# Conservation Biology of New Zealand Sea Lions (*Phocarctos hookeri*)

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# ABSTRACT

New Zealand sea lion (*Phocarctos hookeri*) is a pinniped endemic to New Zealand and is among the rarest of sea lion species. New Zealand sea lions are incidentally caught in the trawl fishery for squid around the Auckland Islands, and a sea lion catch-limit or Fishing Related Mortality Limit (FRML) is used to manage this interaction. Since 2003 such limits have been calculated using an age-structured Bayesian population model. One problem with this approach is that several key demographic parameters have had to be assumed, or are based on very few data.

Archaeological and other historical records demonstrate that New Zealand sea lions were substantially more widespread before the arrival of humans to New Zealand than they are today (Chapter 2 published as Childerhouse & Gales 1998). The present population size is clearly reduced, with subsistence and commercial hunting the most likely cause of historical changes in distribution and abundance. Campbell Island, the only significant breeding site outside the Auckland Islands, was thoroughly surveyed for New Zealand sea lions for the first time in 2003. An estimated 385 pups were born there, comprising 13% of the total pup production for the species for 2003 (Chapter 3 published as Childerhouse *et al.* 2005).

This thesis provides the first robust estimates of several demographic parameters for New Zealand sea lions. These data were gained via the capture, tagging and ageing of 865 individual females, which had come ashore to pup between 1999 and 2001. This research was underpinned by the development of a novel and robust ageing technique for live New Zealand sea lions (Chapter 5 published as Childerhouse *et al.* 2004).

Chapters 6, 7 and 8 used analyses of the age structure of these females, and of subsequent resightings of them, and of known-age females between 1998 and 2005, provided the first estimates of individual growth, mean reproductive rate (0.67, SE = 0.01), mean adult survival (0.81, SE = 0.04), and maximum age (28 years) for females. These data show that New Zealand sea lions are among the slowest growing, slowest reproducing, and longest lived sea lion species. Significant differences in the age structure of the two largest breeding colonies highlight flawed assumptions of the current management approach. The application of this new demographic information has the potential to significantly alter the existing management advice relating to the setting of FRMLs and the impact of the squid fishery on the New Zealand sea lion population.

Taken alone, these results suggest a dim outlook for an already threatened species. In the context that pup production is in significant decline (e.g. 32% since 1998 Chilvers *et al.* 2007), the species' foraging environment is thought to be marginal (Costa & Gales 2000), and that resource competition may also be impacting on the population (Chapter 4 published as Childerhouse *et al.* 2001a), the picture darkens further. Taken as a whole, these data suggest that current management is insufficient to ensure population stasis, let alone meet the Government's statutory goal of recovery.

# ACKNOWLEDGEMENTS

It has been a privilege to be surrounded by so many wonderful, supportive and patient people during this extremely lengthy but satisfying journey. After such a long time in getting to this point, I hope that I have not inadvertently forgotten anyone deserving of thanks.

This project required extraordinarily challenging fieldwork including the capture and sampling of 865 adult female sea lions and several thousand pups. Twenty two New Zealand sea lions captured, anaesthetised and processed in single day remains the world record and what a day that was! My deepest gratitude to the dedication and commitment of all the people who provided help and support to complete this enormous task: Jacinda Amy, Henriette Beikirch, Derek Cox, Padraig Duignan, Nick Gales, Nadine Gibbs, Francis Gulland, Bernie Haberley, Wally Hockly, Gus McAlister, Shaun McConkey, Helen McConnell, Nathan McNally, Dave Sutherland, and Ian Wilkinson. Without all of you this work would not have been possible, nearly as satisfying, or as anywhere near as much fun.

This thesis has grown organically since its original inception due to the input of many talented people. I owe a huge amount to Nick Gales who gave me not only my first introduction to New Zealand sea lions but also my first real job. The thesis has been greatly improved by advice and suggestions from a wide range of people including: Jacinda Amy, Louise Chilvers, Dan Costa, Padraig Duignan, Nick Gales, Nadine Gibbs, Wally Hockly, Rob Mattlin, Gus McAlister, Ian West, and Ian Wilkinson. I have included an Acknowledgement section at the end of most of the Chapters in order to recognise the contributions of people for specific pieces of work. Just because you don't appear here does not mean I don't appreciate your wonderful contributions.

Several of the Chapters in this thesis have been published already and I would like to recognise the contributions of my co-authors in getting the research out there - a key feature of the conservation science process. Thanks to: Bruce Dix, Nick Gales, Nadine Gibbs, Guy Hessel, Gus McAlister, Shaun McConkey, Helen McConnell, Nathan McNally, Dave Sutherland, and Gail Townsend (nee Dickie).

I am extremely grateful to Louise Chilvers, Ian Wilkinson and Ian West for making unpublished data available from the long term DOC New Zealand sea lion research programme. This programme is world class and it was a privilege to be part of it and

contribute to it. Their generous provision of data allowed me to improve the depth and conclusions of this thesis making it considerably better than it would have been otherwise. I would also like to thank Jane McKenzie for making unpublished data available. Louise Chilvers also provided some insightful and useful personal communications.

To my supervisors, Associate Professors Steve Dawson, Liz Slooten and David Fletcher: my greatest admiration and appreciation for your dedication, wisdom, inspiring science and friendship. When I first met you, you were all relatively new lecturers at the University of Otago, and it is satisfying to see your brilliant contributions to science and conservation have been recognised with promotions, despite it making me realise just how long I have been in and out of the University of Otago! My success is due in great part to your leadership, support and the challenges that you have encouraged me to take. Thanks for everything and don't think you have seen the last of me just yet. Professor Richard Barker also filled in as an Acting supervisor for a short period and his help is appreciated. Ian West, while not formally one of my supervisors, filled an equally valuable position as role model, mentor, manager and friend to me both during my time at DOC and afterwards.

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On a personal note, I have had the support of a great many friends and colleagues who provided advice, support and friendship over the years. There are too many of you to mention here but don't think that I value your input any the less. One of the most exciting things about completing this thesis is that I now get to spend more quality time with you all. Special thanks to Lesley Douglas for coming into my life in the latter stages of my thesis and helping to hold everything together, not to mention the magic thesis formatting and editing.

I am not sure that my parents actually believed that I would ever finish this thesis but thankfully they were always too kind to come out and say it! So despite all my deviations and distractions, I am finally finished. Thanks for always being so supportive, loving and all round amazing people. While my supervisors deserve the credit for honing my scientific skills, you deserve the credit for preparing me personally for this and instilling such a fine sense of self belief in me that, even during the difficult times, I never stopped believing that I could accomplish this. Lots of love to you both and please accept a large amount of the credit for me getting here.

# TABLE OF CONTENTS

## CHAPTER 1: GENERAL INTRODUCTION

## CHAPTER 2: HISTORICAL AND MODERN DISTRIBUTION AND ABUNDANCE OF NEW ZEALAND SEA LION

## CHAPTER 3: DISTRIBUTION, ABUNDANCE AND GROWTH OF NEW ZEALAND SEA LION PUPS ON CAMPBELL ISLAND

## CHAPTER 4: DIET OF NEW ZEALAND SEA LIONS AT THE AUCKLAND ISLANDS

## CHAPTER 5: AGEING LIVE NEW ZEALAND SEA LIONS USING THE FIRST POST-CANINE TOOTH

## CHAPTER 6: INTER-ANNUAL AND INTER-SITE VARIATION IN AGE DISTRIBUTION OF LACTATING NEW ZEALAND SEA LIONS

## CHAPTER 7: GROWTH AND REPRODUCTION OF FEMALE NEW ZEALAND SEA LIONS

## CHAPTER 8: MODELLING DEMOGRAPHIC PARAMETERS OF FEMALE NEW ZEALAND SEA LIONS

# CHAPTER 9: CONSERVATION BIOLOGY OF NEW ZEALAND SEA LIONS: GENERAL DISCUSSION AND CONCLUSIONS

# LIST OF TABLES

# LIST OF FIGURES

# Chapter 1

# General Introduction

# CHAPTER 1: GENERAL INTRODUCTION

This thesis is presented as a series of manuscripts that are at various stages of publication, including several Chapters that have already been published. Each Chapter has been written as a stand alone paper but I have also provided a General Introduction Chapter (this Chapter) and a Discussion and Conclusion Chapter that places the work into a coherent context with a single over-arching focus. This Chapter focuses on summarising the state of knowledge of New Zealand sea lions (NZSL) but also includes an introduction to the two main research areas of this thesis: population demography and population modelling. Each subsequent Chapter includes additional detail and background to the relevant research areas that it covers.

## 1.1 NEW ZEALAND SEA LION BIOLOGY

### *1.1.1 Distribution*

The New Zealand sea lion *Phocarctos hookeri* (also known as Hooker's sea lion) is an otariid endemic to New Zealand (NZ). The present distribution of New Zealand sea lions (NZSLs) was significantly reduced from its pre-human range by subsistence and commercial sealing. The pre-human range was the whole of NZ (Smith 1989; Childerhouse & Gales 1998 (Chapter 2); Gill 1998). The species' range was reduced to a remnant population in the NZ sub-Antarctic during the 19th Century and has since shown a slow recolonisation of parts of its former range (Childerhouse & Gales 1998 (Chapter 2); McConkey *et al.* 2002b).

The present distribution is centred on the NZ sub-Antarctic islands with the majority of individuals living and breeding on Campbell Island and the Auckland Islands group (Figure 1.1) (Gales & Fletcher 1999; McNally *et al.* 2001; Childerhouse *et al.* 2005 (Chapter 3)). NZSLs are also found on The Snares, the South Island and Stewart Island of mainland NZ (Crawley & Cameron 1972; McConnell 2001; McConkey *et al.* 2002a, 2002b). Distribution around the South Island is primarily restricted to the Southland and Otago regions. Vagrant NZSLs have also been reported in Canterbury, and very occasionally on the southern beaches of the North Island (Cawthorn *et al.* 1985). The western-most extent of their distribution is Macquarie Island in the sub-Antarctic, where a few males are regularly seen (McMahon *et al.* 1999; Robinson *et al.* 1999). The species breeds almost exclusively (>99%) on Campbell Island and the Auckland Islands group (Chilvers *et al.* 2007). A few individuals breed occasionally on The Snares, Stewart Island, Codfish Island and around Otago (Childerhouse & Gales 1998 (Chapter 2); Gales & Fletcher 1999; McConkey *et al.* 2002a). Adult males disperse between breeding colonies within breeding seasons and across the species' range before and after the breeding season, suggesting that the entire NZSL population could be considered as a single population unit (Robertson *et al.* 2006).

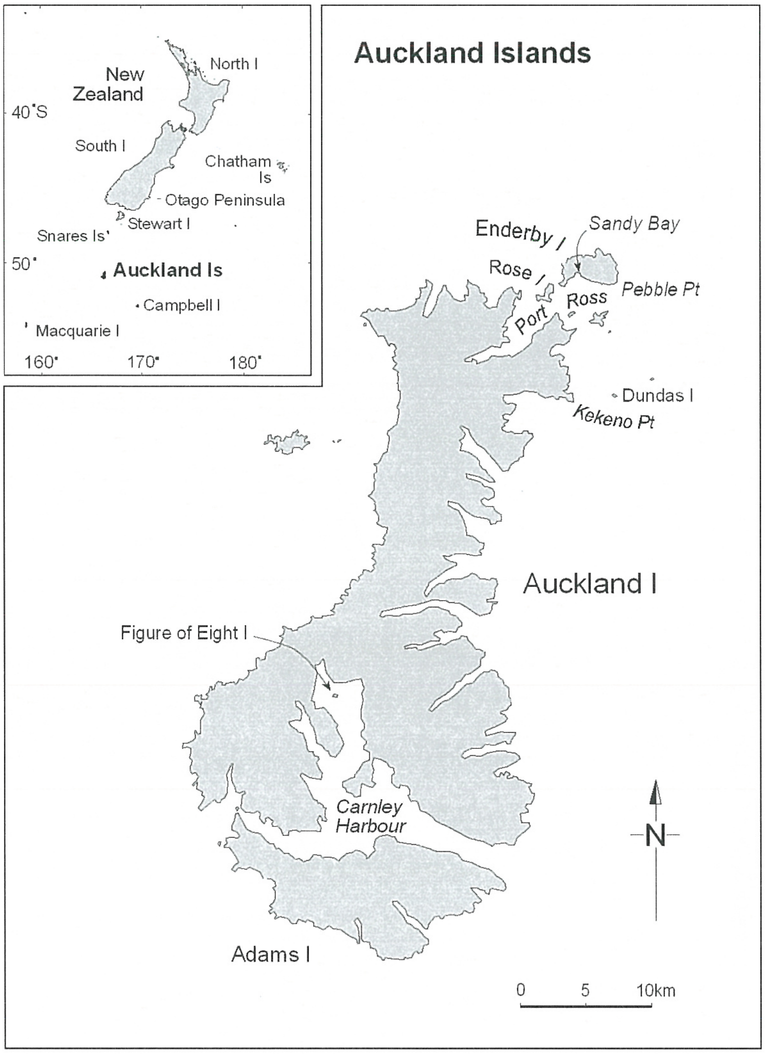

**Figure 1.1** Map showing location of Auckland Islands and sites mentioned in the text

### *1.1.2 Abundance and trends*

Population size of NZSLs at the Auckland Islands was estimated at 11,914 (95% CI 10,311-13,699) individuals for the 2004/05 breeding season (Chilvers *et al.* 2007). There is no evidence of a trend in population size from the 1940s through until 1998 (Childerhouse *et al.* 1998), but there is now evidence to suggest that the population is currently in decline. Annual pup production has declined by 32% since 1998 (Figure 1.2) (Chilvers *et al.* 2007). The 1998 peak in pup production coincided with an unusual mortality event that killed over 50% of the pups born that year and at least 100 adults (Baker 1999; Gales & Childerhouse 1999). Since 1998 there have been two further unusual mortality events, one each in 2002 and 2003, that resulted in significantly higher (i.e. two to three times) than normal pup mortality (Wilkinson *et al.* 2006).

The cause of the 1998 event remains unclear but the most plausible explanation is that of a naïve population being exposed to an unidentified bacterial pathogen, possibly a strain of *Campylobacter* bacteria (Baker 1999; Duignan 1999; Stratton *et al.* 2001). The bacterium *Klebsiella pneumoniae* has been implicated in the latter two events but not in the 1998 event (Wilkinson *et al.* 2006). While these bacterial strains are implicated, it is still unclear whether they were primary or secondary agents and whether there were also unidentified viral pathogens involved.

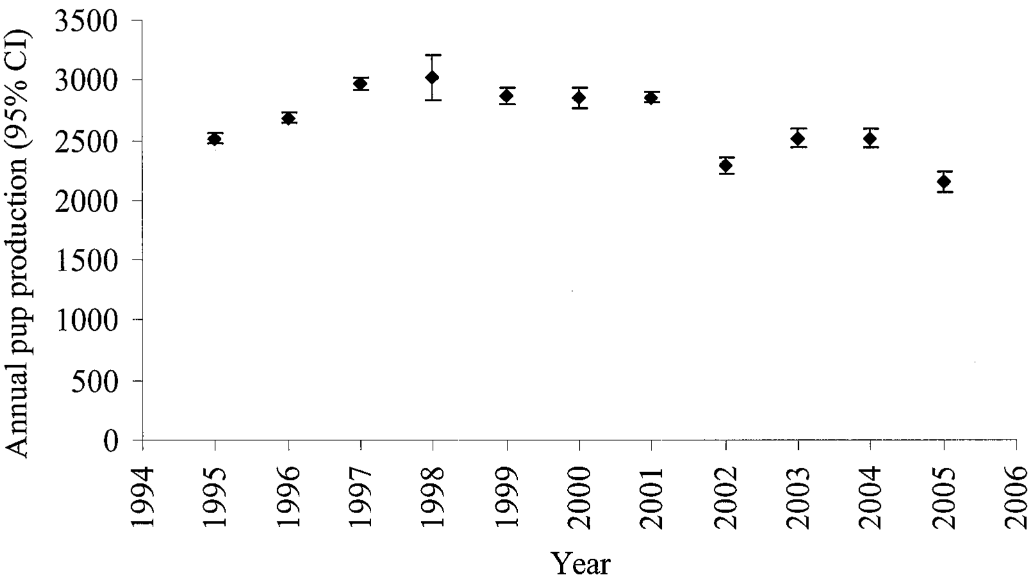

**Figure 1.2** Estimates of New Zealand sea lion annual pup production for the Auckland Islands. Source: Chilvers *et al.* 2007

While the exact relationship between pup production and absolute population size remains unclear, the observed decline in pup production is likely to be indicative of a real population decline. This is supported by evidence of declines in the number of breeding females on the breeding colonies from long term counts while observed reproductive rates show no significant change (Chilvers *et al.* 2007). There are insufficient data to clearly identify the casual agents involved in declining pup production, but there are several potential contributing factors, including fisheries bycatch, the introduction of new pathogens, resource competition with commercial fisheries, density dependence, and environmental stochasticity. Both fisheries bycatch and the recent unusual mortality events have had direct impacts on the population by increasing mortality of adults and/or pups. It is more difficult to establish the impact of the other potential factors as they require more detailed and long term data sets. It is possible that the cause of the decline is a combination of two or more of these factors, which will make it more difficult to determine the true cause of the observed decline.

