investigated using Spearman's rank correlation. Differences in mean dose rate between levels and groups were tested using Student's *t*-tests. The Mann-Whitney *U*-test was used to test for differences in the level of immobilisation and dose rate between groups if the data were not normally distributed. The median value was used to summarise level of immobilisation across groups. The influence of physiological condition on dose-response was investigated by assigning animals to one of two condition categories, good or poor. For animals with available morphometric data, a body condition index (BCI) was calculated as the residual value of the linear regression between the logged body mass and standard body lengths. Animals with negative BCI values were considered to be in relatively poor condition compared to animals with positive values. Homogeneity of variances were tested using Levene's equality of variances *F* test and the Kolmogorov-Smirnov and Shapiro-Wilk tests were used to

determine whether data were normally distributed. Mean values are given with \pm standard deviation. Statistical analysis was performed using SPSS® (Version 10.0, SPSS Inc. 1999). Results were considered significant if probability values were below 0.05.

RESULTS

Initial behavioural response to darting

Of the 52 adult females darted during the combined behavioural and midazolam trial, 4% ($n = 2$) immediately reacted by fleeing to the sea. Alert (46%, $n = 24$) and short-flight responses (35%, $n = 18$) were the most frequent reactions (Fig. 1), and were not significantly different in occurrence ($\chi^2 = 0.86$, $df = 1$, $P = 0.355$). Females that were darted were 5-50 m from the water's edge, with most of them 20-25 m away. During a short-flight response the median distance females moved away from their original position was 2.5 m (range 2-5 m, $n = 18$) and during a long-flight response it was 20 m (range 10-25 m, $n = 6$). There was no correlation between the distance an animal fled and its original distance from the water (Pearson's $r = 0.286$, $P = 0.156$, $n = 26$), and the intensity (low-moderate vs. severe) of the response was not related to whether an animal was close to (5-20 m) or further away (> 20 m) from the water (Fisher's Exact test $P = 0.123$, $n = 52$). The direction of flight was typically in the direction of the sea (85%, $n = 22$), which was also the direction away from the darter. Three animals (11%) moved along the colony and one (4%) moved inland towards the darter.

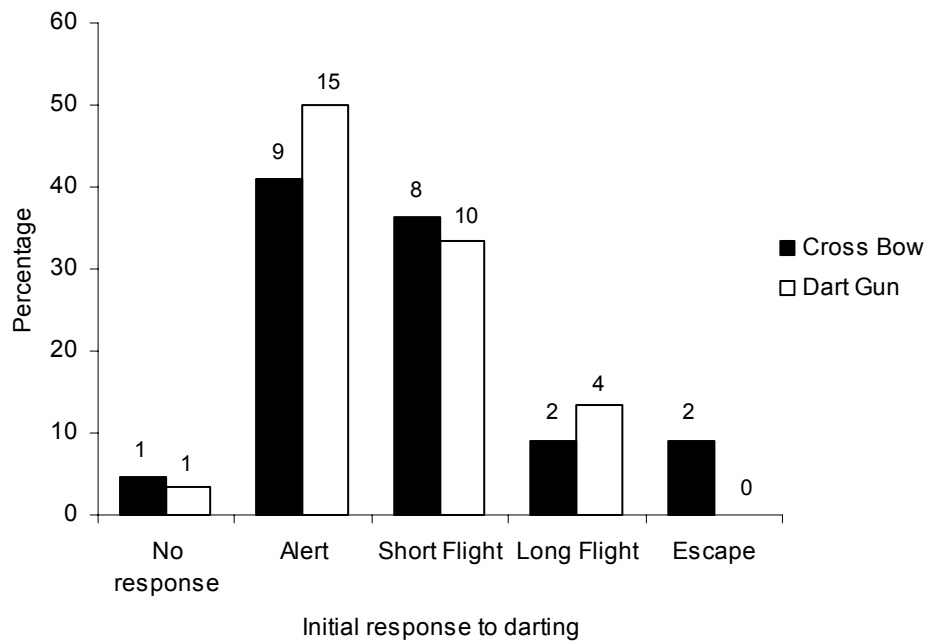
The two females that escaped to the sea were darted with sterile water using the crossbow. However, there were no significant differences (Fisher's Exact test $P = 0.708$, $n = 52$) between delivery systems (cross bow vs dart gun) in the intensity (low-moderate vs severe) of the responses observed (Fig. 1a). Both females that escaped were > 20 m from the sea nursing their pup with other seals nearby. In one case the arrow hit the animal's shoulder and stayed in for 5 m as the animal fled. In the second case the arrow hit mid-back, but bounced out. Both seals were darted on the same day which was sunny and hot with little breeze. Relatively high temperatures or painful hits may have agitated animals. All other shots were rump or side hits and occurred on relatively cooler days.

Of the females that were darted, 37 were with a pup (nursing or resting alongside) and 15 were alone. The intensity of the initial reaction to darting was not related to the presence or absence of a pup ($\chi^2 = 1.36$, $df = 2$, $P = 0.506$) (Fig. 1b). Of the females darted with water that remained ashore ($n = 28$), most (78.5%) stayed at their original location or moved back towards their original location within 30 min. Five females (18%) settled closer to the water or further alongshore and one (3.5%) went to sea after 12 min. Females with pups ($n = 16$) were typically reunited with their pup (75%). Two females (12.5%) went looking for pups that had moved off and two females settled without their pups (12.5%). Those females that returned to their original location, typically settled quickly.

The level of disturbance to surrounding animals was also low. Of the 52 animals darted, 50 had other seals present within a 10 m radius. Surrounding seals typically showed no reaction (78%) or displayed an alert response (14%) for a short period. Non-target animals only fled towards the water (8%) when a darted animal ran through the colony in a long-flight response.

The initial reaction of darted seals was recorded on 73 occasions (23 females and 50 males) when TZ was used. The initial reaction of females was similar to that observed in the earlier trial ($\chi^2 = 1.36$, $df = 2$, $P = 0.506$, $n = 75$). When results from all darting events were combined (Fig. 2) the frequency of low-moderate and severe responses did not differ significantly between sexes ($\chi^2 = 1.31$, $df = 1$, $P = 0.253$, $n = 125$). However, females displayed an alert response more frequently than no response compared to males ($\chi^2 = 10.69$, $df = 1$, $P = 0.001$, $n = 75$). Overall, 7% ($n = 9$) of animals reacted by immediately escaping to the water and 14% ($n = 18$) reacted severely (long-flight and escape).

(a)



(b)

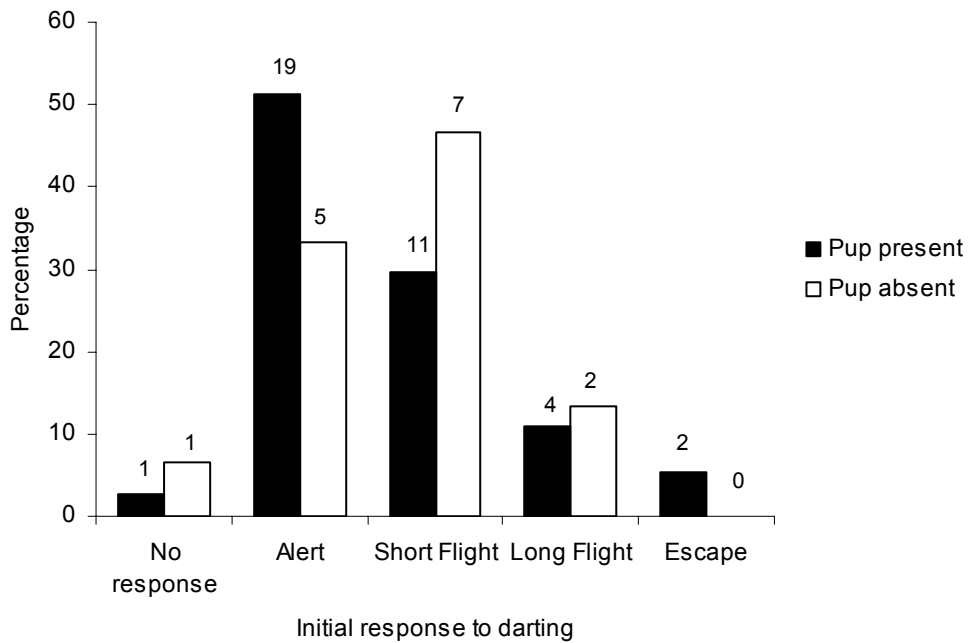


Fig. 1. Percent of initial responses to darting displayed by adult female New Zealand fur seals in relation to (a) the dart delivery system used (cross bow or dart gun) and (b) the presence of absence of a pup. Numbers above each bar indicate number of individuals.

Midazolam trial

Twenty-two adult females were darted with midazolam. Of these, only eight are considered in further analyses due to the failure of the other darts to inject. The level of immobilisation appeared to increase with dose rate (Table 3), with the relationship approaching significance for the dose range tested ($r_s = 0.655$, $P = 0.078$, $n = 8$). Of the eight animals darted, one reached level 3; four were level 2; one was level 1; and two level 0. Because most animals displayed low-intensity responses to darting, it was difficult to determine whether a seal was sedated or resting until it was approached. Animals that were level 1-2 became aroused when netted or disturbed by fleeing animals. No adverse effects of midazolam were encountered during immobilisation. However, during recovery animals were extremely uncoordinated and appeared restless and distressed. All females that were immobilised with midazolam had returned to their site of capture and were with their pups by the following day.

Table 3. Level of immobilisation reached for female New Zealand fur seals following a single dose of midazolam (mean \pm SD). Data are for animals of known mass.

Immobilisation level	Dose mg/kg	Range mg/kg	<i>n</i>
0	0.37 \pm 0.07	0.32 – 0.42	2
1	0.41	0.41	1
2	0.55 \pm 0.13	0.42 – 0.73	4
3	0.49	0.49	1

Tiletamine-zolazepam

There were 120 TZ darting events (35 females and 85 males) between 2001 and 2005. The initial dose of TZ delivered to females of known mass ranged from 0.86-2.37 mg/kg (mean 1.74 \pm 0.37 mg/kg, $n = 21$) and for males ranged from 0.90-1.89 mg/kg (mean 1.39 \pm 0.27 mg/kg, $n = 62$). For both sexes, the level of immobilisation reached following the first dart (Table 4, Fig. 3), was positively correlated to dose rate of TZ (females: $r_s = 0.738$, $P < 0.001$, $n = 20$; males: $r_s = 0.631$, $P < 0.001$, $n = 55$). However, for a given dose there was considerable variation in the level of immobilisation induced, particularly for males. At all degrees of immobilisation, the mean dose administered to

females was significantly greater than that administered to males (Partial immobilisation $t = 3.19$, $df = 36$, $P = 0.003$; Moderate: $t = 3.73$ $df = 21$, $P = 0.001$; Complete: $t = 3.88$, $df = 12$, $P = 0.002$).

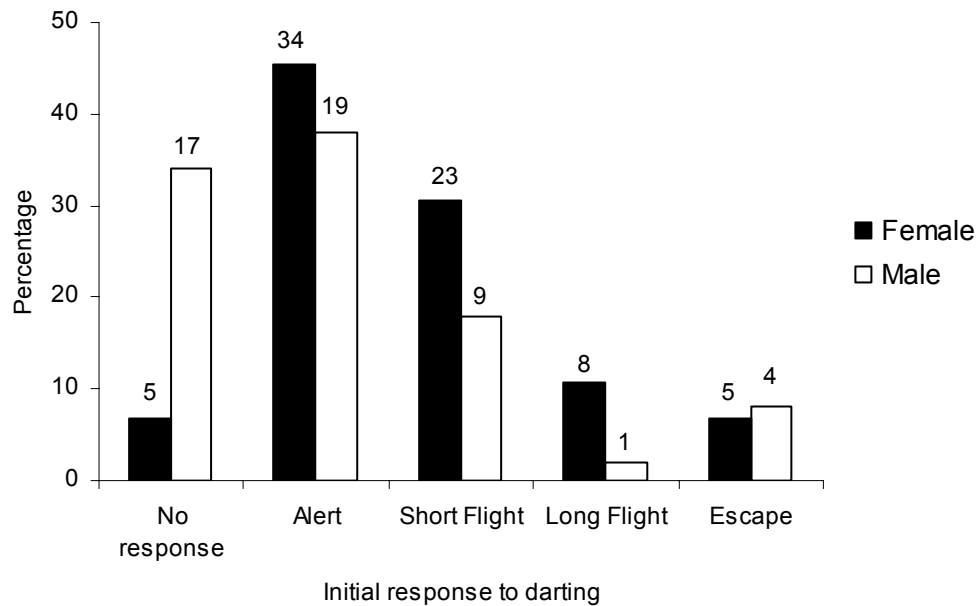
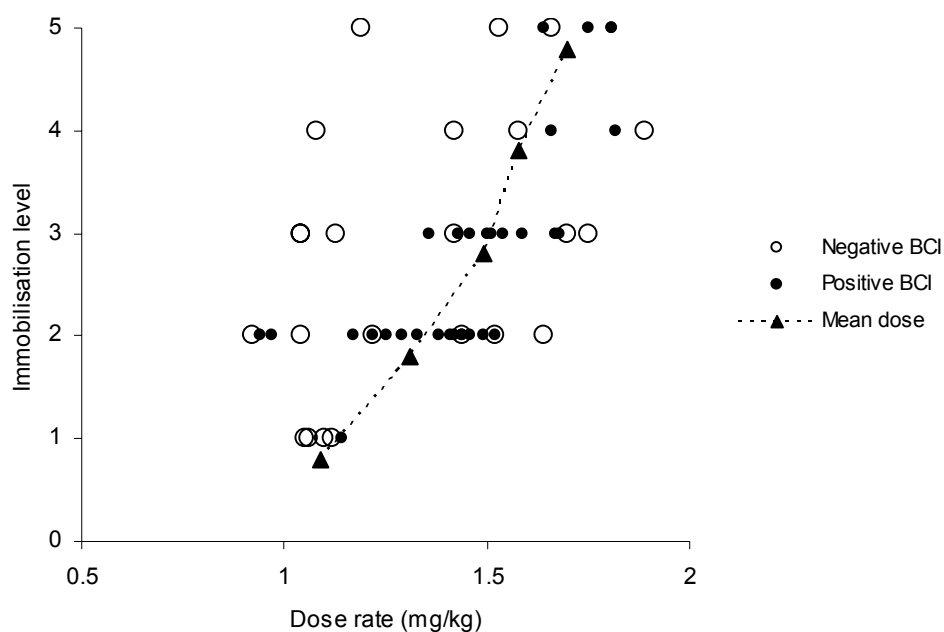


Fig. 2. Percent of initial responses to darting by New Zealand fur seals in relation to sex. Data are combined results from the behavioural trial and subsequent darting events using tiletamine-zolazepam. Numbers above bars indicate number of individuals.

Table 4. Level of immobilisation reached following an initial dose (mean \pm SD) of tiletamine-zolazepam for female and male New Zealand fur seals. Data are for animals of known mass and exclude animals that escaped immediately following darting.

Immobilisation level	Dose mg/kg	Range mg/kg	<i>n</i>
Females			
1	1.22 \pm .50	0.86 – 1.57	2
2	1.59 \pm 0.22	1.26 -1.88	10
3	1.87 \pm 0.18	1.71 -2.11	6
4	2.28 \pm 0.11	2.20 – 2.35	2
Males			
1	1.09 \pm 0.04	1.05 – 1.14	5
2	1.31 \pm 0.21	0.92 – 1.64	21
3	1.49 \pm 0.23	1.04 – 1.77	17
4	1.58 \pm 0.30	1.08 – 1.89	6
5	1.70 \pm 0.11	1.53 – 1.81	6

(a)



(b)

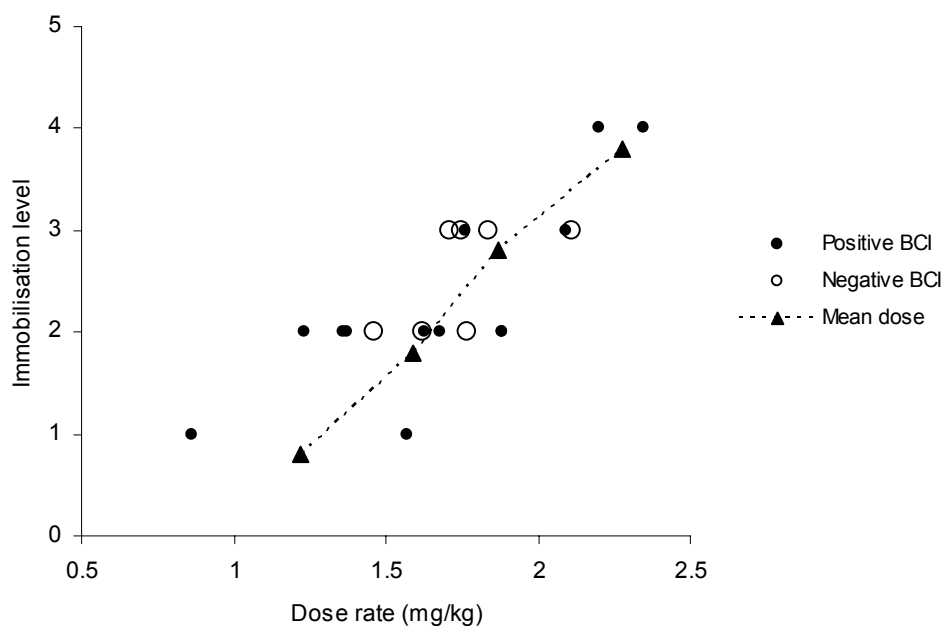


Fig. 3. The relationship between initial dose and maximal level of immobilisation reached for (a) male ($n = 54$) and (b) female ($n = 20$) New Zealand fur seals and the influence of relative body condition. Positive BCI indicates animals are in relatively good condition compared to those with negative BCI. Mean doses for each level of immobilisation are for all animals combined and include additional males for which BCI values were unavailable.

Body condition index

The level of immobilisation achieved did not differ significantly between males in relatively good body condition compared to those in poor condition ($U = 346.00$, $P = 0.848$, $n_1 = 31$, $n_2 = 23$). However, the mean dose required to immobilise males in relatively good condition (1.45 ± 0.23 mg/kg) was slightly higher than that required to immobilise those in poor condition (1.33 ± 0.27 mg/kg), with the difference approaching significance ($t = 1.762$, $df = 40.579$, $P = 0.086$ unequal variances). For males in good condition (Fig. 3a), the mean dose delivered increased significantly with increasing degree of immobilisation ($F = 21.744$, $df = 2$, $P < 0.001$). However, for males in relatively poor condition there was no significant relationship between dose and degree of immobilisation ($F = 1.979$, $df = 2$, $P = 0.164$, $n = 23$). For females, there was no significant difference between condition categories in the level of immobilisation achieved ($U = 34.50$, $P = 0.344$, $n_1 = 13$, $n_2 = 7$) or mean dose required ($t = -0.417$, $df = 18$, $P = 0.682$). However, the sample size of females in relatively poor condition (Fig. 3b) was small ($n = 7$).

Multiple darts

In 15 cases it was necessary to increase the dose delivered by using a second or third dart due to individual variability in dose-response, underestimation of dose, or incomplete injection. In cases where multiple darts were required, the initial dose and level of immobilisation induced were significantly lower than in cases where only a single dart was used (Females: dose $t = 3.79$, $df = 18$, $P = 0.001$; effect $U = 10.50$, $P = 0.001$, $n_1 = 11$, $n_2 = 9$; Males: dose $t = 3.21$, $df = 55$, $P = 0.002$; effect $U = 49.00$, $P < 0.001$, $n_1 = 44$, $n_2 = 12$). The mass of females immobilised with a single dart was significantly less than that of females immobilised using two darts ($t = -2.32$, $df = 18$, $P = 0.032$), indicating a conservative approach to dose rates in larger animals and/or underestimation of mass. In contrast, the mass of males that required multiple darts was not significantly different from that of males that were immobilised after a single dart ($U = 275.50$, $P = 0.994$, $n_1 = 46$, $n_2 = 12$).

Behaviour of drugged seals in the water

Of the 120 animals darted with TZ, 16 seals (6 females and 10 males) escaped to the water. Eight (7%) escaped immediately after they were darted, two (2%) were darted on the waters edge and entered the water following disturbance by other animals and six (5%) escaped when they were approached. Of the six animals (1 female and 5

males) that escaped when approached, three occurred when appropriate dose rates were being established and three were likely due to underestimation of mass.

Of the six females that escaped, two returned to shore within 1.5 hrs and were captured (one by net and the other by dart). One of the females had received 2.37 mg/kg, the highest single dose of TZ administered to a female. Following darting, the female began to show signs of immobilisation but was spooked by another animal, hit by a wave and entered the water 8 min after darting. On entering the water the female remained on the surface, and breathed regularly with jerky movements. The female moved alongshore for 1.5 hrs, until returning to land. When captured, the female was groggy and did not attempt to move away. Similar surface swimming behaviour was observed in a second female, which was darted with 1.89 mg/kg. The second female regained normal swimming behaviour about 50 min after darting and was then lost from view. Of the remaining four females, three were estimated to have received 1.40-1.42 mg/kg and the fourth a partial dose (< 1.89 mg/kg). All four females displayed normal swimming behaviour. The dose rates of females that escaped (range 1.20-2.37 mg/kg, mean 1.7 ± 0.43 mg/kg) were within the range of dosages administered to females that were partially to completely immobilised (Table 4).

Of the 10 males that escaped, five were recaptured within 1.5 hrs, one was captured the following day, and one was captured two days later. Of the three males that were not recaptured, one was previously marked and was observed alive the next day. The remaining two males were observed until normal swimming behaviour was regained by 60 min post-darting. The doses delivered to the five males that were of known mass ranged from 1.12 -1.63 mg/kg (mean 1.39 ± 0.21 mg/kg), which is within the dose range of partially to completely immobilised males (Table 4). Temporary depression of swimming behaviour was observed in males that escaped to the water following estimated doses of 1.40-1.69 mg/kg. The male with the highest dose (~ 1.69 mg/kg) escaped immediately after darting with 118 mg. On entering the water the male swam slowly at the surface, but held its head above the water and breathed regularly. After 15 min the male hauled out and moved inland before lying down and becoming completely immobile (Level 4). The male was immediately administered 5 ml of Anexate and recovered without any further complications.

On another occasion a large male went into the water immediately after darting with ~ 1.40 mg/kg. The male swam on the surface, predominantly on his back, raising his

head every 60-68 sec to breathe, and drifted alongshore. After 30 min his breathing became more frequent (every 40-48 sec) and head movement more controlled. At 45 min, the male was breathing every 28-24 sec and it commenced grooming, appearing similar in behaviour to other surrounding seals. At 60 min the male was lost from view.

Adverse effects and mortality

Most seals immobilised with TZ breathed regularly (82%, $n = 93$), but prolonged periods of respiratory depression or apnoea occurred in 20 (18%) cases following darting (3 female and 17 male). Fourteen (70%) cases occurred within 5-17 min of darting, five (25%) during Isoflurane anaesthesia and one (5%) during recovery. Respiratory depression and apnoea following darting were more common (89%, $n = 8$) in animals that reached immobilisation levels 5 and 4 (23%, $n = 3$), compared to animals that reached levels 3 (4%, $n = 2$) or 2 (4%, $n = 1$). The dose of TZ (including multidoses) administered to females that experienced respiratory depression, ranged from 2.20-2.77 mg/kg (mean 2.49 ± 0.29 , $n = 3$) and from 1.17-1.81 mg/kg (mean 1.51 ± 0.22 mg/kg, $n = 14$) for males. Additional incidents of respiratory depression may have been avoided by the administration of Anexate following capture ($n = 9$), as a precautionary measure in males that had been darted with 1.25-1.81 mg/kg TZ (mean 1.55 ± 0.20 mg/kg).

In two cases of respiratory depression, physical stimulation (pinching of flippers and gentle rocking) and supplementary oxygen delivered via a face mask was sufficient to induce regular respiration. In 14 cases animals were administered 2-15 ml (mean 5.5 ± 4 ml) of Anexate and regained regular respiration and gum colour. In four of these cases, animals were also administered 4-10 ml (mean 8.5 ± 5 ml) of Dopram. On one of these occasions, an adult male that had been darted with a relatively low dose of TZ (~ 1.17 mg/kg) was moderately immobilised (Level 3), but stopped breathing when netted. The seal was immediately intubated and Anexate (4 ml) and Dopram (5 ml) administered intravenously (IV). Supplementary doses of Anexate (5 ml) and Dopram (5 ml) were administered and artificial respiration maintained until spontaneous breathing was regained. Coordination was regained 1.5 hrs after darting.

Of the 120 animals darted four (3.3%) died (2 females and 2 males): two within 10 min of capture, one 30 min after capture during Isoflurane anaesthesia, and one during recovery. Of the two males that died, both doses of TZ were within the range that had moderately to completely immobilised males without complication (1.04–1.89 mg/kg).

One adult male reached level 5 within 5 min of darting with a relatively low dose of TZ (1.19 mg/kg). Anexate and Dopram were administered IV after which the male began to gasp. Although gum colour improved following intubation and artificial respiration, respiratory and cardiac arrest occurred within 20 min of darting. Administration of adrenaline and CPR were unsuccessful. The second male received a dose of 1.66 mg/kg and reached level 3 before capture, but died during Isoflurane anaesthesia from unknown causes.

Both adult females that died received multiple doses totalling 2.51 mg/kg and 2.77 mg/kg, which were within the range of multiple doses administered to moderately immobilised females without complication (2.44–2.96 mg/kg, $n = 3$). One female was darted twice (1.37 and 0.91 mg/kg), but was still mobile (Level 2) when netted and was given a supplementary dose of TZ (0.23 mg/kg) intramuscularly while physically restrained. Respiration quickly deteriorated and the female died. The second female was partially immobilised following two darts, totalling 2.77 mg/kg. Respiration was shallow but regular during Isoflurane anaesthesia and was normal during early recovery. However, respiratory and cardiac arrest occurred during recovery about 60 min after the first dart.

DISCUSSION

Risk of drugged animals entering the water and drowning

This study has demonstrated that by using TZ, free-ranging New Zealand fur seals can be effectively and safely immobilised using a dart gun, with low risks of animals escaping to the water and drowning. Although New Zealand fur seals are typically flighty, both females and males exhibited low to moderate behavioural responses to darting (Fig. 2). Reactions to darts fired from the cross-bow and the dart gun were similar (Fig. 1a), despite the larger size and weight of the arrows. Following the initial trial, the dart gun was chosen over the cross bow for further captures because of its wider shooting range and the benefit of using disposable darts. Disturbances to surrounding seals, which may have prompted darted seals to react more severely, were also low allowing work to be conducted in crowded and active areas of the colony. Following darting, seals typically resettled and most of those that initially moved away returned to their original location allowing immobilisation drugs to take effect with minimal agitation.

Of the 120 seals administered TZ, 16 (13%) escaped to the water. However, a large proportion of escapes occurred early in the trial period, while dose rates and protocols were being refined. Had all animals received an appropriate dose and target animals been selected more conservatively, the likelihood of a drugged animal escaping may have been closer to 8 in 120 (7% of animals). More importantly drugged animals that did escape to the water were able to maintain a reduced but effective swimming response.

Tiletamine-zolazepam caused moderate depression of swimming behaviour and respiratory function in animals that escaped to the water at doses of < 2.37 mg/kg, which would otherwise have induced moderate or complete immobilisation. Females that received 1.89-2.37 mg/kg and males that received 1.40-1.69 mg/kg, displayed a characteristic period of surface swimming with occasional sudden jerky movements before regaining normal swimming behaviour or hauling out on land. Normal swimming behaviour was typically regained within 30-60 min of darting, but other animals hauled out within 90 min in a moderate to heavily sedated state.

In the case reported by Trillmich (1983) of two Galapagos fur seals that escaped following darting, one was assumed to have drowned and the other was observed to breathe normally, but swam with jerky movements. Both seals received doses of ketamine-xylazine within the range administered to seals, which were effectively immobilised (Trillmich 1983). It therefore appears that at some dose rates the stimulus of the water and/or action of swimming reduces the immobilisation effects of some drugs, allowing seals to maintain sufficient respiration and swimming actions until anaesthetic agents are completely metabolised. In contrast, Heath et al. (1996) reported that two Steller sea lions (*Eumetopias jubatus*) drowned in rock pools following the darting of 51 adult females with tiletamine-zolazepam. Both females had fallen into small rock pools and inhaled water (Heath et al. 1996). However, dose rates for the two animals that died are not given and it is unclear to what degree animals were immobile before falling into or partially into the water. In the present study all animals that entered the water still had some level of mobility.

Although the long-term fate of six out of 16 seals that escaped is not known, no dead seals were observed washed up within the study area in the days or week following the incidents. Of these six animals, three did not appear to be affected in any way on entering the water and the remaining three appeared to regain normal swimming

behaviour before they were lost from view. All six animals had received doses lower than the maximum dose rates (females: 2.37 mg/kg and males: 1.69 mg/kg) of escapees that are known to have survived.

Midazolam

Data on the effectiveness of midazolam was limited; however the response of adult female New Zealand fur seals to the dose range trialled (0.32-0.73 mg/kg) was highly variable and did not facilitate capture nor appear to reduce capture stress. At the higher doses locomotion was moderately affected, but drugged seals were easily aroused by others during induction (~ 30 min), on approach and during capture. Although midazolam at doses > 0.2 mg/kg has been reported to produce moderate sedation in a number of pinniped species, facilitating capture and masking (Gales and Mattlin 1998; Lynch et al. 1999; Gales et al. 2005), the degree of sedation achieved was not adequate for procedures undertaken in the present study.

Problems during recovery associated with high doses of midazolam also prompted me to abandon the trial of midazolam in favour of TZ. Animals recovering from midazolam were less coordinated, appeared highly distressed, and were more likely to flee to the water before regaining full coordination. In addition to the immobilisation trial, 330 New Zealand fur seals (293 females and 37 males) were premedicated IM with midazolam (range 0.07-0.60 mg/kg) to assist with induction by Isoflurane, following physical capture and restraint. At doses of midazolam > 0.20 mg/kg, animals were extremely uncoordinated on recovery and appeared restless and distressed. Doses were gradually reduced to an average of 0.17 ± 0.05 mg/kg, resulting in a smoother and faster recovery (McKenzie unpublished data). Higgins et al. (2002) also reported similar differences in the level of coordination of leopard seals during recovery when comparing seals that were immobilised with Midazolam-Pethidine to those immobilised with TZ.

Tiletamine-zolazepam immobilisation

New Zealand fur seals were remotely immobilised effectively (Level 3) with a 1:1 mixture of tiletamine-zolazepam at a mean dosage of 1.87 mg/kg for adult females and 1.49 mg/kg for adult males. A mean dose of 2.28 mg/kg for females and 1.58 mg/kg for males completely immobilised (Level 4) animals and facilitated minor painful procedures, such as tagging and blood sampling. Most seals respired regularly, but occasional irregular breathing and periods of apnoea accompanied by cyanosis of the

gums occurred, particularly in animals that reached immobilisation levels 4 and 5. Physical stimulus and administration of Anexate and Dopram were generally sufficient to induce regular respiration. However, intubation and artificial respiration were required in four cases and four mortalities occurred.

Induction by TZ was predictable, smooth (uneventful) and short. Animals exhibited gradual loss of coordination and muscle relaxation, accompanied by increased tear production. Loss of coordination and excessive tear production was first noted around 5 min and maximum drug effect was observed between 10-15 min. Typically, induction under 6 min was indicative of an overdose. Determining the exact duration of induction was difficult because animals were typically inactive after darting. Monitoring of tear production and depth and frequency of respiration was critical in the detection of overdose or respiratory depression, particularly in animals that remained prone immediately following darting. Muscle relaxation induced by TZ progressed from the hind quarters to head, as observed by Loughlin and Spraker (1989) and Heath et al. (1996) for Steller sea lions. The reverse sequence occurred during recovery. Recovery was smooth and predictable, with animals appearing to regain full coordination before attempting to move away.

The level of immobilisation produced by TZ in both female and male New Zealand fur seals was positively correlated to dose, but variable, particularly in males (Fig. 3). Males appeared to be more sensitive to TZ than females, with lower doses required to achieve equivalent levels of immobilisation. Greater sensitivity to TZ (administered by dart) has been reported for male Antarctic fur seals (*Arctocephalus gazella*) and may relate to their lower mass-specific metabolic rate (Boyd et al. 1990). Some variation in dose response between individuals is also expected due to variation in dart placement and variable rates of drug absorption in tissue other than muscle (Lynch et al. 1999; Osofsky and Hirsch 2000).

The maximum level of immobilisation achieved and dose required may also be influenced by the physiological state of the animal and level of excitation prior to and during induction (Trillmich and Weisner 1979; Osofsky and Hirsch 2000). Some studies have suggested that animals in relatively good condition are more dose-sensitive and require lower doses than those in poor condition (Boyd et al. 1990; Dabin et al. 2000). The duration of recovery has also been linked to body condition and age of Southern elephant seals (*Mirounga leonina*) administered TZ intravenously, with recovery times

decreasing with increasing body condition and age (Field et al. 2002). In contrast, Wheatley et al. (2006) found no evidence for effects due to age or condition on recovery times of Weddell seals administered TZ intravenously. In the present study, I found no systematic pattern in the dose response of animals to TZ in relation to relative body condition. However, the response of males in relatively poor condition appeared to be less predictable than for males in relatively good condition and variation in dose-response due to other factors, such as drug absorption or partial injection may have masked any significant relationships. The period of fasting on shore or lactation before drugging may also influence individual drug responses (Woods et al. 1989), but were not controlled for in the present study.

Individual variation in the response to immobilising drugs has also been attributed to differences in the degree of activity and excitation of an animal prior to injection (Geraci 1973; Trillmich and Weisner 1979). During the course of my study, five adult females were administered 0.91-1.05 mg/kg TZ following net capture and physical restraint. Females administered TZ during physical restraint displayed greater variability to TZ, in comparison to females that were remotely injected. Maximal immobilisation reached for a given dose was higher in physically restrained seals, but was also highly variable and was not related to dose ($r_s = 0.112$, $P = 0.858$, $n = 5$). One of the five females injected following capture stopped breathing 8 min following administration of 0.93 mg/kg. The female was alert and resisted intubation, but her body was rigid and locomotion restricted. Apnoea continued for 10 min, despite manual stimulation and delivery of Anexate and Dopram. A second injection of Dopram stimulated gasping breaths, which became more regular and the female recovered and moved off 75 min after capture. The female was observed alive two days later. Complications also arose in two other cases where animals that were not adequately immobilised remotely were given additional low doses of TZ following capture. Although my sample size is small, these observations suggest that the dose response of animals that are chased and/or physically restrained prior to TZ injection may differ from that reported for remote injection.

The dose of TZ required to moderately immobilise female New Zealand fur seals (1.71-2.11 mg/kg) is similar to that recommended for the remote immobilisation of female Steller sea lions (1.8-2.5mg/kg: Loughlin and Spraker 1989) and Antarctic fur seals (1.58 mg/kg: Boyd et al. 1990), but higher than the dose reported for the immobilisation of physically restrained subantarctic fur seals (*Arctocephalus tropicalis*)

(0.9-1.3 mg/kg: Dabin et al. 2002). In contrast to the positive correlation between dose and effect observed for New Zealand and Antarctic fur seals (this study; Boyd et al. 1990), Dabin et al. 2002 found no relationship between dose and maximal effect in subantarctic fur seals, although in the later study TZ was administered during physical restraint rather than by remote injection.

In my study, animals that were not adequately immobilised by remotely injected TZ when netted were anaesthetised using Isoflurane. Although some animals required physical restraint, others could be masked through the net or through a special opening at the end of the net without the need for physical restraint. Isoflurane was used to augment the effect of TZ because it allowed good control of anaesthetic depth and rapid induction and recovery (Heath et al. 1996, 1997; Troy et al. 1997). Use of Isoflurane to augment the immobilisation and anaesthetic effect of TZ, rather than the use of TZ alone, reduced the total amount of injectable drugs required. Thus, many of the problems associated with higher doses of TZ, such as prolonged respiratory depression, apnoea and hyperthermia (Trillmich and Wiesner 1979; Loughlin and Spraker 1989; Boyd et al. 1990; Heath et al. 1996; Dabin et al. 2002) were uncommon.

Conclusion and recommendations

Tiletamine-zolazepam (1:1) at a mean dosage of 1.87 ± 0.18 mg/kg for females and 1.49 ± 0.23 mg/kg for males is recommended for the remote immobilisation of New Zealand fur seals. At these doses, induction and recovery are typically smooth and respiratory depression minimal. If further chemical restraint and analgesia are required, Isoflurane provides a safe and effective method of augmenting anaesthesia. I do not recommend the routine use of TZ for complete immobilisation due to the risk of severe respiratory depression and prolonged recovery.

Several improvements were made to the darting protocol over the course of this study and should be considered when developing darting and anaesthetic protocols for other seal species. Firstly, I highly recommend behavioural trials. The importance of prior experience and knowledge of factors influencing the behavioural reactions of age-sex classes to darting should not be underestimated. Second, the administration of additional TZ to increase the level of immobilisation following darting and capture should be avoided, due to unpredictable dose-response of physically restrained seals and the risk of excessive sedation. I recommend that care be taken when applying doses reported for remote injection to immobilisation of physically restrained animals.

Third, if complete (Levels 4 and 5) anaesthesia or increased duration of immobilisation is required, inhalational anaesthetic agents should be utilised when possible. In doing so the risks of respiratory depression and mortality associated with the use of higher doses of TZ may be reduced. Fourth, if complete immobilisation is induced by TZ, I strongly recommend the administration of Anexate before adverse effects become apparent. Finally, drugged animals that escape to the water should be monitored if possible until they regain normal swimming behaviour or return to land. Drugged animals that haul-out should be monitored in case of relapse, as a result of residual anaesthetic.

CHAPTER 3. ESTIMATION OF PREGNANCY RATES AND REPRODUCTIVE FAILURE IN NEW ZEALAND FUR SEALS (*ARCTOCEPHALUS FORSTERI*)

Published as: McKenzie J, Parry LJ, Page B, Goldsworthy SD (2005) ESTIMATION OF PREGNANCY RATES AND REPRODUCTIVE FAILURE IN NEW ZEALAND FUR SEALS (*ARCTOCEPHALUS FORSTERI*). *Journal of Mammalogy*: Vol. 86, No. 6 pp. 1237–1246

With kind permission of Journal of Mammalogy, Alliance Communications Group



INTRODUCTION

For long-lived mammals, adult female survivorship and fecundity are critical parameters in modelling population dynamics (Caughley 1980). Pregnancy rates represent the potential reproductive output of a population, but it is essentially reproductive failure prior to birth that ultimately determines reproductive rates. Understanding the extent and cause of reproductive failure in a population is therefore essential in accurately predicting population growth.

The New Zealand fur seal (*Arctocephalus forsteri* Lesson) is the most abundant fur seal species in the Australian-New Zealand region (Ling 1999). However, between the 18th and early 20th century, unregulated harvesting for the fur industry decimated populations throughout the region. Since the species' full protection in 1919, populations in Australia have rapidly recovered and are now recolonising their former range (Warneke 1982). In Australia, current population estimates based on pup counts, are about 57,400 (Goldsworthy et al. 2003). Despite their increasing abundance and growing importance as a major predator in the marine ecosystem, there is little quantitative data on key population demographic parameters such as pregnancy rates, fecundity and survivorship. As a result, population models for the species have been based on parameters calculated for other fur seal species (e.g., Goldsworthy et al. 2003).