Based on the recent information, NZSLs are approaching the point at which they may become re-classified under the Department of Conservation (DOC) threat classification system from "at risk"[1] to "chronically threatened"[2], which is a higher risk classification within the threatened category (see Molloy *et al.* 2002). This is also likely to be the case for the IUCN threat classification (IUCN 2002). This would mean that robust and appropriate management becomes essential and should provide additional impetus to the Ministry of Fisheries (MFish) and DOC to minimise the impacts of fishing on NZSLs.

### *1.1.3 Breeding biology*

The breeding biology of NZSLs closely follows the same general pattern as other otariid seals (Bonner 1994, Atkinson 1997). NZSLs are polygamous breeders with a breeding season from December through February. Males establish territories in breeding colonies in late November with females arriving in early December. Females usually arrive 1 to 4 days before parturition, and are then mated 5 to 10 days later (Cawthorn *et al.* 1985; Gales 1995; Chilvers *et al.* 2006a). Pups are born in December and January with pupping generally completed by mid January. Mean pupping date for the Auckland Island colonies is approximately the 25th December and the peak of pupping occurs around the 13th January for Sandy Bay and Dundas Island colonies and slightly earlier for South East Point colony in the Auckland Islands (Cawthorn 1993; Gales & Fletcher 1999). Pups are generally nursed for 10 to 12 months but occasionally for up to 2 years (Gales 1995; Childerhouse & Gales 2001). There is considerable sexual dimorphism with mature males (mean = 400 kg) being significantly larger than mature females (mean = 160 kg) (Cawthorn *et al.* 1985). This large difference in body size between sexes combined with sexual aggressive behaviour by males during the breeding season leads to significant female harassment, resulting in injuries and sometimes deaths (Chilvers *et al.* 2005a).

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[1] Taxa that have either restricted ranges or small scattered sub-populations are defined as 'At Risk'. Although these taxa are not currently in decline, their population characteristics mean a new threat could rapidly deplete their population(s) (Molloy *et al.* 2002).

[2] Taxa listed as 'Chronically Threatened' also face extinction, but are buffered slightly by either a large total population, or a slow decline rate (Molloy *et al.* 2002).

### *1.1.4 Diving and foraging behaviour*

NZSLs dive deeper and longer than any other otariid, with dives characterised by a combination of benthic and mid water dives (Gales & Mattlin 1997; Chilvers *et al.* 2006b). While NZSLs have both physiological (e.g. increased blood volume; Costa *et al.* 1998) and behavioural (e.g. increased swimming performance; Crocker *et al.* 2001) adaptations, they have not achieved their high level of diving performance through metabolic adaptations (Costa & Gales 2000). This research has lead to the conclusion that NZSLs are operating at, or near, their physiological limits and that the Auckland Islands shelf is likely to represent a marginal foraging environment for NZSLs (Gales & Mattlin 1997; Costa & Gales 2000; Chilvers *et al.* 2006b). Recent foraging studies have demonstrated a high degree of individual variation in foraging behaviour with a preferential use of the Auckland Island shelf and its edge (Chilvers *et al.* 2005b). In addition to their extraordinary diving abilities, NZSLs have the longest foraging trips and largest foraging areas of any otariid (Chilvers *et al.* 2005b). It has also been shown that NZSL foraging areas overlap both spatially and temporally with the operation of the southern squid fishery (Chilvers *et al.* 2005b).

### *1.1.5 Life history parameters*

There is little published on the life history parameters of NZSLs. All modelling studies so far have assumed values for key parameters, or used estimates from other species (Doonan & Cawthorn 1984; Woodley & Lavigne 1993; Gales & Fletcher 1999; Lalas & Bradshaw 2003; Breen *et al.* 2003; Breen & Kim 2005). Most of the life history estimates utilised have come from anecdotal field observations (Cawthorn 1985; Gales 1995; Gales & Fletcher 1999; Chilvers 2005a) but some have been derived from the autopsy of bycaught individuals (Dickie 1999; Duignan *et al.* 2003a, b). Minimum age at first reproduction is 4 years, indicating that females can be sexually mature as early as 3 years (Cawthorn 1993; Dickie 1999; Gales & Fletcher 1999). Little is known about the proportion of females that achieve maturity at this age and most researchers have treated age at first reproduction as a "knife edge" function (e.g. 100% of females start reproducing at age $x$ and stop at age $y$) in most models. The only estimate of reproductive rate (e.g. proportion of mature females giving birth to a pup) available is 0.75 (95% CI 66 - 84%), estimated from resightings of branded females (Chilvers 2005a). Maximum ages, based on counts of growth layer groups (GLGs) in teeth, are 21 for females (Dickie 1999) and 23 for males (Cawthorn 1985). These observations are based on a small number of individuals and represent estimated rather than known-ages (i.e. no individuals of known-age were available for GLG reading).

There are few estimates of survival available for any age class and none are published. Mean annual survival of adult females was estimated from resighting records of marked individuals analysed in the programme MARK at 0.91 (95% CI 0.87 - 0.93) (Chilvers 2005a). Bayesian modelling using a more extensive data set estimated survival at 0.87 (95% CI 0.83 - 0.91) for the same parameter (Breen & Kim 2005). Both of these estimates are very preliminary as the number and length of individual resighting histories of individuals used is generally small (e.g. <5 years). The latter estimate derived by Breen & Kim (2005) has some serious methodological problems relating to the Bayesian framework used, including poor fits to some of the priors and posteriors, which means that this value should be treated with caution (Goodman 2003, Slooten 2005). While the estimate by Chilvers (2005c) is the first quantitative estimate of adult female survival, it derives from a small sample of individuals and further research is needed to provide more robust estimates from large data sets.

### *1.1.6 Population modelling*

There have been several attempts to model the impact of the southern squid trawl fishery (SQU6T) on NZSLs. SQU6T (or more commonly called 6T) is the code used by the Ministry of Fisheries to designate the area of the southern trawl fishery around the Auckland and Campbell Islands (for a description of this fishery area, see Figure 1.3). Using a simple deterministic logistic model Doonan & Cawthorn (1984) modelled the impact of bycatch on the population using an estimated bycatch of 123 NZSLs per annum and concluded that if bycatch continued at that rate then the population would have declined by half after 64 years. A deterministic Leslie matrix was used by Woodley & Lavigne (1993) who constructed two models to investigate the impact of the bycatch on the NZSL population. The approach used life history parameters derived from two species with a similar estimated lifespan; the northern fur seal (*Callorhinus ursinus*) and Himalayan thar (*Hemitragus jemlahicus*). Both models, using a constant level of bycatch, predicted that NZSLS would have a limited capacity for population increase. None of these models incorporated uncertainty in parameter estimates, or environmental stochasticity. The most recent developments have adapted a Bayesian modelling approach used in fisheries stock assessment to the issue of assessing the relative performance of alternate management strategies (Maunder *et al.* 2000; Breen *et al.* 2003; Breen & Kim 2005). This model has been strongly criticised by Wade (2003), Goodman (2003) and Slooten (2005), chiefly on issues of lack of robustness and sensitivity testing, providing biologically implausible outputs (e.g. mismatches between modelled and current population size, low estimates of population growth), and the underestimation of uncertainly (and therefore risk) in the model. Despite these criticisms, the most recent version of this model is presently used by the MFish as the primary tool for bycatch management (Breen & Kim 2005).

While not an attempt to model population trend, Gales & Fletcher (1999) provided the first estimate of total population size for the species based on simulation modelling of pup production. Reproductive and survival rates were assumed, and the population was assumed to be stable. Based in part on this work, Lalas and Bradshaw (2003) constructed a Leslie matrix model to explore scenarios for female population growth and found that it was not possible for NZSLs to achieve a non threatened status within 20 years as required in the NZ Marine Mammals Protection Act (MMPA) 1978 (Lalas & Bradshaw 2003).

## 1.2 GENERAL INTRODUCTION

The goal of this thesis is to provide data on key biological characteristics of NZSLs that are crucial in managing the impacts on NZSLs of the commercial Arrow squid (*Nototodarus sloanii*) fishery around the Auckland Islands. Bycatch of NZSLs in this fishery was obvious from the first exploratory fishing by the German research trawler Wesermaunde in 1978 (DOC 1996). Since this time, it is estimated that on average more than 70 NZSLs have been killed each year (MFish 2005). As a result of continued reports of bycatch, specific protection was implemented for NZSLs in 1982 when a 12 nautical mile Fisheries Exclusion Zone was declared around the Auckland Islands. This 12 nautical mile Fisheries Exclusion Zone was later amended to become a Marine Mammal Sanctuary in 1994 and, more recently, a Marine Reserve in 2004. While these actions were useful in highlighting the plight of NZSLs, they were ineffective as a management measure as both the squid fishery operates and NZSL forage well outside the 12 nautical mile protection limit (Chilvers *et al.* 2005b).

Bycatch of NZSLs continued despite the introduction of closed areas, leading to the NZ Government imposing a sea lion catch-limit or Fishing Related Mortality Limit (FRML) on the 6T southern squid fishery in 1993. The 6T squid fishery is the NZ Quota Management Area which encompasses the areas around the Auckland and Campbell Islands (Figure 1.3; MFish 2005). The Total Allowable Commercial Catch for the 6T squid fishery is 32,369 tonnes, estimated to be worth up to $49 million per annum (MFish 2005). While recognising the economic value of this fishery, MFish must also ensure that any environmental impacts of the fishery are minimised and sustainable, as required under the Fisheries Act 1996.

The FRML was originally calculated using the Potential Biological Removal (PBR) model as used by the United States National Marine Fishery Service (Wade 1998). Since 2003 FRMLs have been calculated using an age-structured Bayesian model specifically developed for this purpose (Breen *et al.* 2003; Breen & Kim 2005). Since 1993, FRMLs have been the primary management mechanism in this fishery. Since 1996, the fishery has been halted early in eight of the last ten years either by the MFish closing the fishery or the industry voluntarily withdrawing when it was estimated that the sea lion FRML was reached or exceeded by up to 90% (MFish 2005). In 2003 and 2004 legal proceedings by the fishing industry successfully challenged the closure by the MFish and forced the reopening of the fishery, resulting in additional deaths of NZSLs in excess of the originally agreed FRML (MFish 2005).

NZSLs are fully protected under the NZ MMPA 1978. The details of the MMPA mean that while it is illegal to kill a marine mammal deliberately, it is not illegal to kill one accidentally, provided the death is reported to the DOC. Fisheries bycatch is considered as being an accidental or "incidental" death and therefore is not an offence under the MMPA. NZSLs are listed as "threatened" by both the NZ DOC (Hitchmough 2002) and the International Union for the Conservation of Nature (IUCN) (Reijnders *et al.* 1993; IUCN 2002). In 1997 the NZ Government formally gazetted them as a "threatened species" under the MMPA. Concomitant with this is the specified objective that NZSLs shall, "...be managed to a level of human-induced mortality which would allow the species to achieve non-threatened status as soon as reasonably practicable, and in any event within 20 years". Given that the single largest known source of anthropogenic mortality is from bycatch in the commercial squid fishery, one of the major aims of management is to reduce fisheries bycatch to the point that it does not prevent, or significantly delay, recovery of the Auckland Island breeding population (Wilkinson *et al.* 2003).

While FRMLs are used in various fisheries worldwide, NZ is in the near unique position of having closed a fishery when the FRML was exceeded. In the US, exceeding a FRML triggers a formal take-reduction process that can involve years of consultation, gear modification and experimentation. In the sense of taking strong action when bycatch limits are exceeded, NZ is a world leader. However, the underlying caveat of this management method is that the science that underpins the estimation of the FRML must be accurate and of the highest standard to ensure that it is set appropriately. Without high quality science, an inaccurate FRML could be set and may result in either an unsustainable catch of NZSLs or the premature closing of a valuable fishery.

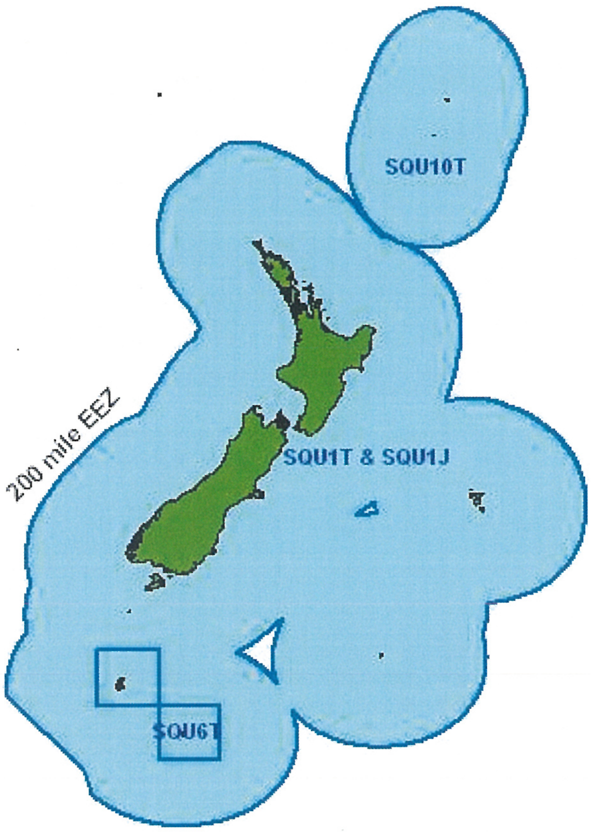

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**Figure 1.3** Location of 6T squid fishery Quota Management Area boundaries. Source: MFish (2006) and available at www.fish.govt.nz

Both the PBR model and the Breen & Kim model require specific data inputs to generate robust estimates of sustainable bycatch levels. At the heart of both of these models is an estimate of population size that cannot be estimated directly for NZSLs for two reasons; (i) the population has a large and variable geographic and temporal spread, and (ii) at any time it is impossible to know what proportion of the population is ashore and available to be counted. The austral summer breeding season is the only time when a significant proportion of the population is in one place at one time. However the potential usefulness of this period for population level monitoring is reduced in that immature and non breeding individuals do not appear consistently on the breeding colonies and hence are unavailable for monitoring or sampling (Gales & Fletcher 1999). The components of the population that can be most accurately assessed and monitored are the breeding females and pups of the year during the summer colonial breeding period. Estimates of pup production are widely considered to be the best index of relative population status for pinniped populations (Berkson & DeMaster 1985; Gales & Fletcher 1999), and such estimates can be extremely useful for exploring relative population changes. However, they are not estimates of absolute population size, as required for the estimation of a FRML.

As population size cannot be estimated directly for NZSLs, the standard approach has been to use estimates of life history parameters (e.g. survival and reproductive rates) to model population size from estimates of pup production (Woodley & Lavigne 1993; Gales & Fletcher 1999; Manly & Walshe 1999; Lalas & Bradshaw 2004; Breen & Kim 2005). While pup production for NZSLs is now well documented (Cawthorn 1993; Childerhouse & Gales 1998 (Chapter 2); Gales & Fletcher 1999; Wilkinson *et al.* 2003; Childerhouse *et al.* 2005 (Chapter 3); Chilvers 2007), there are no robust published estimates of any life history parameter for the species. The key focus of this thesis is provide robust estimates of survival and reproductive rates, both to enable reliable FRML calculation, and to facilitate modelling of population trends and fishery impacts.

A total of 1346 (annual mean = 75 individuals, SE = 9.7) NZSLs are estimated to have been killed in the 6T fishery since observer coverage began in 1988 with a peak of 141 in 1989 (Figure 1.4) (MFish 2005). Estimates of bycatch are calculated from the number of NZSLs recorded killed by Government Scientific Observers aboard fishing vessels adjusted upwards to account for the proportion of tows in the fishery that do not have observer coverage. While the 6T squid fishery is the single largest source of bycatch, it is not the only fishery to kill NZSLs. They have also been reported as bycatch in the vicinity of the Auckland Islands from trawlers targeting scampi (*Metanephrops challengeri*), southern blue whiting (*Micromesistius australis*), orange roughy (*Hoplosthethus atlanticus*) and oreos (predominantly *Psuedocyttus maculates*). While information is patchy as observer coverage in these fisheries has been low, for the most part these captures appear to be infrequent and restricted to a total of only one or two a year (Wilkinson *et al.* 2003). Given the low incidence of sea lion captures in other fisheries, management of NZSL bycatch is currently limited to the squid 6T fishery (MFish 2000). The FRML is calculated specifically for the 6T fishery and no adjustments are made to account for bycatch in other fisheries, nor for other anthropogenic impacts (e.g. shootings, disturbance, food competition, habitat modification).

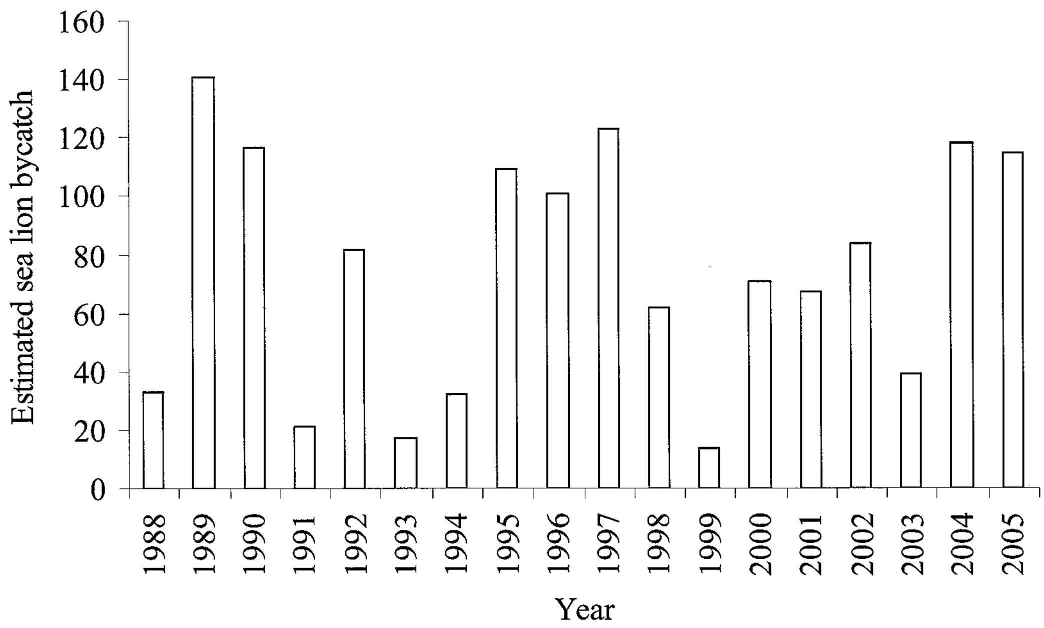

**Figure 1.4** Estimates of annual bycatch levels of New Zealand sea lions in the 6T squid fishery. Estimates of bycatch are calculated from the number of NZSLs recorded killed by Government Scientific Observers aboard fishing vessels adjusted upwards to account for the proportion of tows in the fishery that do not have observer coverage. Source: MFish (2005)

NZSLs are not the only otariid with a known bycatch problem in commercial fisheries. Of the 15 otariid species, ten have been recorded as incidental captures in fisheries, most in trawl fisheries, and in some cases such captures have been linked with population declines (Woodley & Lavigne 1991). Five sea lion species have been recorded as bycatch in various fisheries but bycatch has not been implicated in any population declines despite significant levels (e.g. >1% of estimated abundance per annum) of bycatch for Southern (*Otaria flavescens*) and California sea lions (*Zalophus californianus*), both of which are showing regional population increases (Woodley & Lavigne 1991; Barlow *et al.* 1997; Loughlin & York 2000; Crespo *et al.* 1997). Closer to home, large numbers (e.g. >500 per annum) of NZ fur seals (*Arctocephalus fosteri*) are estimated as being killed in trawl fisheries within NZ fisheries waters (Baird 2005).

While a FRML serves to restrict the number of NZSLs directly killed as bycatch, the 6T fishery also has the potential to impact on NZSLs in other ways. The most likely of these is through indirect competition for limited food resources with the commercial fishery. The fishery removes up to 35,000 tonnes of squid annually plus other species including jack mackerel (*Trachurus* species). NZSLs are known to feed on both squid and jack mackerel and so while some impact from this interaction is likely, its magnitude is unknown (Cawthorn *et al.* 1985; Childerhouse *et al.* 2001a (Chapter 4)). The NZ sub-Antarctic ecosystem around Campbell and the Auckland Islands where NZSLs forage is known to be resource limited and have a low production (Bradford-Grieve *et al.* 2001). Recent research on the diving behaviour of lactating NZSLs has suggested that they are operating at their physiological limits in what is considered a marginal foraging environment (Gales & Mattlin 1997; Costa *et al.* 2000; Chilvers *et al.* 2005b, 2006b). This is likely to increase susceptibility to direct and indirect fisheries impacts and other local environmental changes (Chilvers *et al.* 2005b). To understand any potential indirect impacts of the commercial fishery on NZSLs, it is important to understand the diet of NZSLs at the Auckland Islands in relation to commercial target species. Once this overlap is characterised it may be possible to assess the potential for indirect competition.

Indirect competition between otariids and commercial fisheries has been hypothesised for many otariids, as commercially targeted species have been identified in their diets. To date there has been no clear evidence to demonstrate a negative causal relationship (Thomson *et al.* 2000; Crespo *et al.* 1997; Hennen 2004), though it has to be noted that convincing evidence of this is extraordinarily difficult to obtain. In fact most of the reports in the literature highlight the negative impacts of pinnipeds on fisheries, rather than the other way around (Shima *et al.* 2000; Szteren & Paez 2002; Hückstädt & Antezana 2003), which is probably a reflection on the ease of monitoring this side of the interaction.

In conclusion, the data on the prevalence of squid in NZSL diet, the overlapping locations of NZSL foraging areas with fisheries operations, and the documented bycatch of NZSLs in fishing operations, all indicate that the 6T squid fishery has considerable potential to impact negatively on NZSL populations (Chilvers *et al.* 2005c). Through improved understanding of both potential direct and indirect effects it will be possible to improve the management and sustainability of the NZSL - 6T squid fishery interaction.

## 1.3 POPULATION DEMOGRAPHY & MODELLING

### *1.3.1 Population demography*

A key part of this thesis is the modelling of population demography for NZSLs. A short summary outlining the basic assumptions and underlying principles of population demography and modelling are presented here as background to the main Chapters on these subjects. An understanding of demographic parameters and population dynamics is essential to the appropriate conservation and management of any species, especially so for a threatened species.

### *Population dynamics*

The dynamic behaviour of a population – whether it increases or decreases, or remains stable – is determined by its age-specific mortality and fecundity rates interacting with its age distribution (Caughley 1994). When age-specific rates of mortality and fecundity remain constant, the population's age distribution assumes a stable form even though its size may be changing. Conversely, if these rates change, the age distribution may also change while the population size may increase, decrease or remain stable depending on the specific combination of changes in parameter. An understanding of these age-specific rates of mortality and fecundity are critical to developing an understanding of a population. Population demography, at its simplest, is the investigation and understanding of these vital rates and the assessment of their impact on a population. In a practical sense, an understanding of population demography is essential in underpinning and guiding management decisions for the conservation or sustainable use of a population.

There are many parameters that are relevant to the understanding of population demography. The relative importance of these different parameters will depend on the research question, the methodology that is to be used to address the question, and the desired outcome of the research. At the most fundamental level, the parameters of interest are:

1. Population structure – defining a population is an essential starting point for any demographic study. This definition may vary considerably based on the study animal and the question of interest but is likely to be based on one or more different criteria (e.g. temporal, spatial, ecological, behavioural or genetic dimensions). While the definition of a population can vary, it must be clearly defined as it provides the context for the research;
2. Population size – at its simplest, this is the number of individuals in the population but also can include other assessments such as population densities;
3. Age and sex distributions – a knowledge of the age and sex composition of a population is required to understand demographics; and,
4. Demographic rates – there are many potential demographic rates that can be considered but the most fundamental include rates of birth, death, emigration and immigration.

*Population change*

Population change is one of the most basic questions of interest in population studies and results from the combination of four fundamental demographic processes: births, deaths, immigration and emigration. The change in population (λ) between time intervals is the ratio of the size of the population next year ($t + 1$) to the size this year ($t$), or

$$\lambda = \frac{N_{t+1}}{N_t}$$

Lambda (λ) is called the finite rate of population increase or geometric growth rate. For example, a population with $\lambda = 1.0$ is stationary, $\lambda = 2$ will double in one year, and $\lambda = 0.75$ will decline by 25% in one year. For convenience λ is often expressed as an exponent, or

$$\lambda = e^r$$

where $r$ is the exponential rate of increase (or intrinsic growth rate) and $e$ is the base of the natural logarithms (Mills 2007). For example, a population with $r = 0$ is stationary, $r > 0$ is increasing, and $r < 0$ is decreasing. The use of λ or $r$ will depend on the questions being addressed but the use of $r$ leads to simplified algebra and a better appreciation of the nature of a rate of increase (Caughley 1977). A key assumption of geometric growth rate over time is that it is independent of density. This assumption is reasonable in an ideal world but in reality, eventually there will some form of density dependence (i.e. feedback between the density of a population and its growth rate). A commonly used form of density dependence is the logistic growth model where as density increases, the realised per-capita growth rate declines in a steady, linear fashion (Rockwood 2006).

Changes in population growth can be driven by factors that are deterministic (i.e. that change growth in predictable ways) or stochastic (i.e. that change growth and are not predictable). There are two main kinds of stochasticity: demographic (i.e. random variation around the mean demographic rates) and environmental (i.e. random changes in the mean demographic rates due to extrinsic factors). The combination of these factors will result in population change dictated by the magnitude and extent of each factor.

The point at which per-capita mortality and reproduction are equal so that the population replaces itself and $\lambda = 1$ ($r = 0$), is called the carrying capacity and is denoted by $K$. The carrying capacity is considered to be an equilibrium because if density is greater than $K$ then mortality exceeds reproduction and the population will decrease to $K$; if it is less than $K$ then reproduction exceeds mortality and the population increases to $K$. As discussed above, stochasticity will mean that *K* is unlikely to be fixed over time and will fluctuate depending on various stochastic factors.

### *1.3.2 Population modelling*

*General overview*

Demographic modelling has been widely used to investigate the dynamics of marine mammal populations (Caughley 1977; Slooten & Lad 1991; Brault & Caswell 1993; York 1994; Wickens & York 1994; Barlow & Clapham 1997; Caswell *et al.* 1999; Caswell 2001). At their simplest, population dynamics are characterised by the interaction of births and deaths, immigration and emigration but are also subject to both intrinsic (e.g. senescence, varying fecundity with age) and extrinsic effects (e.g. density-dependent mortality from limited food resources) (Caughley 1977; Boyd *et al.* 1995). Demographic modelling has frequently relied on a specified age structure and age-specific birth and survival rates (Barlow & Boveng 1991; Evans & Hindell 2004). While this information is available for some marine mammal populations, it is partially or completely lacking for most. Statistical models that estimate demographic parameters can be used to explore and understand population dynamics (Caswell 2001).

*Foundations of population modelling*

At its simplest, population modelling is used in population ecology to model the dynamics of wildlife or human populations. There are many different ways of achieving this but the most common foundation for models is the simple equation:

$$\mathrm{N}_{t+1} = \mathrm{N}_t + \mathrm{B} - \mathrm{D} + \mathrm{I} - \mathrm{E},$$

where: $\mathrm{N}_{t+1}$ = abundance at time $t + 1$; $\mathrm{N}_t$ = abundance at time $t$; B = number of births within the population between $\mathrm{N}_t$ and $\mathrm{N}_{t+1}$; D = number of deaths within the population between $\mathrm{N}_t$ and $\mathrm{N}_{t+1}$; I = number of individuals immigrating into the population between $\mathrm{N}_t$ and $\mathrm{N}_{t+1}$; E = number of individuals emigrating from the population between $\mathrm{N}_t$ and $\mathrm{N}_{t+1}$. This equation is called a BIDE model. Although BIDE models are conceptually simple, reliable estimates of the 5 variables contained therein ($\mathrm{N}_t$, B, D, I and E) are often difficult to obtain. Given the difficulties of estimating all of these variables, simple closed population models are often used. For example, one of the simplest forms of closed models is where it is assumed that the population experiences neither losses (i.e. D & E = 0) nor additions (i.e. B & I = 0). If these assumptions do not hold, then a model is considered open. In general, open population models are more complex and build on the same concepts and definitions used in closed models (Mills 2007).

The BIDE equation is a simple approach and provides information useful at the population level. An additional step in complexity is to model populations with an underlying structure that includes information about cohorts or stages (e.g. age). One such approach is the use of life tables (Caughley 1977). A life table requires information such as the number of individuals of each age in the population and age-specific values for reproduction and mortality. This allows for the investigation of age-specific population dynamics and population growth rates. There are two main kinds of life table: (i) a dynamic or horizontal life table monitors a single cohort from birth through to the death of all individuals; and (ii) a static or vertical life table where all individuals in a population are examined within a fixed time period. Both types of life table have different assumptions and these need to be carefully examined to ensure that conclusions from a life table are accurate and robust. The key parameters in a life table are $l_x$ survivorship, $m_x$ reproductive rate, $p_x$ age-specific survival rate, and $q_x$ age-specific mortality rate.

A life table provides a temporal snapshot of the population but often we are interested in investigating changes in a population size and structure over time. The process of projecting a single age class through time and one year at a time is time consuming and tedious (Rockwood 2006). Leslie (1945) showed that populations could be easily projected through the use of matrix algebra. This matrix approach allows quick calculations of changes in age structure and total populations size due to mortality and reproduction, as well as a quick method of finding $\lambda$ when there is a stable age distribution. An extension to this work by Lefkovich (1965), demonstrated that specific age classes could be replaced by "stage classes" based on life stages such as juvenile, young adult, adult, etc. This latter method can be more appropriate where detailed age-specific information is not available. Both of these methods allow for the detailed investigation of vital rates of individuals, cohorts and populations including sensitivity testing useful in the exploration of alternative hypotheses.

Another tool used in population modelling is Population Viability Analysis (PVA). PVA can be broadly described as the use of quantitative methods to predict the likely future status of a population or collection of populations of conservation concern (Morris & Doak 2002). There are many uses for predictions of future population status but almost all research can be divided into two areas: assessment of the risk of extinction and guidance for management decisions. Although the acronym PVA is commonly used as though it signified a single method or analytical tool, PVAs are in fact based upon a range of data analysis and modelling methods that vary widely in both their complexity and in the kinds and amount of data that they require (Morris & Doak 2002).

The focus of research for NZSLs has been on estimating population size, λ, and demographic rates with a view to understanding NZSL population dynamics. With an understanding of dynamics, it is possible to assess any potential effect of bycatch on the NZSL and manage bycatch accordingly. The specific aim of this thesis has been the estimation of survival and reproductive rates.

## 1.4 AUCKLAND AND CAMPBELL ISLANDS

Research for this thesis has focused on the Auckland Islands population as it represents the largest component (~87%; Childerhouse *et al.* 2005 (Chapter 3)) of the NZSL breeding population and is the population from which bycatch in the 6T squid fishery is taken. In addition to work at the Auckland Islands, research was also undertaken on Campbell Island (~13% of breeding population; Childerhouse *et al.* 2005 (Chapter 3)), which is the only significant breeding site outside the Auckland Islands.

The study sites for this research were at the Auckland (50°S 166°E) and Campbell Island groups (52°S 169°E) in the NZ sub-Antarctic zone lying to the south of mainland NZ (Figure 1.1). Both groups lie between the Antarctic and the sub-Antarctic convergence and lack permanent human residents but small numbers of researchers and tourists visit during summer.

The Auckland Island group is situated 480 km south of the NZ mainland and comprises one large main island (Auckland Island - 60km long) and numerous smaller islands including Enderby and Dundas Islands, the sites of field work reported here. Enderby and Dundas Islands are approximately 5 nautical miles apart at the northern end of the island group. Dundas Island is a small (400m long, ~4 ha), low lying island and has the largest breeding colony of the species (~2000 pups born per annum; Gales & Fletcher 1999). A beach on the south eastern point about 100 m long and 50 m wide is the site of pupping and mating. Access to Dundas Island is logistically very difficult as it is in an exposed location, is surrounded by a reef and is without a source of fresh water. Enderby Island (4 km long by 1 km wide, 688 ha) has two breeding colonies, Sandy Bay (~400 pups per annum; Gales & Fletcher 1999) and

South East Point (~70 pups per annum; Gales & Fletcher 1999). Sandy Bay is a protected sandy beach on the southern coast about 400m long and 30m wide where most of the pupping and mating takes place. Pupping and mating at South East Point occurs on a flat area of hard packed sand immediately inshore of a rocky point. Researchers lived in two small huts overlooking Sandy Bay and generally spent short periods (~3 days at a time) on Dundas Island living in a small "Apple" hut. Field trips to the Auckland Islands generally consisted of three months' work from early December until late February.