In the absence of live birth data, many pinniped demographic studies estimate fecundity using pregnancy rates (e.g., Lima and Páez 1997; Wickens and York 1997). Most estimates of pregnancy in pinnipeds have been based on examination of reproductive tracts from culled or harvested animals, which provide accurate estimates of ovulation and pregnancy rates at the time of sampling. However, depending on the period of sampling, significant periods of reproductive failure may be overlooked (Testa 1987), over-estimating reproductive rates (Wickens and York 1997). Although reproductive failure is known to occur at different times in gestation (Craig 1964; Bigg 1969; Pitcher and Calkins 1981), qualitative data on the extent and timing of failures to term is rare. Pregnancy rates also vary between populations and years (Bowen, Capstick and Sergeant 1981; Boyd 1985; Laws and Sinha 1993; Wickens and York 1997).

The only pregnancy rate published for the New Zealand fur seal is 69%, which was derived from examination of reproductive tracts of seals caught as fisheries bycatch in New Zealand (Dickie and Dawson 2003). Full term pregnancy rates are expected to be lower, as animals were only sampled up until September (mid active gestation), after which foetal mortality is still expected to occur. It is not known however to what degree this pregnancy rate positively biases reproductive rates. The estimate may also be biased due to differences in the foraging grounds of pregnant and non-pregnant females and differential overlap with commercial fishing grounds (Dickie and Dawson 2003). Further estimates from other populations and years are needed as well as an understanding of the extent and timing of reproductive failure.

A number of non-destructive techniques for determining pregnancy have been developed and are used widely in other mammal species (Sasser and Ruder 1987; Arthur et al. 1996; Ropstad et al. 1999). These techniques include ultrasonic imaging and the measurement of serum progesterone. Concentrations of circulating progesterone during the reproductive cycle of most mammal species depend on the activity and life span of the corpus luteum (Short 1984). In the absence of fertilization or implantation, the corpus luteum regresses (luteolysis) and the secretion of progesterone decreases, allowing a new ovarian cycle to begin. In some species, the placenta may also secrete progesterone to the extent that the corpus luteum is no longer required for gestation (Heap and Flint 1984). Differences in circulating progesterone between pregnant and non-pregnant females therefore enable pregnancy to be detected.

Changes in circulating progesterone concentrations over the reproductive cycle have been measured in a number of seal species and have been shown to vary in relation to gestational stage (Daniel 1975, 1981; Raeside and Ronald 1981; Boyd 1983, 1984, 1991a, 1991b; Gardiner et al. 1996; Gales et al. 1997; Guinet et al. 1998). In otariids, progesterone concentrations are extremely low to undetectable following birth of the pup and for a few days prepartum, (Boyd 1991a, 1991b; Guinet et al. 1998), and increase rapidly just after ovulation (Boyd 1991a, 1991b). After conception, concentrations decrease, but remain detectable throughout embryonic diapause, increasing again just before implantation (Daniel 1975, 1981; Boyd 1991a, 1991b; Gales et al. 1997). The pattern of progesterone concentrations during active gestation (implanted gestation) is still unclear. After the implantation pulse, progesterone concentrations may decrease (Boyd 1991a, 1991b; Gales et al. 1997) for a period of

time until the corpus luteum and/or the developing placenta increases or maintains progesterone production (Boyd 1984, 1991b; Hobson and Boyd 1984; Reijnders 1990).

In non-pregnant females the corpus luteum remains active over a period equivalent to delayed implantation in pregnant females (Craig 1964). As a result, profiles of progesterone in pregnant and non-pregnant females are indistinguishable between ovulation and implantation (Guinet et al. 1998). After the implantation progesterone pulse, the corpus luteum is thought to decrease in progesterone secretion and regresses rapidly in the absence of a conceptus or failure of the conceptus to implant (Craig 1964). The overlap in progesterone concentrations after implantation will depend on the life span of the non-pregnant corpus luteum and/or the production of progesterone by the developing placenta. In the harbor seal (*Phoca vitulina*), embryonic diapause lasts 2-3 months (Daniel 1981, Reijnders 1990), but the luteal phase in non-pregnant females appears to last for 4-5 months after ovulation based on progesterone concentrations (Reijnders 1990; Gardiner et al. 1999). As a result, differences in progesterone concentrations between pregnant and non-pregnant females may not be detectable until 1-2 months after implantation.

Based on progesterone concentrations, pregnancy rates in the harbor seals were estimated to be 79% (Gardiner et al. 1996). Although pregnancy in females that did not give birth could not be confirmed, estimated pregnancy rates were similar to those reported elsewhere for the species (Gardiner et al. 1996). Guinet et al. (1998) used a similar method for determining pregnancy in culled South African fur seals (*Arctocephalus pusillus pusillus*). Pregnancy rates estimated from examination of reproductive tracts (79%) were similar to those estimated from progesterone concentrations (78.6%), although a small proportion of females sampled for progesterone were incorrectly classified as pregnant.

No work has been published on progesterone concentrations in the New Zealand fur seal or on the rate and timing of reproductive failure. The aims of this study were to (i) establish the patterns of serum progesterone concentrations in mature female New Zealand fur seals, over the early post-implantation period, when differences between pregnant and non-pregnant concentrations are expected to occur; (ii) develop a method for classifying pregnant and non-pregnant females based on progesterone profiles observed and use this method to estimate early active gestation pregnancy

rates; and (iii) estimate the timing and extent of reproductive failure in the females sampled based on observations of live births in the following breeding season.

MATERIALS AND METHODS

Population and study area

Samples were collected over three years (2000, 2001 and 2002) from live New Zealand fur seals at Cape Gantheaume (36°04' S, 137°28' E), Kangaroo Island, South Australia. Estimates of pup production since 1989 indicate the Cape Gantheaume population was increasing rapidly at approximately 16% per annum until 2000-2001 (Shaughnessy and Dennis 2003). In 2000-2001 estimates of pup production dropped by 23% to 1,640, but increased again in 2001-2002 to 2,141 and 2,163 in 2002-2003 (Shaughnessy and Dennis 2003).

Animal capture and sample collection

Individual seals were captured once during the post-implantation period, between May and August. Seals were captured using a hoopnet and sedated using 0.1-0.3 mg/kg IM Midazolam® (Roche Products Pty. Ltd., Sydney, New South Wales, Australia) or remotely immobilized using 1.5-2mg/kg Zoletil® (Virbac Pty. Ltd. Peakhurst, New South Wales, Australia) delivered by a dart gun (Taipan 2000, Tranquil Arms Company, Melbourne, Victoria, Australia). Animals were then restrained using gas anaesthesia (Isoflurane®, VCS, Artarmon, New South Wales, Australia) and individually marked using numbered flipper tags (Supertags®, Dalton, Woolgoola, New South Wales, Australia) and/or bleach marks. A 10 ml sample of blood was collected from the caudal gluteal vein using a non-heparinized syringe and transferred into two 6 ml serum clot activating tubes (Venoject®, Terumo Europe, Leuven, Belgium). Blood samples were allowed to sit for 8–12 hrs until clotted. Serum was then collected and frozen at –20°C until analysis. All research was performed in an ethical manner, following the ASM guidelines (Animal Care and Use Committee 1998), and approved by La Trobe University and South Australia's Department for Environment and Heritage animal ethics committees.

Reproductive cycle

The 12 month reproductive cycle of the New Zealand fur seal population studied is depicted in Fig. 1. Pups are born over a two-month period, between mid November and late January (Chapter 6; McKenzie et al. 2005b). Females come into oestrus

approximately seven days postpartum (Goldsworthy and Shaughnessy 1994), after which females enter a period of delayed implantation (Boshier 1981; Crawley 1990; Riedman 1990; Boyd 1991b). Implantation is thought to occur four months later (Daniel 1981; Riedman 1990) in early May, and active gestation is estimated to last for eight months (Daniel 1981). Lactation occurs throughout most of the gestation period (approximately 10 months, Goldsworthy 1992). In order to determine the pattern of progesterone concentrations during active gestation, gestational stage was standardized by expressing sampling date as the number of days prepartum. Because progesterone concentrations were expected to increase over the active gestation period, the sample period was divided into four 26 days blocks, which represented four stages in active gestation (Table 1). For females that did not give birth to a pup, gestational stage was estimated based on the median birth date for the population (26 December). The median date of birth was calculated according to Caughley (1980) based on twice-daily counts of pups over the breeding season.

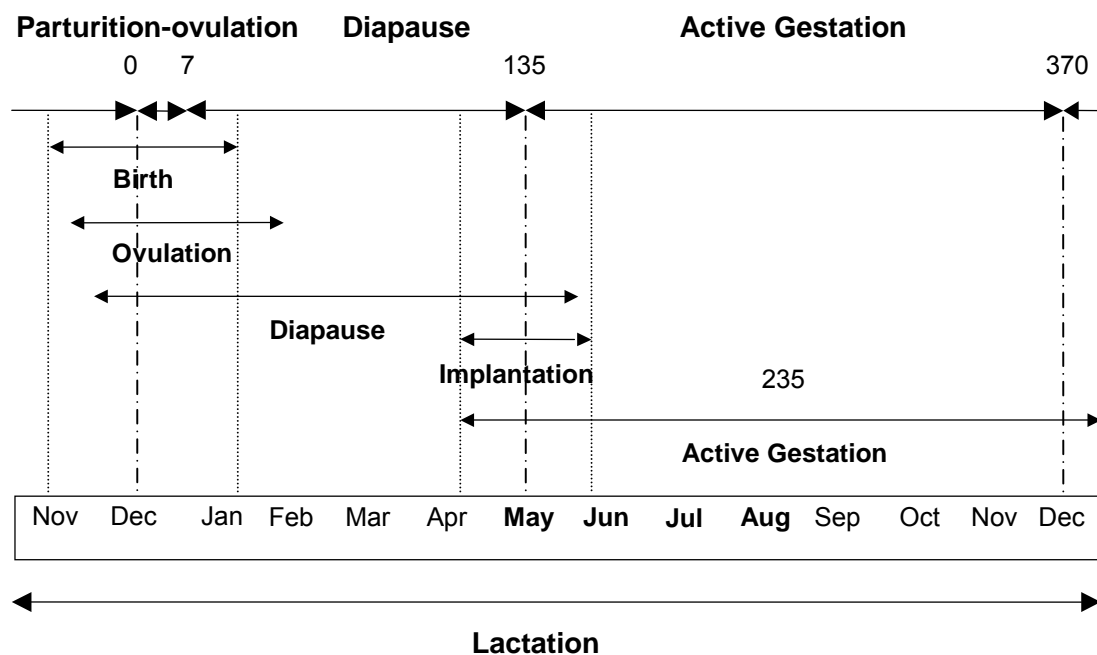


Fig. 1. Reproductive cycle of the New Zealand fur seal at Cape Gantheaume, Kangaroo Island, South Australia, indicating the estimated number of days since parturition at which ovulation, implantation and the following birth occur. Blood samples were taken May-August.

Table 1. Number of individual adult New Zealand fur seals sampled during each gestational stage of 26 days duration and the number that subsequently gave birth (“pupped”) and those that did not (“no pup”).

Gestation stage (Days prepartum)	Month	Active gestation stage	2000		2001		2002		Total	
			Pupped	No pup	Pupped	No pup	Pupped	No pup	Pupped	No pup
I (234-209)	May	Post-implantation			9	10			9	10
II (208-183)	June	Mid 1st trimester		3	14	13	2	2	16	18
III (182-157)	July	Late 1st Trimester	6	13	14	7	29	17	49	37
IV (156-131)	August	Early 2nd Trimester	3	10	2		2		7	10
Total			9	26	39	30	33	19	81	75

Reproductive classifications

Females were classified as sexually mature if they were lactating (milk manually expressed) when captured, or observed nursing a pup in the season of capture or following breeding season. Females not observed with a pup were classified as mature if they were within the size range of other mature females. Females were classified as resident if they were observed with a pup at the study colony in at least one year of the three-year study. Reproductive status was determined by resighting females during twice-daily censuses of the colony, in the breeding season following sample collection. Females were classed as having been pregnant if they were observed with a newborn pup or of unknown pregnancy status if they were not observed with pup. Resident females not observed during a breeding season but observed in subsequent seasons were considered not to have given birth for the season they skipped (Testa 1987; Boyd et al. 1995). The probability of resighting a tagged resident female given she was alive was 0.99 ± 0.01 SE (Chapter 6). The frequency of censuses ensured that pups that died at birth or shortly after birth were not missed; 94% of pups were observed within a day of birth and all others within a week of birth, therefore the accuracy of reproductive status based on resights should be high.

For the purpose of this study, reproductive failure is defined as the failure of a sexually mature female to give birth to a live pup. Two types of reproductive failure are defined following Craig (1964): missed pregnancies and failed pregnancies. Missed pregnancies include failure to ovulate, conceive or implant. Failed pregnancies are implanted pregnancies that are resorbed or aborted. Pregnancy rates were calculated as the estimated number of females that implanted and were pregnant at the time of sampling, divided by the total number of females sampled. Only resident mature females were used in the pregnancy analysis. Reproductive rates were calculated as the proportion of adult females sampled in each year that gave birth to live pups.

Radioimmunoassays

Serum progesterone concentrations were measured in duplicate in three assays, using coated-tube radioimmunoassay kits developed for progesterone measurement in human serum (Spectria[®], Progesterone RIA, Orion Diagnostica, Espoo, Finland). In order to increase assay specificity and ensure measurements coincided with the steepest portion of the standard curve, serum samples were extracted in ethyl acetate and diluted following extraction with MilliQ water (1:4) before assay. A single 750 μ l aliquot of each serum sample was added to 8 ml ethyl acetate (analytical research

grade) and vortexed for 10 min. To allow organic and aqueous layers to separate, extractions were left to stand at room temperature for 10 min. Tubes were placed in a mixture of dry ice and ethanol to freeze the aqueous layer. The organic layer was decanted, placed in a water bath at 35 °C and dried down under a stream of filtered air. Extracts were resuspended in MilliQ water and diluted 1:4. Addition of a known amount of tracer (labelled ligand) to male serum gave an extraction efficiency of 79.57%.

Assay procedure

A 50 µl aliquot of each diluted extract and standards were added to the polyclonal (rabbit) progesterone antibody coated assay tubes and incubated with 500 µl ¹²⁵I-labelled progesterone, at room temperature for 2 hrs. Following incubation assay solutions were decanted and the radioactivity in the antibody-coated tubes counted for 3 min. Non-specific binding tubes were also included in each assay and were under 1% of the total counts for each assay.

Validation of the radioimmunoassay

The sensitivity of the assay, determined as the lowest standard that differed from the zero standard by twice the standard deviation was 0.2 ng/ml. Juvenile male New Zealand fur seal serum gave concentrations of progesterone below the sensitivity of each assay. Two solvent blanks (ethyl acetate) also gave values below the sensitivity of each assay. In each assay a duplicate sample of juvenile male serum was used as a quality control low (QCL) and the 10 nmol/L standard provided with the kit was used as a quality control high (QCH). The QCH was repeated three times in duplicate in each assay to assess assay drift. The inter-assay coefficient of variation was 6.2% QCH and 3.4% QCL (*n* = 3 assays). The mean intra-assay coefficient of variation was 4.2% for the QCH. Specificity was investigated in two ways: 1) known amounts of progesterone (kit standards) were added to male fur seal serum and measured directly without extraction and again following extraction and dilution (1:4), and 2) a female serum sample with known high progesterone concentration (9.7 ng/ml) was serially diluted in assay buffer at 1:1, 1:2, 1:4 and 1:8 and the dilution curve examined for parallelism with the standard curve.

Statistical analyses

Analysis of covariance was used to compare recovery curves and test for similarities in slope. Because samples were not collected in every active gestational stage in each year, data were pooled across years. Changes in progesterone concentrations over the four active gestation stages (Table 1) were examined using analysis of variance. A Tukey-Kramer post hoc test for unequal sample sizes (Zar 1996) was used to test for mean differences in progesterone concentrations between gestational stages.

Because sample sizes for separate stages in active gestation were insufficient to allow statistical analysis of differences between groups, data for stages I and II and for stages III and IV were combined. Student unpaired t-tests were used to test for differences in progesterone concentrations between combined gestational stages within and between each group. Values are given as mean \pm 1 SE. Differences in pregnancy rates, reproductive rates and classes of reproductive failure between years were analysed using chi-square analysis. Because counts of missed pregnancies were too small to analyse for differences between years and there was no significant difference in observed reproductive rates between the two years ($\chi^2 = 0.41$, d.f. = 1, $P = 0.52$), data from 2001 and 2002 were combined. A probability level of 0.05 was used as the upper limit of significance.

RESULTS

Validation of progesterone assay

The log transformed recovery curve of standards in male fur seal serum was parallel ($F_{[1,6]} = 1.75$, $P = 0.24$), but significantly elevated above the standard curve in human serum ($F_{[1,7]} = 35.45$, $P = 0.001$), suggesting some degree of non-specific binding of seal serum to the antibody. Specificity was improved by extraction and dilution of the seal serum ($F_{[1,6]} = 0.03$, $P = 0.88$). The relationship between progesterone recovered and that added was significantly linear ($P < 0.05$) for standards added to male fur seal serum ($y = 0.995x + 0.022$, $R^2 = 0.90$, where y = amount of progesterone recovered, x = amount of progesterone added) and for kit standards prepared in human serum ($y = 0.993x + 0.005$, $R^2 = 0.99$). Parallelism between kit progesterone standards and progesterone in fur seal serum was also demonstrated by serial dilution of a sample from a known pregnant female. The slope of the regression between percentage binding and log of the expected progesterone concentration was parallel to the standard curve ($F_{[1,5]} = 2.97$, $P = 0.15$) and not significantly elevated ($F_{[1,6]} = 4.23$, $P = 0.085$).

Progesterone profile over early active gestation

Of the 156 blood samples collected from resident adult females, 81 were from females that gave birth (known pregnant) and 75 were from females that did not give birth (unknown pregnancy status) (Sizes of samples analysed for each gestational stage are given in Table 1.). As there were no significant differences in progesterone concentrations between years, when sampling block was taken into consideration, for females that gave birth ($F_{[2,75]} = 0.20$, $P = 0.82$) or for females that did not give birth ($F_{[2,69]} = 0.16$, $P = 0.86$), data from the three years was pooled for each gestational stage.

Progesterone concentrations in females that subsequently gave birth varied significantly over the four active gestation stages ($F_{[3,77]} = 6.25$, $P = 0.001$) (Fig. 2). Mean progesterone concentrations were relatively low and not significantly different ($t = 1.94$, d.f. = 23, $P = 0.065$) between the post-implantation and mid first trimester stages and increased significantly ($t = 2.59$, d.f. = 63, $P = 0.012$) towards the end of the first trimester. The mean progesterone concentration during the combined post-implantation and mid first trimester period was 8.62 ± 0.97 ng/ml (range 3.03 – 20.34 ng/ml, $n = 25$), significantly lower ($t = 4.09$, d.f. = 79, $P = 0.000$) than the progesterone concentration observed in females during the combined late first trimester and early second trimester period (14.87 ± 0.92 ng/ml, range 2.59 – 29.85 ng/ml, $n = 56$). The overlap in the range of concentrations between the two gestation periods is due to a few low values of progesterone at the beginning of the late first trimester period. For females that did not give birth to a live pup, progesterone concentrations did not vary significantly over the four early active gestational stages ($F_{[3,71]} = 1.59$, $P = 0.2$; Fig. 2).

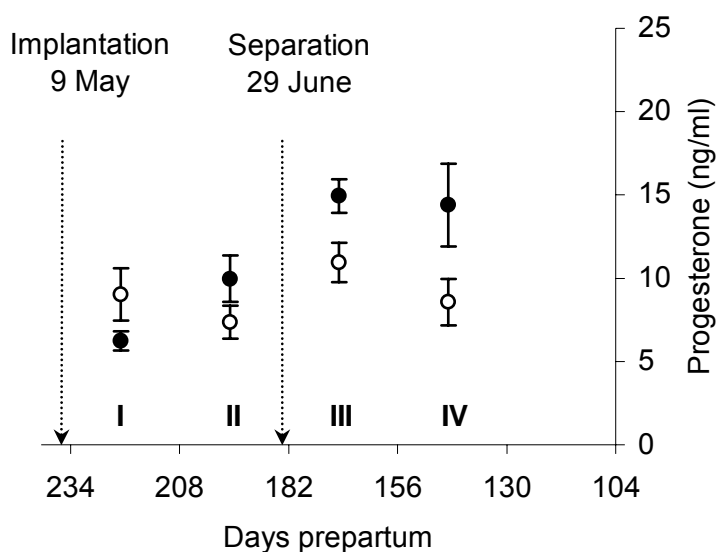


Fig. 2. Serum progesterone concentration at each gestational stage, over days prepartum of female New Zealand fur seals that did not subsequently give birth (○, $n = 75$) compared to females that did (●, $n = 81$), shown as mean \pm SE. Differences in progesterone concentrations between the two groups appears to occur by 29 June.

Over the combined post-implantation and mid first trimester period there was no significant difference in the mean progesterone concentration measured in females that gave birth and those that did not ($t = 0.53$, d.f. = 51, $P = 0.60$). However, progesterone concentrations in females that subsequently gave birth were significantly higher than in females that did not, during the combined late first trimester and early second trimester period ($t = 3.3$, d.f. = 101, $P = 0.001$). Differences in progesterone concentrations were apparent between the two groups around 180 days prepartum (Fig. 2); about 1.5 months after implantation. In terms of the average reproductive cycle, this separation in progesterone concentrations is estimated to have occurred by 29 June (Fig. 1). Elevated progesterone concentrations in pregnant females that did not subsequently give birth may mask any earlier decrease in progesterone concentrations in non-pregnant females. June 29 is therefore likely to be a conservative estimate.

Pregnancy rates

Given the observed profile of serum progesterone concentrations, it is reasonable to suggest that progesterone concentrations in females sampled after 29 June may be used to predict pregnancy. The lowest progesterone concentration for a female sampled after 29 June that subsequently gave birth was 6 ng/ml. This value was taken as the minimum concentration of serum progesterone required to maintain pregnancy during the early active gestation period.

Using the criterion above, of the 110 females sampled after 29 June (35 in 2000, 23 in 2001 and 52 in 2003), 85.5 % ($n = 94$) were diagnosed as pregnant and 14.5% ($n = 16$) as either non-pregnant, having failed to implant, or aborted prior to 29 June (missed pregnancies). All adult females that missed pregnancies were considered to have ovulated as all of their progesterone concentrations were above those measured in juvenile females. Pregnancy rates after 29 June varied between years, with rates lowest in 2000 (68.6%) and increasing in 2001 (86.9%) and 2002 (96.2%) (Fig. 3). Observed reproductive rate the following breeding season reflected the same trend with 25.7% giving birth to a live pup in 2000-2001, 56.5% in 2001-2002 and 63.5% in 2002-2003 (Fig. 3). The variation in reproductive rates between years was significant ($\chi^2 = 12.42$, d.f. = 2, $P = 0.002$).

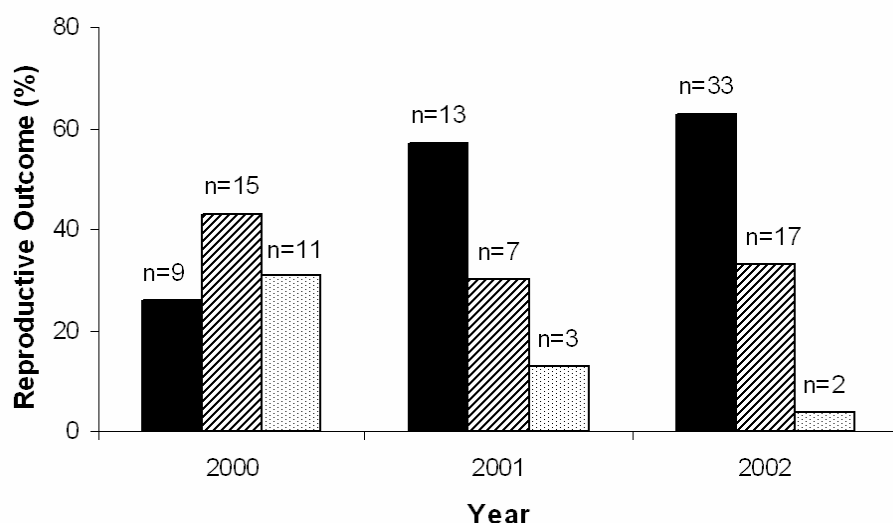


Fig. 3. Variation in reproductive outcome of female New Zealand fur seals sampled. Percentage of full term pregnancies (black bars) compared to failed pregnancies in mid to late active gestation (diagonal lines in bars) and missed pregnancies (light grey bars). Numbers of females in each category are indicated for each year.

Reproductive failure

Overall 29% ($n = 16$) of reproductive failure occurred by early active gestation and 71% ($n = 39$) by the pupping season. The observed reproductive rate in the 2000-2001 breeding season (25.7%) was significantly lower than both the 2001-2002 and 2002-2003 breeding seasons ($\chi^2 = 5.59$, d.f. = 1, $P = 0.018$ and $\chi^2 = 11.94$, d.f. = 1, $P = 0.000$ respectively). In 2000, 62.5% of females estimated as pregnant failed to carry pregnancies to term. In 2001 and 2002, 35% and 34% of pregnant females failed to carry pregnancies to term.

In the year before a season of high reproductive rate (2001 and 2002), when pregnancy rates were high (93.3%), failed pregnancies in mid to late active gestation accounted for 82.8% of reproductive failure, significantly higher ($\chi^2 = 12.45$, d.f. = 1, $P = 0.000$) than missed pregnancies (17.2%) (Fig. 3). In the year before a season of low reproductive rate (2000), pregnancy rates were low (68.6%) and pregnancy failure in mid to late active gestation contribute to 57.7% of reproductive failure, not significantly different ($\chi^2 = 0.62$, d.f. = 1, $P = 0.43$) to the number of missed pregnancies (42.3%) (Fig. 3). Therefore, the pattern of reproductive failure was also significantly different in the year of low observed reproductive rate compared to the years of higher observed reproductive rate ($\chi^2 = 4.18$, d.f. = 1, $P = 0.041$).

Previous reproductive history

Of the 110 females tested for pregnancy, 103 were known to have given birth in the breeding season before sampling as they were lactating on capture or were observed nursing a pup. Of the seven females for which previous reproductive history could not be confirmed, four were diagnosed as pregnant and gave birth in the following season, one aborted in mid to late gestation, and two missed pregnancies.

DISCUSSION

Progesterone profile

Progesterone concentrations in females that successfully gave birth, increased significantly approximately 1.5 months after implantation and remained elevated for at least the following 1.5 months (until early in the 2nd trimester). Elevated progesterone concentrations during the early to mid active gestation period in pregnant New Zealand fur seals were similar to concentrations measured in studies of pregnant South African fur seals (Guinet et al. 1998), Antarctic fur seals (*Arctocephalus gazella*) (Boyd 1991a)

and the northern fur seal (*Callorhinus ursinus*) (Daniel 1975, 1981). In contrast, progesterone concentrations in females that did not give birth remained at the lower immediate post-implantation concentrations. This suggests that the corpus luteum of pregnancy increases in progesterone production soon after post-implantation and/or the developing placenta contributes to circulating progesterone.

The facility of the corpus luteum to produce progesterone depends on its health and life span (Johnson and Everitt 1995). There are only two studies on reproductive tract anatomy of the New Zealand fur seal. Dickie and Dawson (2003) concluded that the anatomy and development of the ovaries and corpus luteum were similar to that of other pinniped species, but provided no information on the timing of regression of the corpus luteum. In a pregnant female sampled in August, Mattlin (1978a) found a corpus luteum in the ovary associated with the foetus. The corpus luteum was larger than that found in females sampled in January; however there is no mention of the condition of the corpus luteum. In October a non-pregnant female was sampled and no corpus luteum was found.

In the northern fur seal, the corpus luteum of pregnancy increases in size after implantation (Craig 1964), which is accompanied by increasing progesterone concentrations (Daniel 1975, 1981). By three months post-implantation, the corpus luteum has begun to regress (Daniel 1975, Yoshida et al. 1978), suggesting that the placenta probably secretes progesterone to maintain pregnancy to term. This has also been suggested for other pinniped species (Boyd 1984; Hobson and Boyd 1984; Reijnders 1990; Laws and Sinha 1993). In the subantarctic fur seal, (*Arctocephalus tropicalis*) and South African fur seal (*Arctocephalus pusillus pusillus*), the corpus luteum of pregnancy also increases in size after implantation, but does not appear to regress until 1-2 month before parturition (Bester 1995; Odendaal et al. 2002). The size of the corpus luteum however, may not reliably reflect secretory activity (Bester 1995). In the process of regression, luteal tissue undergoes vacuolisation and invasion by connective tissue, which may result in little change in size although its steroid hormone production is affected (Craig 1964).

In non-pregnant fur seals or females that fail to implant, the corpus luteum is thought to decrease in progesterone secretion and regresses rapidly shortly after implantation (Craig 1964). In my study any decrease in progesterone concentrations due to luteolysis in non-pregnant females or females that failed to implant would be masked,

as a large proportion of females that did not give birth were most likely pregnant at the time of sampling (aborting later in gestation). In non-pregnant northern fur seals the corpus luteum is also regressing by three months post-implantation but appears smaller than the regressing corpus luteum of pregnancy (Craig 1964). This was also the case for females that had aborted or resorbed pregnancies shortly after implantation (Craig 1964). In the process of luteal regression, luteal cell loss does not occur until after the corpus luteum loses its capacity to synthesize and secrete progesterone (Niswender et al. 2000). This suggests that a decrease in progesterone secretion by the non-pregnant corpus luteum may occur shortly after the implantation pulse and sooner than any drop in the regressing pregnant corpus luteum.

I cannot separate increases in progesterone concentrations due to increased production of progesterone by the corpus luteum from that potentially produced by the placenta. I have however demonstrated that a significant difference in circulating progesterone concentrations between females that successfully gave birth and females that did not was detectable 1.5 months post-implantation, which is similar to the period of overlap observed in pregnant and non-pregnant harbor seals (Reijnders 1990; Gardiner et al. 1999).

Potential error and biases in pregnancy testing

The pattern and absolute concentrations of progesterone over the gestation period vary considerably between individuals and species (Daniel 1981; Raeside and Ronald 1981; Boyd 1991a; Reijnders 1990) and it is not known why (Johnson and Everitt 1995). The range of progesterone concentrations required to maintain pregnancy, during gestation, is unknown for the New Zealand fur seal. The minimum concentration required to maintain pregnancy over the late first trimester-early second trimester period may be lower than 6 ng/ml; however over the three year study no females with progesterone values below 6 ng/ml maintained a pregnancy to term. Although progesterone concentrations may not facilitate precise detection of pregnancy (Guinet et al. 1998), they appear to reflect pregnancy viability.

A significant separation of progesterone concentrations observed in females that gave birth and females that did not occurred 1.5 months after the estimated implantation date. We do not know the exact time of implantation in the New Zealand fur seal nor the duration over which implantation may occur in the population studied. The timing of implantation in the New Zealand fur seal is likely to be affected by maternal age and

condition, age of the unimplanted blastocyst, and day length (Boyd 1991b; York and Scheffer 1997). The mean progesterone concentrations observed during the first two sampling blocks, in females that gave birth (9 ng/ml) and females that did not (8 ng/ml) are lower than progesterone concentrations observed during the progesterone implantation pulse in northern fur seals (25-30 ng/ml, Daniel 1975, 1981), and Antarctic fur seals (35 ng/ml, Boyd 1991a). This suggests I sampled after the implantation pulse, even for females whose gestational or oestrous stage was calculated from median pupping dates. Due to the expected masking of lowered progesterone concentrations by females that were pregnant but aborted later in pregnancy, separation of concentrations may in fact occur at an earlier date. Errors in pregnancy classification due to overlapping progesterone concentrations of pregnant and non-pregnant females measured after 29 June are therefore expected to be small.

I have also assumed that pregnant and non-pregnant females are equally represented in the breeding colony. Little is known about the temporal or spatial separation of pregnant and non-pregnant individuals; however my observations of tagged animals at breeding colonies and haul-out areas suggest that non-breeding and senescent females regularly return to the Cape Gantheaume colony during winter.

Pregnancy rates

Post-implantation pregnancy rates for sexually mature New Zealand fur seals were lowest in 2000 (68.6%) and highest in 2003 (96.2%). Published pregnancy rates for pinnipeds range from 69% to 94% (Bowen et al. 1981; Boyd 1985; Wickens and York 1997; Laws and Sinha 1993; Bester 1995). Care must be taken however in comparing pregnancy rates, as estimates vary depending on the time and location of sampling, and the method of pregnancy determination (York 1983; Wickens and York 1997). The pregnancy rate of 69%, calculated for culled New Zealand fur seal sampled in 1996 by Dickie and Dawson (2003), is the same as my estimated rate for 2000 but is relatively low compared to my estimates for normal pup production years and compared to estimates reported for other fur seal species. Because their sample included animals collected both before and after implantation, I would expect their estimates to be slightly higher. The difference in pregnancy rates estimated by the two studies may reflect differences in sampling females at sea and sampling females from breeding colonies. Differences in age-distribution of females sampled may also contribute to the observed differences. Amongst fur seal species, including the New Zealand fur seal, pregnancy rates are lower in immature females (Lunn, Boyd and Croxall 1994; Lima and Páez

1995,1997; Wickens and York 1997; Dickie and Dawson 2003). This may indicate that my samples were biased towards mature parous females. At the time of analysis reported here, ages of sampled animals were not available.

Interannual differences in pregnancy rates have also been reported for other seal species (Boyd 1985; Lima and Páez 1995). In the South American fur seal (*Arctocephalus australis*), pregnancy rates between years ranged from 52% to 82% (Lima and Páez 1995). Samples were collected from animals harvested at breeding colonies and over a similar reproductive time period as my study. My lowest pregnancy rate of 68.6% in 2000 was similar to intermediate pregnancy rates observed in South American fur seals (68-72%). My highest pregnancy rate (96.2%) was however, higher than the highest rate observed in the South American fur seal (82%).

Overall, 59 % of the New Zealand fur seal females diagnosed as pregnant in mid winter in this study failed to carry their foetuses to term. In years of high observed reproductive rate, the difference between pregnancy rate and observed reproductive rate was 32%. In the year of low observed reproductive rate, foetal mortality reduced the reproductive rate by 43%. Apart from a few studies of captive individuals, no other study has tested wild seals for pregnancy and followed the same individuals through to term with the aim of calculating foetal mortality. For a few species, pregnancy rates and reproductive rates have been calculated separately and differences between rates suggest that foetal mortality occurs (Weddell seals, *Leptonychotes weddellii*, Testa 1987; Antarctic fur seal, Lunn et al. 1994; Payne 1977). However, correction factors based on published pregnancy and reproductive rates calculated for separate populations and years may bias fecundity estimates because the extent and timing of reproductive failure is likely to vary between populations and years.

Timing and extent of reproductive failure

Ovulation rates in mature female pinnipeds are generally high (95-100%) and show little variation between years (Rand 1955; Craig 1964; Bowen et al. 1981; Boyd 1985; Bester 1995; Guinet et al. 1998; Dickie and Dawson 2003). Conception rates are also likely to be equally high in mature females, considering that parturition and mating are highly synchronized. Boyd (1991b) suggested that the critical stage at which reproduction is affected greatest by extrinsic factors is implantation, whereas Guinet et al. (1998) suggested that, abortions during active gestation may also play a significant role in reproductive failure. Results from the present study also suggest that a

considerable level of foetal mortality occurs during the later stages of gestation in the New Zealand fur seal.

In the New Zealand fur seal population studied, reproductive failure in mature females was estimated to be 39% in years of high observed reproductive rate. The greatest percentage of failures (83%), was estimated to occur in mid to late gestation. In contrast, in the year of lower observed reproductive rate, reproductive failure was 74% and the pattern of timing was very different from that in high observed reproductive rate years. Reproductive failure before or around implantation was higher (42% compared to 10-30%) and mid to late gestation abortions were less common than in other years (58% compared to 70-90%), as fewer females had implanted. However, the percentage of females that were still pregnant by implantation, but aborted later in gestation, was considerably higher (62%) than in the years of high observed reproductive rate (34%).

In the Steller sea lion (*Eumetopias jubatus*), Pitcher and Calkins (1981) calculated pregnancy rates in mature females based on culled samples collected throughout active gestation. Initial early post-implantation pregnancy rates were 95%, after which monthly prenatal mortality was estimated to be 4.7% (assuming a linear relationship) (Pitcher and Calkins 1981). Their projected reproductive rate of 63% suggested that 32% of females failed during the active gestation period, which is the same as my estimate for the New Zealand fur seal during years of normal observed reproductive rate.

In years of normal observed reproductive rate, 4-13% of mature females in my study failed to implant, which is similar to rates observed in the South African fur seal (16%, Odendaal et al. 2002), northern fur seal (11.5%, York and Scheffer 1997) and the Steller sea lion (5%, Pitcher and Calkins 1981). In contrast, missed pregnancies in the year of low observed reproductive rate (31%) in this study, were 2-8 times higher. In the South African fur seal, 32% of mature females examined during the period of pre-implantation and implantation were non-pregnant (Rand 1955). Rand (1995) however suggests minute blastocysts may have been missed during dissections or disturbance during sample collection may have caused females to abort. Samples were also collected over 2-3 years and data were pooled, thereby obscuring any possible interannual differences.

Estimates of the timing and number of abortions in a population based on observation of live animals are rare, as pertinent data are inherently difficult to collect (McCafferty 1999). Aborted fetuses during late gestation were commonly observed in the Cape Gantheaume colony between August and December. No attempt was made to estimate abortion rates over this time from observed fetuses, due to difficulties in observation, unequal effort and scavenging by birds and cats. However these observations support my findings that reproductive failure commonly occurs between mid active gestation and the breeding season.

Overlooking this period of significant foetal mortality would considerably overestimate pregnancy rates for the population studied. If I had used early active gestation pregnancy rates to estimate reproductive rates, without adjusting for foetal mortality, reproductive success would have been overestimated by 30-43%. This finding supports Wickens and York's (1997) caution that the use of pregnancy rates without consideration for the timing of data collection can positively bias estimates of reproductive rates. My finding that significant reproductive failure occurs during the later stages of gestation impacts on previous estimates of reproductive success in pinnipeds where no steps were taken to control for the stage of gestation at which measurements were taken.

Factors affecting reproductive failure

Apart from inherent deficiencies of the conceptus, diseases and anatomical abnormalities of the reproductive tract, inadequate maternal support is generally the cause of reproductive failure in mammals (Short 1984). Under-nutrition during foetal and neonatal development may also impact on the subsequent reproductive performance of offspring. Nutritional intake and reproductive success are therefore closely linked in mammalian reproduction (Widdowson 1981). Interannual differences in pup production in pinnipeds have been related to food shortages (Guinet et al. 1998; Trillmich and Ono 1991; Lunn and Boyd 1993a; Lunn et al. 1994), and poor body condition (Guinet et al. 1998). In 2000, dietary studies of female New Zealand fur seals at Cape Gantheaume, suggest that a common fish prey species (redbait, *Emmelichthys nitidus nitidus* Richardson) was less abundant than in 2001-2003 (Page et al. 2005b). Average weight of pups born at Cape Gantheaume in the breeding season 2000-2001, were also below the average for the previous 13 seasons (Shaughnessy and Dennis 2001). Because low food availability can result in lowered nutritional intake and increased energy expenditure (Lunn and Boyd 1993a; Lunn et al.