The Campbell Island group is situated 660 km south of the NZ mainland and comprises one large main island (Campbell Island, 11300 ha) and several smaller islands. The terrain is steep and much of the coastline is inaccessible to sea lions because of sheer cliffs (McNally *et al.* 2001). While research was restricted to the main island, the whole island was surveyed including inland areas as breeding at Campbell Island is both colonial and non colonial (McNally *et al.* 2001). A disused metrological station was used for accommodation. Field trips consisted of two survey periods; one of three weeks in January and February and another of four weeks in March and April in 2003.

## 1.5 THESIS OUTLINE

The research in this thesis was developed to meet identified research needs relating to the interaction between NZSLs and the 6T squid fishery, originally identified in the NZSL Recovery Plan (Gales 1995) and refined in subsequent discussions on management (DOC 1996). The aim of this project was for its outcomes to be directly applied to understanding and improving the management of this interaction. Improved understanding of this interaction should help minimise the impact from the commercial fishery. The NZ MFish and DOC are actively managing this interaction and are relying on science-based approaches to guide decision making. Some of the results of this thesis have already been used to inform this process. The most recent research will be presented to MFish and DOC technical groups to improve ongoing management.

The thesis is titled "Conservation Biology of New Zealand sea lions" to capture the broad scope of this thesis. All of the research was focused towards improving the science underpinning the management of the interaction between the NZSL and the 6T squid fishery. There were three specific aims of the thesis:

1. Investigate life history characteristics and demographics of the Auckland Islands population.
2. Improve knowledge of population status; and,
3. Investigate the potential indirect effects of fishing.

This thesis is presented as a series of manuscripts that are at various stages of publication, including several Chapters that have already been published. Each Chapter has been written as a stand alone paper, which has resulted in some unfortunate but necessary repetition between Chapters. I have attempted to reduce this wherever possible including combining all references into a single list at the end of the thesis. I have also provided a General Introduction and a Discussion and Conclusion Chapter that places the work into a coherent context with a single over-arching focus. Each Chapter builds on the research of the previous Chapters, so the discussion in Chapter 8 (i.e. the final data Chapter) includes a discussion of all of the findings from the previous data Chapters. The thesis is broken into several independent but related sections that focus on different aspects of the NZSL - squid fishery interaction.

**Section 1** provides an introductory summary:

**Chapter 1** is a general introduction with a focus on the biology of NZSL but also includes a review of demography and population modelling to provide some background and context for the later Chapters.

**Section 2** examines population status:

This section was aimed at addressing two areas of NZSL biology that were unknown.

**Chapter 2** provides a general overview of the status of the population and a review of the historic distribution of the species. This Chapter was published in 1998 (Childerhouse *et al.* 1998) and at the time was the first comprehensive review of the status of this species. This Chapter has since been updated in Chilvers *et al.* 2007 of which I am a co-author.

**Chapter 3** provides the first robust estimate of pup production for Campbell Island, which is the only major breeding colony outside of the Auckland Islands. This Chapter was published in 2005 (Childerhouse *et al.* 2005).

**Section 3** provides information relevant to the investigation of the potential indirect effects of fishing:

**Chapter 4** describes the diet of NZSLs at the Auckland Islands and implications for potential overlap with commercial fisheries. This Chapter was published in 2001 (Childerhouse *et al.* 2001a).

**Section 4** investigates life history characteristics and demographics of the Auckland Islands population:

**Chapter 5** introduces a technique for the ageing of NZSLs from a post-canine tooth; an essential element when investigating age-specific parameters. This Chapter was published in 2004 (Childerhouse *et al.* 2004).

**Chapter 6** describes the age structure of the female breeding population between sites and over three years.

**Chapter 7** investigates growth and age-specific reproductive rates from age-structure information and the re-sighting of marked individuals.

**Chapter 8** estimates age-specific survival rates using modelling of age-structured data.

**Section 5** includes a General Discussion and Conclusion, and relevant Appendices.

**Chapter 9** is a General Discussion and highlights Conclusions of the thesis. All of the previous 7 Chapters had detailed discussion sections that were relevant to the focus of each Chapter so this Chapter does not attempt to revisit each discussion but provides a synthesis of the thesis.

**Appendix 1** includes references to several published papers that I lead- or co-authored on NZSLs. These do not appear as part of the thesis as, either they are not directly relevant to the work of the thesis (e.g. Childerhouse & Gales 2001), or represent work where I was not the major contributor. They are listed here as they provide useful additional information on NZSLs.

## 1.6 DIVISION OF LABOUR

In 1994 a comprehensive annual research programme was started in the Auckland Islands by Dr Nick Gales of the DOC. This followed a previous long-term research programme spanning the 1980s and early 1990s from which little was published (Cawthorn *et al.* 1985; Cawthorn 1993). The recent research has primarily focused on attempting to understand the interaction between NZSLs and the commercial squid fishery but has also investigated other facets of NZSL biology and ecology, such as foraging ecology, energetics and breeding behaviour (Gales & Mattlin 1997; Costa & Gales 2000; Chilvers *et al.* 2006b). This has been a multidisciplinary project and this thesis reports results from some components of this long term research programme.

I have been enrolled at Otago University as a part-time student since 1998, originally undertaking an MSc that I later upgraded to a PhD. From 1998 to 2006, I also worked full time at DOC, and on several occasions deferred my thesis, when my job demanded my full attention. I resigned from DOC in late 2006 to work full time on my thesis.

This thesis represents the work of a long-term research programme to which many other researchers have contributed. This ongoing collaboration has been an essential element of this research project and allowed us to increase greatly the quality and quantity of science that I have been able to achieve. As a result, this thesis contains four published papers, all of which have been co-authored with various researchers. It is important to clarify my contribution and those of others to each Chapter for transparency and to ensure that appropriate recognition is given. All the work in this thesis is my own work and all the published papers were lead-authored by me.

Chapter 2 was published in 1998, co-authored with Dr Nick Gales. I undertook all the research and writing with advice, editing and reviewing by Dr Nick Gales.

Chapter 3 was published in 2004, co-authored with Nadine Gibbs, Gus McAlister, Helen McConnell, Shaun McConkey, Nathan McNally and David Sutherland who were all present for various parts of the field work. I designed and led the project, and undertook all the analysis and writing.

Chapter 4 was published in 2001 co-authored with Bruce Dix and Dr Nick Gales. Data collection was shared among us while Mr Dix and I jointly identified prey remains. I undertook all the analysis and writing.

Chapter 5 was published in 2004, co-authored with Gail Townsend (nee Dickie) and Guy Hessel. The tooth ageing technique was originally developed by Gail Townsend and subsequently refined by Guy Hessel and myself. We shared tooth preparation and I led the field collection and undertook all the >3,500 tooth readings, analysis and writing of the paper.

Chapters 6, 7, and 8 are at this stage unpublished. I undertook all the data collection, research, analysis and writing of these Chapters. My supervisors, Associate Professors Steve Dawson, Liz Slooten, and David Fletcher have contributed ideas, editing and advice, especially on data analysis and the development of models. Associate Professor David Fletcher helped with the development and coding of population models.

# Chapter 2

# Historical and Modern Distribution and Abundance of New Zealand Sea Lion[3]

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[3] Originally published as Childerhouse, S.; Gales, N. 1998. Historic and modern distribution and abundance of New Zealand sea lions. New Zealand Journal of Zoology 25: 1-16. This paper has recently been updated as Chilvers, L.; Wilkinson, I.; Childerhouse, S. 2007. New Zealand sea lion, *Phocarctos hookeri*, pup production - 1995 to 2006. New Zealand Journal of Marine and Freshwater Research 41: 205–213

# CHAPTER 2: HISTORICAL AND MODERN DISTRIBUTION AND ABUNDANCE OF NEW ZEALAND SEA LION

## 2.1 ABSTRACT

This paper describes both the modern and the pristine distribution, breeding range and relative abundance of the New Zealand NZSL (*Phocarctos hookeri*) (NZSL). Archaeological data and historical references were used to determine the pristine status of the NZSL and the present status was determined from recent scientific studies and observations. NZSL had a substantially more widespread distribution before the arrival of humans in New Zealand (NZ) than it does today. The species used to range along the whole length of the coast, from the north of the North Island through to Stewart Island and the sub-Antarctic Islands. Although we have no direct estimate of pristine abundance, the present population size is clearly reduced. Subsistence and commercial killing of NZSL is the most likely cause of historical changes in distribution and abundance. Their pristine breeding range extended at least as far north as Nelson and may have extended to the North Island. The present breeding range is restricted to the Auckland Islands and Campbell Island. Within the last ten years a few individuals have started to breed on mainland NZ and Stewart Island, which may reflect a slow recolonisation of earlier breeding grounds. Pup production at Sandy Bay, Enderby Island, has been stable for at least the last three decades, and no major changes in pup production at Dundas Island and Figure of Eight Island are apparent.

Keywords: New Zealand NZSL; *Phocarctos hookeri*; historical trends; distribution; abundance.

## 2.2 INTRODUCTION

The endemic NZSL, *Phocarctos hookeri* (also known as Hooker's NZSL) is one of the world's rarest pinnipeds, and has a highly localised distribution. Most of the population is found in the Auckland Islands although some animals disperse as far as the NZ mainland, Campbell Island and occasionally Macquarie Island (Figure 2.1). The most recent total population estimate, for the 1995/96 breeding season, suggest between 11 600 and 15 200 animals (95% C.I.) (Gales & Fletcher 1999). Approximately 95% of all pups are produced at four colonies in the Auckland Islands. The largest, on Dundas Island, accounts for about 70% of total pup production; the other colonies are on Figure of Eight Island and on Enderby Island, at Sandy Bay and Pebble Point (Gales & Fletcher 1999).

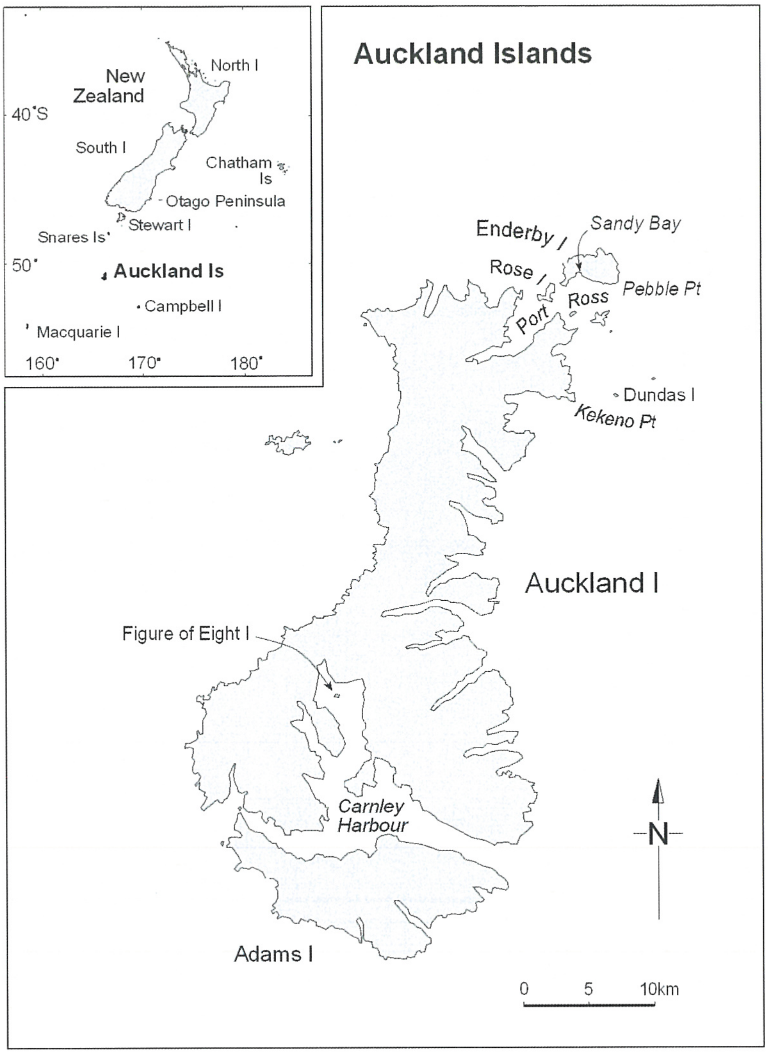

**Figure 2.1** Location of New Zealand sea lion breeding sites at the Auckland Islands.

During the 1970s a trawl fishery for arrow squid (*Nototodarus sloanii*) was established on the Auckland Island and Snares Island shelf. As the fishery developed, a bycatch of NZSLs became apparent; this led to the establishment of a 12 nautical mile fishing exclusion zone around the Auckland Islands in 1982 (Baird 1996). Estimates of NZSL bycatch have varied from year to year, but range from 17 to 140 for the years 1988-95 inclusive (Baird 1996). Doonan & Cawthorn (1984) modelled the impact of bycatch on the population using the reported bycatch figure of 123 NZSLs in a single season and concluded that if bycatch continued at that rate then the population would have declined by half after 64 years. Woodley & Lavigne (1993) constructed two models to investigate the impact of the bycatch on the NZSL population using life history parameters derived from two species with a similar estimated lifespan; the northern fur seal (*Callorhinus ursinus*) and Himalayan thar (*Hemitragus jemlahicus*). Both models, using a constant level of bycatch, predicted that the NZSL would have a limited capacity for population increase.

In an attempt to limit the potential impact of the NZSL bycatch a catch limit or Potential Biological Removal (PBR) of 63 NZSLs was set by the New Zealand Department of Conservation in 1993, on the basis of draft guidelines from the United States National Marine Fisheries Service. This number was used for the 1993-96 fishing seasons. In 1995 the estimated bycatch of NZSLs exceeded the catch limit, but the fishery was not closed as a delay in processing the data resulted in the situation not being recognised until the season had finished for that year. In 1996 the fishery was closed early as the estimated bycatch again exceeded the PBR.

Recent changes in New Zealand legislation require the Department of Conservation to produce Population Management Plans for threatened fauna killed incidentally in fishing operations. The first of these plans, to be produced in 1997, is for the NZSL. It is necessary to understand the current status of NZSL in relation to pristine stocks for managers to make informed decisions on sustainable levels of bycatch that will not limit the ability of this species to recover from previous exploitation.

The pristine abundance and distribution of NZSL is unknown but it is clear from various archaeological and sealing records that significant exploitation for food and skins took place. There has been little previously written about the NZSL but many parallels are evident with the New Zealand fur seal (*Arctocephalus forsteri*) and where possible, we have discussed relevant fur seal examples. Whilst many of the records and much evidence of historical distribution and abundance are dispersed and occasionally ambiguous, they are nevertheless fairly numerous and potentially relevant. The purpose of this paper is to document and interpret this information with the aim of describing the pristine distribution, breeding range, and relative abundance of the NZSL and to compare this with the current situation.

## 2.3 HISTORICAL RECORDS OF SEA LION

There is a wide variety of sources reporting information on NZSL. Much of this work is unpublished or is reported only in the 'grey' literature. We have examined reports from sources such as personal diaries, vessel manifests, expedition reports, unpublished reports, published books, scientific reports and papers, and personal communications. Many of these make only brief reference to NZSL but where possible we have critically reviewed the information. We summarised the information under three main sections; pre-European, 19th Century, and 20th Century.

### *2.3.1 Pre-European*

The remains of NZSLs dated to pre-European times have been reported from at least 47 sites around New Zealand (Figure 2.2). The combined records extend from North Cape to Stewart Island, with almost half occurring in southern half of the South Island (Smith 1989). Fordyce (1988) summarises the records of fossil seals in New Zealand and finds no specimen older than the Pleistocene (2-3 million years ago). A full list of recorded sites with NZSL remains, other than those reported by Smith (1985, Appendix 3), are summarised in Table 2.1.

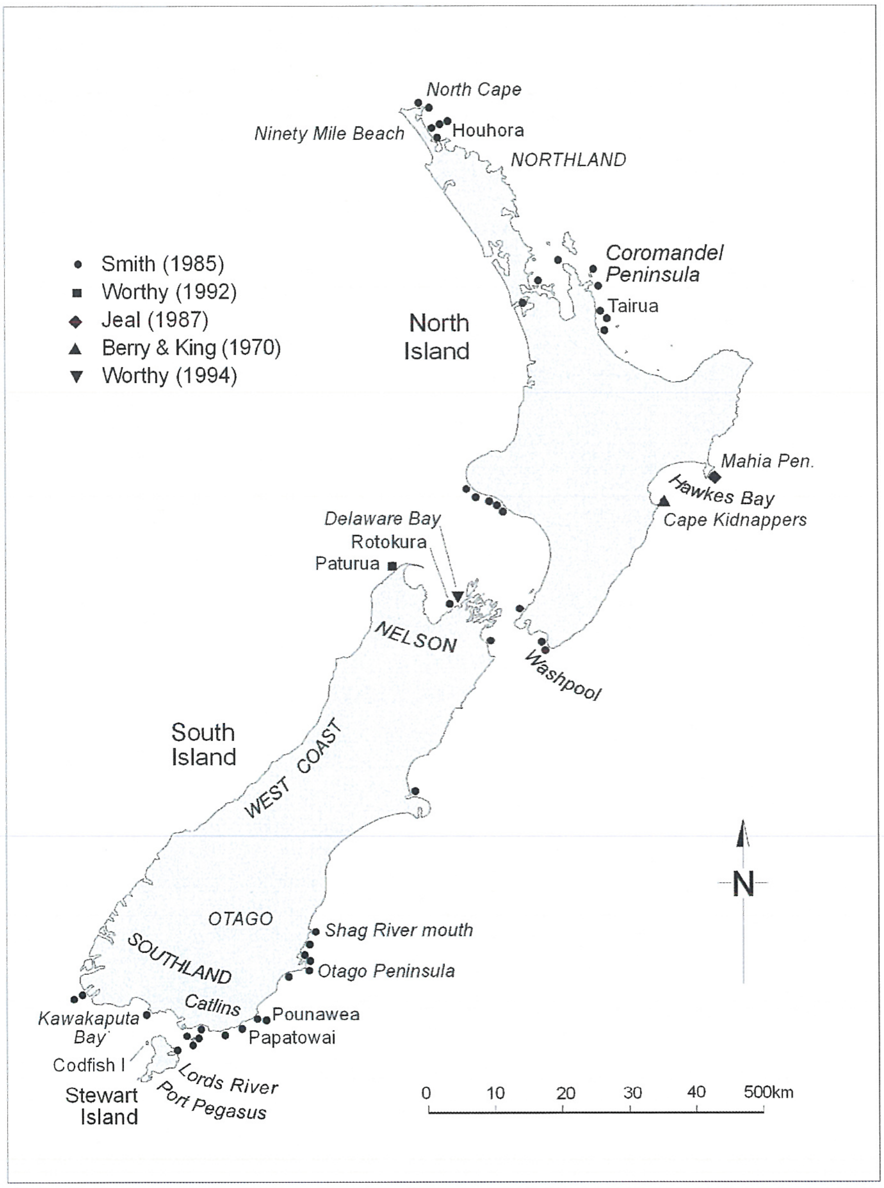

**Figure 2.2** Location of archaeological sites with recorded New Zealand sea lion remains.

Smith (1989) provides a comprehensive summary of what is known of the past distribution and abundance of NZSLs as determined from archaeological records. Smith reports 43 pre-

European sites where NZSL remains have been found. No pup remains were reported, but numerous juveniles and several adult females were found. Most sites are Maori or Moriori middens, indicating that NZSLs were used for food.

**Table 2.1** Description of pre-European archaeological sites with New Zealand sea lion remains

| Location of site | Description of site | Number and type of remains found | Reference |
|---|---|---|---|
| Cape Kidnappers, Hawkes Bay | Maori midden | Description of Berry (1928) specimen as 1 young male. <1,000 years old (Weston & Repenning 1973). Also remains of 1 young female | Berry and King 1970 |
| Mahia Peninsula | Maori midden | 1 NZSL | Jeal 1987 |
| Chatham Islands | Sandy dunes and Moriori middens | Numerous bones from both adults and juveniles and of both sexes. Oldest bones dated at 2,700 years old | McFadgen 1994 |
| Tairua, Coromandel Peninsula | Maori midden | 1 NZSL aged at maximum 700 years old | Smith 1978 |
| Palliser Bay | Maori midden | 1 adult female and 1 juvenile male | Smith 1979 |
| Mainland New Zealand | 42 sites in Maori midden | Female remains from 5 sites and the rest males | Smith 1989 |
| Shag River Mouth, Otago | Maori midden | 14 NZSLs | Smith 1996 |
| Northwest Nelson | Limestone caves | 6 sub adult and adult male fossils aged up to 10,000 years old | Worthy 1992 |
| Delaware Bay, Nelson | Sandy beach dunes | 1 adult and 3 pup fossils aged at least 5,000 years old | Worthy 1994 |

McFadgen (1994) reports on the remains of NZSLs from the Chatham Islands, again including bones from both adults and juveniles, but not from pups. Gastroliths, identified as being from NZSLs, have also been recorded. Some of these remains were found in Moriori middens. The Moriori are reported to have hunted marine mammals, including NZSLs, at Te Whakaru, the north eastern tip of Chatham Island, before European discovery of the Island (Richards 1982).

Fossil bones from NZSLs have been found in caves in north-west Nelson (Worthy 1992). Radiocarbon dating of two bones has yielded ages of approximately 10 000 and 3 000 years old although other evidence suggests that this site was occupied by NZSLs until several hundred years ago. Most of the bones appear to have been from males, as no females have been definitively identified. Sex determination from the bones was made on the basis of tooth and skull structure and skeletal dimensions.

The only pre-European records of pup remains on the New Zealand mainland are from Delaware Bay and Paturau in Nelson (Worthy 1994). Three remains recovered from Delaware Bay have been identified as young pups from skeletal and cranial measurements and dental characteristics. One of the pups was tentatively dated to the late Holocene on the basis of progradation of the site. At Paturau the fossil remains of several NZSLs have been recovered (Worthy 1992), and re-examination of the material yielded the remains of a pup (Worthy 1994). Worthy (1994) cites the finding of pups as strong evidence that NZSLs bred in the Nelson area during the late Holocene. The remains of two young NZSLs have been found at Hawkes Bay, probably in a midden, and the remains are less than 1000 years old (Berry & King 1970; Weston & Repenning 1973).

Remains tentatively identified as female have been recorded from Papatowai (12th century), Pounawea (12th century), Washpool (12th century), Rotokura (14th century) and Houhora (14th century), which may indicate breeding in these areas (Smith 1989) (Figure 2.2). However, it is not possible to determine if these females were breeding at, or close to, the location where their remains were found.

### *2.3.2 19th Century*

*Auckland Islands*

Most of the records from this time are from Auckland Islands sealing expeditions. Many are anecdotal, but they do provide a picture of the exploitation of NZSLs from this area. Taylor (1971) provides a good summary of the history of sealing in the Auckland Islands.

The Auckland Islands were discovered on 18 August 1806 by the vessel Ocean, commanded by Captain A. Bristow. In his log he says "This place, I should suppose abounds with seals, and sorry am I that the time, and the lumbered state of my ship do not allow me to examine" (McNab 1907, pp. 95). It soon became clear that there was an abundance of fur seals, and sealing began shortly thereafter. NZSL (also known as hair seal) skins were not as highly valued as those of the fur seal, and so NZSLs were not targeted initially. It is likely that NZSLs were initially taken in small numbers, and it was not until fur seal stocks were severely depleted that NZSLs were killed in larger numbers. One of the first records of a commercial NZSL take is from the vessel *Commerce*, which arrived in the summer of 1807-08 and found two teams of sealers already ashore (McNab 1907). Owing to heavy exploitation, catches declined, and by 1815 there was little sealing being carried out on the Aucklands (McLaren 1948).

In 1823 the vessel Henry visited the Aucklands and returned with 12 000 fur seal skins. The vessels *Wellington* and *Elizabeth* and *Mary* returned from hunting in the Aucklands and on Campbell Island early in 1825 with a total of 3670 NZSL skins (Cumpston 1968). Although most of the accounts are anecdotal there is little doubt that the NZSL population at the Auckland Islands was depleted, and by about 1826 the southern sealing trade was virtually finished (McNab 1907).

Captain Benjamin Morrell (1832) visited the Auckland Islands in January 1830. When some of his crew spent five days circumnavigating the islands with the express purpose of discovering fur seals, they saw no fur seals and fewer than 20 NZSLs. Morrell wrote "Although the Islands once abounded with numerous herds of fur and hair seals, the American and English seamen engaged in this business have made such clean work of it as scarcely to leave a breed - at all events, there was not one fur seal to be found on the 4th of January, 1830" (Morrell 1832, pp. 363). January is the peak of the breeding season for both NZSL and fur seal and the breeding colonies, had they existed, should have been easily visible. The fact that no seals and few NZSLs were seen at this time strongly suggests that there were few animals remaining of the former population. Morrell also visited The Snares islands and found no fur seals or NZSLs.

Morrell's accounts have not always been found to be accurate and reliable. Best & Shaughnessy (1979) compared Morrell's account of a sealing voyage to Africa with that of an independent private journal of the same trip and found many discrepancies between the two descriptions. They suggest that Morrell frequently used "omission, elaboration, exaggeration or fictionisation" of events, possibly as they may have reflected poorly on his authority or competence (Best & Shaughnessy 1979, pp. 15). There appears to be little to gain for Morrell in falsely reporting numbers of NZSLs at the Auckland Islands but his account cannot be relied upon to be completely accurate. However, it does seem likely that with the large number of skins being taken from the sub-Antarctic Islands that both the fur seal and NZSL population would have been much reduced.

The vessel *Caroline* continued to make frequent sealing trips to the Aucklands and other islands, and landed 1 000 fur seal skins in Sydney in 1833. Is not clear from which sub-Antarctic Island or islands these skins came, but they were a small fraction of the quantities that vessels had landed earlier in the century (Cumpston 1968). After 1830 a small number of sealers frequently visited the Aucklands but without much success (McLaren 1948).

In 1840 McCormick (1884) visited the Auckland Islands and spent several days in Port Ross. He made detailed accounts of the natural history of the area but makes no mention of NZSLs anywhere, although he landed several times at Sandy Bay on Enderby Island during November and December, during what should have been the start of the breeding season. Sandy Bay is a very visible site, and it is unlikely that NZSLs would have escaped observation had they been present. Therefore it is likely that there was no breeding at Sandy Bay in 1840.

The settlement of Hardwicke in Port Ross was founded in 1849, and the capture of NZSLs was apparently an "exciting pastime in which they engaged whenever they could" (McLaren 1948, pp. 52). After three years the settlement failed, and the buildings were dismantled and removed by departing settlers. This was due to the harsh nature of the environment, the lack of whales, and the few visits by whaling vessels (McLaren 1948). It seems likely that fur seals and NZSLs were both in low numbers in the area at the time, as there is no reference to sealing as a source of either food or income in the records. However, Malone (1854) reported that in May 1852, when he arrived to help dismantle the settlement, at least 20 NZSLs were shot by his crew in and around Port Ross.

Musgrave (1866) was shipwrecked on the Auckland Islands in 1864 and spent over a year there, subsisting on a diet of primarily seals and NZSLs. During this time he reports on "great number of seals" and "hundreds of seals" in Carnley Harbour (Musgrave 1866, pp. 10 & 16). Although species identification is not always clear (he refers to tiger seals, black seals, seals, and NZSLs, often switching between the definitions) it is evident from his description that there were NZSLs breeding on Figure of Eight Island. He wrote in his diary "seeing 3 mobs of seals [NZSLs from his description] asleep on the island, we landed. We found 30 to 40 in each mob, including many young calves" (Musgrave 1866, pp. 28). A tally from his diary records the killing of 22 pups from Figure of Eight Island in one season, and many more are mentioned.

An expedition to the sub-Antarctic reported that Rose Island and Enderby Island had "plenty" of NZSLs ashore in 1864 (Anon. 1865, pp. 4). In 1881 the first official steps were taken to close the remaining seal fisheries in New Zealand (Wilson 1893), although some poaching occurred into the 1890s (McGhie 1888, Joyce 1894). Captain Fairchild, who made numerous trips to the sub-Antarctic Islands, reported in 1890 that "The NZSL is numerous everywhere throughout the islands. There are millions of them on the islands at one time of year"

(Cumpston 1968, pp. 148). In 1893 sealing, for both fur seal and NZSL, was prohibited by law in New Zealand. There were still low levels of sealing up until this time and it was believed that if sealing continued it might prevent NZSLs and particularly fur seals from recovering (Cumpston 1968). Since 1893 some open seasons have been declared for fur seals although NZSLs have remained completely protected (Chapman 1893; Falla 1962).

The NZSL population at the Auckland Islands, although depleted in the early 19th century, showed signs of recovering by the end of that century. After returning from a trip to the sub-Antarctic, Joyce (1894, pp. 2) wrote that NZSLs frequented the inlets and harbours of the eastern coastline, and were found "at nearly every point touched at among the Auckland Islands and also Campbell Island. At Rose Island ninety were counted on the beach or among the scrub and tussock."

*Sea lions at other locations*

The only record of NZSLs on Campbell Island was from the 1815-16 season when at least 300 NZSLs skins were taken from there (Warneke 1982).

During his trip to Stewart Island in 1826 and 1827, John Boultbee wrote in his diary that the local Maori annually killed "great quantities" of NZSLs at Lord's River for the purposes of food, and also that NZSLs bred there (Starke 1986, pp. 105). This was apparently an important food resource, some of which the Maori preserved for future use either smoked or in kelp bags (Begg & Begg 1979). Port Pegasus had numerous NZSLs when visited by Thomas Shepherd in 1826 and he reported that they bred there (Howard 1940; Begg & Begg 1979). Boultbee found and killed a "young hair seal" at Kawakaputa Bay near Riverton (Begg & Begg 1979, pp. 186).

Sir James Hector (1892, pp. 257) reported that "About December they [NZSL] take up stations on the coast in warmer latitudes, such as the West Coast of New Zealand, and formerly used also to frequent the islands of Bass Strait and on the west coast of Tasmania. The breeding season is in January after which the males leave and the females remain until May." He described each male securing a harem of 10-20 females which would suggest a reasonable sized colony. He continues: "the mode of life of the hair seals has, however, been much altered since 1863, when I made my first observations, and I believe that the New Zealand hair seals have now become much more solitary, and that they will soon become extinct."

Sea lion tracks were reported in the extreme south of Stewart Island in 1874 by Thomson (1921, pp. 75), but he had "not heard of one being seen for many a long day."

### *2.3.3 20th Century*

Waite (1909, pp. 542) reported from his trip in 1907 that NZSLs were "quite numerous" on The Snares, The Auckland Islands, and Campbell Island. Sea lions were present in the Aucklands year round, scattered mostly around the eastern coastline (Turbott 1952). Most of the records from this period are from the Auckland Islands, and we have compiled them into sections by geographical area, concluding with a summary of all population estimates for the species reported in the literature.

*Enderby Island*

Wilson (1907, pp. 60) reported seeing "numerous NZSLs" on the Auckland Islands when he visited in March 1904. In his diary he wrote that there were about 200 on the beach of Sandy Bay and that there were more animals in the scrub (Wilson 1966). He also saw two young NZSLs that had been born the previous breeding season (Wilson 1907). This is the earliest record of NZSLs breeding, since the population was depleted from sealing in the 19th century.

Coastwatchers were stationed on the Auckland Islands from 1941 and began to make observations of the NZSLs. L. H. Pollock (1941) wrote in his diary on 4 September 1941 that Webling [*a fellow officer*] reported seals to be plentiful on Enderby Island.

Falla made intermittent observations of NZSL behaviour at Sandy Bay over the period 1942-79 and reported that the breeding population of about 1000 animals, and production of about 350-400 pups per annum, was stable over this whole period (Falla 1965; Falla 1975; Falla *et al.* 1979).

Counts of pups during the breeding season at Sandy Bay have been collected most years *(n* = 19) since 1972 and estimates of pup production are shown in Table 2.2. Data from nine seasons spanning 1972/3-95/6 were used to determine whether the number of live pups was stable over this period (Best 1974; Gales & Fletcher 1999; M. Cawthorn unpubl. data). We estimated a mean and standard error for the maximum number of pups in each season using the standard errors associated with the estimated dates of peak pupping (determined from the optimisation routine in Excel), calculated by parametric bootstrapping (Efron & Tibshirani

1993). We then used weighted regressions to test for a linear trend, defining each weight as the reciprocal of the square of the standard error of the estimate (Figure 2.3). There was no evidence of any trend in live pup numbers in estimates from Sandy Bay over this period (t7 = -0.54, p = 0.6) indicating stability over this period. Power analysis showed there to be an 83% chance of detecting a linear trend in live pup numbers of 1% per year (with alpha = 10%).