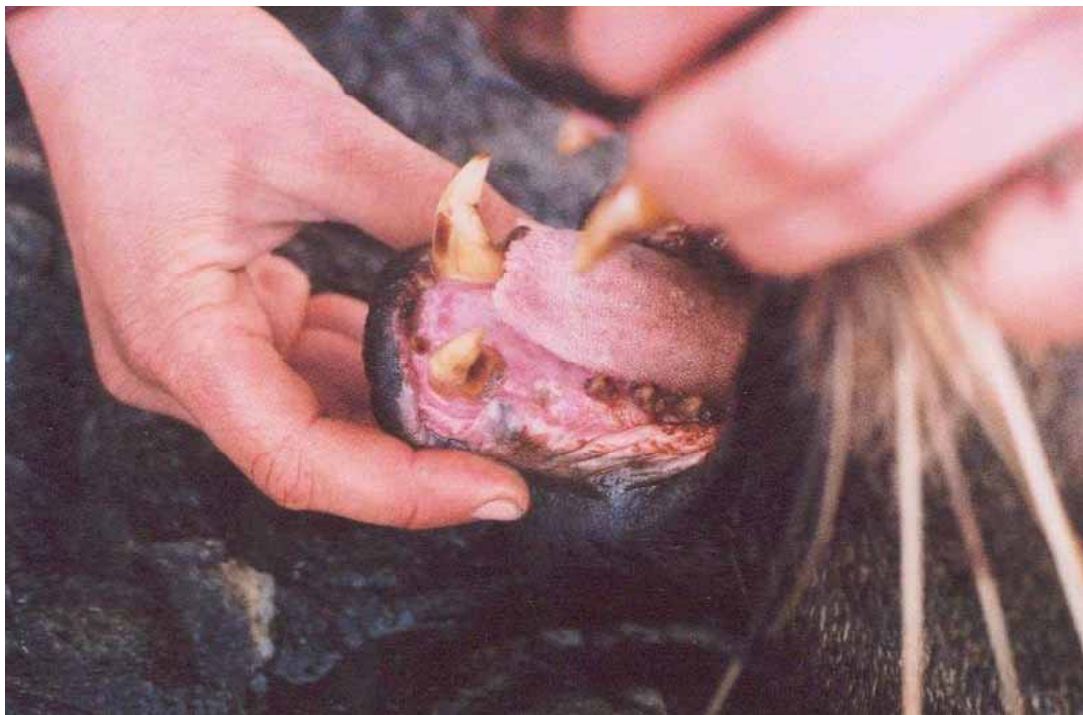
1994), maternal support at implantation and over active gestation may have been reduced in 2000.

My finding that significantly more abortions occur during the later stages of gestation is in contrast to the generalized pattern postulated by Boyd (1991b); that implantation is the point at which extrinsic factors have their greatest impact on reproduction.

Implantation and early gestation are generally less energetically expensive compared to later stages of gestation (Widdowson 1981). Under-nutrition is therefore more likely to come into effect as gestation progresses and energetic demands increase. This is probably truer for pinniped species that have an extended lactation period such as the New Zealand fur seal. Other factors such as age and reproductive history of a female may also influence the impact of extrinsic factors on reproductive success. To examine the role of nutritional stress in reproductive failure a more comprehensive longitudinal study is required than is presented here. Analysis of the effect and interaction between maternal age, body condition and environmental variability on reproductive rates is presented in Chapter 4 and 6.

CHAPTER 4. AGE AND REPRODUCTIVE MATURITY OF NEW ZEALAND FUR SEALS (*ARCTOCEPHALUS FORSTERI*) IN SOUTHERN AUSTRALIA

Published as: McKenzie J, Page B, Shaughnessy PD, Hindell MA (2007) AGE AND REPRODUCTIVE MATURITY OF NEW ZEALAND FUR SEALS (*ARCTOCEPHALUS FORSTERI*) IN SOUTHERN AUSTRALIA. *Journal of Mammalogy*: Vol. 88, No. 3 pp. 639–648.
With kind permission of *Journal of Mammalogy*, Alliance Communications Group



INTRODUCTION

Age at first reproduction and longevity are important life-history parameters required in the estimation and interpretation of population size, age structure, and growth (York 1987; Wickens 1993). The age and size at which individuals mature also provide valuable information for the interpretation of age and sex-specific life-history parameters and behaviours relating to growth and reproduction (e.g., Testa 1987; Clinton and Le Boeuf 1993; Trites and Bigg 1996).

For females of many mammal species, the age at reproductive maturity (ARM) is the age at which a female first gives birth and the age of sexual maturity (ASM) is the age at first conception, which may but not always correspond to the age at first oestrus (puberty). In contrast, for males of many mammal species the age at reproductive maturity is not clearly defined, because males may be mature sexually (i.e. viable sperm are produced and conception is physiologically possible) but they may not have the opportunity to mate until they become 'socially mature'.

In marine mammals, the age at reproductive or sexual maturity is considered a useful index of the reproductive potential or status of a population (Eberhardt and Siniff 1977; DeMaster 1978, 1981; York 1983). This concept is based on the premise that ASM is closely linked with a critical size or body condition (Laws 1956; Widdowson 1981), and growth rates are dependant on per capita prey availability. Thus, decreased food availability, due to increasing population density and/or declining prey abundance, is thought to result in slower growth rates among younger animals and therefore later maturation (e.g., Bowen et al. 1981; Bengtson and Laws 1985; Pistorius et al. 2001). However, due to variation in age at maturity between individuals within a population, this criterion is often difficult to apply, unless reliable estimates of the average age at maturity are available. This in turn requires the collection of age-specific reproductive information from either a large cross-sectional sample of the population or extensive longitudinal studies, both of which have disadvantages and potential biases.

In most pinniped studies, ARM in females has been inferred from age-specific ovulation rates or evidence of past or present pregnancies (i.e. presence of a foetus, placental scarring, corpus luteum or corpus albicans), based on examination of reproductive tracts from culled individuals (e.g., Lima and Páez 1997; Wickens and York 1997; York 1983). Such estimates assume that all sexually mature females become pregnant on

their first ovulation and are equally likely to give birth, regardless of age. However, a number of studies have indicated that pregnancy rates are not always independent of age, and failure to conceive is often associated with initial ovulation (Craig 1964; Pitcher and Calkins 1981; Boyd 1985). Significant intrauterine mortality may also occur late in gestation (Chapter 3; Pitcher and Calkins 1981; McKenzie et al. 2005a). Thus, age-specific ovulation or pregnancy rates may underestimate ARM. Inter-annual differences in the pattern and degree of pregnancy failure may also occur (Chapter 3; Boyd 1985; Lima and Páez 1995; McKenzie et al. 2005a); therefore reproductive parameters collected over a number of years are required to reduce the influence of anomalous seasons on parameter estimates.

Determining the age at first reproduction in male fur seals (i.e. first mating) is more difficult. Although males may be sexually mature, reproductive maturity in polygamous species may be delayed until a male can physically secure a breeding territory, which in turn may depend on attainment of a certain size or fighting ability (Boyd and Duck 1991). Although non-territorial males may mate with females on the periphery of territories (Mattlin 1978a; Troy 1997), the age at first territory tenure is a valuable criterion for estimating age at reproductive maturity in males.

In other pinniped studies, estimates of ARM have been based on observations of marked individuals of known or estimated age, resighted from birth (or marking) until first reproduction (e.g., Huber 1987; Testa 1987; Boyd et al. 1995). Although longitudinal data provide the most accurate estimates of ARM, the collection of continuous reproductive histories is labour intensive, requires some level of predictability in the movement and location of animals and requires sufficient numbers of individuals of different age classes to retain their marks until the age of maturity. Alternatively, ARM has been estimated from age-specific reproductive schedules, which requires a large cross-sectional sample of known-aged individuals across a range of ages (e.g., Testa 1987) or a combination of cross-sectional and longitudinal reproductive data (e.g., Dabin et al. 2004). Where individuals have not been marked at birth a reliable method of aging animals sampled is also required.

The New Zealand fur seal (*Arctocephalus forsteri*) is the most abundant fur seal species in the Australian-New Zealand region (Harcourt 2001; Goldsworthy et al. 2003). Populations throughout the region were greatly reduced by unregulated harvesting in the late 18th and early 19th centuries (Ling 1999), but the species has

since been recovering and recolonising its former range (Shaughnessy et al. 1994; Harcourt 2001). Despite their increasing abundance and a growing interest in their role as a major predator in the marine ecosystem (e.g., Goldsworthy et al. 2003), vital aspects of the species biology are poorly understood. The maximum reported age of female and male New Zealand fur seals are 22 and 15 years, respectively (Mattlin 1978a; Troy et al. 1999; Dickie and Dawson 2003). Sexual maturity in New Zealand fur seals is thought to occur between 4-6 years of age in females and between 5-9 years in males (Dickie and Dawson 2003). Males first attempt to hold territories at 8-9 years (Mattlin 1978a; Dickie and Dawson 2003), but are unlikely to be successful until they are 10 years (Mattlin 1978a).

Accurate determination of the age of individuals is critical to the study of age-specific life-history parameters. The counting of growth layer groups (GLGs) in the structure of teeth is routinely used to age marine and terrestrial mammals, but the accuracy and reliability of estimates vary between species, preparation techniques, and the type of tooth (i.e. postcanine or canine) and layers examined (i.e. dentine or cementum) (Anas 1970; Payne 1978; Arnbom et al. 1992; Stewart et al. 1996; Oosthuizen 1997; Oosthuizen and Bester 1997; Childerhouse et al. 2004). Two techniques have been used to estimate the age of New Zealand fur seals: counting of GLGs in the dentine of acid etched lower canines (e.g., Mattlin 1978a; Dickie and Dawson 2003) and counting of GLGs in the cementum of ground sections of postcanines (e.g., Troy et al. 1999). However, the accuracy of age estimation techniques have not been validated on known-age specimens in this species.

This paper outlines a method of aging New Zealand fur seals through examination of decalcified, stained thin sections of postcanine teeth. This technique is then used to estimate ages of a large cross-sectional sample of live New Zealand fur seals, which is then used to investigate age-specific life-history parameters. I also present a novel approach of assessing reproductive maturity of live female fur seals based on external examination of mammary teats. The objectives of the study are: (i) validate the ageing technique using a sample of known-age teeth, (ii) assess the accuracy in classifying females as reproductively immature or mature based on mammary teat status, (iii) estimate the age and size at reproductive maturity, and (iv) estimate maximum longevity of female and male New Zealand fur seals based on cross-sectional and longitudinal data.

MATERIALS AND METHODS

Study population

Analyses were based on morphometric and tag-resight data of seals captured and observed between 2000 and 2004 at Cape Gantheaume (36°04'S, 137°28'E), on Kangaroo Island, South Australia. The New Zealand fur seal population at Cape Gantheaume has been increasing by about 16% per annum since monitoring began in 1989 (Shaughnessy 2000) and current population size is estimated around 9,100 individuals (Goldsworthy et al. 2003). In the breeding season of 2000-2001 pup production dropped markedly, but recovered in 2001-2002 to numbers slightly higher than 1999-2000 and has since continued to increase (Shaughnessy 2004). Previous tagging programs conducted at Cape Gantheaume provided a pool of known-age individuals for validation of the aging technique and additional individuals for age-specific reproductive analysis. From January 1990 to January 1996, 203-820 pups were tagged annually at Cape Gantheaume (Shaughnessy 1997). In addition, 367 pups were tagged at irregular intervals between January 2001 and September 2003 at Cape Gantheaume (Baylis et al. 2005; Haase 2005).

Animal capture and data collection

Between 2000 and 2003, 331 females and 100 males aged ≥ 1.5 years were selected at random and captured in breeding and haul-out areas at Cape Gantheaume, including 22 known-age animals, which were tagged as pups. Most animals were captured during the non-breeding season between March-October. Seals were captured using a hoop-net and sedated using an intramuscular injection of Midazolam (0.1-0.6 mg/kg; Roche Products Pty. Ltd., Sydney, New South Wales) or remotely immobilized using Zoletil® (0.86-2.37 mg/kg; Virbac Pty. Ltd. Peakhurst, New South Wales) delivered by a dart gun (Taipan 2000, Tranquil Arms Company, Melbourne, Victoria), using 0.5 -1.0 cc barbless darts (Pneu-Dart®, Pennsylvania, USA) (Chapter 2; McKenzie et al. in review). Animals were restrained using gas anaesthesia (0.5-5%; Isoflurane VCS, Artarmon, New South Wales) delivered from an anaesthetic machine (Komesaroff Small Animal Anaesthetic Machine, Medical Developments Australia, Melbourne, Victoria). Each seal was individually marked using uniquely numbered flipper tags (Supertags®, Dalton, Woolgoolga, New South Wales) and/or bleach marks. Animals were weighed using a spring balance (50 kg \pm 0.1 kg or 200 kg \pm 1.0 kg; Salter, Melbourne, Victoria) and their dorsal standard length (straight line nose-tail distance) and axillary girth (AXG) measured to the nearest centimetre.

A first postcanine tooth (PC1) was extracted from each animal for age determination. Before tooth extraction, a local anaesthetic (10 mg lignocaine hydrochloride; Xylocaine[®], Austrazeneca Pty. Ltd., North Ryde, New South Wales) was administered into the gum next to the tooth to reduce the amount of general anaesthetic required and reduce postoperative pain. The lower left PC1 (or right, if the left was missing or broken) was extracted within a few minutes (average time 2.7 ± 1.0 min, $n = 20$), using a dental elevator (3 mm or 4 mm) and stored in 70% ethanol. To assist in defining the first cementum annulus, a sample of teeth was also collected from dead young of the year and known 1 year olds. All research procedures were approved by the Animal Ethics Committees at La Trobe University and the South Australian Department for Environment and Heritage.

Tooth preparation

Age was estimated by counting incremental layers or growth layer groups (GLGs) in the cementum of decalcified, stained, thin longitudinal sections of teeth, using a method modified from Stewart et al. (1996). Teeth that had been stored in ethanol were rinsed in running water for 3 hrs before being decalcified in a hydrochloric acid rapid decalcifying agent (RDO[®], Apex Engineering Products Corporation, Illinois, USA) for 5-12 hrs. After rinsing briefly in water, teeth were checked every 2 hrs for flexibility. To decrease decalcification times, the buccal and lingual sides of larger teeth were trimmed when partly decalcified, taking care not to dislodge the periodontal ligament tissue or damage the anterior or posterior edges of the tooth. Over-decalcification resulted in the swelling and fragmentation of GLGs. Decalcified teeth were rinsed in running water for at least 6 hrs or overnight. Teeth were then embedded in Optimal Cutting Temperature Compound (OTC) (Tissue-Tek[®], Miles Inc. Diagnostic Division, Elkhart, USA) and sectioned (20 μ m) longitudinally through the centre of the tooth from crown to root tip, using a freezing microtome (Minotome cryostat, International Equipment Company, Newark, USA; C35 microtome disposable blades, Feather Safety Razor Co., Ltd., Osaka, Japan) set at -5°C . Sections were rinsed in running water for ~ 5 min to remove the OTC, before being stained using a Hematoxylin stain for 20-25 min. Stained sections were then rinsed in running water until the water ran clear and a sample was checked for darkness under a dissecting microscope. The stained sections were then fixed in a 5% solution of ammonia for 30 sec, then rinsed immediately in running water for ~ 30 min. Sections were floated in distilled water and the 12 best sections for each tooth were selected and mounted on gelatine coated

slides (6 sections per slide). Both central (sections which include the entire length of the pulp cavity) and near to central sections were selected. Slides were air-dried before being mounted under a glass cover slip using DPX Mountant (Fluka[®], Sigma-Aldrich Pty. Ltd., Sydney, Australia). Remaining sections were stored in 99.5% glycerine.

Age estimation

Counts of cementum GLGs were made on a compound microscope 40-100x. A single GLG was defined as a layer that included two distinct incremental growth zones; a wide poorly stained zone that contained lightly stained accessory laminae and a narrow deeply stained zone (Klevezal' 1980). In many individuals, two narrow dark zones occurred in some annual layers, which are thought to occur due to a second period of arrested annual growth (Klevezal' 1980). These 'double layers' were clearest in the region of the root tip. To distinguish GLGs, lines were followed distally and proximally to ensure GLGs were not compressed (fused) and to ensure 'double layers' were counted as one. The first annual layer was not always distinct from the dentine-cementum junction along the length of the tooth. In some regions, the first annulus appeared as a thickened dentine-cementum junction. Equally the most recent layer of growth was not visible in all regions or may have been partially formed or damaged, particularly if the periodontal ligament was not intact. The most complete depositional record of cementum was typically found adjacent to the root tip. In older animals, the more recent GLGs were narrower and appeared compressed in some regions.

For each tooth, the clearest and most complete section (in terms of cementum deposition) was selected from the available sections, and the number of GLGs were counted in repeated reading sessions. During each session, each tooth was given a subjective score of readability (1 to 4, excellent to unreadable, respectively) and detailed notes taken on any damage to the cementum. Three to five reading sessions were undertaken for each tooth without prior knowledge of the previous estimate or animal identification. If three readings were the same, that value was assigned as the final age estimate. If two readings were the same and a third reading differed by no more than one year the modal value was taken as the final age. In the case that a third reading differed by more than one year from the mode or all three readings differed, two more readings were made and the mean and 95% confidence intervals calculated. Individual readings beyond the 95% confidence interval ('outliers') were removed and the final age estimate was calculated as the median of the remaining values (McCann 1993). Age estimates were corrected for date of collection by adjusting ages to the

nearest 0.1 yr (McLaren and Smith 1985), assuming a mean date of birth of the 26th December (Chapter 6; McKenzie et al. 2005a). I conducted all readings in order to eliminate inter-reader biases (Anas 1970; Oosthuizen 1997). Validation of annual GLGs and accuracy of aging was assessed using teeth collected from 22 known-age individuals (17 females and 5 males) that were tagged as pups.

Reproductive maturity and status

For females, reproductive maturity was assessed using two forms of reproductive data: mammary teat status on capture and reproductive status during the breeding season. Females captured in the non-breeding season (2000, 2001 and 2002), were classed as reproductively immature or mature based on the visual appearance of their mammary teats and their state of lactation was recorded. Females with small, non-swollen and unworn teats were classed as reproductively immature (not having previously nursed a pup). Females with medium to large teats, which appeared engorged or worn, with or without milk manually expressed were classed as reproductively mature (having previously nursed a pup at least once). To confirm the presence of a current pup, censuses for tagged females were conducted weekly and less systematically on a daily basis during the 2-3 month capture period.

During four consecutive breeding seasons (2000-2001 to 2003-2004), the annual reproductive status (i.e. given birth or holding a territory) and location of tagged seals (tagged individuals aged by tooth examination and individuals tagged as pups) were recorded during twice-daily censuses of breeding and haul-out areas. Study animals were observed from cliffs, which run adjacent to the colony, using binoculars and spotting scopes. Censuses were conducted from mid November to early February. Additional resight data were also collected from censuses conducted over 6 days during the peak of the 2004-2005 breeding season and over 5 days at the end of the same season. Females were classed as reproductive for a given season if they were observed with a newborn pup and non-reproductive for that season if a pup was not observed. Because some tagged females, which were resighted infrequently during the breeding season, may have given birth to a pup elsewhere, only known-resident females were used in the estimation of reproductive rates. Females were classed as resident if they were observed with a pup in at least one year of the 5 years. This classification ensured that immature females, which may have been resighted infrequently in a given breeding season, but later pupped in the study area were included. Resident females not observed during a breeding season but observed in

subsequent seasons were considered not to have given birth for the season skipped (Huber 1987, Testa 1987, Boyd et al. 1995, McKenzie et al. 2005a). The probability of resighting a tagged resident female given she was alive was 0.99 ± 0.01 SE (Chapter 6). The frequency of censuses (except for 2004-2005) ensured that pups that died at birth or shortly after birth were not missed; 94% of pups were observed within a day of birth and all others within a week of birth, therefore the accuracy of reproductive status based on resights should be high.

The reproductive status of tagged males was assessed based on their territorial status during the breeding season. Males were classed as territorial if they were observed holding a territory containing females or challenging an existing territorial male. Males that attempted to sneak into existing territories without challenging the territory holder or males hauled-out in non-breeding areas were considered non-territorial. The latter classification is likely to underestimate the proportion of territorial males, because some males may have held or attempted to hold territories at other colonies. Males that were observed less than three times over the summer were not included in the analysis.

Data Analysis

Age-specific maturity rates were estimated from the proportion of females within each age class that were classed as mature based on mammary teat status. For analysis, ages were adjusted to age at the previous breeding season (age at breeding season prior to capture). The average age at reproductive maturity and its associated variance was estimated from the age-specific maturity schedule using the algorithms described by DeMaster (1978):

$$(1) \quad \bar{x} = \sum_{x=0}^w x \hat{p}_{(x)}$$

where \bar{x} is the average age at first birth, x is age in years, $\hat{p}_{(x)}$ is the estimated probability of giving birth for the first time at age x , and w is the maximum age in the sample.

The probability that a female first gives birth at age x is estimated from the age-specific maturity schedule by:

$$(2) \quad \hat{p}_{(x)} = f_{(x)} - f_{(x-1)}$$

where $f_{(x)}$ is the proportion of females of age x that were estimated to be mature.

The estimated variance for \bar{x} is:

$$(3) \quad v(\bar{x}) = \sum_{x=0}^{w-1} \frac{f_{(x)}(1 - f_{(x)})}{n_{(x)} - 1} + \frac{w^2 f_{(w)}(1 - f_{(w)})}{n_{(w)} - 1}$$

The 95% confidence limits (CL) are approximated by:

$$(4) \quad 95\% \text{ CL} = \bar{x} \pm 1.96 [v(\bar{x})]^{1/2}$$

To examine the effect on the estimated average ARM, which may have resulted from the unusually low reproductive rates recorded in 2000-2001 breeding season, estimates were also calculated excluding data from captures during the 2001 non-breeding season.

Age-specific reproductive rates were estimated from tag-resight data as the proportion of individuals within each age class that were recorded with a pup or were classed as territorial. Because of small sample sizes in some age classes in any given year, analysis was performed on data pooled across breeding seasons, except for 2000-2001, which was excluded from analysis. Some marked animals were observed in consecutive years and therefore included more than once in the analysis. Age-specific reproductive rates and reproductive histories were primarily based on the sample of seals captured between 2000 and 2003.

The relationship between counts of GLGs and age was investigated using linear least squares regression and analysis of covariance (ANCOVA), to test for similarities in slope between estimated and actual age. The relationship between body size and maturity was investigated based on body length and a body condition index (mass/length ratio). Differences in length between immature and mature females were

compared using ANCOVA. Due to small age-specific sample sizes, differences in morphology (length and condition) between immature and mature individuals were tested for 5 year old females only, using a Student's *t*-test. Low numbers of individuals in each age category precluded meaningful statistical analysis of differences in body size between territorial and non-territorial males. Body condition indices for males captured in the non-breeding season were not representative of the condition of males in the breeding season and therefore were not explored. Homogeneity of variances was tested using Levene's equality of variances *F* test, and the Kolmogorov-Smirnov and Shapiro-Wilk tests were used to determine whether data were normally distributed. Mean values are given with \pm standard deviation unless otherwise stated. Statistical analysis was performed using SPSS® (Version 10.0, SPSS Inc. 1999). Results were considered significant if probability values were below 0.05.

RESULTS

Validation and accuracy of aging technique

Deposition of the deeply stained narrow zone appeared to begin in mid to late autumn and was complete by spring, when deposition of the lightly stained and broader 'growth' zone commenced. Age was correctly assigned to 17 (77.3%) of the known-age individuals ($n = 22$, range 0.9-8.6 yrs), and underestimated by one year in the remaining 5 (22.7%). Actual age and the age estimated from counts of cementum GLGs were positively correlated ($r^2 = 0.96$, $P < 0.001$). The slope of the regression for estimated age was parallel ($F_{1,40} = 0.970$, $P = 0.331$) and not significantly different from that of actual age ($F_{1,42} = 0.139$, $P = 0.712$). The proportion of females correctly assigned age (76.5%) was similar to that of males (80%); however the number of males sampled was small ($n = 5$).

Validation and accuracy of mammary teat classification

Mammary teat status was recorded for 331 females ranging in age from 1-23 years. Females classed as immature ranged in age from 1-7 years ($n = 33$), and none were recorded as lactating nor observed with pups in the census period following capture. Females classed as mature ranged in age from 4 to 23 years ($n = 298$). Of the resident females classified as mature, 217 (82.2%) were observed with a pup following capture and ranged in age from 4-18 years. Mature lactating females not observed with pups ranged in age from 6-15 years ($n = 24$). The age distribution of mature females that were not observed with a pup and were not lactating ranged from 5-23 years ($n = 23$).

and was bimodally distributed, with peaks at 6 and 17 years. The first peak in the bimodal distribution is expected if younger mature females are more likely to skip a breeding season or fail early in the lactation period compared to older, mature females. In contrast, the second peak may indicate reproductive senescence in older females.

Although the reproductive status of females classed as mature that were non-lactating and without a pup could not be verified, the age distribution of females classed as immature or mature agree with the observed age range of known reproductively mature females (females observed with pups). Thus, my classification of mammary teat status appears to provide a reasonable assessment of reproductive maturity.

Age-specific maturity and reproductive rates in females

Based on mammary teat status, females were estimated to first give birth between 4-8 years of age, with an average ARM of 5.2 years (95% CI: 4.8-5.6, $n = 331$; Fig. 1). The average ARM calculated following exclusion of data collected in 2001 was 5.1 years (95% CI: 4.6-5.6, $n = 197$). The two 4 year olds classed as mature based on teat status were both observed attending pups and the maximum age at first birth, among eight tagged females with complete reproductive histories was 8 years. Thus, 4-8 years appears to be a realistic age range for reproductive recruitment in the population studied. I did not attempt to calculate the average ARM from available longitudinal data because only two females in the data set were under the age of 4 years when tagged. Thus, the sample was likely to be biased towards later maturing females.

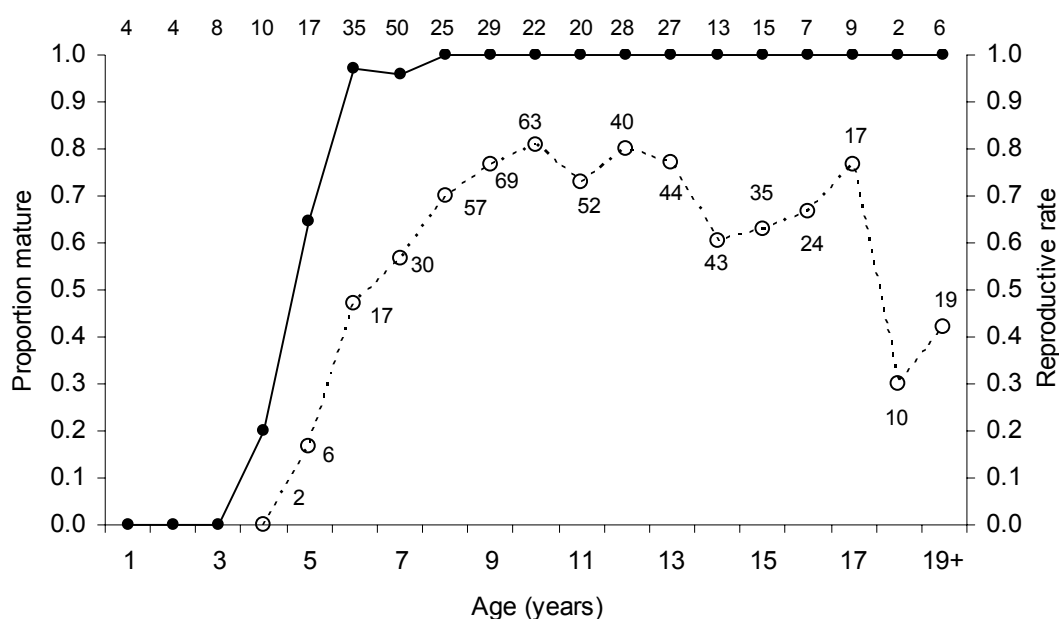


Fig. 1. The proportion of female New Zealand fur seals estimated to have given birth at least once (reproductively mature, solid circles) and the average reproductive rate (open circles) as a function of age. Proportions mature are based on data pooled between 2000 and 2003 ($n = 331$). Reproductive rates are for tag-resight data pooled between 2001 and 2003 ($n = 528$). Numbers on graph are sample sizes and data for females 19-25 years of age are pooled.

Of the 334 females captured and marked between 2000 and 2003, 244 were classed as resident and resighted in at least one breeding season following capture. The youngest resident female observed to give birth was 5 years of age and the major onset of reproduction appears to have occurred at 6 years (Fig. 1). However, sample sizes of available (tagged) 4 and 5 year olds was small, and are likely to have biased reproductive proportions of younger age classes. Age-specific reproductive rates were low at 5 years (17%), but increased rapidly to maximum rates between 8-13 years, by which age all females were considered reproductively mature (Fig. 1). At ages > 13 years the proportion of females that pupped began to decrease, which may indicate the onset of reproductive senescence in some females (Fig. 1). The overall reproductive rate of 4-7 year old females was 47% ($n = 55$), compared to 76% for females aged 8-13 years ($n = 325$).

Longitudinal observations of New Zealand fur seals, which were tagged as pups, support the estimate of females attaining reproductive maturity at 5-6 years of age. Females from the 1995 cohort were observed in relatively low numbers during the winter of 2000 when 4.5 years of age, but none were observed nursing pups. In the winter of 2000, several females from the 1994 cohort (5 yr olds) and the 1993 cohort (6 yr olds) were observed with pups. In the following breeding season (2000-2001), females representing all three cohorts (5, 6 and 7 yr olds) were observed to give birth. No females tagged as pups from the 2000, 2001 or 2003 cohorts (1-3 yr olds) were observed to give birth during this study.

Age-specific territory tenure in males

Longitudinal reproductive histories were available for 6 males (aged 6-7 years), followed over 4 breeding seasons (2001-2002 to 2004-2005). Of these males, five were of exact known-age. Age of first territory tenure ranged from 8-10 years, with an average of 9 years (95% CI: 8.1-9.9). Based on the age-specific reproductive schedule, territorial tenure was low among 8 year olds (17%) and increased to 45-50% among 9-10 year olds (Fig. 2). At 11 years of age only 2 of the 6 males (33%) were territorial. At ages ≥ 12 years the majority of males (75-100%) were territorial in at least one breeding season. These results indicate that the major onset of territorial tenure occurs at ~ 9 years. The overall territorial tenure for males aged 10-19 years was 78%, and 30% for 8-9 year olds (Fig. 2).

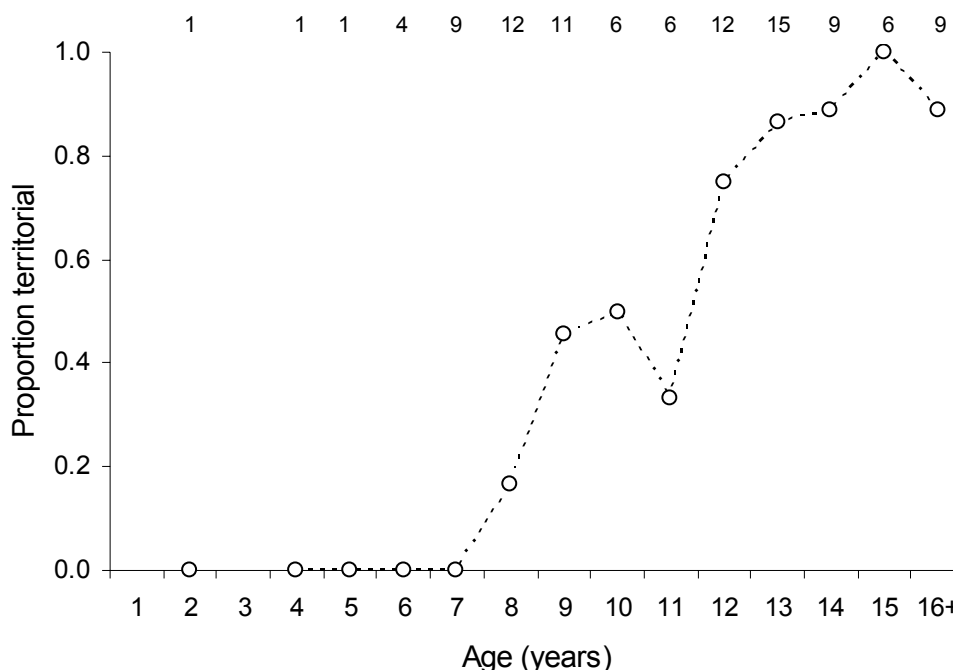


Fig. 2. Age-specific proportion of territorial male New Zealand fur seals based on tag-resight data pooled between 2001 and 2003 ($n = 102$). Numbers above the graph are sample sizes and data for males 16-19 years of age are pooled.

Recording of the territorial status of males tagged as pups from the 1994 and 1995 cohorts commenced in the 2000 breeding season, when males were 6 and 5 years of age, respectively. Males from both cohorts were first observed to first hold territories at 8 years of age, with greater numbers observed to hold territories at 9 years.

Longevity and size at reproductive maturity

The greatest estimated age for females and males based on longitudinal data collected up until 2004-2005 was 25 and 19 years, respectively. The oldest female observed to give birth was a 22-year-old and the oldest male observed to hold a territory was a 19-year-old.

Although there was overlap in length between maturity classes for 1-10 yr old females, immature females between 4-7 years were on average shorter than mature females in the same age range (121.1 ± 6.4 cm, $n = 17$ vs. 129.3 ± 5.2 cm, $n = 93$; ANCOVA, adjusted for age: $F_{1,107} = 7.620$, $P = 0.007$; Fig. 3). The shortest mature female and the longest immature female were 118 cm and 130 cm, respectively. However, the relationship between length and maturity also differed with age (Fig. 3). Females that

were mature at 4 years were among the longest of their age class and females that were still immature at 6 and 7 years were among the shortest of their age classes (Fig. 3). However, at 5 years of age there was no significant difference in length between the two groups (immature: 125.3 ± 5.3 cm, $n = 6$ and mature: 126.7 ± 4.4 cm, $n = 10$; $t_{14} = 0.678$, $P = 0.509$). Failure to detect a difference between maturity classes may be due to small sample sizes or an artifact of the time of sampling. If growth in mature females slows relative to that of immature females of the same age class (due to the energetic cost of reproduction), I expect that any difference in size between the two groups would be reduced by the time animals were measured; 4-8 months after the breeding season.

Among 5 year olds, body condition did not vary significantly between immature and mature females ($t_{14} = 1.357$, $P = 0.196$). However, with the removal of one immature female that was in extremely good body condition, mature 5 year olds had significantly greater mass per unit length ($t_{13} = 2.645$, $P = 0.02$), indicating that body condition may influence reproductive maturity in addition to length and age. Alternatively, it could be argued that the greater condition index of mature females is a result of increased mass due to pregnancy or lactation, rather than an indication of maturity.

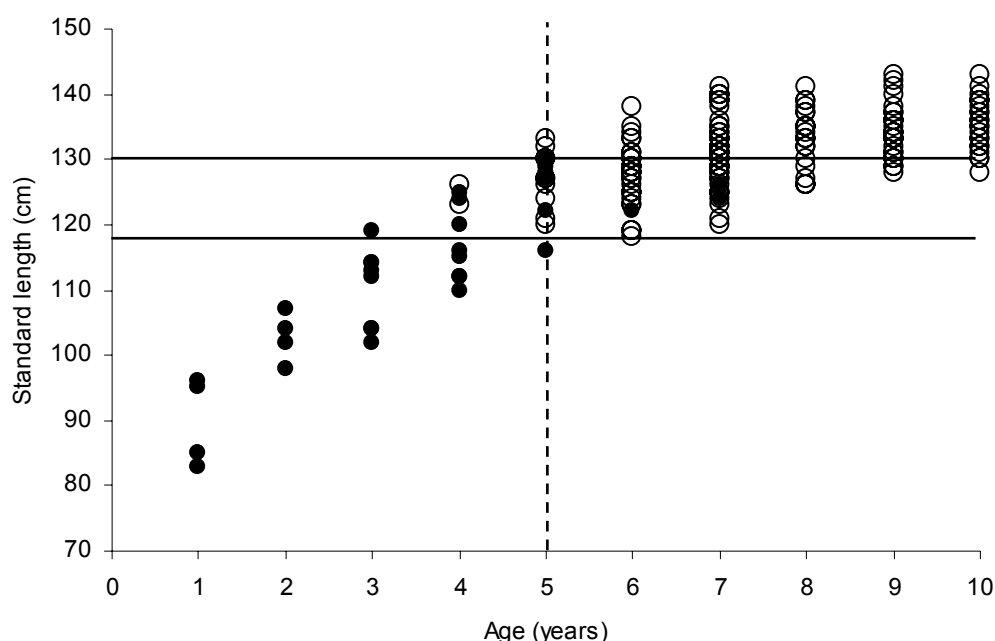


Fig. 3. The relationship between reproductive maturity, standard body length (in non-breeding season) and age (in previous breeding season), in female New Zealand fur seals (1-10 yrs). Open circles indicate mature individuals and closed circles indicate immature individuals (based on mammary teat status). Solid lines indicate the body length of the smallest mature (lower line) and largest immature females (upper line), and the dashed line indicates the estimated average age at first birth.

The shortest male to hold a territory in the following breeding season was 164 cm (12 yr old; Fig. 4). However, morphological data was not available for 8 year old territorial males. Small age-specific sample sizes and high variability in male STDL precluded statistical analysis. However, of the 8-10 year old males sampled, territorial males were longer in STDL (170.0 ± 1.4 cm, $n = 2$) than non-territorial males (150.7 ± 8.4 cm, $n = 8$).

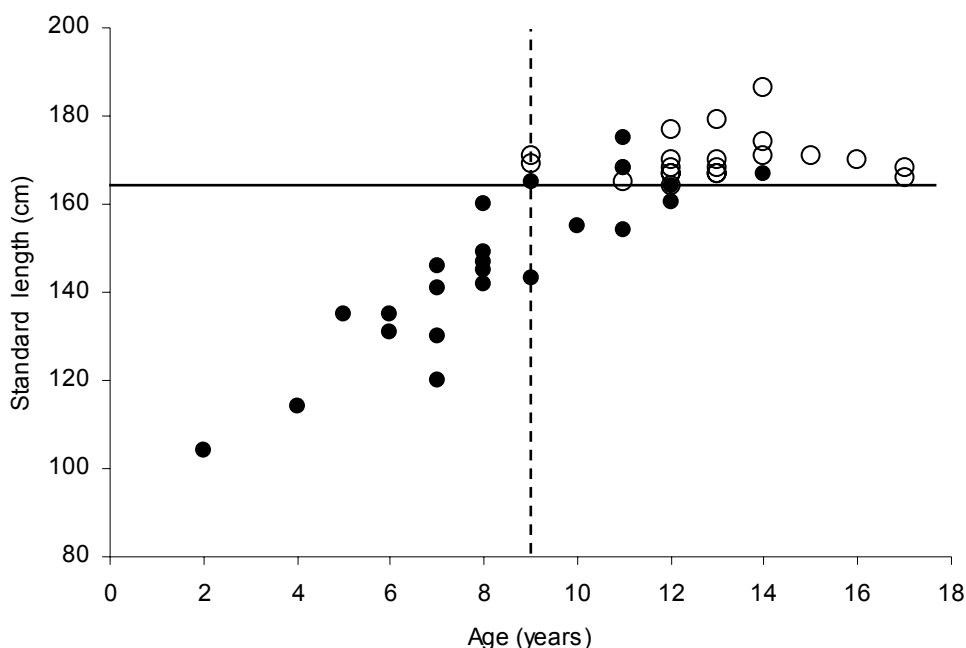


Fig. 4. The relationship between observed territorial status, body length (in non-breeding season) and age (in following breeding-season) in male New Zealand fur seals. Open circles indicate males that were observed to hold territories ($n = 21$) in the summer following capture and closed circles indicate males that were non-territorial ($n = 24$). The solid line indicates the minimum body length of males that attempted to hold territories and the dashed line indicates the estimated average age at reproductive maturity. Body length was not available for 8-year-old territorial males sampled.

DISCUSSION

Age determination

In the present study, GLGs were clear and unambiguous in the cementum of decalcified and stained thin-sections of the first postcanine. Annual deposition of cementum layers was confirmed by comparison of counts of GLGs with actual age, using a sample of known-age individuals (17 females and 5 males). Age was accurately assigned to the correct year in a majority of cases (77.3%) and underestimated by 1 year in all other cases. However, the age range over which the aging technique was assessed was limited to 0.9–8.6 years. Due to the compression of GLGs with increasing age, greater error may occur in assigning ages to older animals. Although

counting GLGs in tooth sections was difficult in older animals, I do not expect compression of GLGs to affect estimated ages significantly. Further collection of samples from older known-age individuals of both sexes will help to evaluate homogeneity of variance in assigning ages to older animals.

The ageing technique described in this paper provides an accurate and consistent estimate of age in live New Zealand fur seals. However, care in the preparation of sections and interpretation of GLGs is important to ensure errors associated with assigning ages are minimised. It is particularly important to retain the periodontal ligament tissue surrounding the cementum. Preliminary comparison of teeth collected from dead individuals, indicated that maceration of teeth during skull preparation can damage the peripheral annulus, resulting in age being underestimated. Quantification of such error would be valuable in correcting ages of individuals aged from skull collections or dried teeth. This finding has considerable implications for other mammal studies that have investigated seasonal deposition of growth layers or season of death based on the characteristics of the peripheral cementum band, and in assessing the accuracy of techniques that utilize dried teeth, particularly where known-age material is lacking.

Longevity

In the present study, the maximum age recorded for female and male New Zealand fur seals was 25 and 19 years respectively, which are comparable to those reported for other otariid species (Wickens 1993; Trites and Bigg 1996; Lima and Páez 1997; Arnold and Warneke 2002). The maximum ages recorded in the present study were greater than previously reported for this species (12+ yr old female and 15 yr old male: Mattlin 1978a; 15 yr old male: Troy et al. 1999; 22 yr old female and 12 yr old male: Dickie and Dawson 2003), but it is likely that older individuals of both sexes may be found in even larger samples. Among fur seal species, maximum ages reported for individuals in the wild are 35 years for a female northern fur seal (*Callorhinus ursinus*; York cited in Wickens 1993) and 21 years for a male South American fur seal (*Arctocephalus australis*; Vaz-Ferreira and Ponce de Leon 1987). The second oldest reported female is a 30-year-old South American fur seal (Lima and Páez 1997). The maximum reproductive longevity reported for female fur seals is 27 years, for a pregnant South American fur seal (Lima and Páez 1997). In the present study no females were recorded to pup beyond 22 years.

Age and size at reproductive maturity

New Zealand fur seals at Cape Gantheaume exhibited maturation patterns similar to those of other otariid species, with both sexes displaying a range of ages at which reproductive maturity is attained. For female fur seals, the earliest estimated ARM ranges from 3-5 years and both ASM and ARM may differ between individuals in the same population by up to 3-4 years (e.g., York 1983; Bester 1995). Comparison of reported ARM between species is impractical because estimates of maturity not only vary between populations and time periods within species, but also in the manner in which parameters were estimated (Wickens and York 1997).

I used both direct and indirect methods to evaluate reproductive maturity in female New Zealand fur seals. Mammary teat characteristics of females suggest that the ARM in the population ranged from 4-8 years, with most females maturing at ~5 years (Fig. 1). The predicted period of maturation was also reinforced with increasing age-specific reproductive rates between 4-8 years (Fig. 1). Although limited, longitudinal data and resighting of females tagged as pups supported my indirect estimates of ARM. Estimated ARM was also consistent with reported estimates of ASM (4-6 yrs) for New Zealand fur seals from New Zealand (Mattlin 1978a; Dickie and Dawson 2003).

Disproportionate representation of mature and immature females in the study area would bias age-specific estimates of the proportion mature, based on mammary teat status. However, in the present study such biases are thought to be minimal because animals were captured from both breeding and haul-out areas during the non-breeding season, when juveniles are more common on land. In the absence of sufficient longitudinal histories, the age-specific maturity rates calculated in the present study provide the best estimate for this population.

The youngest males observed holding territories during this study were 8 year olds, which is consistent with previously reported estimates for New Zealand fur seals (e.g., Mattlin 1978a; Troy 1997). In other fur seal species, the youngest males reported to hold territories range from 7-8 years (Wickens and York 1997). The estimated average age at first territory tenure for New Zealand fur seals was ~9 years, with most males ($\geq 75\%$) between the ages of 12-19 years observed holding territories (Fig. 2). Low rates of territory tenure observed among 11 year olds may be an artifact of small sample size and/or indicate a lack of site fidelity among younger males. Although territory males routinely return to the same site between years (Troy 1997), the level of site fidelity

displayed by younger first time territorial males is not known. Thus, the proportion of younger males that were estimated to be territorial may be underestimated if younger males attempted to hold territories in other breeding areas, between hauling out at the study site. Alternatively, increased mortality rates in males that attempted to hold territories at younger ages (Clinton and Le Boeuf 1993) may account for lower territorial rates.

In accordance with other fur seal species, male New Zealand fur seals appear to attain reproductive maturity several years after they mature sexually, following the development of secondary sexual characteristic such as larger size and fighting ability (Boyd and Duck 1991; Troy 1997). Sexual maturity in males is estimated to occur between 5-9 years (Mattlin 1978a; Dickie and Dawson 2003), when males are predicted to have reached 74-92% of the average maximum adult length (Chapter 5; McKenzie et al. in press a). Of the tagged males for which morphological data was available, none were less than 95% of the average maximum adult length were observed to hold territories (Fig. 4), suggesting that for some sexually mature males reproductive maturity was delayed until they reached a critical size.

Variation in ARM between individuals appears to be correlated in part with body size and/or condition. Females in the present study were estimated to reach reproductive maturity at length ≥ 118 cm and ≤ 131 cm (Fig. 3), which corresponds to 86-96% of the estimated average maximum adult length (Chapter 5; McKenzie et al. in press a). In pinnipeds, as in most other mammals, body size or condition is generally thought to have a greater influence on sexual maturity and reproductive success than age (Laws 1956; Bowen et al. 1981; Widdowson 1981), but distinguishing between causation and correlation is difficult (Bernardo 1993). Laws (1956) hypothesised that female pinnipeds attain sexual maturity at 87% (range 81-92%) of their adult length. However, genetic differences and environmental variation during development are also likely to influence the size and age at which individuals mature (Widdowson 1981). Although a number of pinniped studies have indicated that size and condition may influence the reproductive success of mature females and maternal investment in young (e.g., Pitcher et al. 1998; Georges and Guinet 2001), direct evidence of the effect of growth and condition on maturation is lacking.

Monitoring changes in the age at which individuals in a population first reproduce may be useful in detecting change in factors that influence growth and development

(DeMaster 1978; Eberhardt and Siniff 1977). However, obtaining reliable estimates of the average ARM is difficult and valid comparisons between populations and time periods cannot be made if different methods have been used. Longitudinal studies require extensive tagging and resight programs and are therefore time consuming and expensive. Evaluation of sighting biases is also required (Testa 1987). In contrast, indirect estimation of reproductive maturity in females based on mammary teat characteristics does not require an extensive tag-resight program and can be repeated easily, provided animals can be reliably aged (e.g., tooth extraction, tags, microchips, brands). Because animals can be captured over a relatively short period of time, at any time of the year, biases associated with segregation of age and reproductive classes during the breeding season can be reduced. This method is unlikely to be without error, but may provide an index with which to study trends. Classification of teat status in combination with longitudinal studies would assist in evaluating the level of accuracy in the described method and assist in developing a reliable classification method.

Although population specific, the estimates of ARM and longevity presented here will provide a useful basis for modelling population dynamics of fur seals and assist in the evaluation of survival estimates. These estimates will also provide a basis for comparison among pinnipeds and may be valuable in assessing relative population or environmental change in the future.

CHAPTER 5. INTER-SEXUAL DIFFERENCES IN THE GROWTH OF NEW ZEALAND FUR SEALS (*ARCTOCEPHALUS FORSTERI*) IN SOUTHERN AUSTRALIA



Published as: J. McKenzie, B. Page, S. D. Goldsworthy, M. A. Hindell (2007) Growth strategies of New Zealand fur seals in southern Australia. *Journal of Zoology* 272 (4) , 377–389.
With kind permission Zoological Society of London.

INTRODUCTION

Sex-specific differences in growth strategies are generally thought to have evolved as a result of sexual differences in the factors limiting reproductive success. In mammals, male-biased sexual size dimorphism (SSD) has generally been attributed to sexual selection favouring larger, more competitive males (Bartholomew 1970; Trivers 1972; Stirling 1975; Weckerly 1998). Males are therefore predicted to display phenotypic adaptations such as rapid early growth and delayed maturation (Weckerly 1998). In contrast, reproductive success of females is dependent more on investment in condition and extended reproductive life span. Thus, females are expected to invest available resources in reproduction, rather than body growth, once a minimum size for reproduction is reached (Trivers 1972). Growth in females is therefore expected to be slower and characterised by early maturation (Weckerly 1998). However, sexual selection is unlikely to be the single selective factor directing SSD and growth patterns (Isaac 2005). Sex-specific differences in growth and the degree to which growth strategies diverge are also a product of life-history and environmental constraints and variation in the selective pressures influencing the growth and survival of individuals at different life stages (Post et al. 1999; Badyaev 2002; Isaac 2005). Knowledge of growth patterns is therefore valuable in understanding and investigating sexual differences in life-history characteristics and the evolution and maintenance of SSD.

Because energetic requirements vary according to the age, sex and size of individuals (Boyd et al. 1994; Klausen et al. 1997), knowledge of sex-specific growth patterns provides valuable information for modelling the nutritional requirements and consumption rates of each age-sex class (Lavigne et al. 1986; Boyd et al. 1994). Size is also an important determinant of diving ability and inherently affects the ability and efficiency with which pinnipeds obtain prey (Boyd and Croxall 1996; Schreer and Kovacs 1997; Costa and Williams 1999). Information on growth patterns is therefore valuable in interpreting differences in foraging behaviour between demographic groups and identifying which groups or age classes are more vulnerable to changes in prey availability (e.g., small juveniles undergoing periods of rapid growth). Currently there is particular interest in developing prey consumption models for seal populations, in order to investigate the impact of recovering populations on their marine environment and their trophic interactions with commercial fisheries (e.g., Butterworth et al. 1995; Guinet et al. 1996; Goldsworthy et al. 2003). Critical to the development of such models is data

on population biomass and sex and age-specific growth rates, which can be predicted from growth models based on age-specific size structure of the population.

Variations between populations in growth rates and the average maximum size attained by adults have also been attributed to possible differences in food availability and population density between locations and time periods (Bryden 1968; Innes et al. 1981; McLaren 1993; Trites and Bigg 1992; Bester and Van Jaarsveld 1994; Etnier 2004). In assessing the energetic requirements of pinniped populations and their impact on the marine ecosystem, it is therefore critical that any strong seasonal or regional components of growth are taken into account (Trites and Bigg 1996; Chabot and Stenson 2002).

The New Zealand fur seal (*Arctocephalus forsteri*) is a polygamous species characterised by a large male-biased SSD. Uncontrolled commercial harvesting in the late 18th and early 19th centuries decimated populations throughout Australia, New Zealand and New Zealand's subantarctic islands (Ling 1999), but since the species' full protection in 1919, populations have been recovering and recolonising their former range, particularly in recent decades (Shaughnessy et al. 1994; Harcourt 2001). In Australia, the current population estimate is about 57,400 (Goldsworthy et al. 2003). Despite their increasing abundance, our understanding of the population demographics of New Zealand fur seals is limited by a lack of data, including age-specific morphology and growth.

Although there are several studies on sex differences in pup growth for New Zealand fur seals (Crawley 1975; Mattlin 1981; Chilvers et al. 1995; Lea and Hindell 1997; Haase 2005; Goldsworthy 2006), information on the size and growth of older animals is limited. Several studies have presented morphological measurements of small numbers of adult males (Miller 1975a; Mattlin 1978a; Troy et al. 1999; Harcourt 2001) and females (Miller 1975a; Mattlin 1978a; Schulman 1996 in Wickens and York 1997; Goldsworthy 2006), but few have gathered sufficient samples of known-aged animals to allow for the modelling of growth and comparison of sex-specific growth strategies. Troy et al. (1999) examined the relationship between age and size of adult males at the beginning of the breeding season but were limited by the narrow range of ages sampled. Dickie and Dawson (2003) presented data on the body mass and length of males and females caught as fishery by-catch off the coast of New Zealand and

provided growth models for females aged 1-22 years. Growth of males was not modelled because few physically mature animals were caught.

Geographic variation in the size attained by adult New Zealand fur seals has been suggested through morphometric analysis of skulls collected from across the species range. The skulls of both adult males and females from Australia were typically larger than specimens from higher latitudes in New Zealand and Macquarie Island in the subantarctic (Brunner 1998a). Because samples were pooled from several populations and time periods, it is unclear to what extent the observed differences are due to variability in growth between populations. Examination of differences in body size and growth between New Zealand fur seal populations in New Zealand and Australia is currently limited by a lack of population specific data. Genetic studies of New Zealand fur seals have also suggested that some level of regional segregation may exist, but more extensive sampling is required throughout the entire geographical range to clarify population differences (Shaughnessy 1970; Lento et al. 1997; Wynen et al. 2001).

The aims of this study were to describe and quantify post-weaning growth of New Zealand fur seals based on a cross-sectional sample of animals captured on Kangaroo Island in South Australia. Mathematical growth models are used to predict mean size-at-age and to estimate age and sex-specific growth rates. We compare sex-specific growth patterns and discuss the relationships between growth, size, reproductive maturity and foraging ecology. Age-specific mass and length tables are presented to facilitate the development of biomass and consumption models.

MATERIALS AND METHODS

Study population

Morphometric and age data were collected from live New Zealand fur seals that were captured between June 2000 and January 2003 at breeding and haul-out areas at Cape Gantheaume (36°04'S, 137°28'E), on Kangaroo Island, South Australia. The New Zealand fur seal population at Cape Gantheaume has been increasing by about 16% per annum since monitoring began in 1987 (Shaughnessy 2000) and current population size is estimated around 9,100 individuals (Goldsworthy et al. 2003). To obtain a cross-sectional sample of the population in which all age classes (> 1 year) were represented, females were randomly selected in breeding areas, but in haul-out

areas younger age classes (based on smaller body size) were targeted in order to increase sample sizes. Males were randomly selected in breeding and haul-out areas.

Animal capture and data collection

Seals were captured using a hoop-net and sedated using an intramuscular injection of Midazolam[®] (0.1-0.6 mg/kg; Roche Products Pty. Ltd., Sydney, New South Wales) or remotely immobilized using Zoletil[®] (0.86-2.37 mg/kg; Virbac Pty. Ltd. Peakhurst, New South Wales) delivered by a dart gun (Taipan 2000, Tranquil Arms Company, Melbourne, Victoria), using 1.0 cc barbless darts (Pneu-Dart[®], Pennsylvania, USA). Animals were administered inhalation anaesthesia (0.5-5%; Isoflurane[®] VCS, Artarmon, New South Wales) as described in Page et al. (2006). Each seal was individually marked using uniquely numbered flipper tags (Supertags[®], Dalton, Woolgoolga, New South Wales) and/or bleach marks. Animals were weighed using a spring balance (50 kg \pm 0.1 kg or 200 kg \pm 1.0 kg; Salter, Melbourne, Victoria) and their dorsal standard length (straight line nose-tail distance) and axillary girth (AXG) measured to the nearest centimetre with a tape measure. Axillary girth was measured on full exhalation.

To determine age a postcanine tooth (PC1) was extracted from each animal. Age was estimated from counts of annual growth layer groups (GLGs) in the cementum of decalcified, stained, thin sections of the PC1. This aging technique has been validated for New Zealand fur seals using teeth from animals of exact known-age, which were tagged as pups (Chapter 4; McKenzie et al. in press b). Preparation of teeth and estimation of age follow the methods outlined in Chapter 4 (McKenzie et al. in press b). Age estimations were corrected for date of collection by adjusting ages to the nearest 0.1 yr (McLaren and Smith 1985), assuming a mean date of birth of the 26th December (Chapter 6; McKenzie et al. 2005b). A single reader with prior experience (J.M.) conducted all readings of GLGs in order to eliminate inter-reader biases (Anas 1970; Oosthuizen 1997). No complications related to tooth extraction were observed in any animal resighted (up to 5 years) following initial capture. The gums of 19 animals recaptured within two weeks of tooth extraction were completely healed and showed no signs of infection or inflammation. All research procedures were approved by the Animal Ethics Committees at La Trobe University and the South Australian Department for Environment and Heritage.

Data analysis

Morphological data were examined for outliers with respect to age and season and unusually small or large measurements or animals removed from further analysis to ensure growth models were representative of the population. Growth analysis was restricted to the non-breeding season (autumn-spring period), because few animals were captured during the breeding season (late November to late January).

Post-weaning growth in length and body mass was described using the von Bertalanffy, Gompertz and logistic growth models (Table 1) fitted to cross-sectional size-at-age data using non-linear least squares regression analysis (Nonlinear Regression, SPSS® Version 10.0, SPSS Inc. 1999). Due to the detection of a secondary growth spurt in sub-adult males, a two-component logistic function was also fitted to male size-at-age data (Koops 1986; Clinton 1994). Because growth during the first year of life in pinnipeds differs from that of older animals, no single growth function can adequately describe growth over their entire life span (McLaren 1993). Because my aim was to describe post-weaning growth, I did not 'anchor' models at the beginning of prenatal growth or parturition, which would have introduced biases when fitting models to data of older animals (Winship et al. 2001). The simplest model that best described the data was selected based on correlation coefficients (r^2), mean square residuals (MS_R), parameter standard errors and visual inspection of residuals (Quinn and Keough 2003). Parameters for all models are presented to assist comparison between populations and species (Hammill et al. 1995).

Predicted values from the curve that provided the best fit for each sex were used as a measure of the average size of each age class and used to describe age-specific growth rates. The age at which sexual size differences first became significant was determined by comparing mean size (length and mass) for each age class using Student's *t*-test. The allometric relationships between length, girth and mass were investigated by fitting power functions, using non-linear least squares regression (Peters 1983). Homogeneity of variances was tested using Levenes's equality of variances *F* test, and the Kolmogorov-Smirnov and Shapiro-Wilk tests were used to determine whether data were normally distributed. Mean values are given with \pm standard deviation unless otherwise stated. Statistical analysis was performed using SPSS® (Version 10.0, SPSS Inc. 1999). Results were considered significant if probability values were below 0.05.

Table 1. Growth models used to fit size (S_t) at age (t) data for New Zealand fur seals. S_∞ is the predicted asymptotic size, k determines the rate of approach to the asymptote (growth rate parameter), and t_0 is the hypothetical age at which growth is zero, but should be interpreted with caution (McLaren 1993).

Model	Equation
von Bertalanffy, specific	$S_t = S_\infty (1 - e^{-k(t-t_0)})$
von Bertalanffy	$S_t = S_\infty (1 - e^{-k(t-t_0)})^3$
Gompertz	$S_t = S_\infty e^{-e^{-k(t-t_0)}}$
Logistic	$S_t = S_\infty / (1 + e^{-k(t-t_0)})$
Two-component logistic	$S_t = S_1 / (1 + e^{-k_1(t-t_1)}) + S_2 / (1 + e^{-k_2(t-t_2)})$

RESULTS

Season of capture and age distribution

Growth analysis for females was based on 326 animals captured in late March-August, with 90% captured in June-August (southern hemisphere winter). Males included in analysis ($n = 88$) were captured in late March-early October, with most (90%) captured in May-September (winter-early spring). One female and two males were excluded from analysis due to poor readability of teeth sections caused by over decalcification or incomplete sections. One 13 year-old female that was extremely small for her age and two males that were extremely large for their age were excluded from analysis. The larger of these two adult males (13.5 years) was 187 cm in length and weighed 147 kg in July; 8 cm longer than the longest adult male previously recorded and 20 kg heavier than the mean mass of territory males at the beginning of the breeding season (Mattlin 1978a; Dickie and Dawson 2003; Troy et al. 1999; present study). It is unlikely that this male was incorrectly aged, because all three readings of GLGs were the same and the sections obtained were classed as high quality, in terms of a clear and complete cementum deposition record. Age of animals used in the final analysis ranged from 1.5-23.4 years for females and 1.5-16.7 years for males. Females under 3 years ($n = 7$)

and over 18 years ($n = 8$) were under-represented in the data set (Fig. 1). Males under 3 years ($n = 8$), older than 14 years ($n = 5$) and 9 year old males ($n = 1$) were also under-represented (Fig. 1).

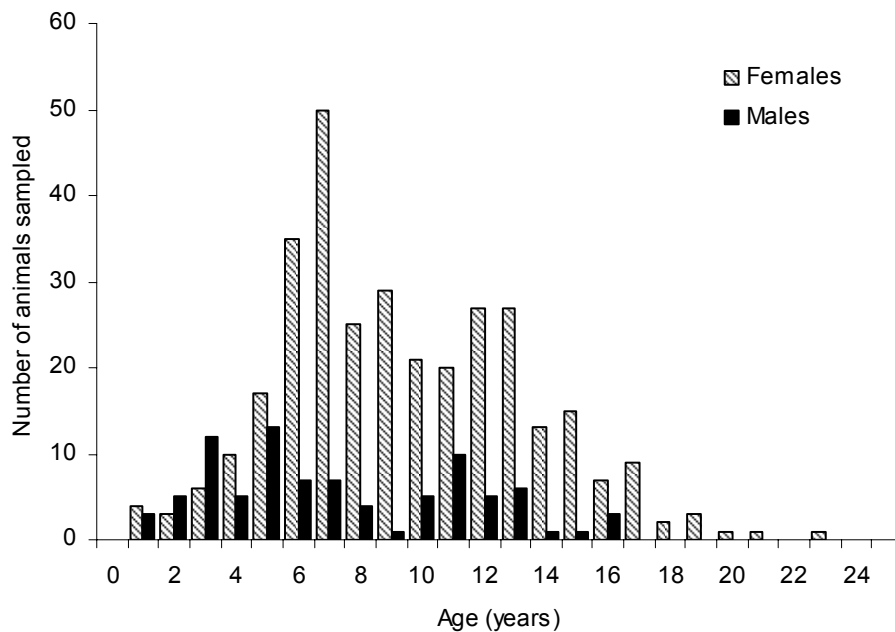


Fig. 1. Age-frequency distribution of female ($n = 326$) and male ($n = 88$) New Zealand fur seals sampled at Cape Gantheaume between 2000 and 2003 that were used for development of growth models in this study.

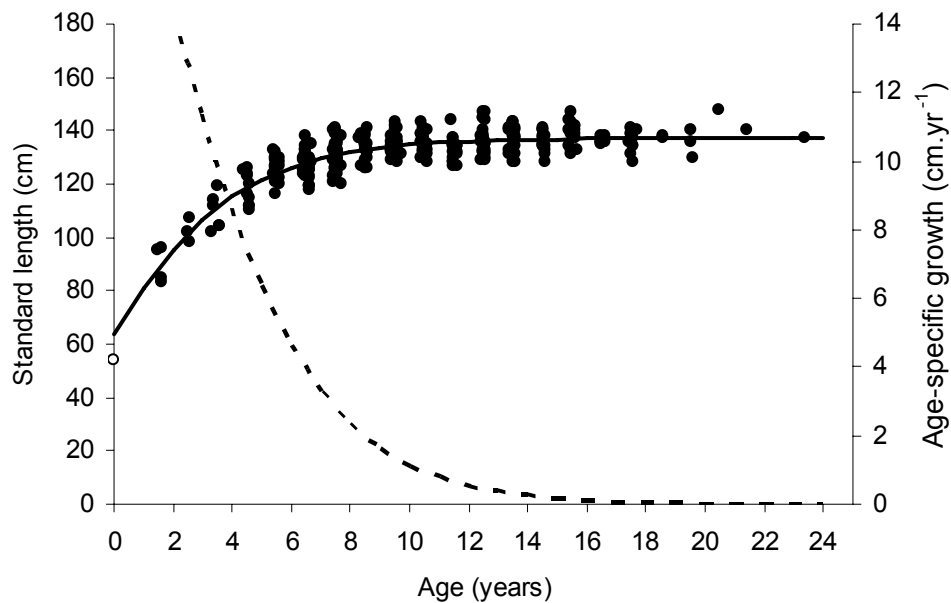
Growth

In females, growth in female length and mass was slightly better described by the Gompertz model compared to other one-component models, although the difference in MS_R was small (Table 2). In contrast, male growth in length and mass was better described by a logistic model. The one-component model explained about 90% of the variation, but this was improved significantly by adding a second component, thereby better describing the second growth spurt between 6-10 years (Figs. 2b and 3b; Table 2).

The calculated growth curves and age-specific growth rates for length and mass are presented in Figures 2 and 3, respectively and illustrate significant sexual differences in growth. Growth in length was asymptotic for females (137 cm), 95% of which was

reached by 7 years. In contrast, males grew in length over a longer period, reaching 95% of their asymptotic length (170 cm) by 10 years. Post-weaning growth rates in length decreased with age in females. Although the growth function continued to approach zero growth rate over a number of years, relative linear growth (growth rate/size) was <2% by 9 years. Although initially similar to that of females, linear growth in males was characterised by a growth spurt between 6-9 years, peaking at 8.3 cm.yr⁻¹ at 7-8 years. Little relative linear growth in males was observed by 12 years. The growth models based on size of animals 1.5 years and older overestimated both length and mass at birth (Figs. 2 and 3).

(a)



(b)

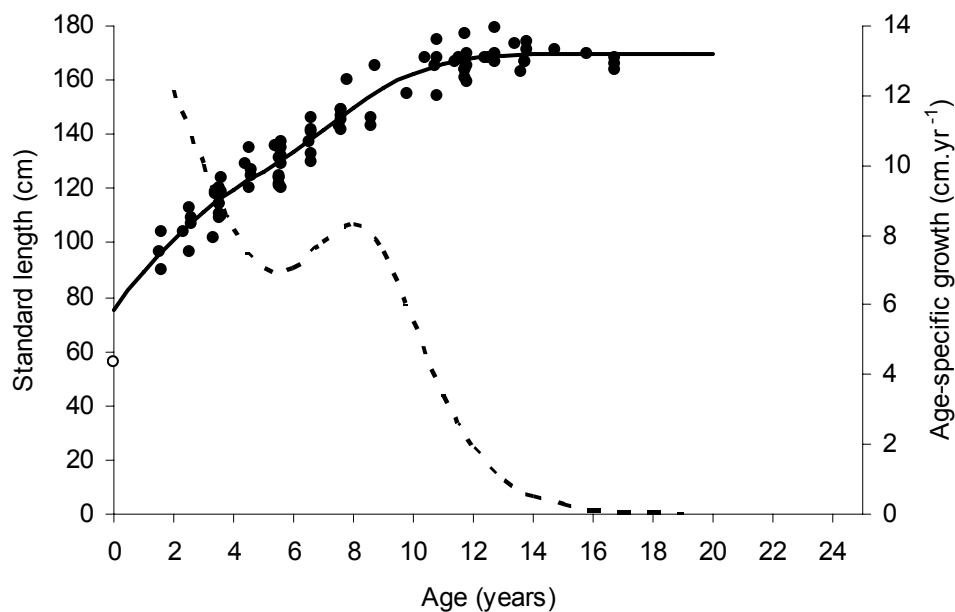
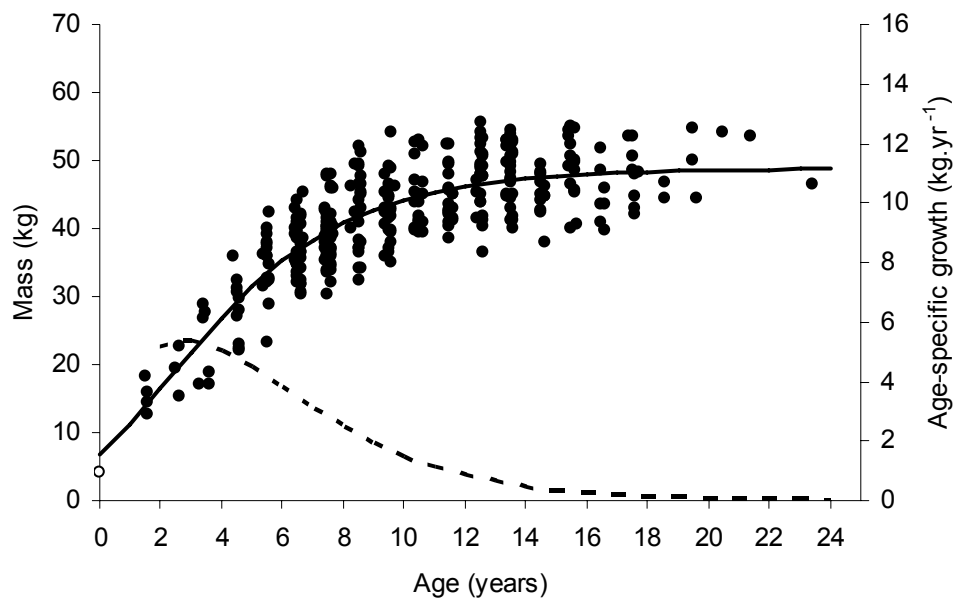


Fig. 2. Standard length growth curves (solid lines) and age-specific growth rates (dashed lines) for (a) female and (b) male New Zealand fur seals at Cape Gantheaume. Fitted growth curves are Gompertz for females and a two-component logistic model for males (see Table 2 for parameter estimates). Solid circles indicate females ($n = 322$) and males ($n = 86$) measured in this study and the open circle indicates mean curvilinear length at birth (0 days) from Mattlin (1978a).

(a)



(b)

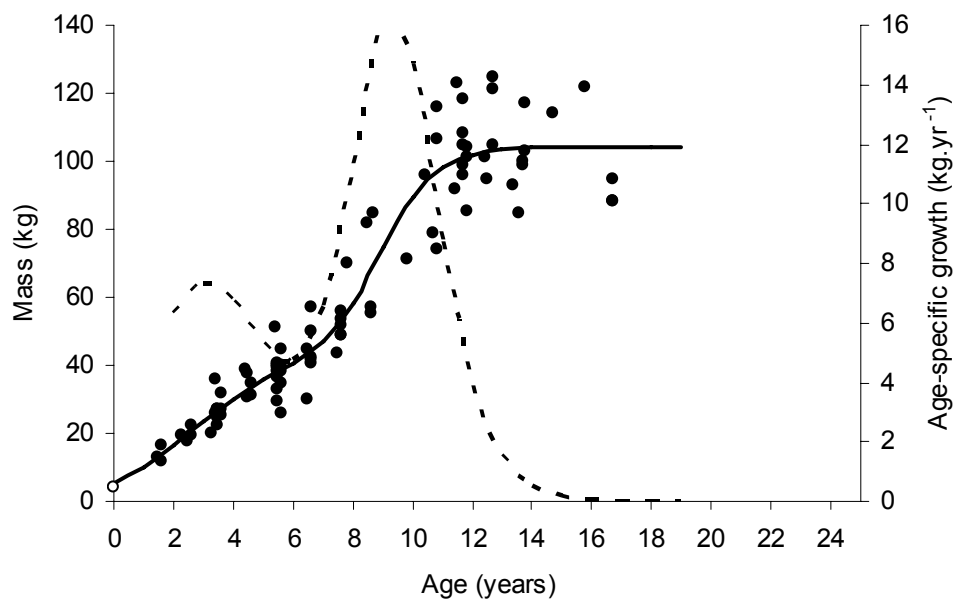


Fig. 3. Body mass growth curves (solid lines) and age-specific growth rates (dashed lines) for (a) female and (b) male New Zealand fur seals at Cape Gantheaume. Fitted growth curves are Gompertz for females and a two-component logistic model for males (see Table 2 for parameter estimates). Solid circles indicate females ($n = 320$) and males ($n = 87$) measured in this study and the open circle indicates mean mass at birth (0 days) from Goldsworthy (2006).

Table 2. Parameter estimates (\pm SE) for growth models fitted to New Zealand fur seal size-at-age data from Cape Gantheaume. See Table 1 for model and parameter details. Sample size for female length, 322; female mass, 320; male length, 86; and male mass, 87.

Growth parameter	Model	S_{∞}	$-k$	t_0	r^2	MS_{Residual}
Females						
Standard length (cm)	Gompertz	137.2 \pm 0.5	0.37 \pm 0.02	-0.72 \pm 0.23	0.721	22.586
	Logistic	136.9 \pm 0.5	0.41 \pm 0.02	-0.03 \pm 0.21	0.721	22.597
	von Bertalanffy, specific	137.4 \pm 0.5	0.33 \pm 0.02	-1.55 \pm 0.26	0.72	22.633
Mass (kg)	Gompertz	48.8 \pm 0.6	0.30 \pm 0.02	2.28 \pm 0.21	0.687	20.299
	von Bertalanffy	49.1 \pm 0.7	0.27 \pm 0.02	-2.34 \pm 0.51	0.686	20.333
	Logistic	48.1 \pm 0.6	0.38 \pm 0.03	3.47 \pm 0.18	0.686	20.344
Males						
Standard Length (cm)	Two-component Logistic					
	First part	132.7 \pm 38.0	0.44 \pm 0.44	-0.59 \pm 0.63	0.944	34.227
	Second part	36.7 \pm 38.2	0.75 \pm 0.48	7.84 \pm 1.19		
	Logistic	179.0 \pm 3.2	0.23 \pm 0.02	0.98 \pm 0.18	0.935	37.908
	Gompertz	182.6 \pm 4.0	0.18 \pm 0.02	-0.75 \pm 0.28	0.933	39.242
	von Bertalanffy	184.2 \pm 4.4	0.17 \pm 0.02	-8.18 \pm 1.06	0.932	39.756
Mass (kg)	Two-component Logistic					
	First part	40.1 \pm 11.77	0.73 \pm 0.49	2.54 \pm 0.86	0.924	94.003
	Second part	64.2 \pm 12.9	1.03 \pm 0.31	8.84 \pm 0.40		
	Logistic	114.6 \pm 5.0	0.38 \pm 0.04	7.30 \pm 0.36	0.902	116.491
	Gompertz	127.3 \pm 9.3	0.21 \pm 0.03	6.11 \pm 0.44	0.888	133.361
	von Bertalanffy	137.3 \pm 13.4	0.16 \pm 0.03	-1.43 \pm 0.80	0.882	140.979

Growth in body mass was asymptotic for both females (48.8 kg) and males (104.3 kg), 95% of which was reached by 12 years in both sexes (Fig. 3; Table 3). Little relative growth in mass was predicted for either sex by 13 years. Females demonstrated a growth spurt in mass between 2-4 years, peaking at 5.4 kg.yr^{-1} between 2-3 years, before decreasing with age. Although mass growth rates of juvenile males initially followed those of females, with a peak between 2-3 years (7.3 kg.yr^{-1}), growth rates remained higher and displayed a secondary growth spurt between 6-10 years; peaking at 16.1 kg.yr^{-1} at 8-9 years, before rapidly decreasing with age. Both sexes therefore appear to stop growing in mass at a similar age, although males continued to grow in length over a longer period than females (Fig. 2). Asymptotic length of males was about 1.2 times that of females and their non-breeding season mass was about 2.1 times that of females.

In both females and males, variation in mass at age was greater than that of length (Figs. 2 and 3). For females, variation in both length and mass did not differ significantly with age (length: Levene Statistic $F_{21,300} = 1.462$, $P = 0.089$; mass: $F_{21,298} = 1.165$, $P = 0.281$), whereas variation in male mass, but not length increased with age (mass: $F_{15,71} = 3.369$, $P < 0.001$; length: $F_{15,70} = 1.379$, $P = 0.182$). Variation in mass was low among males < 8 years old then increased significantly with the onset of the secondary growth spurt. Overall, males displayed significantly greater variance in adult mass and length compared to females (mass: $F_{1,405} = 308.834$, $P < 0.001$; length: $F_{1,406} = 96.542$, $P < 0.001$). However, variance in mass and length were not significantly different between sexes for animals ≤ 8 years old (mass: $F_{1,172} = 3.298$, $P = 0.071$; length: $F_{1,172} = .0416$, $P = 0.520$). Only length was used to explore the age at which sexual differences in size first became apparent because mass was highly variable and likely to be influenced by season and lactation or fasting duration before capture. Length of males differed significantly from that of females at ages 5 ($t_{13} = 2.771$, $P = 0.016$) and 7 ($t_{38} = 4.965$, $P < 0.001$), and for each age class older than 7 years (all $P < 0.05$), but not at 6 years ($t_{27} = 1.076$, $P = 0.291$). Failure to detect a clear difference in size is likely an artifact of small sample sizes for males.

Table 3. Predicted standard length and body mass of New Zealand fur seals in southern Australia. Standard length and mass for animals ≥ 1.5 years calculated using Gompertz growth models for females and two-component logistic models for males (Table 2). Estimated size at birth (0 days old) are observed mean sizes from Mattlin (1978a) Open Bay Is., New Zealand (*) and Goldsworthy (2006) Cape Gantheaume 1988 (**). Maximum ages are based on tag-resight data for the population studied (Chapters 4 & 6; McKenzie et al. in press b).

Age (years)	Standard length (cm)		Mass (kg)	
	Female	Male	Female	Male
0	54*	56*	4.0**	4.2**
1.5	88	95	13.8	12.8
2	95	101	16.4	16.2
3	107	111	21.8	23.5
4	115	119	26.9	30.3
5	122	126	31.4	35.6
6	126	133	35.2	40.4
7	130	141	38.3	47
8	132	150	40.8	58.4
9	133	157	42.7	74.5
10	135	163	44.2	89.2
11	135	166	45.4	98
12	136	168	46.2	101.9
13	136	169	46.9	103.4
14	137	169	47.4	104
15	137	170	47.7	104.2
16	137	170	48	104.3
17	137	170	48.2	104.3
18	137	170	48.4	104.3
19	137	170	48.5	104.3
20	137		48.6	
21	137		48.6	
22	137		48.7	
23	137		48.7	
24	137		48.7	
25	137		48.7	

Allometric relationships between mass, length and girth

Body mass was positively correlated with standard length and with axillary girth, for both females and males. The allometric relationships between mass and standard length and between mass and axillary girth were adequately explained by power functions (Table 4). Due to a growth spurt in males at 8-9 years, the relationships between mass and other linear measurements were best described by separate functions for males smaller than, and larger than, 150 cm in length. For both males and females, age-specific mean mass was also adequately predicted by a regression function incorporating both length and girth (Table 4).