**Table 2.2** Estimates of pup production from Sandy Bay, Enderby Island

| Season | Date of estimate (d/m/y) | Estimated number of live pups (SE) | Estimated number of dead pups | Technique used in calculating the estimate | Source |
|---|---|---|---|---|---|
| 1942-44 | - | about 350 | | anecdotal accounts | Falla (1965) |
| 1965/66 | 22/1/66 | 407 | | single count | Taylor (1971) |
| 1972/73 | 12/1/74 | 460 | | daily count | Best (1974) |
| 1974/75 | 19/1/75 | 368 | | daily count | Cawthorn (1975) |
| 1975/76 | 17/1/76 | 406 | | daily count | Cawthorn unpubl. data |
| 1976/77 | 19/1/77 | 375 | | daily count | Cawthorn unpubl. data |
| 1977/78 | 19/1/78 | 380 | | single count | Falla *et al.* (1979) |
| 1979/80 | 26/1/80 | 180 | | daily count | Mitchell & Ensor (1986) |
| 1980/81 | 18/1/81 | 375 | | daily count | Cawthorn unpubl. data |
| 1981/82 | 17/1/82 | 450 | 41* | daily count | Cawthorn (1986a) |
| 1982/83 | - | - | 142* | - | Cawthorn (1986b) |
| 1983/84 | 14/1/84 | 400 | 30* | daily count | Cawthorn (1986c) |
| 1984/85 | 18/1/86 | 446 | | daily count | Cawthorn unpubl. data |
| 1985/86 | 4/1/86 | 358 | | daily count | Cawthorn unpubl. data |
| 1986/87 | 12/1/87 | 415 | | daily count | Cawthorn unpubl. data |
| 1989/90 | 12/1/90 | 379 | | daily count | Cawthorn unpubl. data |
| 1990/91 | 14/1/91 | 376 | | daily count | Cawthorn unpubl. data |
| 1991/92 | 11/1/92 | 436 | | daily count | Cawthorn unpubl. data |
| 1992/93 | 9/1/93 | 408 | 16* | daily count | Cawthorn (1993) |
| 1994/95 | 14/1/95 | 421 (4) | 46 | mark recapture | Gales & Fletcher (1999) |
| 1995/96 | 15/1/96 | 417 (3) | 38 | mark recapture | Gales & Fletcher (1999) |

* Minimum mortality estimate for the season.

Estimates of live pup numbers from Pebble Point are: 16 pups in the 1981/82 season (Cawthorn 1986a); 25 pups in the 1992/93 season (Cawthorn 1993); and 59 (excluding 12 dead) and 49 (excluding 20 dead) for the 1994/95 and 1995/96 seasons respectively (Gales & Fletcher 1999). All were made by direct counts of pups.

### *Dundas Island*

Estimates of pup production from Dundas Island are shown in Table 2.3. The first record of NZSLs there was made in September 1941 when Dundas was reported by Webling to be "practically covered in them" (Pollock 1941).

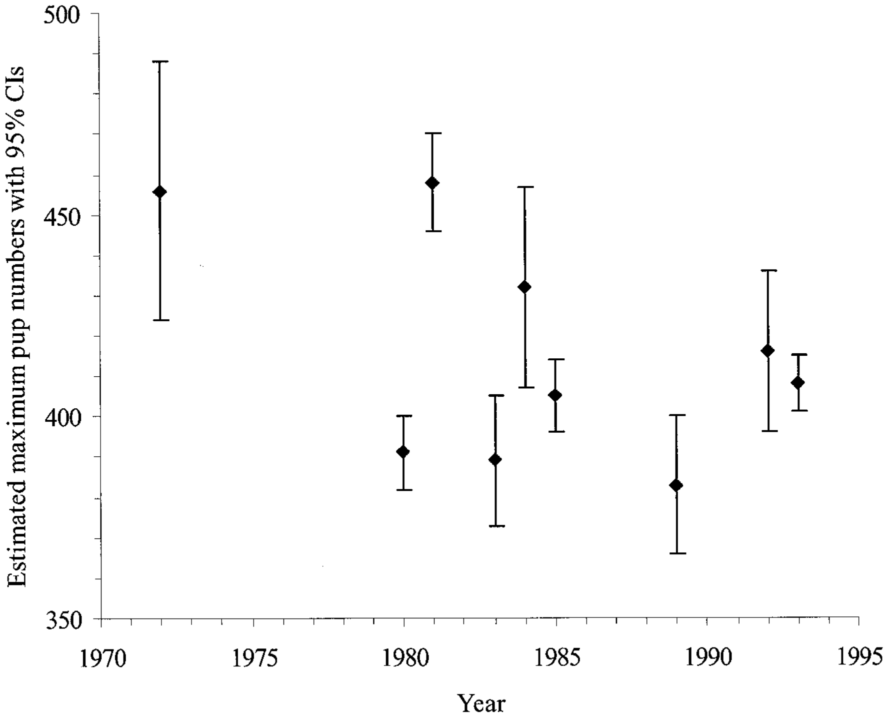

**Figure 2.3** Estimated maximum live pup numbers (with 95% CI) at Sandy Bay, Enderby Island over nine seasons.

The first record of a pup count on Dundas Island was on 25 January 1974 when over 1000 pups were counted (R. Russ, pers. comm. to Falla *et al.* 1979). The colony, at this time, was estimated to be at least twice the size of that at Sandy Bay, i.e. about 2000 animals (Best 1974). Falla *et al.* (1979) conducted a survey of Dundas Island on 21 January 1978. Their total count of 2762 animals was later scaled up to 3550 after an estimate of the number of cows at sea at the time of counting was included. The maximum number of pups counted was 1680, but it was agreed that 1700 would still be a conservative estimate. Falla *et al.* believed that the population at Dundas was increasing, although they acknowledged that the evidence was sketchy.

Sea lions on Dundas Island were counted on 20 February 1985. A total of 253 pups were counted with many other NZSLs seen on nearby Kekeno Beach (Taylor & Sadleir 1985).

*Figure of Eight Island*

Estimates of pup production on Figure of Eight Island are shown in Table 2.4.

**Table 2.3** Estimates of maximum pup production from Dundas Island

| Season | Date of estimate (d/m/y) | Estimated number of live pups (SE) | Estimated number of live pups | Technique used in calculating the estimate | Source |
|---|---|---|---|---|---|
| 1972/73 | 25/1/73 | 1000+ | | single count | Falla *et al.* (1979) |
| 1977/78 | 21/1/78 | 1680 | | single count | Falla *et al.* (1979) |
| 1980/81 | 29/12/80 | 1050 | | single count | Cawthorn unpubl. data |
| 1984/85 | 20/2/85 | 253 | | single count | Taylor & Sadlier (1985) |
| 1985/86 | 19/1/86 | 1087 | | single count | Cawthorn unpubl. data |
| 1986/87 | 20/1/87 | 1121 | | single count | Cawthorn unpubl. data |
| 1990/91 | 12/2/91 | 973 | | single count | Cawthorn unpubl. data |
| 1991/92 | 4/1/92 | 2369 | | single count | Cawthorn unpubl. data |
| 1992/93 | 18/1/93 | 1804 | 66* | multiple counts on same day | Cawthorn (1993) |
| 1994/95 | 20/1/95 | 1603 (20) | 234* | mark recapture | Gales & Fletcher (1999) |
| 1995/96 | 20/1/96 | 1810 (22) | 207* | mark recapture | Gales & Fletcher (1999) |

* Minimum mortality estimate for the season.

**Table 2.4** Estimates of pup production for Figure of Eight Island

| Season | Date of estimate (d/m/y) | Estimated number of live pups | Estimated number of live pups | Technique used in calculating the estimate | Source |
|---|---|---|---|---|---|
| 1863/64 | N/A | 22+ | | tally of pups killed | Musgrave (1866) |
| 1972/73 | 2/1/73 | 24 | | single count | Best (1974) |
| 1980/81 | 29/12/80 | 38 | | single count | Cawthorn unpubl. data |
| 1984/85 | 16/2/85 | 39 | 8* | single count | Taylor & Sadlier (1985) |
| 1986/87 | 10/1/87 | 91 | | single count | Cawthorn unpubl. data |
| 1989/90 | 15/1/90 | 104 | | single count | Cawthorn unpubl. data |
| 1992/93 | 7/1/93 | 67 | | single count | Cawthorn (1993) |
| 1994/95 | 11/1/95 | 123 | | single count | Gales & Fletcher (1999) |
| 1995/96 | 24/1/96 | 113 | 31* | single count | Gales & Fletcher (1999) |

* Minimum mortality estimate for the season

### *Adams Island*

Sea lions have also been reported on Adams Island in the Auckland Islands (Buckingham *et al.* 1991) and 42 animals were found near Lake Turbott on 12 November 1989. The group comprised 4 males with harems, 10 bachelor males, and 28 females. This is unlikely to have been a breeding group because it was observed too early in the season and was more likely part of the pre-breeding build-up. No pups have been reported from this site.

### *Campbell Island*

Most of the reports from Campbell Island have been as a result of opportunistic surveys and encounters and not the result of detailed studies. The data reported therefore reflects a minimum count for most of the references mentioned. Bailey & Sorensen (1962) estimated that on Campbell Island at the end of 1947 there were no more than 20 females and many hundreds of males, the majority of them immature. The NZSLs were mostly concentrated at Northwest Bay and Northeast Harbour although young pups have been seen all across the Island. They also reported that there may have been a slight increase in the number of NZSLs on Campbell Island between 1941 and 1958. Bailey & Sorensen (1962, pp. 52) wrote of Campbell Island that "while of regular occurrence, the sea lion is not an abundant animal." Degerbol (1956, pp. 205) reported seeing "only a few" NZSLs in Perseverance Harbour in 1951.

Russ (1980) counted 78 animals on the Island on 21 December 1975, with only a single female being seen. He reports that NZSLs can be found all over the Island but particularly at Perseverance and Northeast Harbours, and Northwest Bay. Southeast and Monumental Harbours are also used as resting areas. During the 1991/92 breeding season 98 pups were tagged on Campbell (M. Frazer, pers. comm.) and the 24 dead untagged pups counted give a minimum production estimate of 122 pups. This study was undertaken on an opportunistic basis and pups were tagged when encountered all across the Island. Taylor & Sadleir (1985, pp. 4) reported approximately 30 pups born on Campbell Island during the 1984/85 summer and that this "represents a continuing gradual increase of breeding animals there." Moore & Moffat (1990) report that a minimum of 51 pups were born on Campbell in the summer of 1987/88 with most being seen in Capstan Cove, Northwest Bay, and Tucker Cove. Cawthorn (1993) estimated pup production to be 150 for the 1992/93 season.

### *Sea lions at other locations*

Sea lions have been reported from The Snares islands, where small numbers breed (Falla 1948). Waite (1909) reported a single pup and female found at The Snares in 1907. Basaltic pebbles assumed to be NZSL gastroliths have also been found there (Fleming 1951). In a visit in the summer of 1970/71 a maximum of 47 animals were counted consisting of 36 males and 11 females (Crawley & Cameron 1972). Crawley & Cameron (1972) also reported the presence of two pups that were probably born on the islands in 1969 and 1971 respectively. Cawthorn (1993) estimated pup production for the Snares Island at 10 for the 1992/93 season. Gales & Fletcher (1999) reported that no NZSL pups have been reported born on the Snares islands for the past few years despite frequent visits by scientific parties during the pupping season.

Male NZSLs visit Macquarie Island, and some individuals stay for several years or return over several consecutive years (Gwynn 1953; Csordas 1963). Csordas (1963) noted that there was no evidence of NZSLs breeding on Macquarie Island when it was discovered in 1810.

Stewart Island has been reported as a frequent haul out site for immature and sub-adult males during 1971 and 1974 (Wilson 1979); the maximum number of animals counted in a single day was 15. Lone males are reported to visit these shores during winter (Begg & Begg 1979). Fleming (1951) reported some animals, mostly immature, hauled out on the coast of Stewart Island and Southland which he classified as a non-breeding overflow from the Auckland Island population.

The Otago coastline is now a regular haul-out site for immature and subadult males (Hawke 1986; Beentjes 1989; Hawke 1993; McConkey 1994). A small number are resident for the whole year with many remaining for several months before leaving (McConkey 1994). Some have returned over successive years (Beentjes 1989). Most of these NZSLs leave early in summer months and are not seen again until late March. These individuals may have been travelling to the sub-Antarctic Islands for the breeding season (Beentjes 1989). Hawke (1993) reported the first post-sealing record of a female on the New Zealand mainland. In 88 surveys conducted on the coast of Otago between 1984 and 1992 Hawke sighted 28 NZSLs, four of which were female; at least two different females were individually identified.

McConkey (1994) estimated a population of about 20 animals for the Otago Peninsula in 1994. The number of resident individuals and maximum haul-out numbers indicate a doubling of the population size over the last 10 years. The population is composed almost exclusively males with only one or two females. Six NZSLs have been reported killed by humans in the Catlins (four shot and two run over) in 1993 and 1994, from a population with an estimated size similar to that of Otago's. This population is also composed almost exclusively of males.

Single females have given birth on the Otago coast in the summers of 1992/93, 1993/94 and 1995/96 (McConkey 1994, S. McConkey pers. comm.); at Butterfield Beach on Stewart Island in 1988/89 and 1991/92, and on Codfish Island in 1989/90 and 1995/96 (L. Chadderton, pers. comm.).

*Total population estimates*

Estimates of total population size for NZSL are shown in Table 2.5.

**Table 2.5** Total population estimates for New Zealand sea lion

| Date of estimate | Total population estimate* | Method used to calculate estimate | Reference |
|---|---|---|---|
| 1974/75 season | 3 000 | sum of counts at 3 main breeding colonies | Best (1974) |
| 1974/75 season | 3 144[1] | sum of counts with estimation of other parameters | Cawthorn (1975) |
| 1978/79 season | 6 000[2] | calculated from counts and estimates at breeding colonies | Falla *et al.* (1979) |
| 1982 | 4 000 | based on reports of Best (1974) and G.J.Wilson pers. comm. | Warneke (1982) |
| 1984 | 6 655 | sum of counts at breeding colonies and from aerial photographs | Doonan & Cawthorn (1984) |
| 1984/85 season | 6 440-7 300 | method not described | Cawthorn (1986b) |
| 1985 | 6 500-7 000 | calculated from tagging and survey programmes | Cawthorn *et al.* (1985) |
| 1992/93 season | 14 083 | modelled from counts of pup production | Cawthorn (1993) |
| 1992/93 season | 8 587-15 393 | modelled from counts of pup production | Gales (1995) |
| 1994/95 season | 10 900-14 300 | modelled from mark recapture estimate of pup production | Gales & Fletcher (1999) |
| 1995/96 season | 11 600-15 200 | modelled from mark recapture estimate of pup production | Gales & Fletcher (1999) |

[1] Estimate for Auckland Islands only

[2] Estimate excludes non breeding males and juveniles

* Values provided are mean estimates and ranges are 95% confidence intervals.

## 2.4 DISCUSSION

Archaeological evidence demonstrates that NZSLs were once more widespread than they are today. Before the occupation of New Zealand by humans, NZSLs ranged all along the coast from the far north of the North Island through to Stewart Island and the sub-Antarctic Islands to the south.

There are several potential biases arising from examination of archaeological records to infer distribution patterns of pinnipeds. First, archaeological research has a patchy distribution around the New Zealand coastline, and the reported location of NZSL bones and other remains is concentrated in areas of greatest effort. Selection of sites for excavations has usually not been based on an investigation of NZSL distribution, but rather on other criteria such as history. For instance, there have been few systematic investigations of sites for marine mammal remains on the west coast of the South Island (Smith 1989) although R. Hooker (pers. comm.) reported that no NZSL and only a few fur seal bones were found during a survey of 45 sites while investigating Maori occupation of the area. Consequently, the pattern of NZSL remains shown in Figure 2.2 implies a widespread distribution, but gives no clear clues as to areas of relative abundance. Second, the location of bones may or may not relate to the site where the animal was originally found and killed. Fortunately this is unlikely to be a significant problem with large animals such as NZSLs, because Maori traditionally dressed out the meat for transport and storage, leaving the bones in situ (Smith 1989).

A further potential bias is in the interpretation of the significance of a find of bone material at a particular site. If remains are from only one animal, it is possible that the animal was beyond its normal range when killed and butchered. When bone remains from several animals are found (e.g. 8 at Houhora and 15 at Kaupokonui - Smith 1989) it is more likely that the find of bones is from within the normal range of NZSLs. It is possible that sites where the remains of several NZSL have been found could reflect the accumulation of material over a long period of time, potentially several hundred years or longer. However, this seems unlikely given the range of coastline from which remains have been found and the number of sites that have yielded multiple remains.