Table 4. Allometric regression of non-breeding season body mass on standard length, axillary girth, and volume for New Zealand fur seals (≥ 1.5 years) from Kangaroo Island, South Australia.

Regression	Equation	<i>n</i>	<i>r</i> ²
Females			
Standard length (L)	$0.0000719 \times L^{2.717}$	316	0.75
Axillary girth (G)	$0.0445 \times G^{1.611}$	319	0.74
Volume Index	$0.00198 \times L^{1.654} \times G^{0.983}$	315	0.89
Immature males (L < 150 cm)			
Standard length (L)	$0.0000321 \times L^{2.872}$	51	0.91
Axillary girth (G)	$0.00358 \times G^{2.200}$	51	0.83
Volume Index	$0.0000673 \times L^{1.927} \times G^{0.918}$	51	0.96
Adult males (L > 150 cm)			
Standard length (L)	$0.00000153 \times L^{3.514}$	34	0.59
Axillary girth (G)	$0.0269 \times G^{1.783}$	34	0.79
Volume Index	$0.0000411 \times L^{1.662} \times G^{1.344}$	34	0.87

DISCUSSION

Potential sources of bias

Ideally, growth curves should be fitted to longitudinal age data of individuals recaptured and measured numerous times over their life span. This is not possible for many wild populations due to low probabilities of recapture. In these cases, growth curves are fitted to cross-sectional data and need to be interpreted as a summary of the average size at age of that population over a given time period (Kingsley 1979; McLaren 1993). Although growth models based on cross-sectional data provide a means of predicting growth for an average individual, the patterns predicted are likely to be influenced to some degree by differential size-dependent survival. In addition, due to the manner in which it is collected, cross-sectional data is often characterised by some error in estimating ages and non-uniform sample distributions in terms of age, maturity status, size and season of measurement. Such characteristics can lead to biased estimates of growth parameters and should be taken into consideration when assessing growth patterns and comparing growth studies (Leberg et al. 1989; McLaren 1993; Winship et al. 2001).

In the present study, GLGs in the cementum of stained decalcified thin sections were used to assign ages by an experienced reader. This method has been validated in New Zealand fur seals and has been shown to provide reliable and accurate estimates of age to within ± 1 year (Chapter 4; McKenzie et al. in press b). However, because the age range over which the aging technique was validated (0.9 – 8.6 years) did not cover the entire range of ages sampled, greater error may have occurred in assigning ages to older animals. Because little to no growth was observed in both sexes after the age of 13 years, and the readability of GLGs did not become noticeably difficult until around 15 years (due to the compression of GLGs), such biases are considered minimal.

Obtaining an adequate sample of a population which is representative of the true distribution of sizes and age classes can be difficult when age classes are segregated or unequally represented in the area of collection. At Cape Gantheaume during the non-breeding season adult females and pups still occupy breeding areas. Although juveniles and sub-adult and adult males occupy breeding areas during this time, many occur in haul-out areas adjacent to breeding areas (Troy 1997). To reduce possible sampling biases related to uneven distribution of age and size classes, animals were captured from both breeding and haul-out areas, and included males that were actively

holding winter territories. In the present study, some variation in mass between individuals is also likely to occur due to differences in the period of fasting and/or lactation before capture, which was not controlled for.

Despite my attempts to sample all size groups, some age classes were under-represented. The number of older females (> 18 years) and males (> 14 years) in the total sample was small. Because females and males appear to undergo very little growth after the age of 13 years, the overall shape of the growth curves is unlikely to be affected by small sample sizes of older age classes. However for males, the smaller sample of data falling on the horizontal section of the curve affects the relative precision of asymptotic size estimates, as indicated by the larger standard errors (Table 2). Asymptotic sizes may also be biased if larger or smaller animals live longer. The small number of animals sampled under 3 years may have biased early growth estimates, particularly that of 1-2 year olds. Following weaning at 8-11 months of age (Crawley 1975; Mattlin 1981; Haase 2005; Goldsworthy 2006), both sexes are thought to be largely pelagic during the first year of independence (Goldsworthy and Shaughnessy 1994) and it is unclear how representative my sample is of this age class. The number of males between 9-10 years was also unexpectedly low and may have influenced the magnitude and timing of peaks in growth rates around this period. The magnitude of the secondary growth spurt predicted for males may also be artificially high if larger individuals have a greater probability of survival and/or displayed greater site fidelity than smaller immature males within the same age class.

Because fur seals undergo marked seasonal fluctuation in mass and body condition in relation to the breeding season (Boyd and Duck 1991; Baker et al. 1994; Trites and Bigg 1996; Guinet et al. 1998), the season of sampling may also bias growth models. In the present study, most animals were captured during the winter-spring period, prior to the summer breeding season. The growth curves therefore underestimate breeding season asymptotic mass, particularly in adult males, but are representative of the average size of the population over a significant part of the year. We did not control for the mass of foetuses in females because pregnancy status at the time of capture was not known for all females. Because most females were sampled during the early period of active gestation, biases due to foetal mass are expected to be low. Although seasonal fluctuations in length, possibly as a result of mass displacement or body water content, have been suggested in a number of studies, length varies less with season

and is therefore a more reliable indication of size for comparative studies (McLaren 1993; Trites and Bigg 1996; Winship et al. 2001; Chabot and Stenson 2002).

Sexual differences in growth

Like other pinnipeds that are highly polygamous, adult New Zealand fur seals display pronounced male-biased sexual size dimorphism (SSD). The ratio of adult female to male length was about 1:1.2, which is similar to the ratio of 1:1.3 observed in the congeneric Australian fur seal (*Arctocephalus pusillus doriferus*) and other temperate-latitude otariids, such as the subantarctic fur seal (*Arctocephalus tropicalis*) and the Southern (*Otaria flavescens*) and Steller (*Eumetopias jubatus*) sea lions (Rosas et al. 1993; Bester and Jaarsveld 1994; Arnould and Warneke 2002; Winship et al. 2001). In comparison, New Zealand fur seals were less dimorphic than the Antarctic (*Arctocephalus gazella*) and northern fur seals (*Callorhinus ursinus*), which exhibit a SSD length ratio of about 1:1.5 and inhabit the cooler and highly seasonal but predictable environment of the polar regions (Payne 1979; McLaren 1993; Trites and Bigg 1996). In the present study, non-breeding season adult mass of male New Zealand fur seals was about 2.2 times that of females. At the onset of the breeding season, when males are expected to be at their maximum seasonal mass, the mass ratio of females to males has previously been estimated as 1:3.5 (Miller 1975a). Utilising the mean and maximum adult sizes reported by Troy et al. (1999) for males at the start of the breeding season (mean 126 kg, max. 160 kg) and those reported here for females during the non-breeding season (mean 43 kg, max. 56 kg), the estimated mass ratio of females to males is 1:2.9 or less, because females at the start of the breeding season should be relatively heavier than during the winter months.

Sexual size dimorphism in animals is produced by sex-specific differences in two general developmental processes: growth duration and growth rate, but the relative contribution that each process makes to SSD observed in adults is variable amongst species (Badyaev 2002; Isaac 2005). In many SSD mammals, sexes show significant differences in the number, timing, and duration of growth phases, which may reflect sexual differences in reproductive development, environmental effects or other selective pressures (Koops 1986; Badyaev 2002; Isaac 2005). Detection of multiple growth phases and sexual differences in developmental pathways (seasonal and lifetime) are also dependent on the frequency and quality of available data, and on the mathematical function used to describe growth (Zullinger et al. 1984; Koops 1986; McLaren 1993). In the present study, growth curves were fitted to cross-sectional data

collected during winter-spring. Although they describe the average age-specific size structure of the population, and thus can be used to predict age-specific growth patterns, they have a limited ability to predict seasonal patterns in age-specific growth (cf. Trites and Bigg 1996; Chabot and Stenson 2002)

Although the juvenile pattern of growth in length and mass was similar for the sexes, males were predicted to display a distinct secondary (or sub-adult) growth phase. In males, the second phase was characterised by a period of accelerated growth in both length and mass, followed by an acute decline in growth rates once adult size was reached. Studies of the skull development of New Zealand fur seals by Brunner (1998b) also suggest a secondary growth phase in males but not females. Skull development in females and the initial growth spurt in males was monophasic, with the period of rapid growth thought to coincide with puberty (Brunner 1998b). The secondary growth spurt in male skull development occurred after growth in skull length had ceased and related primarily to the development of characteristics related to biting ability and structural strength. Brunner (1998b) suggested that this second period of skull development may coincide with social maturity, because it related to components that were likely to enhance fighting ability.

Periods of accelerated growth followed by a marked slowing or cessation of growth are typically associated with sexual or social maturation, because energetic resources previously used for growth are directed towards reproductive development, production of secondary sexual characteristics (other than size) and sexual behaviours (Bryden 1972; Bernardo 1993). In the New Zealand fur seal population studied, females first give birth between 4-8 years, with an average age at reproductive maturity estimated as 5 years (Chapter 4; McKenzie et al. in press b). Assuming little intrauterine mortality takes place, the estimated average age at sexual maturity is therefore about 4 years. For females, sexual and reproductive maturity therefore coincided with the period immediately after the juvenile mass growth spurt (2-4 years), which was followed by a marked slowing of growth, particularly in length (Figs. 2a and 3a). Dickie and Dawson (2003) also predicted a marked slowing of growth at 4-5 years corresponding to sexual maturity for females sampled in New Zealand. By 4 and 5 years of age, females in the present study were had attained about 55-64% of their estimated adult mass and 84-89% of their adult length. The proportion of adult length attained by an average 4 year old female is consistent with Laws' (1956) hypothesis that female pinnipeds attain

puberty (sexual maturity) when they reached about 87% (range 81-92%) of their adult length.

Reproductive (or social) maturity in males occurs long after the juvenile growth phase and is preceded by a distinct period of accelerated growth. At Cape Gantheaume, this growth spurt occurs between 6-10 years (Figs. 2b and 3b), while social maturity is estimated to occur between 7-12 years (Chapter 4; McKenzie et al. in press b) and sexual maturity between 5-9 years (Mattlin 1978a; Dickie and Dawson 2003). The average age of social maturity (~9 years) corresponded to the age at which 92% of adult length and 71% of adult mass was reached. The transition between the juvenile, sub-adult and adult growth phases is also marked by a significant change in body shape, as indicated by the changes in the allometric relationship between body measurements with age (Table 4). This suggests that the development of secondary sexual characteristics is delayed until later in life. Males not only become longer and heavier with age but become more robust as they approach social maturity.

Growth spurts in male body mass in relation to sexual or social maturity have been observed for a number of pinniped species (Scheffer and Wilke 1953; Bryden 1968; Payne 1979; McLaren 1993; Bester and Van Jaarsveld 1994; Clinton 1994; Trites and Bigg 1996; Winship et al. 2001; Arnould and Warneke 2002). Growth spurts in pinniped length have also been associated with sexual or social maturation in a number of studies (Scheffer and Wilke 1953; McLaren 1993; Clinton 1994; Oosthuizen and Miller 2000), but not all (McLaren 1993; Rosas et al. 1993; Bester and Van Jaarsveld 1994; Arnould and Warneke 2002). Identification of growth spurts in length also differ between conspecific studies (cf. McLaren 1993; Knutsen and Born 1994; Winship et al. 2001). Discrepancies within and between species in the detection and timing of growth spurts are possibly due in part to the difficulty in collecting sufficient data from each age class, which also directs the choice of growth function (Koops 1986; Knutsen and Born 1994). In a study of the cranial ontogeny of fur seals and sea lions, Brunner et al. (2004) identified a secondary growth spurt in the late development of the male skull for all 12 otariid species studied. Although the pattern of growth of different body parts may vary, biphasic growth in skull development suggests that the absence of a linear growth spurt in post-weaning development of males warrants further investigation in a number of species.

New Zealand fur seal females appear to stop growing in length by 9 years (~133 cm), by which age males are predicted to have attained about 92% (~157 cm) of their maximum adult length. Although males appear to continue to grow in length until about 12 years (~168 cm), differences in the duration of growth only contributed to 31% of adult linear SSD. In contrast, sexual differences in growth rates over the first 9 years contributed to around 69% of SSD in adult length, indicating that sexual differences in adult length were largely due to the post-weaning growth spurt in male length. Sexual size dimorphism in adult mass also appears to be largely produced by sex-based differences in growth rates. Growth in mass for both sexes is predicted to cease by 13 years (Fig. 3). As with length, the initial pattern of post-weaning growth in mass was similar between sexes, but diverged when males underwent a secondary growth spurt (Fig. 3). Compared to the relatively small growth spurt in male length (Fig. 2b), relative growth rates in mass during the secondary growth spurt were higher (14-22% per year) and maintained for a slightly longer period (Fig. 3b). Predicted growth by males between 6-10 years contributed to about 87% of SSD in mass. However, as stated earlier growth rates of males during this period may be overestimated due to size-related survival biases and/or limited sample sizes.

Growth after reproductive maturity

Predicted growth slowed considerably after reproductive maturity in both sexes but continued at a slower rate until later in adulthood. Although females appeared to stopped growing in length by about 9 years, growth in mass continued until about 13 years. Continued growth in mass but not length of adult females following reproductive maturity is also suggested by growth curves of Australian, subantarctic and Antarctic fur seals and Steller sea lions (Payne 1979; Bester and Van Jaarsveld 1994; Winship et al. 2001; Arnould and Warneke 2002). In contrast, female South American fur seals (*Arctocephalus australis*) appear to stop growing in both mass and length at 10 years (Lima and Páez 1995). If larger/heavier females live longer than smaller/lighter females, cross-sectional growth curves may be biased towards increasing mass. However, some level of continued growth in females after reproductive maturity is probable, given the positive relationship shown for a number of pinniped species between maternal age, body condition and reproductive performance (Boyd and McCann 1989; McCann, Fedak and Harwood 1989; Bowen, Oftedal and Boness 1994; Lunn et al. 1994; Guinet et al. 1998; Boltnev and York 2001). Declining mass in older age classes has been suggested for female northern fur seals, but it is unclear if the

apparent decline is a result of a decrease in body condition due to senescence or a consequence of size-related survival biases (Trites 1991; Boltnev and York 2001).

In contrast to females, the period of physical maturation in males seems to be somewhat brief, which may reflect the shorter reproductive life span of males. For males, growth in both mass and length appear to stop by 12-13 years, by which age most males in the population studied were estimated to have held a territory at least once (Chapter 4; McKenzie et al. in press b). In a study of the mating success of male New Zealand fur seals, mass at the beginning of the breeding season was shown to be important in determining whether a male held a territory long enough to mate, but once a territory was successfully obtained, mating success appeared to be influenced by a complex relationship between age, previous experience (including non-breeding season territoriality), and the number of females within the territory (Troy 1997). Larger body size in males undoubtedly increases a male's ability to attain and defend a breeding territory for an extended period of time. However, after some threshold size is reached it may be that continued growth does not increase lifetime reproductive success or, alternatively, the cost (both energetic and survival) of attaining and maintaining greater mass may outweigh the reproductive benefit (Boyd and Duck 1991; Troy 1997). Balancing the costs and benefits of increased mass and energy storage may explain why males appear to delay accumulation of extensive body mass and fat reserves until much later in development. Such behaviour would reduce the energetic cost of attaining, maintaining and transporting additional mass and possibly reduce the survival risk associated with increased foraging activity, such as predation (Beck et al. 2003). This growth pattern may allow males to direct more energy towards somatic growth and development of foraging, fasting and social skills during their sub-adult life-stage.

Growth and foraging ecology

In general, increased rates of growth require increased food consumption. However, the relationship between growth and consumption rates can be influenced by the added energetic costs of reproduction (i.e. gestation, lactation and territory defence) and foraging behaviour (i.e. locomotion, diving effort, and travel time). Individuals are therefore likely to display different foraging strategies in accordance to their size, sex and developmental stage. Studies of the foraging ecology of New Zealand fur seals at Cape Gantheaume indicate that individuals display different foraging strategies, in relation to their sex and developmental stage (Page et al. 2005a, 2005b, 2006).

The initial peak in growth rates between 2-4 years coincides with the period of development when juveniles of both sexes undertake long duration foraging trips in pelagic waters and utilise prey in near-surface waters (Page et al. 2005b, 2006). Lactating females typically conduct relatively brief foraging trips (while provisioning pups) and feed closer to the colony over the continental shelf, where they utilise both mid-water and benthic habitats (Page et al. 2005a, 2005b, 2006). In contrast, socially mature males are able to utilise mid-water and benthic habitats in deeper waters over the shelf break, where larger, more energy rich prey may be more abundant (Page et al. 2005b, 2006). The foraging behaviour of sub-adult males during the second period of accelerated growth (6-10 years) is unknown. Given that body size restricts the available depth range, sub-adult males may increasingly utilise continental shelf break habitats as they grow in size, or they may increase their foraging effort in pelagic waters.

Equally, little is known of the foraging behaviour of non-lactating females and of adult males and females during the seasonal period of accelerated mass gain 1-2 months prior to the breeding season. In order to maximise growth during this period, unconstrained females and males may be expected to search out more profitable foraging grounds (Page et al. 2005a), increase their foraging effort and/or target higher quality prey.

Comparisons between populations

Comparison of the mean length of adult females from different locations (Table 5) suggests that New Zealand fur seals from Kangaroo Island are larger than those from New Zealand. This apparent difference in size between populations is also supported by comparison of predicted length growth curves for females (Fig. 4). Using the Gompertz growth function and adjusting ages to age at last breeding season, as used by Dickie and Dawson (2003), females from Kangaroo Island were predicted to grow to a greater asymptotic length ($137.2 \text{ cm} \pm 0.5 \text{ SE}$, 95% CI: 136.2 – 138.2) than females sampled from New Zealand ($119.2 \text{ cm} \pm 1.8 \text{ SE}$, 95% CI: 115.6 – 122.8). Growth curves fitted to age-specific length for the two locations begin to diverge at about 3 years (Fig. 4). Although females from Kangaroo Island were predicted to exhibit a slightly longer growth period compared to females sampled in New Zealand (95% asymptotic length reached by 7 years vs. 5 years), differences in growth rate accounted for 81% of the difference in asymptotic length.

Comparative growth curves, for males from New Zealand are not available. However, comparisons of available mean length estimates (Table 5) suggest that the size of males from the two regions may be similar. Mattlin (1978a) reported a mean length of adult males from the Open Bay Islands, New Zealand of 158 cm (SD = 11.8, $n = 10$), which is similar to the mean length of males of similar age (7-14 years: STDL 159 cm \pm 17.6, $n = 11$) measured at Kangaroo Island (ANCOVA, adjusted for differences in age: $F_{1,18} = 0.001$, $P = 0.971$). However, nine of the 10 males sampled by Mattlin (1978a) were territorial males; therefore the Open Bay Islands estimate is likely to be biased towards larger males. Males sampled at sea in New Zealand were also similar in size to males of similar age (5 – 12 years) sampled at Kangaroo Island (Table 5; $t_{87} = 1.74$, $P > 0.05$).

Unfortunately effective evaluation of the degree and possible cause of regional size-dimorphism based on available data is not feasible. Because each study varies in the manner in which the data were collected (i.e. pelagic, breeding or haul-out area sample), serious error in comparisons may be introduced, especially if local segregation of various size classes of individuals of the same ages exist. Within and between regions variation may also exist between populations due to differences in per capita food availability, latitudinal effects and/or genotypic traits (Trites and Bigg 1992; McLaren 1993; Bester and Van Jaarsveld 1994; Isaac 2005). The pooling of data in the pelagic sample of animals caught over a wide geographical area and therefore incorporating individuals from a number of populations from both temperate and subantarctic regions is likely to distort the true variability in growth between populations. However, the possible variability in the growth of females between regions identified in the present study highlights the need for population specific size-at-age and size-related survival data in order to address the question of regional variation in growth rates and maximal sizes.

Table 5. Reported mean standard lengths (\pm SD and 95% confidence interval) for New Zealand fur seals from Australia and New Zealand. Approximate values estimated from published graphs are indicated by *. Age range of animals sampled at Kangaroo Island have been adjusted to assist comparison (i.e. females > 22 years and males > 12 years have not been included).

Location & Season	Mean \pm SD (SE)	95% CI	Range	<i>n</i>	Age range (Mean \pm SD)	Source
Females						
Kangaroo I., Aust. (Non-breeding season)	133 \pm 5.7	132 - 134	116 - 148	298	5 – 21 (10 \pm 3.5)	This study
Pelagic sample, NZ (Non-breeding season)	117 \pm (1.2)	115 - 119	104*-133	46	5 - 22	Dickie & Dawson (2003)
Open Bay Is., NZ (Non-breeding season)	119 \pm 5.0	114 - 124	113-127	6	5 – 12+ (8.0 \pm 2.9)	Mattlin (1978)
Males						
Kangaroo I., Aust. (Non-breeding season)	150 \pm 17.2	145 - 155	120 - 179	50	5 – 12 (8 \pm 2.6)	This study
Pelagic sample, NZ (Non-breeding season)	144 \pm (2.3)	139 - 149	100*-179	39	5 - 12	Dickie & Dawson (2003)
Open Bay Is., NZ (early breeding season)	158 \pm 11.8	149 -167	140-175	10	7 - 14 (10.2 \pm 1.9)	Mattlin (1978)

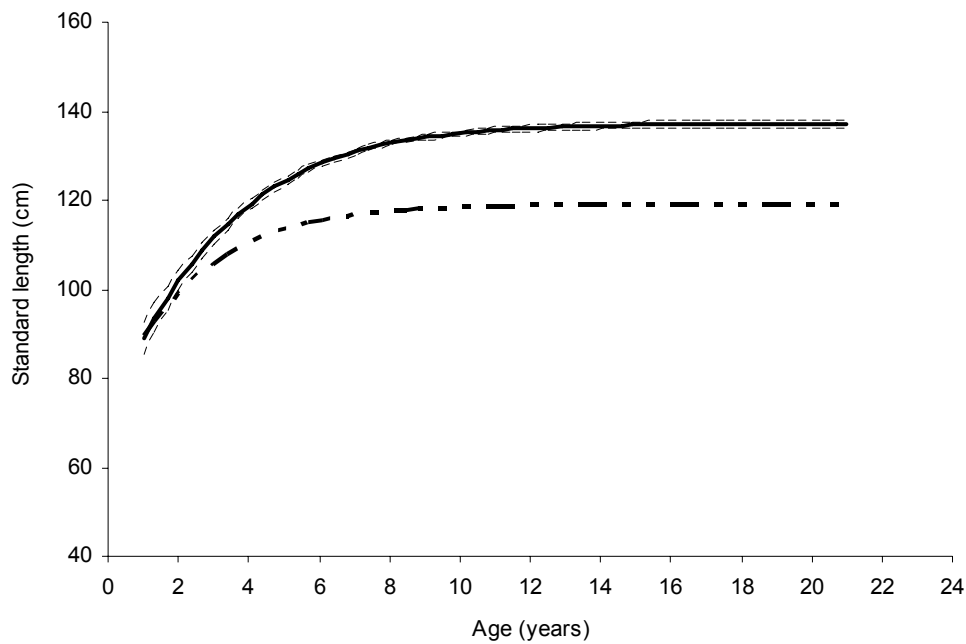


Fig. 4. Comparison of growth in standard length of female New Zealand fur seals from Kangaroo Island, South Australia (solid line \pm 95% confidence interval) and New Zealand (dashed line). For comparison, growth curves are calculated using the Gompertz growth function, where t equals age at last breeding season, following Dickie and Dawson (2003).

Summary

The post-weaning growth curves presented for female and male New Zealand fur seals in the present study are the most comprehensive currently available for this species in Australia. Further seasonal samples of adult females are required to determine the pattern and magnitude of mass gain between winter and the breeding season. A focused longitudinal and seasonal study of growth and mass fluctuations of sub-adult and adult males during the secondary growth period coupled with foraging ecology studies would greatly improve our understanding of the development of secondary sexual characteristic. Although population specific, the growth parameters presented will provide a useful basis for modelling biomass and consumption models, and will facilitate evaluation of the impact of recovering fur seal populations on the marine environment. However, in the absence of sufficient longitudinal growth data consideration for potential biases due to the cross-sectional nature of the data should be taken into account when developing such models.

**CHAPTER 6. POPULATION DYNAMICS OF NEW ZEALAND FUR SEALS IN
SOUTH AUSTRALIA: GENERAL PATTERNS AND VARIATION IN VITAL RATES**



INTRODUCTION

Recovery of a number of fur seal species from over-exploitation during the commercial sealing era of the 18th and 19th centuries and the rapid expansion of human exploitation of global fish stocks has seen a surge in the interest and concern among conservation and fisheries managers in monitoring and understanding seal-fisheries interactions (Harwood and Rohani 1996). Attempts to develop trophic interaction models to examine interactions between increasing seal populations and commercial fisheries and the development of management regimes to ensure long-term persistence of fisheries and pinniped populations have highlighted the lack of available data and understanding of the population dynamics of many fur seal species (Eberhardt and Siniff 1977; Butterworth et al. 1995; Wickens and York 1997; Goldsworthy et al. 2003).

Understanding how basic demographic parameters, such as survival and reproductive rates, vary with age is essential to understanding population dynamics in long-lived vertebrates (Charlesworth 1980). For most marine mammal species, age-specific life-history parameters are lacking, and as a consequence, most population models are simple stage-structured models, which assume two or three survival rates: survival from birth to 1yr or survival from birth to the first reproductive event and constant adult survival (e.g., Eberhardt and Siniff 1977; Harwood and Prime 1978; Wickens and York 1997). Although estimates of age-specific reproductive rates may be available, fecundity is generally reduced to a single value for ease of modelling. In many cases not all parameters are known for the time period in question or are known for only some life-stages (e.g., from birth to end of the breeding season or to weaning). Modelling then requires the substitution of possible estimates available from other populations, other time periods or similar species. This can result in unrealistic estimates of population growth and distorted relationships between vital parameters (York 1987), and can result in significant loss of information and biological meaning. In age-structured populations, determination of age-specific survival and reproductive rates and reliable estimates of their variation are essential for the development of more realistic and accurate population models (Caughley 1980). However, obtaining reliable estimates of fecundity and survival at various life-stages can be difficult, particularly for long-lived species that inhabit remote locations and spend a considerable portion of their life dispersed at sea.

Population growth, over both the short and long term, is also determined by fluctuations in vital rates in response to fluctuations in environmental conditions and population density (Caswell 1989). Understanding the factors which influence population growth are essential in forecasting future population trends and the impact of environmental or anthropogenic stressors (Sibly and Hone 2002). Changes in the density of a population can result from temporal variations in fecundity, survival, immigration and dispersal or through a combination of changes in these parameters. However, comparatively few population studies are conducted at an appropriate resolution to determine the relative contribution of each vital rate to the observed change in population growth. Even in populations which are not subject to significant levels of immigration or emigration, determining if fluctuations in population indices such as pup abundance are a result of shifts in reproductive success, survival rates or a combination of both is difficult without concurrent and accurate information on several parameters (Trillmich 1993). In many situations, by the time a significant change in population growth has been detected, the opportunity to measure factors influencing the dynamics of the population have passed, particularly where changes are relatively slow. Information gained on the variation in vital rates during periods of contrasting pup production is therefore invaluable for interpreting past or future oscillations in population numbers and for providing realistic limits for parameter estimates in the modelling of population growth.

The New Zealand fur seal (*Arctocephalus forsteri*) is the most abundant fur seal species in the Australian-New Zealand region (Harcourt 2001; Goldsworthy et al. 2003). Despite their increasing abundance and a growing interest in their role as a major predator in the marine ecosystem (e.g., Goldsworthy et al. 2003), vital aspects of the species biology are poorly understood. Quantitative data on key demographic parameters such as age-specific fecundity and survival are unknown. As a result, local and regional population estimates for the species have been based largely on parameters calculated for other fur seal species and assumptions about life history patterns (Crawley and Brown 1971; Taylor 1982; Taylor et al. 1995; Goldsworthy et al. 2003).

New Zealand fur seal populations in Australia are increasing rapidly and it has been suggested that populations may treble over the next 15-30 years (Goldsworthy et al. 2003). The current overall population estimate is around 57,400 animals (Goldsworthy et al. 2003). Most of the breeding population occurs in South Australia (77%), spread over 18 breeding colonies (Goldsworthy et al. 2003). The second largest breeding

colony in Australia is located on Kangaroo Island, at Cape Gantheaume and accounts for about 15% of annual pup production in Australia (Goldsworthy et al. 2003). Pup production at Cape Gantheaume has been monitored since January 1989 (Shaughnessy et al. 1995). Including a nearby site (Berris Point) into which the population at Cape Gantheaume appears to have overflowed in recent years, pup production in 2005-2006 was estimated to be 3,829 with an average rate of increase over the past 18 years of 12.5% per annum (Shaughnessy 2006).

In order to establish species and age-specific life-history parameters for the New Zealand fur seal, a life-history study commenced in June 2000 at Cape Gantheaume based on tagging and resighting individuals over a number of years. Between 2000 and January 2003, 330 female and 100 male seals were captured live, marked and aged through examination of a postcanine tooth removed from each animal (Chapter 4; McKenzie et al. in press b), which provided a means of investigating age-specific life-history parameters. Data collected during this study has provided information on pregnancy rates and interannual differences in reproductive failure (Chapter 3; McKenzie et al. 2005a), ranges in age and size at reproductive maturity in females and first territory tenure in males (Chapter 4; McKenzie et al. in press b), reproductive longevity (Chapter 4; McKenzie et al. in press b), and age and sex-specific growth patterns in juveniles, sub-adults and adults (Chapter 5; McKenzie et al. in press a). Monitoring of tagged known-age animals over consecutive breeding seasons since 2000-2001 has also allowed age-specific reproductive and survival estimates to be calculated from both cross-sectional and longitudinal data. Fluctuations in annual pup production over this period have also provided the unique opportunity to examine annual variation in vital rates and their relationship with pup abundance indices for this species.

This paper presents information on age-specific rates of survival and reproductive performance of adult females and early mortality rates in pups based on data collected between the 2000-2001 and 2003-2004 breeding seasons. The aims of this study were to (i) describe for the first time the general pattern of age-specific reproductive and survival rates for a population of New Zealand fur seals, (ii) measure annual variation in vital rates (fecundity and survival), (iii) assess the influence of annual variation in vital rates on short-term changes in pup abundance, and (iv) present a model life-table for the population at the time of measurement.

MATERIALS AND METHODS

Population and animals studied

Analyses were based on reproductive and resight data of known-age tagged seals observed between November 2000 and January 2004 at Cape Gantheaume (36°04'S, 137°28'E), on Kangaroo Island, South Australia. Pup numbers at Cape Gantheaume have generally increased at an average annual rate of $r = 0.110$ (11.6% per annum) over the past 18 years (1988-1989 and 2005-2006) (Fig.1). Until 1999-2000, pup numbers were increasing at an average rate of 16% per annum. However, in 2000-2001 pup numbers at Cape Gantheaume declined markedly (-23%) from the previous years estimate. In 2001-2002 pup numbers recovered to numbers slightly higher than recorded in 1999-2000, but remained stable in 2002-2003 before increasing again in 2003-2004 (Fig. 1). A similar pattern in pup numbers was observed at other breeding sites on Kangaroo Island during the same period (Shaughnessy 2006). Population parameters measured in the present study coincided with the period of fluctuating pup production.

Throughout 2000, 2001 and 2002 a cross-section of adult females was selected at random from breeding areas and haul-out areas within the colony, captured, tagged and aged (Chapter 4; McKenzie et al. in press a). Most animals were captured during the non-breeding season between March-October. Seals were captured using a hoop-net and sedated using an intramuscular injection of Midazolam® (0.1-0.6 mg/kg; Roche Products Pty. Ltd., Sydney, New South Wales) or remotely immobilized using Zoletil® (0.86-2.37 mg/kg; Virbac Pty. Ltd. Peakhurst, New South Wales) delivered by a dart gun (Taipan 2000, Tranquil Arms Company, Melbourne, Victoria), and administered inhalation anaesthesia (Isoflurane® 0.5-5%; VCS, Artarmon, New South Wales) (Chapter 2; McKenzie et al. 2005a; Page et al. 2005a). Each seal was marked using uniquely numbered flipper tags (Supertags®, Dalton, Woolgoolga, New South Wales) and/or bleach marks. For age determination, a postcanine tooth (PC1) was extracted from each animal. Age was estimated from counts of annual growth layer groups (GLGs) in the cementum of decalcified, stained, thin sections of the PC1 (Chapter 4; McKenzie et al. in press b). All research procedures were approved by the Animal Ethics Committees at La Trobe University and the South Australian Department for Environment and Heritage.

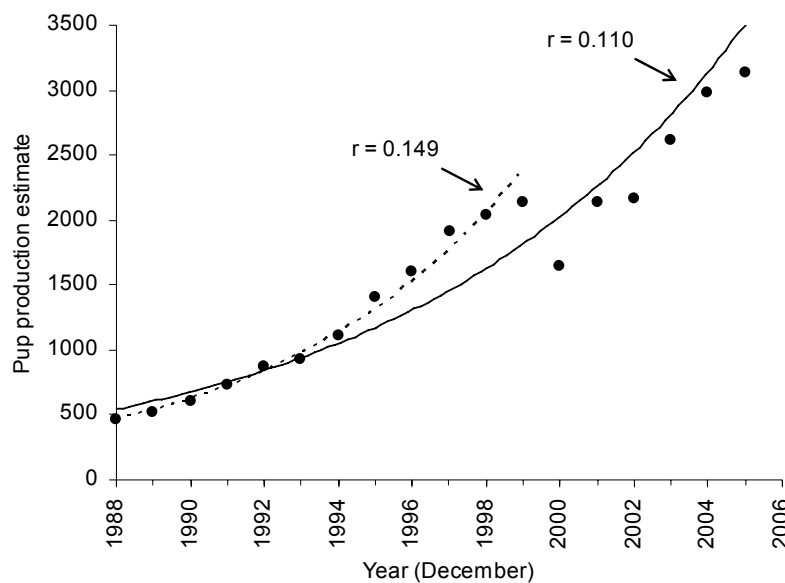


Fig. 1. Estimated number of New Zealand fur seal pups born at Cape Gantheaume, based on mark-recapture at the end of the breeding season (calculated from data in Shaughnessy 2006). Trendlines are based on exponential rate of growth from 1988-1989 to 2005-2006 (solid line) and from 1988-1989 to 1999-2000 (dashed line).

Reproduction

In this study a reproductive female was defined as a female that gave birth to a pup during a given season, whereas mature females were those that had given birth at least once during their life (primiparous or multiparous). Females were classified as reproductively mature or immature based on external classification of mammary teats when first captured (Chapter 4; McKenzie et al. in press b). Attendance, location, reproductive status and parturition date of tagged known-age females and survival of their pups until the end of the breeding season were recorded during twice-daily censuses of the colony over four breeding seasons (Chapters 3 & 4; McKenzie et al. 2005a, in press b). To calculate the duration of each pupping season and estimate median date of birth for the population, pups were counted twice a day over the entire colony throughout the breeding season. The highest of the two counts was taken as the daily estimate of live pups. The duration over which 90% of births occurred, median birth date and its standard deviation were calculated using a modified probit analysis based on the cumulative counts of pups (Caughley 1980).

In the population studied, the age at which females first gave birth was estimated at 4-8 years (Chapter 4; McKenzie et al. in press b). Age-specific reproductive rates were therefore calculated as the proportion of reproductively mature females that gave birth for each age class ≥ 4 yrs. These values differ from those presented in Chapter 4 (McKenzie et al. in press b), which included immature 4-7 yr olds in age-specific samples for comparison with maturation rates. Sample sizes were generally too small to allow for comparison of age-specific rates among years. Consequently age classes were grouped according to the general pattern described by the average reproductive schedule (see below): “young females” consisted of age classes over which age-specific reproductive rates increased rapidly (4-7 yrs), “prime-age” females consisted of the most productive age classes in which reproductive rates were relatively high (8-13 yrs), and the “older females” consisted of age classes where age-specific rates appeared to decline (≥ 14 yrs) (Chapter 4; McKenzie et al. in press b).

To describe an average reproductive schedule for the study period, data from 3 breeding seasons: 2001-2002, 2002-2003, and 2003-2004 were combined; data from 2000-2001 was excluded due to unusually low pup production (Fig.1). Data for age classes ≥ 19 years were combined due to small sample sizes. The three years for which data were combined correspond to the years for which adult survival data were calculated (2000, 2001 and 2002: see below). The relationship between reproductive rate and age was explored using two functions; a rectangular hyperbola model with a quadratic term to account for a decline in reproductive rates in older animals (Lunn et al. 1994) and a quadratic model (Arnould et al. 2003; Dabin et al. 2004) fitted using non-linear least squares regression analysis (Nonlinear Regression, SPSS® Version 10.0, SPSS inc. 1999). Goodness of fit was evaluated by comparing correlation coefficients, mean square residuals and visual inspection of residuals (Quinn and Keough 2003). Predicted values from the curve that provided the best fit were then used to calculate an average schedule of fecundity.

Age-specific fecundity (m_x , average number of female offspring produced by each female in each age class) was estimated by multiplying the predicted proportion of reproductively mature females (proportion of primiparous or multiparous females) within each age class by half the predicted age-specific reproductive rate (York 1994). Age-specific maturity rates were based on pooled data collected over the same time interval (Chapter 4; McKenzie et al. in press b), smoothed using a logistic function. This

analysis assumed the sex ratio of pups was 1:1 (but see Bradshaw et al. 2003) and that all mature females were equally likely to give birth to a female pup in a given year.

Survival

Pup mortality over the breeding season was assessed from twice-daily resight records of tagged females and the presence or absence of their pups. Most pups that died were observed within a day of death. Pups that were not observed dead were assumed to have died the day after they were last observed alive. Resight histories of mother/pup pairs were used to examine distributions of age at death for pups of known birth date and to estimate survival from birth to 15 days of age, 30 days of age and overall mortality for the breeding season.

Mark-recapture data of tagged known-age adult females resighted over 4 consecutive breeding seasons (2000-2001 to 2003-2004) was used to explore between-season (annual) and age-specific patterns of survival and recapture probabilities, using maximum likelihood estimation. One of the main assumptions of mark-recapture analysis is that individuals within the marked population have the same probability of resighting and survival. To reduce heterogeneity in the data due to unequal resighting effort in space and time, data were restricted to resights within the study area during the breeding season. All sightings of an individual made between 22 November and 30 January constituted a single record for that animal in a given year. It was also assumed that emigration rates were minimal, because mark-recapture methods cannot distinguish between mortality and permanent emigration unless data are available for multiple colonies. To reduce heterogeneity in the data due to transient animals or temporary absence due to maturity status, only females that were known to be residents and reproductively mature were used in the analysis. Analysis was therefore based on the marked population ≥ 4 years of age that had pupped at the study site at least once. Females were considered “marked” on their first encounter during the breeding season following their initial winter capture. A second assumption of mark-recapture analysis is that marks are not lost or that survival rates can be corrected for loss of marks. Because most seals in the present study were doubled tagged, estimates of survival were adjusted for estimates of tag loss. A small number of females that were only marked using bleach were excluded from analysis, because bleach marks were only visible for 1 or 2 breeding seasons.

Models of survival and encounter probabilities, parameter values and estimates of variance were obtained using program MARK (Gary White, Montana State University). Model selection began with the most complex model (global model) containing all factors of interest (the effects of time and age on survival and capture rates), which adequately fitted the available data. A bootstrap goodness-of-fit (GoF) approach was used to test if the global (starting) model in each set of candidate models adequately fitted the data, by comparing the observed model deviance with deviances derived from simulated data that exactly met the assumptions of the model (i.e. no over-dispersion due to heterogeneity among animals or data sparseness). In all cases no significant over-dispersion was indicated. Models were then simplified by constraining variables to derive the most parsimonious model (model with the least number of parameters) that was supported by the available data. Because survival parameters were of primary interest, recapture probabilities (p) were modelled first, followed by apparent survival (s) (Lebreton et al. 1992). Both recapture and survival probabilities were tested to see if they were constant over time (.) or were time-dependent (t). Model selection followed the parsimony principle where the model with the lowest Akaike Information Criterion (AICc) was selected as the best model if the difference between AICc values was >2 (Lebreton et al. 1992; Anderson and Burnham 1999). Significant differences between the relative fit of nested models where ΔAICc was <2 were tested using a likelihood ratio test (LRT; Lebreton et al. 1992). Simpler models were accepted if the significance level of the LRT test was >0.10 (Lebreton et al. 1992). The best models were then used to estimate apparent survival after adjustment for tag loss.

To test for possible senescence in adult survival, the overall survival rates of prime-age females (8-13 yrs) were compared to those of older females (≥ 14 yrs). Because the number of recaptures was limited to 3 occasions and all animals were captured as adults, recapture histories of females first observed after capture as 8-12 yr olds were pooled and classified as prime-age females and those first observed when 14 yrs or older were pooled and classed as older females. Senescence was then investigated by comparing models with and without the main effects of time (t) and age group (AG) to models with time and age group interactions (AG*t) or main effects of time and age group only (AG+t).

Age-specific survival rates were estimated by combining resights from all years and calculating return rates for each age class (i.e. the proportion of seals of age x that survived and were resighted at age $x + 1$). Although return rates are known to bias

estimates of survival, due to variation in encounter probability, encounter rate of adult females over the 4 breeding seasons based on mark-recapture models was high (0.986, SE = 0.010). Therefore, return rates should provide a reasonable estimate of apparent survival. Recapture histories were too sparse to estimate return rates for 4 and 5 yrs olds and data for seals >16 years were combined due to small sample sizes. Variances and 95% confidence intervals for age-specific survival rates were calculated using program MARK, which adjusted CI to be bounded by 0 or 1.

Tag loss

Annual and age-dependent survival rate estimates were adjusted for tag loss and variance calculated following Arnason and Mills (1981) by:

$$\hat{S}_c = \frac{\hat{S}}{\hat{\theta}}$$

$$Var(\hat{S}_c) = \hat{S}_c^2 \left[\left(\frac{Var(\hat{S})}{\hat{S}^2} \right) + \left(\frac{Var(\hat{\theta})}{\hat{\theta}^2} \right) \right]$$

where \hat{S}_c is estimated survival corrected for tag loss, \hat{S} is estimated survival from year i to $i+1$ and $\hat{\theta}$ is tag retention rate (probability of retaining at least one tag over an annual interval).

Tag loss was estimated from double tagged females resighted over 4 breeding seasons (2000-2003), following Eberhardt et al. (1979). The loss rate of a single independent tag and its variance were estimated by:

$$T_1 = \frac{n_1}{(n_1 + 2n_2)}$$

$$Var(T_1) = T_1^2 (1 - T_1)^2 (1/n_1 + 1/n_2)$$

where T_1 is the estimated loss rate of a single tag, n_1 is number of animals returning in the next period with only a single tag, and n_2 is the number returning with both tags. The rate of tag loss for females tagged as adults was independent of tag age (regression weighted for sample size $F = 1.073$, $df = 3$, $P = 0.409$). All data were therefore combined to provide an overall estimate of annual single tag loss of 0.027 (SE = 0.006).

The loss rate of either the left or right tag was not significantly different ($\chi^2 = 0.182$, $df = 1$, $P = 0.670$, $n = 22$). The probability of losing both tags was therefore estimated as the squared probability of losing a single tag (T_1^2). However, tag retention rate from any given period to the next depended on the combination of single and double tagged animals in the sample examined. Average tag retention rates ($\hat{\theta}$) were therefore weighted by the proportion of single- and double-tagged animals in a sample by:

$$\hat{\theta} = 1 - (p_1 T_1 + p_2 T_1^2)$$

where p_1 is the proportion of seals in the sample which had a single tag, p_2 is the proportion which had two tags, and T_1 is the probability of losing one tag.

Population age structure

The population age structure at the time of the study was estimated from the age distribution of resident females captured between 2000 and 2003. To represent the age structure at the birth pulse, females captured in winter were “re-sampled” at the first breeding season following capture. Although this slightly reduced the sample size, due to tag loss and or mortality, age distributions were largely unaffected. Interpretation of the age distribution assumed that sampling of the mature population was random. However, achieving a random sample in the present study was confounded by the problem of age-structuring within the breeding colony. As the population has been increasing, younger animals have generally occupied the most recently established breeding areas (Goldsworthy and Shaughnessy 1994; McKenzie unpublished data). Females were therefore sampled in proportion to the number of pups born in each of the breeding areas (referred to as “sectors” in Shaughnessy et al. 1995). All sectors of the breeding area were sampled except for one small sector (< 2% of total pup production), due to problems of accessibility. Establishment of new sectors and pup numbers within each sector have been monitored by direct counts and mark-recapture since 1988 (Shaughnessy 2006).

Life table analysis

To describe the general pattern of mortality for the population a survival curve was developed by fitting a modified Siler competing-risk model (Eberhardt 1985) to age-specific survival data using non-linear least squares regression. This model was chosen as it has been shown to adequately fit the expected mortality patterns of a wide range of long-lived animals including marine mammals (Siler 1979; Eberhardt 1985;

Barlow and Boveng 1991; Stolen and Barlow 2003). Siler's (1979) three component competing-risk model separates mortality processes into three major life stages: an exponentially decreasing risk due to immature or early mortality factors, a constant risk through the mature stage, and an exponentially increasing risk due to senescent mortality factors. Survival to age x (l_x) is given as the product of the three competing risks and can be written following Eberhardt (1985) as:

$$l_x = \exp[-a_1(1 - e^{-b_1x}) - a_2x - a_3(e^{b_3x} - 1)]$$

where a_1 and b_1 are the coefficients for the immature hazard, a_2 relates to the mature hazard, and a_3 and b_3 are the coefficients for the senescence component. Because data on juvenile mortality were absent in the present study, the above function was modified following Eberhardt (1985) and fitted to age classes ≥ 4 yrs of age. Survival (l_x) of adult females to age x was therefore described by:

$$l_x = \exp[-a_1 - a_2x - a_3(e^{b_3x} - 1)]$$

where the single coefficient a_1 represents survival through the early stage of mortality.

Because juvenile and sub-adult age classes (which included both immature and mature individuals) were under-represented in the sample, age classes 1-5 years were treated as missing. Expected survival rates of 4 and 5 year olds were based on observed annual survival rates of juvenile female subantarctic fur seals (*Arctocephalus tropicalis*) prior to their first breeding (0.964) as measured by Beauplet et al. (2005). Survival from birth to 4yrs was estimated as 0.50 also based on Beauplet et al.'s (2005) study. These values were used because subantarctic fur seals display a maturation pattern similar to that of the New Zealand fur seal (Chapter 4; Bester 1995; Dabin et al. 2004; McKenzie et al. in press b) and the population of subantarctic fur seals on which survival estimates were based was considered stationary (Guinet et al. 1994; Beauplet et al. 2005). Goodness of fit was evaluated by examination of parameter standard errors and visual inspection of residuals (Quinn and Keough 2003).

To check that the estimated parameters approximated the true demographic parameters at the time of measurement, the rate of population change (r_s) implied by the estimated schedule of survival and fecundity was calculated and compared to the rate of population growth inferred from the observed rate of increase in pup numbers (r)

measured over the same time period. Calculation of r_s (survival-fecundity rate of increase) followed Caughley (1980) by interpolation of values of r_s to balance the equation:

$$\sum l_x e^{-r_s x} m_x = 1$$

RESULTS

Parturition period

Births occurred between mid-November and late-January in all years with a peak in births in late December. Over the 4 year study one tagged female gave birth to a live pup in early October 2001. The pup was fully developed and was last observed with its mother in September the following year (~1 yr old). Live births outside the breeding season were otherwise rare, although aborted fetuses or stillborns were frequently observed between August and December. Most births (90%) occurred over a 43 ± 3.3 (SD) day period, with a median date of 26 December (Table 1). Median birth dates calculated for the overall population were similar but slightly later than the mean date of parturition for tagged females monitored over the 4 years. There was no difference in the mean date of parturition between years (Analysis of variance $F = 0.234$, $df = 3$, $P = 0.874$).

Table 1. Parturition period for New Zealand fur seals at Cape Gantheaume for 2000 to 2003 calculated for tagged females and total population based on daily pup counts during the breeding season. Values are \pm SD (sample size).

	Breeding season			
	2000-2001	2001-2002	2002-2003	2003-2004
Tagged females				
Mean	23 Dec \pm 6.6 (18)	22 Dec \pm 11 (89)	23 Dec \pm 10 (124)	22 Dec \pm 10 (134)
Overall population				
Median	26 Dec \pm 12	26 Dec \pm 14	25 Dec \pm 12	26 Dec \pm 14
90% births (days)	39	46	41	45

Annual and age-specific reproductive rates

The proportion of reproductively mature females that pupped varied significantly between years (Chi-square $\chi^2 = 77.47$, $df = 3$, $P < 0.001$, $n = 586$). Reproductive rates were lowest in 2000-2001 (26.5%), intermediate in 2001-2002 and 2002-2003 (58.6% and 65.8% respectively), and highest in 2003-2004 (85.2%). Excluding data from 2000-2001, the average rate (\pm SD) measured over 3 seasons was $69.9 \pm 13.8\%$ for mature females and $76.9 \pm 13.1\%$ for prime-aged females (8-13 yrs). Overall young mature females (5-7 yrs) and older females (≥ 14 yrs) showed significantly lower reproductive rates (46.7% and 55.4% respectively) than prime-age females (8-13 yrs: 72.3%) ($\chi^2 = 24.17$, $df = 2$, $P < 0.001$, $n = 586$). However, age-specific reproductive patterns differed both within and between years (Fig. 2). The proportion of prime-age females that pupped in 2001-2002 and 2002-2003 was similar (70.5% and 68.3% respectively), but significantly lower than the proportion that pupped in 2003-2004 (92.0%), and higher than the proportion that pupped in 2000-2001 (33.3%) ($\chi^2 = 45.56$, $df = 3$, $P < 0.001$, $n = 358$). In contrast, the proportion of older females that pupped appeared to increase steadily over consecutive years, with a significant increase between 2001-2002 and 2002-2003 (39.0% to 62.0% respectively; $\chi^2 = 4.76$, $df = 1$, $P = 0.029$, $n = 91$). Among younger females the proportion pupping also increased each year over the course of the study. In contrast to the older age group, the greatest increase in reproductive rates of younger females was observed between 2002-2003 and 2003-2004 (58.8% and 100% respectively; Fisher's Exact test $P = 0.023$, $n = 28$) and rates in 2001-2002 (31.3%) and 2002-2003 (58.8%) were not significantly different ($\chi^2 = 2.53$, $df = 1$, $P = 0.112$, $n = 33$).

Excluding data from 2000-2001, age-specific reproductive rates were low at 5 years of age (50%), increased to maximum rates (70-81%) between 8-13 years, and decreased in older females (≥ 14 yrs) (Fig. 3, Table 2). The relationship between reproductive rate and age was best described by a quadratic model ($r^2 = 0.61$) (Fig 3). Mean fecundity (female births per female) for the age classes over which reproductive rates were approximately constant (8-13 yrs) was 0.362.

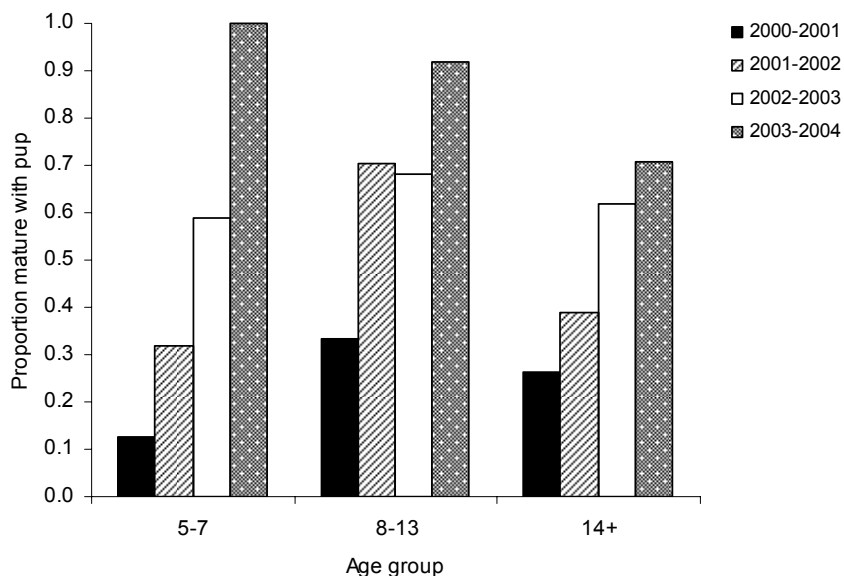


Fig. 2. Annual variation in the reproductive rates of young (5-7 yrs), prime-age (8-13 yrs) and older (14-25 yr) New Zealand fur seal females monitored at Cape Gantheaume. Numbers of resident adult females sampled each year were; 2000-2001 = 68, 2001-2001 = 162, 2002-2003 = 187, and 2003-2004 = 169.

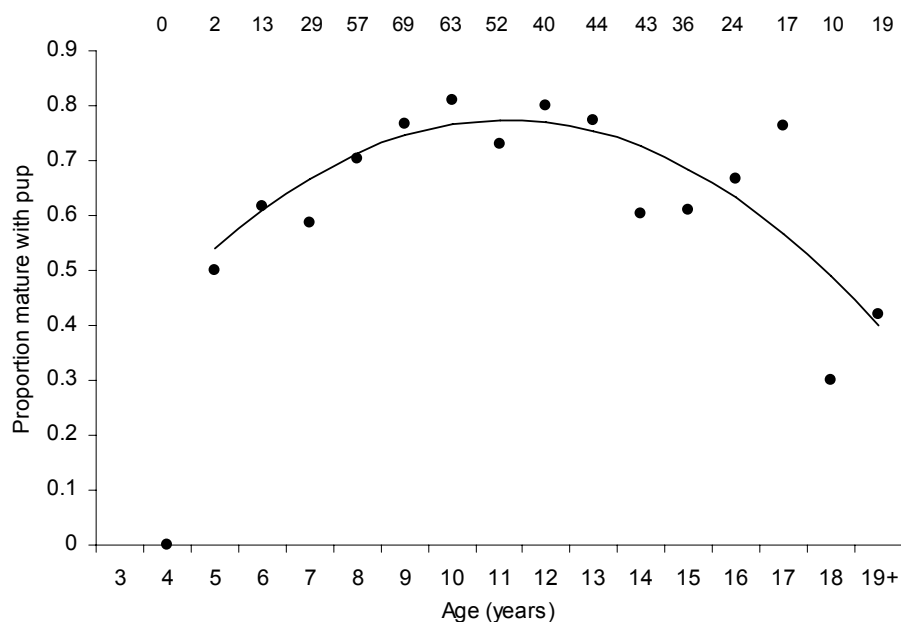


Fig. 3. Age specific reproductive rates for New Zealand fur seals at Cape Gantheaume, pooled over three years (2001-2003). Data for females 19-25 years of age are pooled. Sample sizes are shown at the top of the graph. The regression equation is $y = 0.00915x + 0.137x - 0.00613x^2$.

Table 2. Age-specific proportions reproductively mature for New Zealand fur seals at Cape Gantheaume (Chapter 4; McKenzie et al. in press b) and reproductive rates of mature females pooled over three years (this study) at Cape Gantheaume. SE is standard error and n is sample size. Predicted values from the fitted curves (see text).

Age x	Proportion mature (Px)	SE	n	Predicted Px	Reproductive rate (Rx)	SE	n	Predicted Rx
0								
1	0.00		4	0				
2	0.00		4	0				
3	0.00		8	0				
4	0.20	0.13	10	0.18				0.46
5	0.65	0.12	17	0.66	0.50	0.35	2	0.54
6	0.97	0.03	35	0.94	0.62	0.13	13	0.61
7	0.96	0.03	50	0.99	0.59	0.09	29	0.67
8	1.00		25	1.00	0.70	0.06	57	0.71
9	1.00		29	1.00	0.77	0.05	69	0.75
10	1.00		22	1.00	0.81	0.05	63	0.77
11	1.00		20	1.00	0.73	0.06	52	0.77
12	1.00		28	1.00	0.80	0.06	40	0.77
13	1.00		27	1.00	0.77	0.06	44	0.75
14	1.00		13	1.00	0.60	0.07	43	0.73
15	1.00		15	1.00	0.61	0.08	36	0.68
16	1.00		7	1.00	0.67	0.10	24	0.63
17	1.00		9	1.00	0.76	0.10	17	0.57
18	1.00		2	1.00	0.30	0.14	10	0.49
19+	1.00		3	1.00	0.42	0.11	19	0.40

Early pup mortality (0-30 days)

By the end of each breeding season census period (22 January), pups of known birth date ranged in age from 0 to 60 days (mean age 30.4 ± 9.9 (SD) days, $n = 365$). Pup mortality until the end of the breeding season ranged from 9.6-22.2% over the four breeding seasons (Table 3). The proportion of pups monitored that died by the end of the breeding season was not significantly different between years ($\chi^2 = 2.87$, $df = 3$, $P = 0.412$, $n = 375$). However, the number of pups monitored in 2000-2001 was small. Mean survival from birth to the end of the breeding season was 0.86 (SE = 0.05). Over all years, of the 375 pups monitored, 12.0% ($n = 45$) had died by the end of the breeding season. The distribution of age at death of pups did not differ between years (Kruskal-Wallis test $\chi^2 = 1.74$, $df = 3$, $P = 0.629$, $n = 45$). Of the 45 deaths recorded, 33.3% ($n = 15$) died within the first day of life, 84.4% ($n = 38$) within the first 12 days of life, and 95.6% ($n = 43$) within the first 17 days of life. Mortality rates of pups between ~1.5 months of age and weaning at 9-10 months (Table 3) were calculated in the Beach Sector of the colony over 3 yrs during a concurrent study by Haase et al. (in review). Combining the mortality rates, estimated mortality of pups from birth to weaning varied from 0.21-0.36 among years, with a mean survival rate of ~ 0.73 from birth to weaning (~9.8 months of age; Haase 2005).

Table 3. Pup mortality for New Zealand fur seals at Cape Gantheaume. Sample sizes of pups monitored are in parentheses.

Age	Breeding season			
	2000-2001	2001-2002	2002-2003	2003-2004
Birth to 22 January (mean age 30 days)	0.222 (18)	0.096 (94)	0.106 (123)	0.136 (140)
Birth to 15 days	0.222 (18)	0.090 (89)	0.103 (117)	0.134 (134)
Birth to 30 days	0.182 (11)	0.098 (51)	0.078 (64)	0.113 (80)
~1.5 months to weaning ¹	0.14	0.15	0.10	

¹ Values from Haase et al. (in review).

In most years, early pup mortality was related to indices of female condition in the preceding gestation period. Early pup mortality (0-15 days and 0-30 days) was not significantly correlated with reproductive rate of adult females when all years were considered (Pearson correlations 0-15 days $P = 0.299$ and 0-30 days $P = 0.270$). However, with the exclusion of data from 2003-2004, when reproductive rates were highest, early pup mortality (0-30 days) was negatively correlated with reproductive rates of adult females in concurrent years (linear regression $r^2 = 1.000$, $F = 11560.017$, $df = 2$, $P = 0.006$). A similar relationship was suggested by comparison of early pup mortality with measures of reproductive failure over the preceding gestation period. Estimates of early and mid-late term reproductive failure were available for 2000, 2001 and 2002 (Chapter 3; McKenzie et al. 2005a). Early pup mortality rates for both 0-15 days and 0-30 days approached a significant positive correlation with mid-late term reproductive failure in the preceding gestation period (0-15 days: $r^2 = 0.986$, $F = 68.332$, $df = 2$, $P = 0.077$; 0-30 days: $r^2 = 0.977$, $F = 43.020$, $df = 2$, $P = 0.096$). When incorporating early reproductive failure (implantation and early active gestation failure), early pup mortality (0-30 days) was strongly positively correlated with reproductive failure in the preceding gestation period ($r^2 = 1.000$, $F = 18849.613$, $df = 2$, $P = 0.005$). These observations suggest that in some years early pup mortality is strongly influenced by the condition of females during the preceding gestation period. In contrast, early pup mortality (0-15 days and 0-30 days) was not significantly correlated

with pup abundance estimates adjusted for measured mortality when all years were considered (0-15 days: $P = 0.612$ and 0-30 days: $P = 0.578$), nor with the exclusion of 2000-2001 (0-15 days: $P = 0.164$ and 0-30 days: $P = 0.407$), which suggested that pup mortality was not density-dependent.

Annual and age-specific survival rates of breeding age females

Of 243 reproductively mature females tagged over three winters, 222 individuals were resighted in at least one breeding season following marking. Assuming survival of adult females was independent of age, annual survival rates of the breeding population were estimated from data pooled across age classes. Starting with the full time dependent model (Table 4, model 2), there was no significant effect of year (time) on recapture probability (models 1 vs. 2; LRT $\chi^2 = 1.34$, $df = 1$, $P = 0.246$), but a model with time effect on survival had approximately 22-times more support than one of constant survival (model 1 vs. 3; $\Delta AICc > 2$). Survival rates based on the time variable survival model (model 1) ranged from 0.782 to 0.915 after correction for tag loss (Table 5). The mean annual survival rate of breeding age females between 2000 and 2003 was 0.853 (SE = 0.021) and 0.856 after correction for tag loss. Recapture rate of adult females over the study period was estimated to be constant and high (0.986, SE = 0.010), suggesting high precision of survival estimates for the marked population.

Table 4. Results of model selection using program MARK and resight data for tagged resident adult female New Zealand fur seals at Cape Gantheaume, 2000 to 2003. Models are ranked according to their Akaike weights (AICc W). Values are Akaike's Information Criterion (AICc), difference in AICc (Δ AICc) between models and number of parameters (No. Par.).

Model ¹	AICc	Δ AICc	AICc W	No. Par.
Modeling annual survival rate				
1 S(t) p(.)	358.754	0.000	0.563	4
2 [#] S(t) p(t)	359.462	0.708	0.395	5
3 S(.) p(.)	364.976	6.222	0.025	2
4 S(.) p(t)	365.830	7.076	0.016	4
Testing for senescence				
1 S(AG+t) p(.)	305.615	0.000	0.429	5
2 S(AG*t) p(.)	307.333	1.718	0.182	7
3 S(AG) p(.)	308.088	2.473	0.125	3
4 S(AG*t) p(t)	308.106	2.491	0.124	8
5 S(AG*t) p(AG)	308.989	3.374	0.079	8
6 S(t) p(.)	310.602	4.987	0.035	4
7 [#] S(AG*t) p(AG*t)	311.914	6.299	0.018	10
8 S(.) p(.)	313.649	8.034	0.008	2

¹ See methods for model nomenclature.

[#] Global (starting) model.

In modelling possible differences in survival between prime-age and older females, there was no significant effect of time (Table 4, model 2 vs. 4), age group (model 2 vs. 5) or the term for the interaction between time and group (model 2 vs. 7) on recapture probability. The top three models based on AICc all indicated that age group had a significant effect on survival probability. Examination of parameter estimates from the model with group effect alone (model 3), indicated that average survival of prime-age females (0.867, SE = 0.024) was higher than that of older females (0.733, SE = 0.046), suggesting senescence at older age classes. However, within each group, survival also varied between years (model 2 vs. 3; $\chi^2 = 9.05$, df = 4, $P = 0.0598$). Incorporation of an additive effect of time and age group (model 1 vs 3; $\chi^2 = 6.53$, df = 2, $P = 0.037$) improved the model, suggesting parallelism in survival rates of prime-age and old females overtime. Following adjustment for tag loss, apparent survival rates of prime-age and older females ranged from 0.813 to 0.918 and 0.644 to 0.818, respectively (Table 5).

Table 5. Annual survival rates of mature New Zealand fur seal females at Cape Gantheaume based on resight data of tagged animals between the 2000-2001 and 2003-2004 breeding seasons. S_{xc} are survival rates corrected for tag loss, S_x are uncorrected survival estimates, SE are standard errors, CI are confidence intervals and n is sample size.

Year	S_{xc}	S_x	SE	95% CI	n
Overall annual adult survival					
2001	0.847	0.844	0.046	0.731 - 0.915	63
2002	0.782	0.779	0.034	0.705 - 0.838	149
2003	0.915	0.911	0.024	0.850 - 0.997	177
Prime age (8-13 yrs) females					
2001	0.886	0.883	0.045	0.762 - 0.946	30
2002	0.813	0.810	0.040	0.720 - 0.876	79
2003	0.918	0.914	0.027	0.844 - 0.954	101
Older age (14+ yrs) females					
2001	0.761	0.761	0.078	0.578 - 0.881	18
2002	0.644	0.644	0.066	0.507 - 0.760	39
2003	0.818	0.817	0.053	0.691 - 0.899	38

Age-specific survival rates based on mark-recapture histories pooled across years ranged from 0.655 to 0.947 (Table 6). Survival rates generally declined with increasing age. Survival rates were above average among 7-13 yr olds (0.947 – 0.818) and lowest among 17-24 yr olds (0.655, SE = 0.087). Available data suggested survival rates were low among 6 yr olds (0.800, SE = 0.103), which may indicate a drop in survival among early age breeders. However, the estimate is subject to substantial sampling error due to small sample size. Sample sizes of females < 6 yrs were too sparse for analysis. No females in the sample were resighted beyond 25 years of age.

Table 6. Age-specific annual survival rates (S_x) of adult female New Zealand fur seals at Cape Gantheaume using return rates. S_{xc} are survival rates corrected for tag loss, S_x are uncorrected survival estimates, SE are standard errors, CI are confidence intervals and n is sample size.

Age x	S_{xc}	S_x	SE	95% CI	n
4	-	-			
5	-	-			
6	0.803	0.800	0.103	0.530 - 0.934	15
7	0.940	0.931	0.047	0.762 - 0.983	29
8	0.953	0.947	0.030	0.849 - 0.983	57
9	0.835	0.830	0.055	0.695 - 0.913	47
10	0.823	0.818	0.058	0.677 - 0.906	44
11	0.913	0.909	0.050	0.753 - 0.970	33
12	0.931	0.929	0.049	0.755 - 0.982	28
13	0.835	0.833	0.068	0.657 - 0.929	30
14	0.758	0.757	0.071	0.595 - 0.868	37
15	0.762	0.762	0.093	0.540 - 0.897	21
16	0.790	0.789	0.094	0.554 - 0.919	19
17+	0.656	0.655	0.087	0.471 - 0.802	29

Relationships between vital rates and pup production

The relative change in pup numbers observed over the study period (Fig. 4) was positively correlated with reproductive rates of prime-age females (linear regression $r^2 = 0.933$, $F = 27.753$, $df = 3$, $P = 0.034$), approached a significance linear correlation with reproductive rates of all females combined ($r^2 = 0.838$, $F = 10.334$, $df = 3$, $P = 0.085$), but not those of young or old age groups (all $P \geq 0.20$). Relative change in pup numbers was also strongly correlated with survival rates of adult females (≥ 7 yrs of age) over the year prior to the breeding season (linear regression $r^2 = 1.000$, $F = 2208.958$, $df = 2$, $P = 0.014$), and both survival of prime-age and older females approached an exponential relationship with relative change in pup numbers ($r^2 = 0.988$, $F = 79.323$, $df = 1$, $P = 0.071$ and $r^2 = 0.981$, $F = 52.591$, $df = 1$, $P = 0.087$ respectively).

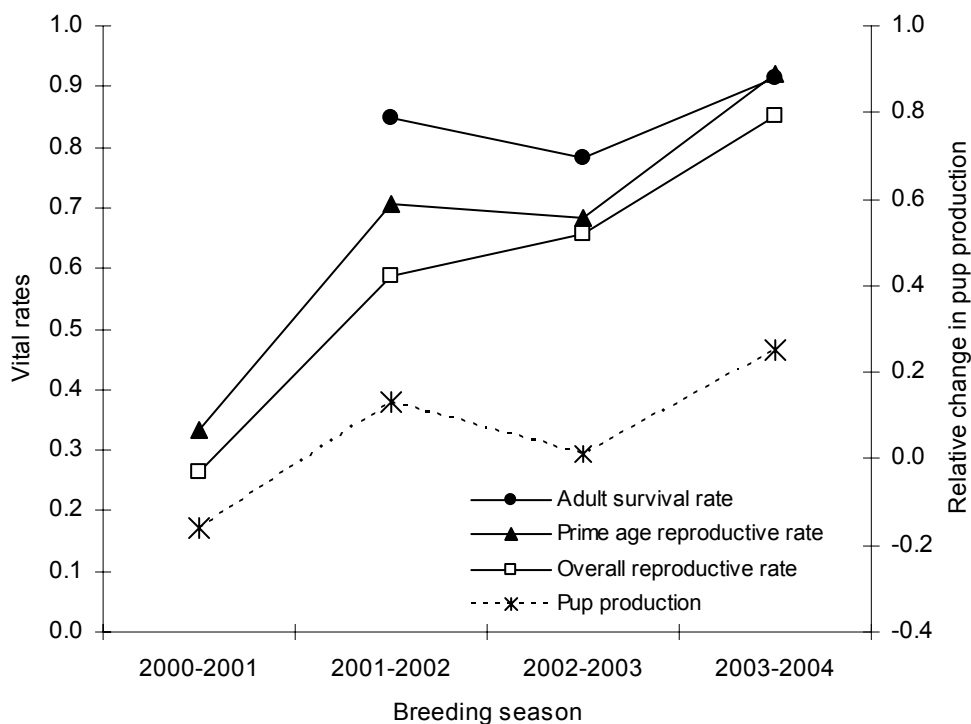


Fig. 4. Relationships between relative change in pup production and variation in vital rates of mature age New Zealand fur seal females at Cape Gantheaume, 2000-2003. Relative change in pup production was calculated based on pup abundance at the end of the breeding season as calculated by Shaughnessy (2006), adjusted for early pup mortality (this study). Survival rates correspond to the periods between breeding seasons.

Adult female age structure

The mean age (\pm SD) of mature females sampled in 2000-2001 (10.8 ± 3.6 , $n = 72$) and 2001-2002 (11.3 ± 3.6 , $n = 104$) was slightly higher than the mean age of females sampled in 2002-2003 (10.2 ± 3.2 , $n = 69$). However, the overall distribution of ages did not differ significantly between years (Kruskal-Wallis Test $\chi^2 = 4.284$, $df = 2$, $P = 0.117$, $n = 244$). This result suggests the age distribution may have been relatively stable during the study period. However, annual cross-sectional age samples were small and subject to an unknown level of sampling error due to age-structuring of the colony. There may therefore be insufficient power to detect any significant shifts in age distribution.

On a broad scale the age composition appears to fluctuate between years, with the ratio of prime-age females to young females varying among years (Table 7). As the reproductive rates of prime-age females are considerably higher than those of younger or older females (Fig. 3), the number of prime-age females in the population will have a large effect on the number of pups produced each year. Although the proportion of prime-age females sampled in each of the 3 seasons was not significantly correlated with the relative change in pup numbers ($P = 0.417$), the proportion of prime-age and older females combined was positively correlated (linear regression $r^2 = 0.997$, $F = 316.901$, $df = 2$, $P = 0.036$). Although some variation in the proportion of mature females ≥ 8 yrs sampled is likely to have resulted from sampling biases between years, the shift closely reflects the observed change in pup production.

Table 7. Age structure of adult female New Zealand fur seals resighted at Cape Gantheaume in the first breeding season following their initial capture. Sample sizes n are indicated in parentheses.

Age group	Breeding season		
	2000-2001	2001-2002	2002-2003
	%	%	%
Young (5-7 yrs)	22.5 (16)	13.5 (14)	17.4 (12)
Prime (8-13 yrs)	49.3 (35)	61.5 (64)	65.2 (45)
Older (≥ 14 yrs)	28.2 (20)	25.0 (26)	17.4 (12)
Total n	71	104	69

To describe the general age structure of the mature female population and to reduce any deviations from a stable age distribution due to annual variation in births and deaths, summer age distributions sampled over the three years were pooled. The pooled age distribution of mature resident females reflected the three different life-history stages of adult females (Fig. 5). The proportions of mature 5-7 year olds were low, but steadily increasing with age, reflecting the gradual recruitment of females into the breeding population over a number of age classes. The most frequently sampled age class (8 yrs) corresponded to the age by which all females are considered fully recruited into the breeding population (Chapter 4; McKenzie et al. in press b).

Prime-age females made up the greatest proportion of the age distribution and numbers rapidly declined among the older age classes (Fig. 5). The mean age of adult females in the pooled sample was 10.8 ± 3.5 yrs (SD).

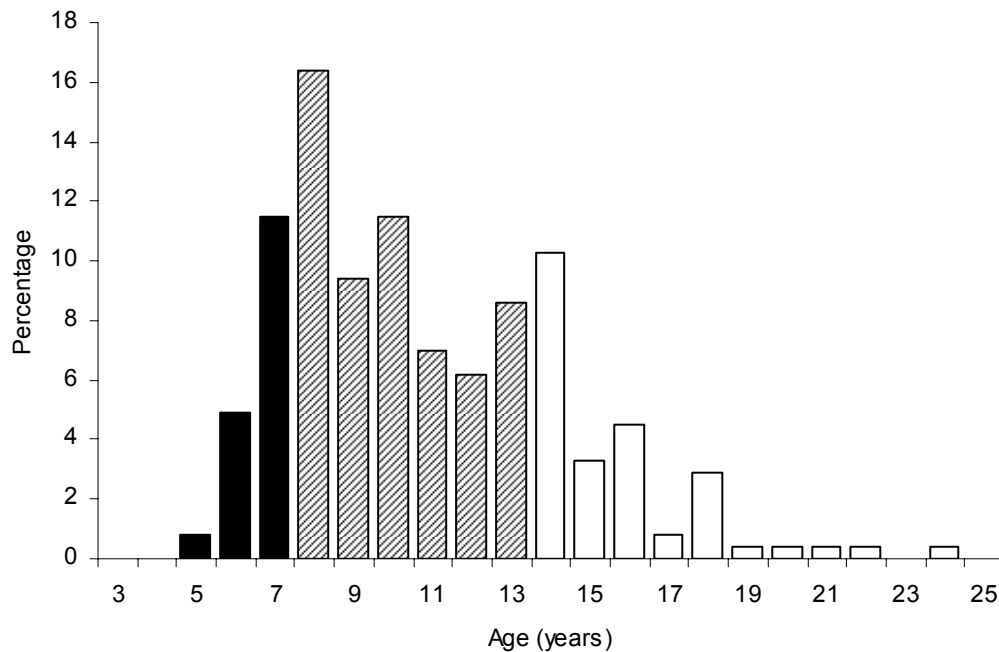


Fig. 5. Pooled age distribution of mature female New Zealand fur seals sampled over three breeding season at Cape Gantheaume, 2000-2001 to 2002-2003 ($n = 244$). Shading indicates the three major life-stages of breeding age females: recently mature young females (black bars), prime-age females (hatched) and senescent older female (white).

Life table analysis

Age-specific rates of survival calculated from mark-recapture data were used to generate the model life table. Due to the large standard error around the survival rate of 6 year olds, the expected rate was initially set equal to that observed for 7 year olds (0.940). The maximum likelihood fit of the modified Siler model to age classes ≥ 4 years adequately described the available data (Fig. 6). Estimated parameters for the modified Siler function are presented in Table 8, and predicted values of age-specific survival and mortality rates are presented in Table 9. Fecundity in the life table is based on the smoothed proportion of mature and reproductive rates in Table 2. Fecundity for females ≥ 19 yrs was assumed constant at 0.200.

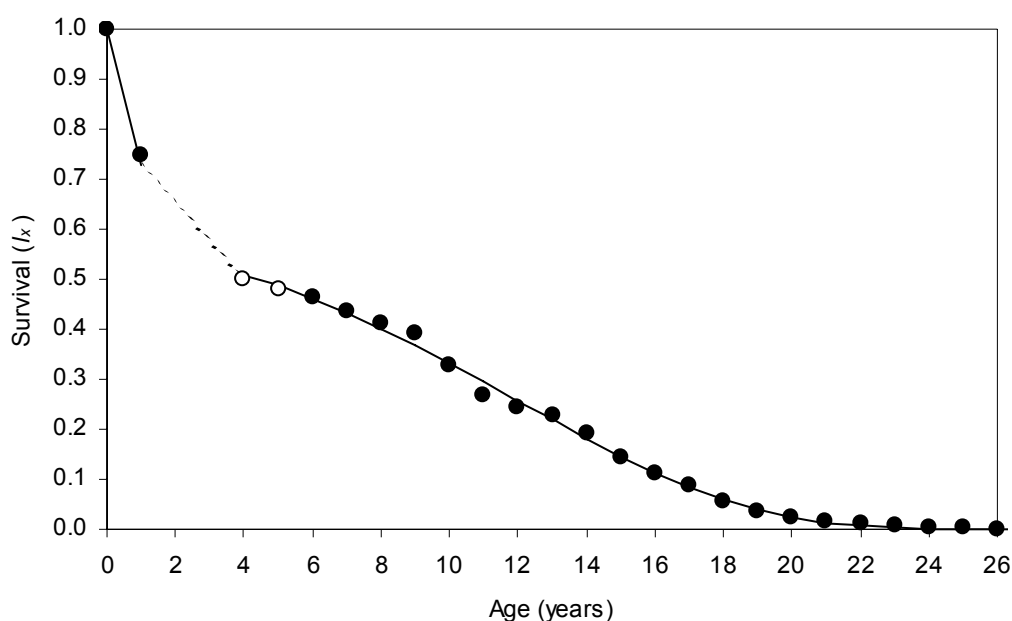


Fig. 6. Survival (I_x) curve for female New Zealand fur seals at Cape Gantheaume, 2000-2003, based on maximum likelihood fit of a modified Siler model to survival data for mature age animals (4-25 yrs). Closed circles indicate estimates derived from measured survival rates and open circles indicate values based on estimated survival rates (see text).