The pre-European distribution of fur seal remains is very similar to that of NZSLs (Smith 1989). Abundance estimates from this time are not available for NZSLs, but fur seals were estimated to number between 1.5 and 2 million animals before exploitation (Richards 1994). Remains of fur seals are recorded at 103 archaeological sites around New Zealand (Smith 1989), compared with 47 sites for NZSLs. Sea lion and fur seal remains are often found in the same midden, the fur seals usually being more abundant than NZSLs, e.g. the remains of 14 NZSLs and 57 fur seals from a midden at Shag Mouth (Smith 1996). It is likely that fur seals have always been more abundant than NZSLs (see Smith 1989; Reijnders *et al.* 1993), and so this bias is not surprising. Nevertheless, as the number of sites with NZSL remains is close to half that for fur seals, this index of abundance - although fairly crude - would suggest that the current NZSL population is significantly reduced in numbers as well as distribution. This seems likely if it is assumed that NZSLs were not preferred as a food resource over fur seals.

Direct exploitation is the most likely cause of the decrease in distribution of NZSL with Moriori, Maori, and later Europeans all hunting them to some degree. The evidence suggests that there was opportunistic hunting of NZSLs around the whole country whereas regular, seasonal hunts were known to occur in at least two places - Lord’s River and Shag Mouth (Stark 1986; Smith 1996). All age classes were hunted, but juveniles and sub-adult males are represented in higher proportions than their incidence in the total population (Smith 1989). As juveniles and sub-adult males disperse more widely than other age/sex classes, this finding is not unexpected.

Smith (1985) states that NZSLs disappeared from the northern North Island by about AD 1500 and elsewhere they appear to be to have become scarce. Worthy (1992, pp. 38) continues: "The implication is that there were resident populations in New Zealand and that hunting by Polynesians exterminated these. The remaining population was much reduced and its usual range extended only to southern New Zealand. Then nineteenth century hunting by sealers further reduced the population so that NZSLs only survived on the inaccessible southern islands." The apparent disappearance of NZSL from the Chatham Islands occurs about the same time as European contact began (Smith 1989). The coincidence of European settlement and the disappearance of NZSLs indicate that the NZSLs were probably driven from the Chatham Islands by human predation.

Smith (1989) suggested that human disturbance may have caused the abandonment of some NZSL colonies. We feel that this is unlikely as in our experience, NZSLs appear to be tolerant of human disturbance, and further, NZSLs are now colonising sites with relatively high levels of disturbance i.e. Otago Peninsula.

There is little evidence that environmental changes have affected the distribution of the NZSL. This partly reflects the fact that the habitat requirements of the NZSL are unknown, but Smith (1989) suggests that as both the Australian (*Neophoca cinerea*) and the South American (*Otaria byronia*) NZSLs inhabit lower latitudes (Vaz-Ferreira 1981; Gales *et al.* 1994) then it is possible that the NZSL could as well.

Environmental factors have been suggested as a constraint on the distribution of breeding colonies of fur seal (Wilson 1974, Mattlin 1978). North of the present breeding limit, fur seals ashore may be disrupted by higher air temperatures and longer hours of sunshine, through effects such as heat stress. As a result, it is likely that fur seals would spend more time in the water cooling and less time ashore maintaining territory and bearing and suckling pups. It follows that NZSLs may also be affected by heat stress, but to what extent is unknown.

Climate change has also been suggested as a possible explanation for the change in distribution of NZSLs. Smith (1989) acknowledges that some climatic changes have occurred, but that they are unlikely to account for a decline in NZSL range. The changes have been small (±0.7°C), and although there was a slightly warmer and more settled period between the

10th and 16th centuries it was followed by a minor deterioration between the 17th and 19th centuries (Leach & Leach 1979) which may in fact have favoured NZSLs breeding at lower latitudes.

That NZSL used to breed on the mainland is indicated by the presence of pups and females in the archaeological record. Although female remains do not constitute direct evidence of breeding, temporal changes in their distribution are likely to reflect changes in distribution of breeding sites. Currently females breed throughout their known range, from Campbell Island in the south to Otago in the north. The fact that they breed at the northern limit of their present distribution suggests that their breeding range may be the same as their geographic range. The presence of female remains in Northland is therefore possible evidence for a more northern breeding range prior to the arrival of Europeans to New Zealand.

The relative lack of pup remains in the archaeological record could be interpreted as evidence against breeding on the mainland or Stewart Island. However, Worthy (1994) states that the finding and identification of pup remains, particularly in dune deposits, is unlikely given that their small, porous bones are the least likely to remain intact. Furthermore, pup bones are unlikely to be found unless they are specifically looked for as most investigations target the larger, well preserved bones. There have been no archaeological investigations carried out at either Lord's River or Port Pegasus where NZSLs where known to breed. Smith (1989) reports that only 28 fur seal pup remains have been recovered from sites across mainland New Zealand. This is an extremely small archaeological representation of the previously extensive breeding range and population size of the fur seal on the mainland. The same pattern appears to be true for the NZSL.

Berry & King (1970) report the remains of two young NZSLs from Hawkes Bay, and conclude that they either bred as far north as Hawkes Bay or close enough that the young animals could swim there. Without a more specific age determination for these specimens it is impossible to say whether they were in fact young pups and probably born there, or juveniles, which are known to disperse widely after weaning. However, juveniles have not been reported from this area recently and this would imply that their present range is reduced from former times.

The two clear references to breeding on Stewart Island in the 1820s, at Lord's River and Port Pegasus (Howard 1940; Starke 1986) describe NZSLs as "numerous" and in "great quantities." Hector (1892) refers to breeding on the west coast of the South Island and makes reference to the occurrence of NZSL on Bass Strait and in Tasmania. This is likely to have been a misidentification of the Australian NZSL as there are no other records of NZSL reaching Australia. Not withstanding this misidentification, it seems unlikely that an accomplished naturalist like Hector would have confused a NZSL with a fur seal and that consequently the breeding range of the NZSL did indeed extend up the west coast of the South Island. The only subsequent records of breeding on the mainland have been recent ones (post 1988) involving seven pups born on Stewart Island, Codfish Island, and the Otago coastline. These are rare events and may reflect a slow recolonisation of past breeding sites rather than an expanding population that is colonising new areas.

Most of the records from the 19th century are accounts by sealers, and they provide only a rough estimation of NZSL abundance and distribution. Few records refer specifically to NZSLs, as most are concerned with the more commercially valuable fur seal. The 3670 NZSL skins landed by the sealing vessels *Wellington* and *Elizabeth* and *Mary* in 1825 represent the only real quantitative reference available from this period. This actually reflects a larger number of NZSLs killed, as pelts were often damaged during skinning and curing; these were not retained and hence were never reported (McNab 1907).

Given that fur seals and NZSLs had been reduced to very low numbers around the New Zealand mainland and offshore islands by 1830, both species were faced with recovery from severe depletion - a long and slow process. Fur seals are now abundant and expanding around much of the South Island and breeding colonies are establishing in the North Island. Fur seals commonly haul out, and are seen throughout their pristine range distribution, although at population levels estimated to be as low as 2% of pristine abundance (Richards 1994). This 'early recovery phase' has not yet been observed for the NZSL.

Why has the apparent partial recovery of NZSL observed in the Auckland Islands in the latter half of the 19th century not continued through the 20th century? We offer no explanation in response to this question, but make the following observations. Throughout the Southern Hemisphere fur seals are likely always to have been more abundant than the three NZSL species (Australian, South American and New Zealand), and many fur seal populations, while still at a small fraction of their pristine abundance, are now rapidly increasing in size and recolonising their previous range (Reijnders *et al.* 1993). By comparison, the populations of all three southern NZSL species appear to be stable and showing no real increase in population size (Reijnders *et al.* 1993). Further work on the ecological differences between fur seals and NZSLs towards understanding the mechanisms that facilitate population expansion is prudent for agencies responsible for protecting NZSL stocks. In particular, and given the current lack of such knowledge, it is important to maximise efforts to reduce anthropogenic factors that may limit the ability of pinniped populations to recover.

Many counts and estimates of the various breeding colonies in the Auckland Islands made in the latter part of the 20th century have been reported. The technique most used to estimate numbers, direct counts, is the easiest and most convenient and provides a good estimate of visible pups, but takes no account of pups hidden by terrain or other pups. This observational bias is likely to be inconsistent, and is impossible to correct for (Gales & Fletcher 1999). There are also likely to be differences between years as personnel and conditions change. Despite these drawbacks successive counts over the years are the only means available to monitor changes in NZSL numbers and especially pup production. At colonies such as Sandy Bay, where pups are fairly easily viewed from the sand bank behind the beach, these biases are likely to be minimised.

The time of year at which estimates are made has a strong influence on the outcome, as peak pup numbers in the colony occurs consistently in mid January (Gales & Fletcher 1999). Estimates that are not made close to the date of peak pup production will not reflect the maximum for that year. Estimates of total pup production require the inclusion of mortality estimates with live pup numbers. Most of the past estimates are only of live pup numbers and do not include any estimate of mortality. Therefore, total pup production estimates are not available for most seasons.

Pup production is the best index of relative population status (Berkson & DeMaster 1985; Gales & Fletcher 1999). There is no evidence of either an upward or downward trend in estimates from Sandy Bay over the last 20 years, indicating that the number of live pups has been stable over at least this period. There was a high likelihood of detecting any such trend. Of all the seasonal estimates used to investigate population trends, only the first in 1973/74 was made before the southern squid fishery became active. It is not known whether the impact of bycatch from this fishery has influenced later pup production estimates. Modelling by Doonan & Cawthorn (1984) and Woodley & Lavigne (1993) suggests that the population would have been affected by a high level of bycatch. Other reports (e.g. Falla 1965; 1975) suggest that production may have been stable, at approximately 350-400 pups at Sandy Bay, since the 1940s. Unfortunately there are no good long term records from any of the other breeding colonies from which to compare the stability of pup production.

Six NZSLs have been reported killed by humans in 1993 and 1994 in the Catlins from a population of approximately 20 males (McConkey 1994). If this mortality rate continues, it would severely threaten the viability of this population and would limit the possibility of the Catlins population increasing. With NZSLs still rare on the mainland, even such localised human induced mortality could affect the ability of NZSLs to recolonise the mainland.

There have been several estimates of the total NZSL population size, employing a range of techniques. The most recent, with 95% confidence intervals, is between 11 600 and 15 200 (Gales & Fletcher 1999) and is based on modelling from pup production estimates from the 1995/96 breeding season. This is the best estimate to have been derived for total NZSL population, and is similar to the figures previously calculated by Cawthorn (1993) and Gales (1995). The NZSL is therefore currently one of the least abundant of any pinniped in the world.

## 2.5 ACKNOWLEDGMENTS

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# Chapter 3

# Distribution, Abundance and Growth of New Zealand Sea Lion Pups on Campbell Island[4]

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# CHAPTER 3: DISTRIBUTION, ABUNDANCE AND GROWTH OF NEW ZEALAND SEA LION PUPS ON CAMPBELL ISLAND

## 3.1 ABSTRACT

Nine weeks field work was completed during two trips in January/February and March/April 2003 to investigate the distribution and abundance of New Zealand sea lion *Phocarctos hookeri* pups at Campbell Island. A total of 161 pups were tagged and a further 138 dead pups were found. A closed mark-recapture model was used to estimate the total number of live pups (e.g., tagged plus untagged pups) at Campbell Island in April as 247 (SE = 28, 95% CI 198-308). Pup production at Campbell Island is estimated at 385, which comprises 13% of the total pup production for the species in the 2003 season. This is the first robust estimate of pup production for New Zealand sea lions at Campbell Island. The figure of 385 pups is considerably higher than any of the previous estimates reported from Campbell Island. The high level of pup mortality (36%) at Campbell Island for approximately the first two months after birth is higher than the 17% reported for the Auckland Islands for approximately the same period in 2003, but is similar to usually high levels of mortality (20-30%) reported at the Auckland Islands in recent years. It was not possible to determine the cause of death of the 138 dead pups owing to scavenging and decomposition. Pups were found over the whole Island, with the exception of its northern end. Male pups were significantly heavier and faster growing than female pups over the same period.

Keywords *Phocarctos hookeri*; subantarctic; sea lion; New Zealand; Campbell Island; survey; breeding; distribution; abundance; pup growth.

## 3.2 INTRODUCTION

The breeding distribution of the New Zealand (Hooker's) sea lion *Phocarctos hookeri* is centred on the New Zealand subantarctic islands (Figure 3.1) with over 95% of all pups of the species born at four colonies in the Auckland Islands (Gales & Fletcher 1999). The only other significant breeding population is at Campbell Island (McNally *et al.* 2001). Occasional births have been recorded at the Snares (Crawley & Cameron 1972), Stewart Island (Childerhouse & Gales 1998 (Chapter 2)) and Otago Peninsula (McConkey *et al.* 2002a). The mean population size of New Zealand sea lions is estimated at 13 608 (95% CI 11 812-15 663) individuals for the 2003 breeding season (Wilkinson unpubl. data) and the population appears to be stable at c. 12 000-14 000 individuals since the mid 1990s (Gales & Fletcher 1999;

Wilkinson *et al.* 2003). New Zealand sea lions are gazetted as a threatened species by the New Zealand Government and are also listed as threatened by the IUCN (IUCN 1996; Wilkinson *et al.* 2003).

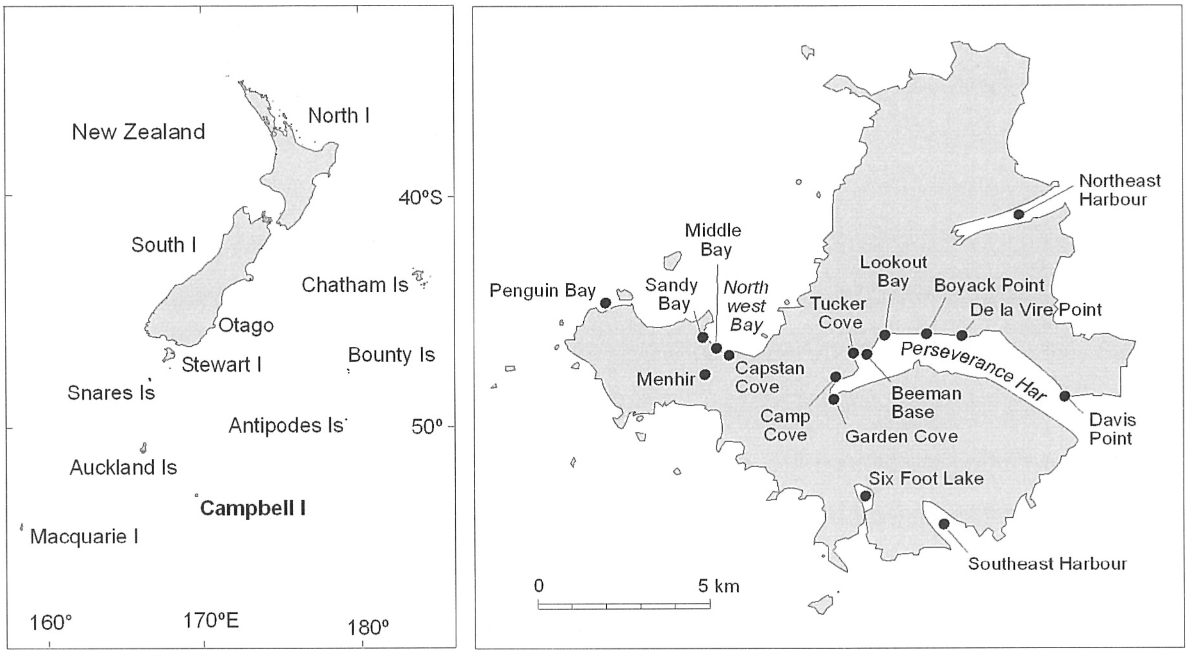

**Figure 3.1** The location of Campbell Island in the New Zealand subantarctic, and sites where New Zealand sea lions (*Phocarctos hookeri*) were seen on Campbell Island.

Campbell Island was discovered in 1810, and both fur seals and sea lions were quickly reduced to low numbers by commercial sealing (McNab 1907; Warneke 1982). By 1830, sealing had declined to an unprofitable level and the industry collapsed (Kerr 1976), after which sea lion numbers on Campbell Island appear to have recovered by the late 19th century (Joyce 1894; Thomson 1912). Sea lions were again reduced to low numbers in the early 20th century from hunting by whalers based at the island (Timms 1978). Reports since the 1940s have documented a slow recovery of sea lions on Campbell Island (Bailey & Sorenson 1962; Russ 1980; Moore & Moffat 1990; McNally *et al.* 2001). A more detailed account of historical records from Campbell Island is provided in McNally *et al.* (2001).

There have been few estimates of pup production at Campbell Island and most have been derived from opportunistic surveys. Sea lion pups are born in December and January spanning two years. In this paper we use the year in January to refer to the breeding season (e.g., 2003 refers to the 2003 season). The following estimates have been reported from Campbell Island: 30 pups in 1985 (Taylor & Sadleir 1985), 51 pups in 1988 (Moore & Moffat 1990), 122 pups in 1992 (M. Fraser pers. comm.), 150 in 1993 (Cawthorn 1993), and 78 from an incomplete survey in 1998 (McNally *et al.* 2001). As New Zealand sea lions are listed as threatened based on their limited number of breeding locations, with Campbell Island comprising the only breeding location outside the Auckland Islands, it is important to have recent and accurate estimates of pup production from Campbell Island.