Table 8. Parameter estimates for the modified Siler model fitted to New Zealand fur seal survival data for mature age animals (4-25 yrs).

a_1	a_2	a_3	b_3
0.5475	0.0000	0.1480	0.1555

The population rate of increase implied by the modelled age-specific survival and fecundity pattern in Table 9 was $r_s = 0.0265$, suggesting the population's capacity for growth at the time of measurement was low (~3% per annum). This result is in close agreement with low rate of growth indicated by pup censuses over the same period 1999-2003 (Fig 1): ~5% per annum (pup numbers adjusted for early mortality). Similarities between estimated rates of population growth suggest the life-history parameters in the present study are in close approximation to the true parameters for the population at the time of measurement.

Table 9. Life table for female New Zealand fur seals based on maximum likelihood fit of a modified Siler model to population parameters for ages 4-25 yrs, measured between 2000 and 2003. Survival to age 1yr is estimated survival to weaning at 8-11 months and is likely to be positively biased. Survival to age 4yrs and annual survival rates for ages 4 and 5 are estimated based on reported rates for subantarctic fur seals (Beauplet et al. 2005).

Age x	Probability of survival (l_x)	Probability of dying (d_x)	Mortality rate (q_x)	Survival rate (p_x)	Fecundity (m_x)	$l_x m_x$
0	1.000	(0.27)	(0.27)	(0.73)	0.000	0.000
1	(0.73)				0.000	0.000
2					0.000	0.000
3					0.000	0.000
4	0.509	0.023	0.045	0.955	0.041	0.021
5	0.486	0.026	0.053	0.947	0.178	0.087
6	0.460	0.028	0.061	0.939	0.287	0.132
7	0.432	0.031	0.071	0.929	0.331	0.143
8	0.401	0.033	0.083	0.917	0.356	0.143
9	0.368	0.035	0.096	0.904	0.373	0.137
10	0.333	0.037	0.111	0.889	0.383	0.127
11	0.296	0.038	0.129	0.871	0.387	0.115
12	0.258	0.038	0.149	0.851	0.385	0.099
13	0.219	0.038	0.171	0.829	0.377	0.083
14	0.182	0.036	0.197	0.803	0.363	0.066
15	0.146	0.033	0.226	0.774	0.342	0.050
16	0.113	0.029	0.259	0.741	0.316	0.036
17	0.084	0.025	0.295	0.705	0.283	0.024
18	0.059	0.020	0.336	0.664	0.245	0.014
19	0.039	0.015	0.380	0.620	0.200	0.008
20	0.024	0.010	0.428	0.572	0.200	0.005
21	0.014	0.007	0.479	0.521	0.200	0.003
22	0.007	0.004	0.533	0.467	0.200	0.001
23	0.003	0.002	0.589	0.411	0.200	0.001
24	0.001	0.001	0.647	0.353	0.200	0.000
25	0.000	0.000	0.703	0.297	0.200	0.000
26	0.000	0.000	0.758	0.242	0.200	0.000
27	0.000	0.000	0.809	0.191	0.200	0.000
28	0.000	0.000	1.000	0.000	0.200	0.000

DISCUSSION

Age-specific reproductive patterns in New Zealand fur seals

Female New Zealand fur seals exhibited age-specific reproductive patterns similar to those reported for other fur seal species (Lander 1981; York 1987; Trites 1991; Lunn et al. 1994; Bester 1995; Boyd et al. 1995; Lima and Páez 1995; Arnould et al. 2003; Dabin et al. 2004). In the population studied, the average age at first birth was ~5 yrs, although females did give birth to their first pup as early as 4yrs or as late as 8 yrs (Chapter 4; McKenzie et al. in press b). Reproductive rates increased rapidly from age at first parturition to ~8 yrs of age and remain relatively constant at 70-81% until ~13 yr of age, before declining during a period of apparent reproductive senescence. A decline in the reproductive performance of older females has also been documented for the northern (*Callorhinus ursinus*), South American (*Arctocephalus australis*), Cape (*Arctocephalus pusillus pusillus*), Australian (*Arctocephalus pusillus doriferus*), Antarctic (*Arctocephalus gazella*) and subantarctic fur seals (Trites 1991; Lunn et al. 1994; Butterworth et al. 1995; Lima and Páez 1995; Arnould et al. 2003; Dabin et al. 2004).

In the present study, reproductive rates in older females started to decline around 13 years of age, with no females recorded pupping beyond 22 yrs of age, although females are known to live to at least 25 yrs (Chapter 4; McKenzie et al. in press b). Examination of reproductive tracts of New Zealand fur seals caught as fisheries bycatch in New Zealand also identified a 22 yr old that appeared to be post-reproductive (Dickie and Dawson 2003). In the northern fur seal, Trites (1991) attributed the apparent decrease in size of older females and their foetuses to a general decrease in body condition of females as they age (senesce). In the New Zealand fur seal, cessation of growth is predicted from age-growth curves at ~13 yrs (Chapter 5; McKenzie et al. in press a) and this corresponds to the age at which a decline in reproductive and survival rates becomes apparent in older females. Cessation of growth may therefore mark the commencement of senescence both physically and reproductively.

Lower reproductive rates among younger females have been reported in a number of pinniped species and are commonly associated with smaller size and poorer body condition of younger females, or with inexperience of primiparous animals (Clutton-Brock et al. 1983; Huber 1987; Reiter and Le Boeuf 1991; Lunn and Boyd

1993b; Lunn et al. 1994; Boyd et al. 1995). In this study, I did not distinguish between primiparous and multiparous females in age class samples or nor did I examine individual reproductive histories. However, based on cross-sectional samples, age at reproductive maturity in New Zealand fur seals appears to be correlated in part with body size and condition (Chapter 4; McKenzie et al. in press b). In addition, although growth slows after sexual and reproductive maturity at 4-5 yrs of age, females appear to continue to grow in length until ~ 9 years of age based on cross-sectional data (Chapter 5; McKenzie et al. in press a), which corresponds to the age at which peak reproductive performance is reached. This suggests that size and/or condition of younger females and the continued cost of growth and development may influence reproductive success over a number of years.

Compared to reproductive rates among both younger and older females, reproductive rates of prime-age females appeared to show the least annual variation, suggesting that the reproductive rates of prime-age females may be less sensitive to environmental fluctuations relative to those of younger or older females. Given that body size also influences diving ability among seals (Kooyman 1989; Mori 2002), younger, smaller females may be restricted in their capacity to obtain sufficient resources to meet the energetic demands of both gestation and lactation. Shifts in the distribution or abundance of prey may therefore have greater effect on younger animals. However, little is known of the effect of increasing age on foraging ability in pinnipeds, which may also affect reproductive performance in older females. Overall, reproductive rates among young females were typically lower than those of prime-age and older females, although this pattern appeared to differ between years. While variation in reproductive success between age groups or individuals may be largely influenced by intrinsic factors such as age, size or experience, the relative costs of reproduction in a given year are also likely to be influenced by extrinsic factors such as prey availability and distribution. In both the present study and the growth study, analysis was based on cross-sectional data rather than individual life-histories. If larger, later maturing females lived longer than smaller, earlier maturing females, the age-specific patterns described may be largely a consequence of size- and reproductive-survival biases rather than reflecting significant changes in individual patterns of reproduction and growth with age. Examination of longitudinal reproductive histories and the response of individuals to varying environmental conditions are required to clarify reproductive patterns over the life time of individuals.

Annual reproductive rates in the population varied from 27-85%. With the exclusion of data from 2000-2001, the average rate measured over 3 seasons was 70% for mature females and 77% for prime-aged females (8-13 yrs). At the same colony in 1989-1991, Goldsworthy and Shaughnessy (1994) reported an average rate of 67%, which falls within the range reported for 2000-2003. Reproductive rates in terms of birth rates have only been reported for a few other otariid species and range from 48-88% (Higgins and Gass 1993; Lunn et al. 1994; Boyd et al. 1995; Wickens and York 1997; Dabin et al. 2004). In most other pinniped studies, reproductive rates are based on pregnancy rates rather than estimates of live births and are therefore likely to overestimate birth rates to some extent due to prenatal mortality (Chapter 3; Pitcher and Calkins 1981; Wickens and York 1997; McKenzie et al. 2005a). Published pregnancy rates for other otariids range from 52-97% (Bester 1995; Lima and Páez 1995; Wickens and York 1997; Pitcher et al. 1998; Odendaal et al. 2002; Arnould et al. 2003). For comparison, annual post-implantation pregnancy rates based on progesterone levels in mature New Zealand fur seals, ranged from 68.6-96.2% (Chapter 3; McKenzie et al. 2005a), which covers most of the values previously reported for other otariid species. However, reported rates may vary considerably depending on the stage of gestation at which measurements were taken (Chapter 3; McKenzie et al. 2005a). Substantial variation in annual reproductive and pregnancy rates within individual populations have also been reported for other pinnipeds and are commonly associated with temporal variation in food availability (Testa 1987; Reiter and Le Boeuf 1991; Trillmich and Ono 1991; Lunn and Boyd 1993a; Lunn et al. 1994; Guinet et al. 1998; Pitcher et al. 1998). In a population of South American fur seals sampled over an 8 year period, annual pregnancy rates ranged from 52-82% (Lima and Páez 1995) and for Antarctic fur seals at South Georgia reproductive rates ranged from 60-88% over an 11 yr period (Lunn et al. 1994; Boyd et al. 1995).

Age-specific survival patterns in New Zealand fur seals

In long-lived mammals, age-specific mortality is typically characterised by initially high but rapidly decreasing juvenile mortality, followed by relatively low but steadily increasing adult mortality particularly at older ages (Caughley 1966; Spinage 1972; Siler 1979; Eberhardt 1985). In the few studies with sufficient data, marine mammals have also shown this general pattern (Lander 1981; Barlow and Boveng 1991; York 1994; Stolen and Barlow 2003). Although the life table presented in this study lacks data on juvenile survival, mortality rates in New Zealand fur seals demonstrated a

similar pattern with high mortality among pups, lower mortality among prime-age females and increasing mortality evident among older animals.

Pup survival

Mean pup survival from birth to the end of the breeding season in the present study was 0.86, with an interannual range of 0.78-0.90, and within the ranges reported for other fur seal species (Boyd et al. 1995; Wickens and York 1997; Chambellant et al. 2003). In accordance with other otariid studies, most mortality occurred within the first month (DeVilliers and Roux 1992; Harcourt 1992; Trites 1992; Georges and Guinet 2000), with 84% of deaths occurring within the first 12 days of life in the present study. Survival estimates from birth to the end of the breeding season were also consistent with previously reported estimates for New Zealand fur seal pups (0.86: Miller 1974; 0.79: Mattlin 1978b; 0.92: Lalas and Harcourt 1995), but low compared to previous estimates (Shaughnessy et al. 1995) for the same population and other populations within the region (0.978-0.998). However, the survival estimates of Shaughnessy et al. (1995) are based on the number of dead pups found during pup censuses at the end of the breeding season. They noted that such estimates are likely to underestimate mortality because some pups that die over the breeding season will have disappeared due to high tides, storms, natural decomposition or scavenging by predators (Shaughnessy and McKeown 2002). At Cape Gantheaume mortality rates based on counts at the end of the breeding season have been calculated since January 1989. Over the course of the present study, mortality rates calculated at the end of the breeding season were 2.0%, 1.2%, 1.5% and 2.6% (2000-2001 to 2002-2004 respectively, based on data in Shaughnessy and Dennis 2001, 2002, 2003; Shaughnessy 2004). Excluding 2000-2001 where the difference between estimates was exceptionally high, mortality rates based on monitoring individual pups from birth were on average 6.8 ± 1.4 (SD) times greater than estimates based on counts of dead pups at the end of the season.

Reported estimates of survival to weaning or to 1 year of age are scarce among other otariids. New Zealand fur seal pups wean between 8-11 months of age (Crawley 1975; Mattlin 1981; Haase 2005; Goldsworthy 2006). Bradshaw et al. (2003) estimated survival from ~12-155 days as 0.88, while Mattlin (1978b) speculated survival from birth to weaning (~300 days) may be around 0.60. In the present study, combining data on mortality rates from birth to the end of the breeding season and from ~1.5 months to weaning (Haase et al. in review) suggested survival from birth to weaning was ~0.73. This estimate is comparable to estimates of pre-weaning survival reported for

subantarctic fur seals, which wean at ~10 months (0.37-0.89; Chambellant et al. 2003). Survival post-weaning to the end of the year is expected to be lower due to the transitional period to nutritional independence, when foraging efficiency may still be low (Mattlin 1978b; Baylis et al. 2005), but as yet no empirical estimates are available.

Adult survival

Among adult New Zealand fur seals, age-specific survival rates were significantly higher among prime-age females (0.867, SE = 0.024) than among older females (0.733, SE = 0.046), supporting the suggestion of senescence in older animals. In the few studies where age-distribution data has been sufficient to allow modelling of age-specific survival, a similar pattern of declining survival has also been described for northern (Lander 1981; Barlow and Boveng 1991) and South American (Lima and Páez 1997) fur seals. Age-specific survival estimates of Antarctic fur seals based on a mark-recapture study exhibited a similar pattern of declining survival, although after accounting for variation in survival due to reproduction and calendar year there appeared to be no consistent effect of age on survival (Boyd et al. 1995). However, sample sizes of older females (≥ 15 yrs) were small. In a longitudinal study of southern elephant seals, Pistorius and Bester (2002) also found no evidence of senescence in survival rates. However, they suggest relatively low adult survival in the population studied is likely to result in no individuals surviving to the age where senescence became apparent.

In the present study, sample sizes for 4 and 5 yr olds were too small to estimate age-specific survival of recently mature females. However, a number of studies have suggested that survival rates among primiparae or recently mature females are low relative to older females due to the higher cost of reproduction among younger animals (Clutton-Brock et al. 1983; Huber 1987; Reiter and Le Boeuf 1991; Lunn et al. 1994; Boyd et al. 1995), which may explain the low rate of survival estimated for 6 yr olds. However, there is considerable uncertainty in this estimate, due to small sample size. Because results were averaged across individuals rather than following individual life-histories, differences in survival and reproduction between individuals due to age at first birth are obscured. However, an increase in the proportion of first-time sexually mature females that failed to pup could also explain the low numbers of reproductively mature females sampled aged 4-6 years.

Estimates of annual adult survival for New Zealand fur seal females based on mark-recapture (0.78-0.92) were similar to estimates for other pinnipeds based on longitudinal studies (Testa and Siniff 1987; Le Boeuf and Reiter 1988; Boyd et al. 1995; Cameron and Siniff 2004). In Antarctic fur seals, annual survival rates varied from 0.65-0.93 for a population increasing at around 10% per annum (Boyd et al. 1995), while in northern elephant seals (*Mirounga angustirostris*) survival rates varied from 0.65-0.85 (Le Boeuf and Reiter 1988).

Recruitment (juvenile survival)

Estimates of juvenile survival are lacking for most pinniped species or have been derived indirectly from harvest data (Lander 1975) or age-distribution data (Wickens and York 1997). For many species including the New Zealand fur seal, pups disperse at sea after weaning and typically display low breeding site fidelity until approaching reproductive age (Stirling 1971; Baker and Fowler 1992; Goldsworthy and Shaughnessy 1994; Baker et al. 1995; Beauplet et al. 2005; McKenzie unpublished data). Estimates of juvenile survival based on mark-recapture therefore require long-term resighting programs involving a large sample of marked animals, particularly as return rates may be low and tag loss high (Testa 1987). Although mortality rates of juveniles are expected to be high post-weaning, due to the transition to independent foraging, mortality rates should decrease steadily as juveniles develop their foraging skills and increase their diving ability as they increase in size. Based on a long-term mark-recapture study on juvenile Weddell seals, mortality was estimated to be highest during the first 2 years of life, but after 2 yrs of age annual survival was comparable to that of adults and showed little variation from 2-6 yrs of age (Hastings et al. 1999). A similar pattern of juvenile mortality has also been demonstrated for the subantarctic fur seal (Beauplet et al. 2005) where juvenile survival rates were low for the first few years post-weaning, but increased following return of the seals to their natal island and remained relatively constant until the age of first reproduction. Pre-weaning survival rates were also typically higher than post-weaning rates (Beauplet et al. 2005), as observed in northern fur seals (Trites 1989).

Based on the assumption that juvenile survival in the New Zealand fur seal followed a similar pattern to that observed in the subantarctic fur seal, the modified Siler model fitted to age-specific survival of female New Zealand fur seals ≥ 4 yrs provided a good fit to available and substituted data. However, until representative survival rates for juvenile and recently mature New Zealand fur seal are obtained, the mortality pattern

presented should be interpreted with caution. Despite the uncertainty surrounding the pattern of mortality among younger adults and survival to first age at reproduction, the predicted survival schedule in combination with the fecundity estimates measured over the same period provided a comparable rate of population growth as estimated from concurrent pup censuses. Using the adaptation of Lotka's equation by Wickens and York (1997: Equation 1) for estimating juvenile survival with parameters estimated in the present study for age at first reproduction (4 yrs), reproductive longevity (22 yrs), average fecundity (0.349), and average adult survival (0.856), and assuming a stationary population ($\lambda = 1$), juvenile survival from birth to age 4 yrs was estimated as 0.435. For a population rate of increase of $\lambda = 1.027$, juvenile survival was estimated as 0.548. Survival to 4 yrs of age presented in the life table (0.509) falls within this range, suggesting the value presented is not unrealistic.

Variation in adult reproductive and survival rates in relation to pup production

Changes in annual pup production were strongly correlated with reproductive rates, particularly those of prime-age females. However, the extent of change in pup production was also strongly influenced by survival rates of adult females between breeding seasons. During the study period reproductive rates varied significantly (27-85%) among years. Rates in 2000-2001 were extremely low, moderate in 2001-2002 and 2002-2003 and high in 2003-2004. Variation in reproductive rates between years most likely reflected a response to fluctuations in the distribution and/or abundance of prey across years (Chapter 3; McKenzie et al. 2005a). Differences in the pattern of reproductive failure over 2000-2002 (Chapter 3; McKenzie et al. 2005a), suggested the timing and or degree of nutritional stress differed significantly in 2000 compared to 2001 and 2002, with significant reproductive failure at or before implantation in 2000 compared to the following two seasons. Pregnancy data was not collected in 2003 for comparison with the preceding two years in which reproductive rates were still considered moderate.

Lower birth mass, higher pup mortality and lower pup growth rates have been associated with a decrease in available prey for females during gestation and lactation in a number of pinniped studies (Lunn et al. 1994; Boltnev et al. 1998; Chambellant et al. 2003). In the present study, the positive relationship between the extent of reproductive failure and early pup mortality also supports the suggestion that the condition of breeding females prior to giving birth varied among years. Following parturition, New Zealand fur seals typically remain ashore for about 7 days before

departing on their first foraging trip (Goldsworthy and Shaughnessy 1994). During this perinatal period, all energy transferred to the pup is derived from stored maternal body reserves (Costa and Trillmich 1988). Thus, food shortages just before or during gestation may result in reduced maternal condition. Most deaths in this study occurred within the perinatal period or soon after, and were most likely due to starvation or underdevelopment at birth. Density-dependant related mortality, such as crushing and trampling by adult animals has been reported for other species (Doidge et al. 1984; Harcourt 1992), but it generally occurs in populations at much higher densities than in the New Zealand fur seal population studied.

Concurrent dietary and pup growth studies at Cape Gantheaume between 2000-2003 suggest the distribution and/or abundance of prey is likely to have fluctuated between years. In winter 2000, a common fish prey species (Redbait, *Emmelichthys nitidus*) was less abundant in the diet of adult females compared to 2001 and 2002 (Page et al. 2005b). Growth rates of pups from ~1.5 month of age also varied among years with early, late and overall growth considerably higher in 2003 compared to 2001 and 2002 (Haase 2005). Lactating females monitored over 2001-2003 also demonstrated shorter foraging trips in 2003 compared to the previous two years (Haase 2005), suggesting greater food availability in 2003. Lower reproductive rates in 2001-2002 and 2002-2003 were also paralleled by low adult survival, suggesting environmental fluctuations were substantial. Unfortunately, due to the timing of data collection, the relationships between adult survival and low reproductive rates and pup production in 2000-2001 are unknown. However, given the magnitude of the decline in pup production in 2000-2001, a decline in adult survival over 2000 is also suspected.

Fluctuations in the survival rates of prime-age females appear to be paralleled by changes in survival rates of older females, suggesting the shifts in mortality affected the adult age group as a whole. However, given the greater variation in reproductive rates of young females between years, mortality rates among younger breeding females may have been greater than older age classes. Low recruitment of young females and/or high mortality among younger, first-time pregnant or recently mature females may also explain in part the reduction in pup production over the study period and the high mean age of mature females (10.8 yrs) in cross-sectional sample in 2000-2001 to 2002-2003.

Another factor that could account for declines in apparent pup production and relatively high mean age of breeding females is emigration of adult females or first-time breeders to other colonies. As the population has been increasing at Cape Gantheaume, the colony has expanded along the coast and into vacant areas between existing breeding sites. Recent increases in pup numbers at a near by site (Berris Point) are most likely due to an overflow of animals from Cape Gantheaume (Shaughnessy 2006) which is ~4.5km away. Although pup production at this site has been increasing rapidly from four pups in January 1997 to 697 in 2005 (Shaughnessy 2006), pup numbers at Berris Point were relatively low over the study period (66, 109, 143 and 264 from 2000-2001 to 2003-2004). During the study period, variation in annual reproductive and survival rates appears to account for most of the change in pup production observed. Significant emigration to other colonies on Kangaroo Island is also unlikely as fluctuations in pup production were also reflected at other sites on Kangaroo Island at the time (Shaughnessy 2006). As the population at Cape Gantheaume and other sites continues to increase, emigration is likely to have a significant effect on pup production estimates in the not too distant future.

Population modelling of a number of fur seal species suggest that changes in reproductive rates have less effect on long-term population growth than adult survival (Eberhardt 1985; York 1987; Trites and Larkin 1989). In the New Zealand fur seal population at Cape Gantheaume, significant oscillations in reproductive rates over the study period do not appear to have greatly affected population trends over the short-term, as demonstrated by the return to an average annual exponential rate of increase 0.110 in recent years (Fig 1.). However, the impact of shifts in adult and possibly juvenile survival on long-term trends may be greater, and may not become apparent for several years.

The life-history traits presented here reflect the population dynamics of the female population at the time the data were collected. To complete the life table for the New Zealand fur seal, estimates of survival over the juvenile life stage and early reproductive maturity are still required in addition to survival rates and age-specific patterns among males. Although the parameter estimates presented here may not be directly applicable to other New Zealand fur seal populations or to the same population under different environmental conditions, the average rates measured and their variance provide a realistic range of values on which to base future population models. Examination of individual reproductive and resight histories and individual traits

recorded over the course of this study are likely to shed further light on the life-history of New Zealand fur seals and the dynamics of its population growth. Given that fur seals as a group share similar life-history patterns (York 1987; Wickens and York 1997), the parameters and range of values presented here may also assist in modelling the dynamics of other species for which data is lacking.

REFERENCES

- Anas, R.E. (1970) Accuracy in assigning ages to fur seals. *Journal of Wildlife Management*, 34, 844-852.
- Anderson, D.R., and Burnham, K.P. (1999) Understanding information criteria for selection among capture-recapture or ring recovery models. *Bird Study*, 46 (Suppl.), 261-270.
- Animal Care and Use Committee. (1998) Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy*, 79, 1416-1431.
- Arnason, A.N., and Mills, K.H. (1981) Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. *Canadian Journal of Fisheries and Aquatic Sciences*, 38, 1077-1095.
- Arnbom, T.A., Lunn, N.J., Boyd, I.L., and Barton, T. (1992) Aging live Antarctic fur seals and southern elephant seals. *Marine Mammal Science*, 8, 37-43.
- Arnould, J.P.Y., Boyd, I.L., and Warneke, R.M. (2003) Historical dynamics of the Australian fur seal population: evidence of regulation by man? *Canadian Journal of Zoology*, 81, 1428-1436.
- Arnould, J.P.Y., and Warneke, R.M. (2002) Growth and condition in Australian fur seals (*Arctocephalus pusillus doriferus*) (Carnivora : Pinnipedia). *Australian Journal of Zoology*, 50, 53-66.
- Arthur, G. H., Noakes, D. E., Pearson, D. E., and Parkinson, T. J. (1996) Pregnancy and its diagnosis. *Veterinary Reproduction and Obstetrics* (eds. G. H. Arthur, D. E. Noakes, D. E. Pearson, and T. J. Parkinson) pp. 63-10. Saunders, London.
- Badyaev, A.V. (2002) Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends in Ecology and Evolution*, 17, 369-378.
- Baker, J.R., Fedak, M.A., Anderson, S.S., Arnbom, T., and Baker, R. (1990) Use of a tiletamine-zolazepam mixture to immobilise wild grey seals and southern elephant seals. *The Veterinary Record*, 126, 75-77.
- Baker, J.D., and Fowler, C.W. (1992) Pup weight and survival of northern fur seals, *Callorhinus ursinus*. *Journal of Zoology (London)*, 227, 231-238.
- Baker, J.D., Antonelis, G.A., Fowler, C.A., and York, A.E. (1995) Natal site fidelity in northern fur seals, *Callorhinus ursinus*. *Animal Behaviour*, 50, 237-247.
- Baker, J.D., Fowler, C.W., and Antonelis, G.A. (1994) Mass change in fasting immature male northern fur seals. *Canadian Journal of Zoology*, 72, 326-329.
- Barlow, J., and Boveng, P. (1991) Modeling age-specific mortality for marine mammal populations. *Marine Mammal Science*, 7, 50-65.

- Bartholomew, G.A. (1970). A model for the evolution of pinniped polygyny. *Evolution*, 24, 546-559.
- Baylis, A.M.M., Page, B., Peters, K., McIntosh, R., McKenzie, J., and Goldsworthy S.D. (2005) The ontogeny of dive behaviour in New Zealand fur seal pups (*Arctocephalus forsteri*). *Canadian Journal of Zoology*, 83, 1149-1161.
- Beauplet, G., Barbraud, C., Chambellant, M., and Guinet, C. (2005) Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: influence of pup sex, growth rate and oceanographic conditions. *Journal of Animal Ecology*, 74, 1160-1172.
- Beck, C.A., Bowen, W.D., and Iverson, S.J. (2003) Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. *Journal of Animal Ecology*, 72, 280-291.
- Bengtson, J.L., and Laws, R.M. (1985) Trends in crabeater seal age at maturity: An insight into Antarctic marine interactions. *Antarctic Nutrient Cycles and Food Webs* (eds. W.R. Siegfried, P.R. Condry and R.M. Laws). pp. 669-675. Springer-Verlag, Berlin.
- Bernardo, J. (1993) Determinants of maturation in animals. *Trends in Ecology and Evolution*, 8, 166-173.
- Bester, M. N. (1995) Reproduction in the female subantarctic fur seal, *Arctocephalus tropicalis*. *Marine Mammal Science*, 11, 362-375.
- Bester, M.N., and Van Jaarsveld, A.S. (1994) Sex-specific and latitudinal variance in postnatal growth of the Subantarctic fur seal (*Arctocephalus tropicalis*). *Canadian Journal of Zoology*, 72, 1126-1133.
- Bigg, M. A. (1969) The harbour seal in British Columbia. *Fisheries Research Board of Canada Bulletin*, 172, 1-33.
- Bodley, K., Petel, T.P., and Gales, N. (2005) Immobilisation of free-living Weddell seals *Leptonychotes weddellii* using midazolam and isoflurane. *Polar Biology*, 28, 631-636.
- Boltnev, A.I., and York, A.E. (2001) Maternal investment in northern fur seals (*Callorhinus ursinus*): interrelationship among mothers' age, size, parturition date, offspring size and sex ratios. *Journal of Zoology (London)*, 254, 219-228.
- Boltnev, A.I., York, A.E., and Antonelis, G. (1998) Northern fur seal young: interrelationships among birth size, growth, and survival. *Canadian Journal of Zoology*, 76, 843-854.
- Bonner, W.N. (1984) Lactation strategies in pinnipeds: problems for a marine mammalian group. *Symposia of the Zoological Society of London*, 51, 253-272.

- Boshier, D. P. (1981) Structural changes in the corpus luteum and endometrium of seals before implantation. *Journal of Reproduction and Fertility, Supplement*, 29, 143-149.
- Bowen, W.D., Capstick, C.K., and Sergeant, D. (1981) Temporal Changes in the Reproductive Potential of Female Harp Seals (*Pagophilus groenlandicus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 38, 495-503.
- Bowen, W.D., Oftedal, O.T., and Boness, D.J. (1994) The effect of maternal age and other factors on birth mass in the harbour seal. *Canadian Journal of Zoology*, 72, 8-14.
- Boyd, I. L. (1983) Luteal regression, follicle growth and the concentration of some plasma steroids during lactation in grey seals (*Halichoerus grypus*). *Journal of Reproduction and Fertility*, 69, 157-164.
- Boyd, I. L. (1984) Development and regression of the corpus luteum in grey seal (*Halichoerus grypus*) ovaries and its use in determining fertility rates. *Canadian Journal of Zoology*, 62, 1095-1100.
- Boyd, I. L. (1985) Pregnancy and ovulation rates in grey seals (*Halichoerus grypus*) on the British coast. *Journal of Zoology (London)*, 205, 265-272.
- Boyd, I. L. (1991a) Changes in the plasma progesterone and prolactin concentrations during annual cycle and the role of prolactin in the maintenance of lactation and luteal development in the Antarctic fur seal (*Arctocephalus gazella*). *Journal of Reproduction and Fertility*, 91, 637-647.
- Boyd, I. L. (1991b) Environmental and physiological factors controlling the reproductive cycles of pinnipeds.(Review). *Canadian Journal of Zoology*, 69, 1135-1148.
- Boyd, I. L., Croxall, J. P., Lunn, N. J., and Reid, K. (1995) Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. *Journal of Animal Ecology*, 64, 505-518.
- Boyd, I.L, Lunn N.J., Duck C.J., and Barton, T. (1990) Response of antarctic fur seals to immobilisation with ketamine, a ketamine-diazepam or ketamine-xylazine mixture, and zoletil. *Marine Mammal Science*, 6, 135-145.
- Boyd, I.L., and Croxall, J.P. (1996) Diving durations in pinnipeds and seabirds. *Canadian Journal of Zoology*, 74, 1696-1705.
- Boyd, I.L., and Duck, C.D. (1991) Mass Changes and Metabolism in Territorial Male Antarctic Fur Seals (*Arctocephalus gazella*). *Physiological Zoology*, 64, 375-392.
- Boyd, I.L., and McCann, T.S. (1989) Pre-natal investment in reproduction by female Antarctic fur seals. *Behavioural Ecology and Sociobiology*, 24, 377-385.

- Boyd, I.L., Arnborn, T.A., and Fedak, M.A. (1994) Biomass and Energy Consumption of the South Georgia Population of Southern Elephant Seals. *Elephant Seals: Population Ecology, Behaviour, and Physiology* (eds. B.J. Le Boeuf and R.M. Laws), pp. 98-117. University of California Press, London, England.
- Boyd, I.L., Croxall, J.P., Lunn, N.J., and Reid, K. (1995) Population demography of Antarctic fur seals - the costs of reproduction and implications for life-histories. *Journal of Animal Ecology*, 64, 505-518.
- Bradshaw, C.J.A., Baker, R.J., and Davis, L.S. (2000b) Modeling Tag Loss in New Zealand fur Seal Pups. *Journal of Agricultural, Biological, and Environmental Statistics*, 5, 475-485.
- Bradshaw, C.J.A., Baker, R.J., Harcourt, R.G., and Davis, L.S. (2003) Estimating survival and capture probability of fur seal pups using multistate mark-recapture models. *Journal of Mammalogy*, 84, 65-80.
- Bradshaw, C.J.A., Davis, L.S., Purvis, M., Zhou, Q., and Benwell, G.L. (2002). Using artificial neural networks to model the suitability of coastline for breeding by New Zealand fur seals (*Arctocephalus forsteri*). *Ecological Modelling*, 148, 111-131.
- Bradshaw, C.J.A., Harcourt, R.G., and Davis, L.S. (2003). Male-biased sex ratios in New Zealand fur seal pups relative to environmental variation. *Behavioural Ecology and Sociobiology*, 53, 297-307.
- Bradshaw, C.J.A., Lalas, C., and Thompson C.M. (2000a) Clustering of colonies in an expanding population of New Zealand fur seals (*Arctocephalus forsteri*). *Journal of Zoology* (London), 250, 105-112.
- Brunner, S. (1998a) Cranial morphometrics of the southern fur seals *Arctocephalus forsteri* and *A. pusillus* (Carnivora: Otariidae). *Australian Journal of Zoology*, 46, 67-108.
- Brunner, S. (1998b) Skull development and growth in southern fur seals *Arctocephalus forsteri* and *A. pusillus doriferus* (Carnivora : Otariidae). *Australian Journal of Zoology*, 46, 42-66.
- Brunner, S., Bryden, M.M., and Shaughnessy, P.D. (2004) Cranial ontogeny of otariid seals. *Systematics and Biodiversity*, 2, 83-110.
- Bryden, M.M. (1968) Control of growth in two populations of elephant seals. *Nature (London)*, 217, 1106-1108.
- Bryden, M.M. (1972) Growth and development of marine mammals. *Functional Anatomy of Marine Mammals* (ed. R.J. Harrison), pp. 1-79. Academic Press, London, England.

- Butterworth, D.S. (1992) Will more seals result in reduced fishing quotas? *South African Journal of Science*, 88, 414-416.
- Butterworth, D.S., Punt, A.E., Oosthuizen, W.H., and Wickens, P.A. (1995) The effect of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 3: Modelling the dynamics of the Cape fur seal *Arctocephalus pusillus pusillus*. *South African Journal of Marine Science*, 16, 161-183.
- Cameron, M.F., and Siniff, D.B. (2004) Age-specific survival, abundance, and immigration rates of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. *Canadian Journal of Zoology*, 82, 601-615.
- Caswell, H. (1989) *Matrix population models*. Sinauer Associates, Sutherland.
- Caughley, G. (1966) Mortality patterns in mammals. *Ecology*, 47, 906-918.
- Caughley, G. (1980) *Analysis of vertebrate populations*. The Blackburn Press, New Jersey, U.S.A.
- Chabot, D., and Stenson, G. B. (2002) Growth and seasonal fluctuations in size and condition of male Northwest Atlantic harp seals *Phoca groenlandica*: an analysis using sequential growth curves. *Marine Ecological Progress Series*, 227, 25-42.
- Chambellant, M., Beauplet, G., Guinet, C., and Georges, J-Y. (2003) Long-term evaluation of pup growth and preweaning survival rates in subantarctic fur seals, *Arctocephalus tropicalis*, on Amsterdam Island. *Canadian Journal of Zoology*, 81, 1222-1232.
- Chapman, D.G., and Robson, D.S. (1960) The analysis of a catch curve. *Biometrics*, 16, 354-368.
- Charlesworth, B. (1980) *Evolution in age-structured populations*. Cambridge University Press, Cambridge.
- Childerhouse, S., Dickie, G., and Hessel, G. (2004) Ageing live New Zealand sea lions (*Phocarctos hookeri*) using the first post-canine tooth. *Wildlife Research*, 31, 177-181.
- Chilvers, B.L., Wilson, K-J., and Hickling, G.J. (1995) Suckling behaviour and growth rates of New Zealand fur seals, *Arctocephalus forsteri*, at Cape Foulwind, New Zealand. *New Zealand Journal of Zoology*, 22, 263-270.
- Clinton, W.L. (1994) Sexual Selection and Growth in Male Northern Elephant Seals. *Elephant Seals: Population Ecology, Behaviour, and Physiology* (eds. B.J. Le Boeuf, and R.M. Laws), pp 154-168. University of California Press, London, England.

- Clinton, W.L., and Le Boeuf, B.J. (1993) Sexual selection's effect on male life history and the pattern of male mortality. *Ecology*, 74, 1884-1892.
- Clutton-Brock, T.H., Guinness, F.E., and Albon, S.D. (1983). The cost of reproduction to red deer hinds. *Journal of Animal Ecology*. 52: 367-383.
- Costa, D.P., and Williams T.M. (1999) Marine mammal energetics. *The biology of marine mammals* (eds. J.E. Reynolds III and S.A. Rommel), pp 176-217. Smithsonian Institution Press, Washington, D.C., USA.
- Costa, D.P., and Trillmich, F. (1988) Mass changes and metabolism during the perinatal fast: a comparison between Antarctic (*Arctocephalus gazella*) and Galapagos fur seals (*Arctocephalus galapagoensis*). *Physiological Zoology*, 61, 160-169.
- Craig, A. M. (1964) Histology of reproduction and estrus cycle in the female fur seal, *Callorhinus ursinus*. *Journal of Fisheries Research Board of Canada*, 21, 773-811.
- Crawley, M. C. (1990) New Zealand fur seal *Arctocephalus forsteri* (Lesson, 1828). Pp. 246-25 in *The Handbook of New Zealand Mammals* (C. M. King, ed.). Oxford University Press, Auckland.
- Crawley, M.C. (1975) Growth of New Zealand fur seal pups. *New Zealand Journal of Marine and Freshwater Research*, 9, 539-545.
- Crawley, M.C., and Brown, D.L. (1971) Measurements of tagged pups and a population estimate of New Zealand fur seals on Taumaka, Open Bay Islands, Westland. *New Zealand Journal of Marine and Freshwater Research*, 5, 389-395.
- Crawley, M.C., and Wilson, G.J. (1976) The natural history and behaviour of the New Zealand fur seal (*Arctocephalus forsteri*). *Tuatara*, 22, 1-29.
- Dabin, W., Beauplet, G. and Guinet, C. (2002) Response of wild subantarctic fur seal (*Arctocephalus tropicalis*) females to ketamine and tiletamine-zolazepam anesthesia. *Journal of Wildlife Diseases*, 38, 846-850.
- Dabin, W., Beauplet, G., Crespo, E.A., and Guinet, C. (2004) Age structure, growth, and demographic parameters in breeding-age female subantarctic fur seals, *Arctocephalus tropicalis*. *Canadian Journal of Zoology*, 82, 1043-1050.
- Daniel, J. C. (1975) Concentrations of circulating progesterone during early pregnancy in the Northern fur seal (*Callorhinus ursinus*). *Journal of Fisheries Research Board of Canada*, 32, 65-66.
- Daniel, J. C. (1981) Delayed implantation in the northern fur seal (*Callorhinus ursinus*) and other pinnipeds. *Journal of Reproduction and Fertility, Supplement*, 29, 35-50.

- David, J.H.M., Hofmeyr, J.M., Best, P.B., Meyer, M.A., and Shaughnessy, P.D. (1988) Chemical immobilisation of free-ranging South African (Cape) fur seals. *South African Journal of Wildlife Research*, 18, 154-156.
- DeMaster, D.P. (1978) Calculation of the Average Age of Sexual Maturity in Marine Mammals. *Journal of Fisheries Research Board of Canada*, 35, 912-915.
- DeMaster, D.P. (1981) Estimating the average age of first birth in marine mammals. *Canadian Journal of Fisheries and Aquatic Sciences*, 38, 237-239.
- DeVilliers, D.J., and Roux, J-P. (1992) Mortality of newborn pups of the South African fur seal *Arctocephalus pusillus pusillus* in Namibia. *South African Journal of Marine Science*, 12, 881-889.
- Dickie, G.S., and Dawson, S.M. (2003) Age, growth, and reproduction in New Zealand fur seals. *Marine Mammal Science*, 19, 173-185.
- Doidge, D.W., Croxall, J.P., and Baker, J.R. (1984) Density dependent pup mortality in the Antarctic fur seal, *Arctocephalus gazella*, at South Georgia. *Journal of Zoology (London)*, 202, 449-460.
- Eberhardt, L.L. (1985) Assessing the dynamics of wild populations. *Journal of Wildlife Management*, 49, 997-1012.
- Eberhardt, L.L. (1988) Using age structure data from changing populations. *Journal of Applied Ecology*, 25, 373-378.
- Eberhardt, L.L. and Siniff, D.B. (1977) Population dynamics and marine mammal management policies. *Journal Fisheries Research Board of Canada*, 34, 183-190.
- Eberhardt, L.L., Chapman, D.G., and Gilbert, J.R. (1979) A review of marine mammal census methods. *Wildlife Monographs*, 63, 1-46.
- Erickson, A.W., and Bester, M.N. (1993) Immobilization and capture. *Antarctic seals Research methods and techniques*. (ed. R.M. Laws), pp. 46-88. Cambridge University Press, Cambridge UK.
- Etnier, M.A. (2004) Reevaluating evidence of density-dependent growth in northern fur seals (*Callorhinus ursinus*) based on measurements of archived skeletal specimens. *Canadian Journal of Fisheries and Aquatic Science*, 61, 1616-1626.
- Fea, N.I., Harcourt, R., and Lalas, C. (1999) Seasonal variation in the diet of New Zealand fur seals (*Arctocephalus forsteri*) at Otago Peninsula, New Zealand. *Wildlife Research*, 26, 147-160.
- Field, I.C., Bradshaw, C.J.A., McMahon, C.R., Harrington, J., and Burton, H.R. (2002) Effects of age, size and condition of elephant seals (*Mirounga leonina*) on their

- intravenous anaesthesia with tiletamine and zolazepam. *The Veterinary Record*, 151, 235-240.
- Gales, N. J. (1989) Chemical restraint and anaesthesia of pinnipeds: a review. *Marine Mammal Science*, 5, 228-256.
- Gales, N. J., and Mattlin, R.H.(1998) Fast, safe, field-portable gas anaesthesia for Otariids. *Marine Mammal Science*, 14, 355-361.
- Gales, N. J., Williamson, P., Higgins, L. V., Blackberry, M. A., and James, I. (1997) Evidence of prolonged post-implantation period in the Australian sea lion (*Neophoca cinerea*). *Journal of Reproduction and Fertility*, 111, 159-163.
- Gales, N., Barnes, J., Chittick, B., Gray, M., Robinson, S., Burns, J., and Costa, D. (2005) Effective, field-based inhalation anesthesia for ice seals. *Marine Mammal Science*, 21, 717-727.
- Gardiner, K. J., Boyd, I. L., Follett, B. K., Racey, P. A., and Reijnders, P. J. H. (1999) Changes in pituitary, ovarian, and testicular activity in harbour seals (*Phoca vitulina*) in relation to season and sexual maturity. *Canadian Journal of Zoology*, 77, 211-221.
- Gardiner, K. J., Boyd, I. L., Racey, P. A., Reijnders, P. J. H., and Thompson, P. M. (1996) Plasma progesterone concentrations measured using enzyme-linked immunosorbent assay useful for diagnosing pregnancy in harbor seals (*Phoca vitulina*). *Marine Mammal Science*, 12, 265-273.
- Gentry, R.L., and Kooyman, G.L. (Editors) (1986) *Fur seals: maternal strategies on land and at sea*, Princeton University Press, NJ.
- Georges, J-Y. and Guinet, C. (2001) Prenatal investment in the subantarctic fur seal, *Arctocephalus tropicalis*. *Canadian Journal of Zoology*, 79, 601-609.
- Georges, J-Y., and Guinet, G. (2000) Early mortality and perinatal growth in the subantarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island. *Journal of Zoology (London)*, 251, 277-287.
- Goldsworthy, S.D. (1992) Maternal care in three species of southern fur seal (*Arctocephalus spp.*). Ph.D. dissertation, Monash University, Victoria, Australia.
- Goldsworthy, S.D. (2006) Maternal strategies in the New Zealand fur seal: evidence for inter-annual variability in provisioning and pup growth strategies. *Australian Journal of Zoology*. 54, 31-44.
- Goldsworthy, S.D. and Shaughnessy, P.D. (1994) Breeding Biology and Haul-out Patterns of the New Zealand Fur Seal, *Arctocephalus forsteri*, at Cape Gantheaume, South Australia. *Wildlife Research*, 21, 365-376.

- Goldsworthy, S.D., Bulman, C., He, X., Larcombe, J., and Littnan, C. (2003) Trophic interactions between marine mammals and Australian fisheries: an ecosystem approach. *Marine Mammals: fishing, tourism and management issues* (eds N. Gales, M. Hindell, and R. Kirkwood), pp. 62-99. CSIRO Publishing, Melbourne.
- Griffiths, D., Wiig, Ø., and Gjertz, I. (1993) Immobilization of Walrus with etorphine hydrochloride and Zoletil®. *Marine Mammal Science*, 9, 250-257.
- Guinet, C., Cherel, Y., Ridoux, V., and Jouventin, P. (1996) Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962-85. *Antarctic Science*, 8, 23-30.
- Guinet, C., Jouventin, P., and Georges, J-Y. (1994) Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St. Paul and Amsterdam) islands and their possible relationship to El Niño Southern Oscillation. *Antarctic Science*, 6, 473-478.
- Guinet, C., Roux, J. P., Bonnet, M., and Milson, V. (1998) Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. *Canadian Journal of Zoology*, 76, 1418-1424.
- Haase, T.J. (2005) *The determinants of weaning in the New Zealand fur seal*. PhD thesis, La Trobe University, Melbourne, Australia.
- Haase, T.J., Goldsworthy, S.D., and McKenzie, J. (in review) Determining Weaning in the New Zealand fur seal, *Arctocephalus forsteri*. *Behavioural Ecology and Sociobiology*.
- Hamill, M.O., Kingsley, M.C.S., Beck, G.G., and Smith, T.G. (1995) Growth and condition in the Northwest Atlantic harp seal. *Canadian Journal of Fisheries and Aquatic Science*, 52, 478-488.
- Harcourt, R.G. (1992) Factors affecting early mortality in the South American fur seal (*Arctocephalus australis*) in Peru: density-related effects and predation. *Journal of Zoology (London)*, 226, 259-270.
- Harcourt, R.G. (2001) Advances in New Zealand mammalogy 1990–2000: Pinnipeds. *Journal of the Royal Society of New Zealand*, 31, 135–160.
- Harcourt, R.G., Bradshaw, C.J.A., Dickson, K., and Davis, L.S. (2002) Foraging ecology of a generalist predator, the female New Zealand fur seal. *Marine Ecology Progress Series*, 227, 11-24.
- Harcourt, R.G., Schulman, A.M., Davis, L.S., and Trillmich, F. (1995) Summer foraging by lactating female New Zealand fur seals (*Arctocephalus forsteri*) off Otago Peninsula, New Zealand. *Canadian Journal of Zoology*, 73, 678-390.

- Harwood, J., and Prime, J.H. (1978) Some factors affecting the size of British grey seal populations. *Journal of Applied Ecology*, 15, 401-411.
- Harwood, J., and Rohani, P. (1996) The population biology of marine mammals. *Frontiers of Population Ecology* (eds. R.B. Floyd, A.W. Sheppard, and P.J. De Barro). pp 173-190. CSIRO Publishing, Melbourne, Australia.
- Hastings, K.K., Testa, J.W., and Rexstad, E.A. (1999) Interannual variation in survival of juvenile Weddell seals (*Leptonychotes weddellii*) from McMurdo Sound, Antarctica: effects of cohort, sex and age. *Journal of Zoology (London)*, 248, 307-323.
- Heap, R. B., and Flint, A. P. F. (1984) Pregnancy. *Reproduction in mammals, Book 3 Hormonal control of reproduction* (eds. C.R. Austin, and R.V. Short), pp 153-194. Cambridge University Press, Sydney, Australia.
- Heath, R.B., Calkins, D., McAllister, D., Taylor, W., and Spraker T. (1996) Telazol and Isoflurane field anaesthesia in free-ranging Steller's sea lions (*Eumetopias jubatus*). *Journal of Zoo and Wildlife Medicine*, 27, 35-43.
- Higgins, D.P., Rogers, T.L., Irvine, A.D., and Hall-Aspland, S. (2002) Use of midazolam/pethidine and tiletamine/zolazepam combinations for the chemical restraint of Leopard seals (*Hydrurga leptonyx*). *Marine Mammal Science*, 18, 483-499.
- Higgins, L.V., and Gass, L. (1993) Birth to weaning: parturition, duration of lactation and attendance cycles of Australian sea lions (*Neophoca cinerea*). *Canadian Journal of Zoology*, 71, 2047-2055.
- Hobson, B. M., and Boyd, I. L. (1984) Gonadotrophin and progesterone concentrations in placentae of grey seals (*Halichoerus grypus*). *Journal of Reproduction and Fertility*, 72, 521-528.
- Huber, H.R. (1987) Natality and weaning success in relation to age at first reproduction in northern elephant seals. *Canadian Journal of Zoology*, 65, 1311-1316.
- Innes, S., Stewart, R.E.A., and Lavigne, D.M. (1981) Growth in Northwest Atlantic Harp seals *Phoca groenlandica*. *Journal of Zoology (London)*, 194, 11-24.
- Isaac, J.L. (2005) Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mammal Review*, 35, 101-115.
- Johnson, M.H., and Everitt, B.J. (1995) *Essential reproduction*. Blackwell Science, Carlton, Australia.
- Kingsley, M.C.S. (1979) Fitting the von Bertalanffy growth equation to polar bear age-weight data. *Canadian Journal of Zoology*, 57, 1020-1025.

- Klausen, B., Toubro, S., and Astrup, A. (1997) Age and sex effects on energy expenditure. *American Journal of Clinical Nutrition*, 65, 895-907.
- Klevezal, G.A. (1980) Layers in the hard tissues of mammals as a record of growth rhythms of individuals. *Report of the International Whaling Commission*, 3, 89-94
- Knutsen, L.Ø., and Born, E.W. (1994) Body growth in Atlantic walruses (*Odobenus rosmarus rosmarus*) from Greenland. *Journal of Zoology (London)*, 234, 371-385.
- Koops, W.J. (1986) Multiphasic growth curve analysis. *Growth*, 50, 169-177.
- Kooyman, G.L. (1989) *Diverse Divers: physiology and behaviour*. Springer-Verlag, Berlin.
- Lake, S. (1997) Analysis of the diet of New Zealand fur seals, *Arctocephalus forsteri*, in Tasmania. *Marine mammal research in the southern hemisphere, Vol 1: status, ecology and medicine* (eds. M. Hindell, and C. Kemper), Surrey Beatty and Sons, Sydney.
- Lalas, C., and Harcourt, R. (1995) Pup production of the New Zealand fur seal on Otago Peninsula, New Zealand. *Journal of the Royal Society of New Zealand*, 25, 81-88.
- Lander, R.H. (1975) Methods of determining natural mortality in the northern fur seal (*Callorhinus ursinus*) from known pups and kill by age and sex. *Journal of the Fisheries Research Board of Canada*, 32, 2447-2452.
- Lander, R.H. (1981) A life table and biomass estimate for Alaskan fur seals. *Fisheries Research*, 1, 55-70.
- Lavigne, D.M., Innes, S., Worthy, G.A.J., Kovacs, K.M., Schmitz, O.J., and Hickie, J.P. (1986) Metabolic rates of seals and whales. *Canadian Journal of Zoology*, 64, 279-284.
- Laws, R. M., and Sinha, A. A. (1993) Reproduction. *Antarctic Seals research methods and techniques* (ed. R. M. Laws), pp. 228-267. Cambridge University Press, Cambridge, Great Britain.
- Laws, R.M. (1956) Growth and sexual maturity in aquatic mammals. *Nature*, 178, 193-194.
- Le Boeuf, B.J., and Reiter, J. (1988) Lifetime reproductive success in northern elephant seals. *Reproductive Success* (ed. T.H. Clutton-Brock), pp 344-362. University of Chicago Press, Chicago.

- Lea, M-A, and Hindell, M.A. (1997) Pup Growth and Maternal Care in New Zealand Fur Seals, *Arctocephalus forsteri*, at Maatsuyker Island, Tasmania. *Wildlife Research*, 24, 307-318.
- Leberg, P.L., Brisbin Jr., I.L., Smith, M.H., and White, G.C. (1989) Factors affecting the analysis of growth patterns of large mammals. *Journal of Mammalogy*, 70, 275-283.
- Lebreton, J-D., Burnham, K.P., Clobert, J., and Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, 62, 67-118.
- Lento, G.I.H., Haddon, M., Chambers, G.K., and Baker, C.S. (1997) Genetic variation, population structure, and species identity of Southern Hemisphere fur seals, *Arctocephalus* spp. *Journal of Heredity*, 88, 202-208.
- Lima, M., and Páez, E. (1995) Growth and reproductive patterns in the South American fur seal. *Journal of Mammalogy*, 76, 1249-1255.
- Lima, M., and Páez, E. (1997) Demography and population dynamics of South American fur seals. *Journal of Mammalogy*, 78, 914-920.
- 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.
- Loughlin, T.R., and Spraker, T. (1989) Use of Telazol® to immobilise female Northern sea lions (*Eumetopias jubatus*) in Alaska. *Journal of Wildlife Diseases*, 25, 353-358.
- Lunn, N. J., and Boyd I. L. (1993a) Influence of maternal characteristics and environmental variation on reproduction in Antarctic fur seals. *Symposia of the Zoological Society of London*, 66, 115-129.
- Lunn, N. J., and Boyd I. L. (1993b) Effects of maternal age and condition on parturition and the perinatal period of Antarctic fur seals. *Journal of Zoology (London)*, 229, 55-67.
- Lunn, N. J., Boyd I. L., and Croxall, J. P. (1994) Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *Journal of Animal Ecology*, 63, 827-840.
- Lynch, M. J., Tahmindjis, M. A., and Gardner, H. (1999) Immobilisation of pinniped species. *Australian Veterinary Journal*, 77, 181-185.
- Mattlin, R.H. (1978a) Population biology, thermoregulation and site preference of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson, 1928), on the Open Bay Islands, New Zealand. PhD thesis. University of Canterbury, New Zealand.

- Mattlin, R.H. (1978b) Pup mortality of the New Zealand fur seal (*Arctocephalus forsteri* Lesson). *New Zealand Journal of Ecology*, 1, 138-144.
- Mattlin, R.H. (1981) Pup growth of the New Zealand fur seal *Arctocephalus forsteri* on the Open Bay Islands, New Zealand. *Journal of Zoology (London)*, 193, 305-314.
- Mattlin, R.H. (1987) New Zealand fur seals, *Arctocephalus forsteri*, within the New Zealand Region. *Status, Biology, and Ecology of Fur Seals* (eds. J.P. Croxall, and R.L. Gentry), NOAA Technical Report NMFS, 51, 49-51.
- Mattlin, R.H., Gales, N.J., and Costa, D.P. (1998) Seasonal dive behaviour of lactating New Zealand fur seals (*Arctocephalus forsteri*). *Canadian Journal of Zoology*, 76, 350-360.
- McCafferty, D. J. (1999) Premature pupping in Antarctic fur seals (*Arctocephalus gazella*). *Marine Mammal Science*, 15, 882-885.
- McCann, T.S. (1993) Age determination. *Antarctic seals research and methods and techniques* (ed. R.M. Laws), pp. 199-227. Cambridge University Press, Cambridge.
- McCann, T.S., Fedak, M.A., and Harwood, J. (1989) Parental investment in southern elephant seals, *Mirounga leonina*. *Behavioural Ecology and Sociobiology*, 25, 81-87.
- McDougall, J. (2006) A recipe for disaster. *Ausmarine*, March 2006, 14-15.
- McKenzie, J., Parry, L.J., Page, B., and Goldsworthy, S.D. (2005a) Estimation of pregnancy rates and reproductive failure in New Zealand fur seals (*Arctocephalus forsteri*). *Journal of Mammalogy*, 86, 1237-1246.
- McKenzie, J., Goldsworthy, S. D., Shaughnessy, P. D., and McIntosh, R. (2005b) *Understanding the impediments to the growth of Australian sea lion populations*. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, Australia.
- McKenzie, J., Page, B. Goldsworthy, S.D., and Hindell, M.A. (*in press a*). Growth strategies of New Zealand fur seals (*Arctocephalus forsteri*), in southern Australia. *Journal of Zoology (London)*.
- McKenzie, J., Page, B. Goldsworthy, S.D., and Hindell, M.A. (*in review*) Behavioural responses of New Zealand fur seals (*Arctocephalus forsteri*) to darting and the effectiveness of midazolam and tiletamine-zolazepam for remote chemical immobilisation. *Marine Mammal Science*.

- McKenzie, J., Page, B., Shaughnessy, P.D., and Hindell, M.A. (*in press b*) Age and reproductive maturity of New Zealand fur seals (*Arctocephalus forsteri*), in southern Australia. *Journal of Mammalogy*.
- McLaren, I.A. (1993) Growth in pinnipeds. *Biological Review*, 68, 1-79.
- McLaren, I.A., and Smith, T.G. (1985) Population ecology of seals: retrospective and prospective views. *Marine Mammal Science*, 1, 54-83.
- McNab, A.G., and Crawley, M.C. (1975) Mother and pup behaviour of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson). *Mauri Orca*, 3, 77-88.
- Miller, E.H. (1971) Social and thermoregulatory behaviour of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson, 1828). MSc thesis, University of Canterbury, Christchurch, New Zealand.
- Miller, E.H. (1974) Social behaviour of the New Zealand fur seal on the Open Bay Islands, Westland. Fisheries Technical report No. 131, New Zealand Ministry of Agriculture and Fisheries, Wellington, New Zealand.
- Miller, E.H. (1975a) Body and organ measurements of fur seals, *Arctocephalus forsteri* (Lesson), from New Zealand. *Journal of Mammalogy*, 56, 511-513.
- Miller, E.H. (1975b) Annual cycle of fur seals, *Arctocephalus forsteri* (Lesson), on the Open Bay Islands, New Zealand. *Pacific Science*, 29, 139-152.
- Mori, Y. (2002) Optimal diving behaviour for foraging in relation to body size. *Journal of Evolutionary Biology*, 15, 269-276.
- National Seal Strategy Group (2005) National Assessment of Interactions between Humans and Seals: Fisheries, Aquaculture and Tourism. Australian Government Department of Agriculture, Fisheries and Forestry.
- Niswender, G. D., Juengel, J. L., Silva, P. J., Rollyson, M. K., and McIntush, E. W. (2000) Mechanisms controlling the function and life span of the corpus luteum. *Physiological Review*, 80, 1-29.
- Odendaal, P. N., Bester, M. N., van der Merwe, M., and Oosthuizen, W. H. (2002) Seasonal changes in the ovarian structure of the Cape fur seal, *Arctocephalus pusillus pusillus*. *Australian Journal of Zoology*, 50, 491-506.
- Oosthuizen, W.H. (1997) Evaluation of an effective method to estimate age of Cape fur seals using ground tooth sections. *Marine Mammal Science*, 13, 683-693.
- Oosthuizen, W.H., and Bester M.N. (1997) Comparison of age determination techniques for known-age Cape fur seals. *South African Journal of Zoology*, 32, 106-111.

- Oosthuizen, W.H., and Miller, E.H. (2000) Bacular and testicular growth and allometry in the Cape fur seal *Arctocephalus p. pusillus* (Otariidae). *Marine Mammal Science*, 16, 124-140.
- Osofsky, S.A., and Hirsch, K.J. (2000) Chemical restraint of endangered mammals for conservation purposes: a practical primer. *Oryx*, 34, 27-33.
- Page, B., McKenzie, J., and Goldsworthy, S.D. (2005a) Inter-sexual differences in New Zealand fur seal diving behaviour. *Marine Ecological Progress Series*, 304, 249-264.
- Page, B., McKenzie, J., and Goldsworthy, S.D. (2005b) Dietary resource partitioning among sympatric New Zealand and Australian fur seals. *Marine Ecological Progress Series*, 293, 283-302.
- Page, B., McKenzie, J., McIntosh, R., Baylis, AMM., Morrissey, A., Calvert, N., Haase, T., Berris, M., Dowie, D., Shaughnessy, P.D., and Goldsworthy, S.D. (2004) Entanglement of Australian sea lions and New Zealand fur seals in lost fishing gear and other marine debris before and after Government and industry attempts to reduce the problem. *Marine Pollution Bulletin*, 49, 33-42.
- Page, B., McKenzie, J., Sumner, M.D., Coyne, M., and Goldsworthy, S.D. (2006) Spatial separation of foraging habitats among New Zealand fur seals. *Marine Ecology Progress Series*, 323, 263-279.
- Payne, M. R. (1977) Growth of a fur seal population. *Philosophical Transactions of the Royal Society, London B*, 279, 647-79.
- Payne, M.R. (1978) Population size and age determination in the Antarctic fur seal, *Arctocephalus gazella*. *Mammalian Review*, 8, 67-73.
- Payne, M.R. (1979) Growth in the Antarctic fur seal *Arctocephalus gazella*. *Journal of Zoology (London)*, 187, 1-20.
- Peters, R.H. (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge, England.
- Phelan, J.R., and Green, K. (1992) Chemical restraint of Weddell seals (*Leptonychotes weddellii*) with a combination of tiletamine and zolazepam. *Journal of Wildlife Diseases*, 28, 230-235.
- Pistorius P.A., Bester, M.N., Kirkman, S.P., and Taylor, F.E. (2001) Temporal changes in fecundity and age of sexual maturity of southern elephant seals at Marion Island. *Polar Biology*, 24, 343-348.
- Pistorius, P.A., and Bester, M.N. (2002) A longitudinal study of senescence in a pinniped. *Canadian Journal of Zoology*, 80, 395-401.

- Pitcher, K.W., and Calkins, D.G. (1981) Reproductive biology of Steller seal lions in the Gulf of Alaska. *Journal of Mammalogy*, 62, 599-605.
- Pitcher, K.W., Calkins, D.G., and Pendleton, G.W. (1998) Reproductive performance of female Steller sea lions: an energetics-based reproductive strategy? *Canadian Journal of Zoology*, 76, 2075-2083.
- Post, E., Langvatn, R., Forchhammer, M.C., and Stenseth, N.C. (1999) Environmental variation shapes sexual dimorphism in red deer. *Proceedings of the National Academy of Sciences of the United States of America*, 96, 4467-4471.
- Quinn, G.P., and Keough, M.J. (2003) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, England.
- Raeside, J. I., and Ronald, K. (1981) Plasma concentrations of oestrone, progesterone and corticosteroids during late pregnancy and after parturition in harbour seals, *Phoca vitulina*. *Journal of Reproduction and Fertility*, 61, 135-139.
- Rand, R. W. (1955) Reproduction in the female Cape fur seal, *Arctocephalus pusillus*. *Proceedings of the Zoological Society of London*, 124, 717-740.
- Reijnders, P. J. H. (1990) Progesterone and oestradiol-17 β concentration profiles throughout the reproductive cycle in harbour seals (*Phoca vitulina*). *Journal of Reproduction and Fertility*, 90, 403-409.
- Reiter, J., and Le Boeuf, B.J. (1991) Life history consequences of variation in age at primiparity in northern elephant seals. *Behavioural Ecology and Sociobiology*, 28, 153-160.
- Riedman, M. (1990) *The pinnipeds: Seals, Sea Lions and Walruses*. University of California Press, Los Angeles.
- Ropstad, E., Johansen, O., King, C., Dahl, E., Albon, S. D., Langvatn, R. L., Irvine, R. J., Halvorsen, O., and Sasser, G. (1999) Comparison of plasma progesterone, transrectal ultrasound and pregnancy specific proteins (PSPB) used for pregnancy diagnosis in reindeer. *Acta Veterinaria Scandinavica*, 40, 151-162.
- Rosas, F.C.W., Haimovici, M., and Pinedo, M.C. (1993) Age and growth of the South American sea lion, *Otaria flavescens* (Shaw, 1800), in southern Brazil. *Journal of Mammalogy*, 74, 141-147.
- Roux, J-P. (1987) Recolonization Processes in the Subantarctic Fur Seal, *Arctocephalus tropicallis*, on Amsterdam Island. *Status, Biology, and Ecology of Fur Seals* (eds. J.P. Croxall, and R.L. Gentry), NOAA Technical Report NMFS, 51, 189-194.

- Ryan, C.J., Hickling, G.J., and Wilson, K-J. (1997) Breeding habitat preference of the New Zealand fur seal (*Arctocephalus forsteri*) on Banks Peninsula. *Wildlife Research*, 24, 225-235.
- Sasser, R. G., and Ruder, C. A. (1987) Detection of early pregnancy in ruminants. *Journal of Reproduction and Fertility*, 34, 261-271.
- Scheffer, V.B., and Wilke, F. (1953) Relative growth in the northern fur seal. *Growth*, 17, 129-145.
- Schreer, J.F., and Kovacs, K.M. (1997) Allometry of diving capacity in air-breathing vertebrates. *Canadian Journal of Zoology*, 75, 339-358.
- Sepúlveda, M.S., Ochoa-Acuña, H., and McLaughlin, G.S. (1994) Immobilization of Juan Fernandez fur seals, *Arctocephalus philippii*, with ketamine hydrochloride and diazepam. *Journal of Wildlife Diseases*, 30, 536-540.
- Shaughnessy, P. (2004) 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 the Department for the Environment Heritage.
- Shaughnessy, P. (2005) Population assessment of New Zealand fur seals and Australian sea lions at some South colonies in South Australia, 2004-2005. Report to Department for Environment Heritage, South Australia. CSIRO, Canberra, Australia.
- Shaughnessy, P. (2006) *Population assessment of fur seals and sea lions at some South colonies in South Australia, 2005-2006*. Report to Department for Environment Heritage, South Australia. CSIRO, Canberra, Australia.
- Shaughnessy, P., and Dennis, T. (2001) *Research on New Zealand fur seals and Australian sea lions in South Australia, 200-2001*. Report to National Parks and Wildlife South Australia, Department for Environment and Heritage. CSIRO, Canberra, Australia.
- Shaughnessy, P., and Dennis, T. (2002) *Population assessment of some colonies of New Zealand fur seals and Australian sea lions in some South Australian, 2001-2002*. National Parks and Wildlife South Australia, Department for Environment and Heritage. CSIRO, Canberra, Australia.
- Shaughnessy, P., and Dennis, T. (2003) *Population assessment of New Zealand fur seals and Australian sea lions in some South Australia colonies, 2002-2003*. Report to National Parks and Wildlife South Australia, Department for Environment and Heritage. CSIRO, Canberra, Australia.
- Shaughnessy, P.D. (1970) Serum protein variation in southern fur seals, *Arctocephalus* spp., in relation to their taxonomy. *Australian Journal of Zoology*, 18, 331-343.

- Shaughnessy, P.D. (1995) *The Action Plan for Australian seals*. Environment Australia, Canberra, ACT, Australia.
- Shaughnessy, P.D. (1997) *Abundance of New Zealand fur seals *Arctocephalus forsteri* at some colonies in South Australia, 1995/96*. Report to the South Australian National Parks and Wildlife Service, Department of Environment and Natural Resources, July 1997.
- Shaughnessy, P.D. (2000) *Seal Research in South Australia, 1999/2000: Abundance of New Zealand Fur Seal Pups on Kangaroo Island and the Neptune Islands*. Report to National Parks and Wildlife, South Australia, Department of Environment and Heritage, November 2000.
- Shaughnessy, P.D., and McKeown, A. (2002) Trends in abundance of New Zealand fur seals, *Arctocephalus forsteri*, at the Neptune Islands, South Australia. *Wildlife Research*, 29, 363-370.
- Shaughnessy, P.D., Gales, N.J., Dennis, T.E., and Goldsworthy, S.D. (1994) Distribution and abundance of the New Zealand fur seal *Arctocephalus forsteri* in South Australia and Western Australia. *Wildlife Research*, 21, 667-695.
- Shaughnessy, P.D., Goldsworthy, S.D., and Libke, J.A. (1995) Changes in the Abundance of New Zealand fur seals, *Arctocephalus forsteri*, on Kangaroo Island, South Australia. *Wildlife Research*, 22, 201-215.
- Shaughnessy, P.D., Kirkwood, R., Cawthorn, M., Kemper, C., and Pemberton, D. (2003) Pinnipeds, cetaceans and fisheries in Australia: a review of operational intractions. *Marine Mammals: fishing, tourism and management issues* (eds. N. Gales, M. Hindell and R. Kirkwood), pp. 124-140. CSIRO Publishing, Melbourne.
- Short, R. V. (1984) Oestrous and menstrual cycles. *Reproduction in mammals, Book 3 Hormonal control of reproduction* (eds. C.R. Austin and R.V. Short), pp. 115-152. Cambridge University Press, Sydney, Australia.
- Sibly, R.M., and Hone, J. (2002) Population growth rate and its determinants: an overview. *Philosophical Transactions of the Royal Society of London, Series B*, 357, 1153-1170.
- Siler, W. (1979) A competing-risk model for animal mortality. *Ecology*, 60, 750-757.
- Smith, I.W.G. (1989) Maori impact on the marine megafauna: pre-European distribution of New Zealand sea mammals. *Saying so doesn't make it so* (ed. D.G. Sutton), *New Zealand Archaeological Association Monographs*, 7, 76-108.
- Sorenson, J.H. (1969) New Zealand fur seals with special reference to the 1946 open season. *New Zealand Marine Department Fisheries Technical Report*, 39.

- Spelman, L.H. (2004) Reversible anesthesia of captive California sea lions (*Zalophus californianus*) with medetomidine, midazolam, butorphanol, and isoflurane. *Journal of Zoo and Wildlife Medicine*, 35, 65-69.
- Spinage, C.A. (1972) African ungulate life tables. *Ecology*, 53, 645-652.
- Stewart, R.E.A., Stewart, B.E., Stirling, I., and Street, E. (1996) Counts of growth layer groups in cementum and dentine in ringed seals (*Phoca hispida*). *Marine Mammal Science*, 12, 383-401.
- Stirling, I. (1971) Studies of the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson). Part II, Adult females and pups. *Australian Journal of Zoology*, 19, 267-273.
- Stirling, I. (1983) The evolution of mating systems in pinnipeds. *Advances in the Study of Mammalian Behaviour* (eds. J.F. Eisenberg and D.G. Kleiman), pp. 489-527. American Society of Mammalogists, Shippensburg, Pennsylvania.
- Stolen, M.K., and Barlow, J. (2003) A model life table for bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon system, Florida, U.S.A. *Marine Mammal Science*, 19, 630-649.
- Tahmindjis, M.A., Higgins, D.P., Lynch, M.J., Barnes, J.A. and Southwell, C.J. (2003) Use of pethidine and midazolam combination for the reversible sedation of crabeater seals (*Lobodon carcinophagus*). *Marine Mammal Science*, 19, 581-589.
- Taylor, R.H. (1982) New Zealand fur seals at the Bounty Islands. *New Zealand Journal of Marine and Freshwater Research*, 16, 1-9.
- Taylor, R.H., Barton, K.J., Wilson, P.R., Thomas, B.W., and Karl, B.J. (1995) Population status and breeding of New Zealand fur seals (*Arctocephalus forsteri*) in the Nelson-northern Marlborough region, 1991-94. *New Zealand Journal of Marine and Freshwater Research*, 29, 223-234.
- Testa, J. W. (1987) Long-term reproductive patterns and sighting bias in Weddell seals (*Leptonychotes weddellii*). *Canadian Journal of Zoology*, 65, 1091-1099.
- Testa, J.W., and Siniff, D. (1987) Population dynamics of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. *Ecological Monographs*, 57, 149-165.
- Trillmich, F. (1983) Ketamine xylazine combination for the immobilisation of Galapagos sea lions and fur seals. *The Veterinary Record*, 112, 279-280.
- Trillmich, F. (1993) Influence of rare ecological events on pinniped social structure and population dynamics, *Symposia of the Zoological Society of London*, 66, 95-114.

- Trillmich, F., and Wiesner, H. (1979) Immobilisation of free-ranging Galapagos sea lions (*Zalophus californianus wollebaeki*). *The Veterinary Record*, 105, 465-466.
- Trillmich, F., and Ono, K. A. (1991) *Pinnipeds and El Nino: Responses to Environmental Stress*. Springer-Verlag, Berlin.
- Trites, A.W. (1989). Estimating juvenile survival rates of male northern fur seals (*Callorhinus ursinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 46, 1428-1436.
- 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. (1992) Reproductive synchrony and the estimation of mean date of birth from daily counts of Northern fur seal pups. *Marine Mammal Science*, 8, 44-56.
- Trites, A.W., and Bigg, M.A. (1992) Changes in body growth of northern fur seals from 1958 to 1974: density effects or changes in the ecosystem? *Fisheries Oceanography*, 1, 127-136.
- Trites, A.W., and Bigg, M.A. (1996) Physical growth of northern fur seals (*Callorhinus ursinus*): seasonal fluctuations and migratory influences. *Journal of Zoology (London)*, 238, 459-482.
- Trites, A.W., and Larkin, P.A. (1989) The decline and fall of the Pribilof fur seal (*Callorhinus ursinus*): A simulation study. *Canadian Journal of Fisheries and Aquatic Sciences*, 46, 1437-1445.
- Trivers, R.L. (1972) Parental investment and sexual selection. *Sexual selection and the descent of man* (ed. B. Campbell), pp. 136-179. Aldine Press, Chicago, Illinois.
- Troy S.K. (1997) *Territorial behaviour and mating success in male New Zealand fur seals*, *Arctocephalus forsteri*, PhD thesis, University of Melbourne, Melbourne
- Troy, S.K., Mattlin, R., Shaughnessy, P.D., and Davie, P.S. (1999) Morphology, age and survival of adult male New Zealand fur seals, *Arctocephalus forsteri*, in South Australia. *Wildlife Research*, 26, 21-34.
- Troy, S.K., Middleton, D., and Phelan, J. (1997) On capture, anaesthesia and branding of adult male New Zealand fur seals *Arctocephalus forsteri*. *Marine mammal research in the southern hemisphere Volume 1: status, ecology and medicine* (eds. M. Hindell and C. Kemper), pp. 179-83. Surrey Beatty and Sons, Chipping Norton, Australia.
- Vaz-Ferreira, R., and Ponce de Leon, A. (1987) South American fur seal, *Arctocephalus australis*, in Uruguay. *Status, Biology, and Ecology of Fur Seals* (eds. J.P.Croxall, and R.L. Gentry), NOAA Technical Report NMFS, 51, 29-32.

- Walzer, C., and Huber, C. (2002) Partial antagonism of tiletamine-zolazepam anesthesia in cheetah. *Journal of Wildlife Diseases*, 38, 468-472.
- Warneke, R. M. (1982) The distribution and abundance of seals in the Australian region, with summaries of biology and current research. *Mammals in the Seas*, Vol. IV. Small Cetaceans, Seals, Sirenians and Otters. Food and Agriculture Organization, Fisheries Series No. 5, 431-475.
- Weckerly, F.W. (1998) Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy*, 79, 33-52.
- Wheatley, K., Bradshaw, C., Harcourt, R., Davis, L. and Hindell, M. (2006) Chemical immobilization of adult female Weddell seals with tiletamine and zolazepam: effect of age, condition and stage of lactation. *BMC Veterinary Research* 2, 8.
- Wickens, P.A., Japp, D.W., Shelton, P.A., Kriel, F., Goosen, P.C., Rose, B., Augustyn, C.J., Bross, C.A.R., Penney, A.J., and Krohn, R.G. (1992) Seals and fisheries in South Africa - competition and conflict. *Benguela Trophic Functioning* (eds. A.I.L. Payne, K.H. Brink and R. Hilborn) *South African Journal of Marine Science*, 12, 773-789.
- Wickens, P., and York, A.E. (1997) Comparative population dynamics of fur seals. *Marine Mammal Science*, 13, 241-292.
- Wickens, P.A. (1993) Life expectancy of fur seals, with special reference to the South African (Cape) fur seal. *South African Journal of Wildlife Research*, 23, 101-106.
- Widdowson, E.M. (1981) The role of nutrition in mammalian reproduction. *Environmental factors in mammal reproduction* (eds D. Gilmore and B. Cook), pp 145-159, Macmillan Publishers, London.
- Winship, A.J., Trites, A.W., and Calkins, D.G. (2001) Growth in body size of the Steller sea lion (*Eumetopias jubatus*). *Journal of Mammalogy*, 82, 500-519.
- Woods, R. McLean, S., Nicol, S., and Burton, H. (1995) Antagonism of some cyclohexamine-based drug combinations used for chemical restraint of southern elephant seals (*Mirounga leonina*). *Australian Veterinary Journal*, 72, 165-171.
- Woods, R. McLean, S., Nicol, S., Slip, D.J., and Burton, H. (1996) Use of the respiratory stimulant doxapram in southern elephant seals (*Mirounga leonina*). *The Veterinary Record*, 138, 514-517.
- Woods, R., Hindell, M., and Slip, D.J. (1989). Effects of physiological state on duration of sedation in southern elephant seals. *Journal of Wildlife Diseases*, 25, 586-590.

- Woods, R., McLean, S., Nicol, S., and Burton, H. (1994) A comparison of some cyclohexamine based drug combinations for chemical restraint of southern elephant seals (*Mirounga leonina*). *Marine Mammal Science*, 10, 412-429.
- Wynen, L.P., Goldsworthy, S.D., Insley, S.J., Adama, M., Bickham, J.C.V., Francis, J., Gallo, J.P., Hoelzel, A.R., Majluf, P., White, R.W.G., and Slade, R. (2001) Phylogenetic relationships within the eared seals (Otariidae : Carnivora): Implications for the historical biogeography of the family. *Molecular Phylogenetics and evolution*, 21, 270-284.
- York, A. E. (1983) Average age at first reproduction of the Northern fur seal (*Callorhinus ursinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 40, 121-127.
- York, A. E., and Scheffer, V. B. (1997) Timing of implantation in the northern fur seal, *Callorhinus ursinus*. *Journal of Mammalogy*, 78, 675-683.
- York, A.E. (1987) On Comparing the Population Dynamics of Fur Seals. *Status, Biology, and Ecology of Fur Seals* (eds J.P. Croxall and R.L. Gentry), NOAA Technical Report NMFS, 51, 133-140.
- York, A.E. (1994) The population dynamics of northern sea lions, 1975-1985. *Marine Mammal Science*, 10, 38-51.
- Yoshida, K., Baba, N., Oya, M., and Mizue, K. (1978) Seasonal changes in the ovary of the northern fur seal. *Bulletin of the Far Seas Fisheries Research Laboratory*, 16, 93-101.
- Zar, J.H. (1996) *Biostatistical Analysis*. 3rd ed. Prentice-Hall, Inc., Englewood, New Jersey.
- Zullinger, E.M., Ricklefs, R.E., Redford, K.M., and Mace, G.M. (1984) Fitting sigmoidal equations to mammalian growth curves. *Journal of Mammalogy*, 65, 607-636.