This paper is an update from previous survey work for New Zealand sea lions on Campbell Island in 1998 reported in McNally *et al.* (2001). The 1998 survey was suspended before completion owing to an unusual mortality sea lion event (reported in Baker 1998). The main aims of this study were to: (1) estimate total number of live pups; (2) investigate and estimate pup mortality; (3) describe adult and pup distribution; and (4) estimate pup growth rates on Campbell Island.

## 3.3 METHODS

The Campbell Island group (52°33'S, 169°09'E) is situated 660 km south of the New Zealand mainland and comprises one large main island and several smaller islands, with a total land area estimated at 11 331 ha (Anon. 1983). Campbell Island is covered with dense vegetation forming distinct plant communities (Meurk *et* a*l.* 1994) including tussock meadows (*Poa* spp.), dwarf forest/scrub (*Dracophyllum* spp. and *Coprosma* spp.) and herb fields. The terrain is steep and much of the coastline is inaccessible to sea lions because of sheer cliffs (McNally *et al.* 2001).

Typically the breeding behaviour of sea lions on Campbell Island is non-colonial with most pups born in the scrub away from the coast in December and January (McNally *et al.* 2001). Pups are difficult to find in the scrub but by March or April, many pups can be found around the coastline and are more accessible (P. Moore pers. comm.). Colonial breeding, when it occurs, takes place in December–January. Two trips were timed to target different periods in the breeding cycle of sea lions in 2003: Trip 1 (from 29 January to 19 February) to investigate any colonial breeding sites and Trip 2 (from 23 March to 27 April) to find pups that had been born in the scrub and had subsequently moved to the coast. Visual surveys were conducted by searching the coastline and inland areas for sea lions. A total of 49 days of survey effort were completed, comprising 19 and 30 days on Trips 1 and 2 respectively. Based on previous surveys and reports, locations identified as sea lion breeding or haul out sites were visited at least once during each trip.

Most sea lion breeding habitat on Campbell Island is characterised by dense, low *Dracophyllum* and *Coprosma* scrub. Most land-based searches were done by either crawling or walking along sea lion and penguin pathways through the scrub. These pathways are common across most of the island and generally lead inland (and invariably uphill) from the coast. Land-based searches were carried out at known sea lion sites with teams of either four or five researchers systematically searching through an area while keeping in visual (where possible) and vocal contact. Streams and the sides of streams were also surveyed. Any areas showing signs of sea lion activity (e.g., recent tracks, scats, calls) were investigated to determine if a sea lion was present and, if so, to establish the sex and age. Some sites were surveyed more than once if there were extensive signs of sea lion activity. All survey track lines and the locations of all sea lions seen were recorded on a map. Locations of pups and track lines were estimated from local topographical features as it was not possible to get a GPS signal under the scrub canopy.

During Trip 2, a 4 m aluminium Stabicraft with 25 Hp Yamaha outboard was used to survey the shoreline of Perseverance Harbour (Figure 3.1). This increased the area that could be covered and was especially useful in March and April when pups were commonly found along the coast. Vessel survey track lines were also recorded on a map.

All individuals found were checked and the sex, age class (adult male, sub adult male, juvenile male, female, pup (following McConkey *et al.* 2002b)), identifying marks (e.g., tag, brand, bleach) and location noted. Pups were identified from their distinctive natal pelage (Walker & Ling 1981). All pups encountered were caught, physically restrained, then sexed, weighed to nearest 0.1 kg, measured (length, girth) to nearest 1 cm and tagged. All pups were tagged in both pectoral flippers with uniquely numbered blue or pink “coffin” shaped Dalton “Jumbotags” (Dalton ID systems, Oxon RG9 5AA, England). Pups removed from their mothers or companions were released back with them or as close to them as possible after handling. Pups were not re-caught after tagging to minimise disturbance but sightings of tagged pups were recorded. Movements of pups were investigated using subsequent resightings of tagged individuals. The location of all dead pups found was recorded and carcases marked to avoid recounting.

### *3.3.1 Data analysis*

Differences in the spatial distribution of pup sightings (e.g., altitude and distance from shore) between Trip 1 and Trip 2 were investigated using Mann-Whitney nonparametric tests as the data had a non-normal distribution. Differences in weights between sexes and trips were investigated using Analysis of Variance (ANOVA) tests. All tests were completed in SPSS statistical software (v12.0.1; LEAD Technologies, United States of America) with a significance level of $P < 0.05$. The mean growth rate for each sex was estimated by combining all weights across both trips (i.e., cross-population estimates) and calculating a simple linear regression.

Total pup production was calculated by adding estimates of the number of live and dead pups on the island. The number of dead pups was estimated from a direct count of dead pups seen on the island during both trips. The number of live pups was estimated using Chapman's modification of the Lincoln/Peterson estimator (Seber 1982) for closed populations using Trip 1 as a marking period (e.g., tagging) and Trip 2 as a recapture period (e.g., tagging and re-sighting). Log (base-10) normal 95% CIs were calculated.

## 3.4 RESULTS

A total of 161 pups were tagged (Trip 1 $n = 44$; Trip 2 $n = 117$) and a further 138 dead pups were found (Trip 1 $n = 137$; Trip 2 $n = 1$). The single dead pup found during Trip 2 had not been tagged. The number of pups tagged at each location is shown in Table 3.1. The following tag numbers were used: 2529–2575, 2601–2643 (pink) and 4579–4650 (blue). The sex ratio of pups tagged ($n = 161$) was biased towards males in both trips with an overall female : male sex ratio of 1 : 1.5.

The total number of live pups on Campbell Island estimated from the mark-recapture model was 247 (SE = 28; 95% CI 192–302). This was estimated using $n_1 = 44$, $n_2 = 142$ and $m_2 = 25$. This, combined with the number of dead pups estimated from a direct count, gives an estimate of total pup production for Campbell Island as 385 (95% CI 330–440) for the 2003 breeding season (Figure 3.2). Using only direct counts (e.g., number of dead pups plus number of pups tagged) provides a minimum estimate for total pup production of 299.

Most (136 out of 138) dead pups were found at Davis Point the first time it was surveyed on 31 January. All but two of these dead pups were found on the coastal rock platform, with the remaining two found in the tussock above the rock platform. It was estimated that the pups had been dead for 2-3 weeks but because of decomposition and scavenging it was not possible to determine the cause of death for any of the carcases. Of the remaining two pups found dead, one was on Menhir with its head wedged tightly in the crook of a tree at ground level and the other was at Duris Point in a mud wallow. Cause of death could not be determined for either pup.

Pups were found over the whole island, with the exception of the northern end (Figure 3.1). Most (65%) pups were found in and around Perseverance Harbour which reflects where most of the survey effort occurred. Other locations with significant numbers of pups were various sites in Northwest Bay (comprising Capstan Cove, Middle Bay and Sandy Bay) ($n = 35$) and Six Foot Lake ($n = 12$). Most (80%) pups were found within 325 m of the shoreline and at altitudes of less than 60 m above sea level, although the distances from shore were significantly greater (Mann-Whitney: $U = 1627$, $Z = -2.350$, $P = 0.019$) and altitudes were significantly higher (Mann-Whitney: $U = 637$, $Z = -7.833$, $P < 0.001$) in the first trip than the second (Table 3.2). Pups were found in a variety of vegetation and habitat types including tussock meadows and coastal sward but most were found in the low *Dracophyllum* and *Coprosma* scrub that covers much of the lower reaches of the island. Almost all pups were found in this low scrub during Trip 1 but during Trip 2 many were also found in or near the water along streams and along the coastline.

**Table 3.1** Number of New Zealand sea lion (*Phocarctos hookeri*) pups tagged at Campbell Island in 2003 by location and trip (Trip 1: January–February; Trip 2: March–April).

| **Location** | **Trip 1** | **Trip 2** | **Total** |
|---|---|---|---|
| Davis Point | 30 | 0 | 30 |
| Lookout Bay | 3 | 23 | 26 |
| Camp Cove | 0 | 23 | 23 |
| Capstan Cove[1] | 0 | 19 | 19 |
| Six Foot Lake | * | 12 | 12 |
| Middle Bay[1] | 0 | 11 | 11 |
| Between De La Vire and Boyack Point | 0 | 11 | 11 |
| Garden Cove | 2 | 7 | 9 |
| Beeman Base | 4 | 1 | 5 |
| Sandy Bay[1] | 0 | 5 | 5 |
| Menhir | 3 | 0 | 3 |
| Northeast Harbour | 0 | 3 | 3 |
| Tucker Cove | 2 | 0 | 2 |
| Penguin Bay | 0 | 1 | 1 |
| Southeast Harbour | 0 | 1 | 1 |
| Total | 44 | 117 | 161 |

* This site was not visited during Trip 1.

[1] Northwest Bay includes these three sites

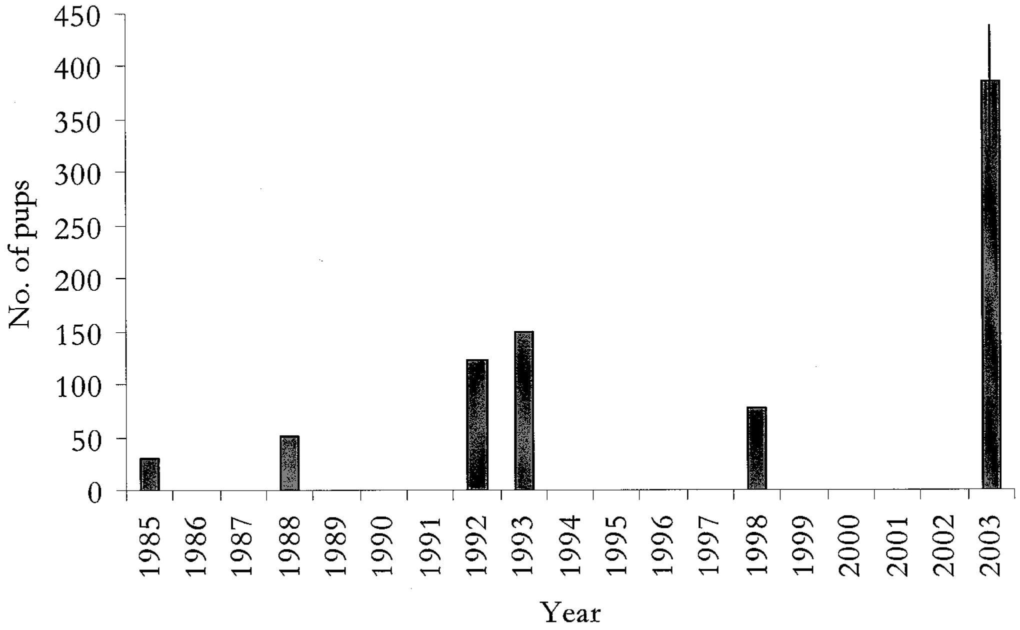

**Figure 3.2** Estimates of New Zealand sea lion (*Phocarctos hookeri*) pup production at Campbell Island from 1985-2003. Estimates are taken from the following sources: 1985 (Taylor & Sadleir 1985), 1988 (Moore & Moffat 1990), 1992 (M. Fraiser pers. comm.), 1993 (Cawthorn 1993), 1998 (McNally *et al.* 2001), and 2003 (this study). 95% confidence intervals are shown for 2003 but were not available for any other estimate. Note: The estimate for 1998 is derived from an incomplete count.

**Table 3.2** Distance from the coast and altitude of locations where New Zealand sea lion (*Phocarctos hookeri*) pups were tagged on Campbell Island in 2003. Details include mean, standard deviation (SD), maximum and the 80th percentile of observations. Sample sizes are *n* = 44 for Trip 1 (January–February) and *n* = 117 for Trip 2 (March–April).

| | **Distance from shore (m)** | | | **Altitude above sea level (m)** | | |
|---|---|---|---|---|---|---|
| | Trip 1 | Trip 2 | Trip 1 and 2 | Trip 1 | Trip 2 | Trip 1 and 2 |
| Mean | 238 | 172 | 190 | 54 | 11 | 23 |
| SD | 168 | 184 | 181 | 31 | 14 | 28 |
| Maximum | 800 | 625 | 800 | 160 | 60 | 160 |
| 80th percentile | 225 | 350 | 325 | 60 | 20 | 60 |

There were 178 observations of pups released after tagging (e.g., resights) over the period January–April. Sixty-two percent *(n* = 111) of resightings were of pups at the location where they were tagged. The remainder *(n* = 67) document the movement of pups around the island. The mean distance of these observed pup movements was 3.5 km (SD = 4.0, range 0.5–19.0); however most (70%) movements were less than 3 km. The longest recorded movements were from Camp Cove and Lookout Bay (in Perseverance Harbour) to the head of North East Harbour and another from Perseverance Harbour to Six Foot Lake. There were no observed interchanges between the eastern sites (e.g., Perseverance Harbour, North East Harbour) and western sites (e.g., Northwest Bay).

The large number of both live and dead pups found at Davis Point indicate that this was a significant site of colonial breeding in 2003 with a minimum estimate of 166 pups, c. 43% of total pup production for the island. The site is characterised by a large bedrock platform above all tides, giving way to *Dracophyllum* and tussock grasses further inland.

Some (37 of 161) of the pups tagged were unable to be both weighed and sexed (e.g., due to protective mothers) and were excluded from weight analysis. There was a significant difference in mean pup weights between the two trips and both sexes and also a significant interaction effect of trip and sex (two-way ANOVA, total SS = 5341, *df* = 123; trip: $F_{1,3996}$ = 287.0, $P < 0.001$; sex: $F_{1,362}$ = 26.1, $P < 0.001$; interaction $F_{1,806}$ = 12.7, $P < 0.001$). Male pups were significantly heavier than females in both trips and the mean weights of pups were heavier in the second trip (Table 3.3). The linear regression equations for growth were $y = 0.2808\text{ x} + 14.977$ ($R^2 = 0.8431$, SE = 0.014) and $y = 0.1816\text{ x} + 14.543$ ($R^2 = 0.6753$, SE = 0.019) for males and females respectively (Figure 3.3). These growth equations give an estimated mean growth rate of 0.281kg/day (or 1.84%/day) for males and 0.182 kg/day (or 1.23%/day) for females over the period January to April (e.g., 90-day period). Male pups had a significantly higher estimated mean growth rate than females over the period January–April (ANOVA : $F_{123,7124} = 10.4$, $P < 0.01$).

Twenty-three sea lions tagged as pups before 2003 were seen, including five sea lions tagged at Campbell Island in 1998, with the remainder being tagged at either Enderby or Dundas Island, in the Auckland Islands. Although most of these were males, four 4-year-old females were seen. Of the males seen, most were aged between two and five years, but three 10 and a single 12-year-old were also seen. In addition, 14 adult males that had been bleach marked at

Enderby Island in December 2002 or January 2003 by B. Robertson were recorded at Campbell Island.

The highest counts of sea lions (of all ages and sexes) were made at Sandy Bay and Beeman Base (Table 3.4). Other sites where sea lions were seen in reasonable numbers (e.g., >20) included Camp Cove, Garden Cove, and North East Harbour.

**Table 3.3** Weights of tagged New Zealand sea lion (*Phocarctos hookeri*) pups by sex and trip (Trip 1: January–February; Trip 2: March–April) at Campbell Island in 2003. Details include count (*n*) and weight data (mean, standard deviation (SD), minimum and maximum observations). Note: Some (37 of 161) of the pups tagged were unable to be both weighed and sexed and were excluded from this analysis.

| | **Male** | | **Female** | |
|---|---|---|---|---|
| | Trip 1 | Trip 2 | Trip 1 | Trip 2 |
| *n* | 27 | 50 | 16 | 31 |
| Mean weight (kg) | 17.1 | 32.0 | 16.0 | 25.7 |
| SD | 3.7 | 3.6 | 3.4 | 4.2 |
| Minimum | 11.6 | 22.8 | 10.4 | 14.0 |
| Maximum | 24.0 | 37.8 | 23.0 | 33.0 |

## 3.5 DISCUSSION

This project has provided the first robust estimate of pup production for New Zealand sea lions at Campbell Island. Although this estimate is considerably higher than previous estimates, it is not possible to make direct comparisons with the recent estimate as earlier estimates were generally non systematic and either anecdotal or opportunistic. To quantify any future changes in pup production at Campbell Island it will be necessary to undertake further dedicated surveys using similar methodologies.

The total estimated pup production for New Zealand sea lions for the 2003 season was 2903 pups with 2518 (87%) born at the Auckland Islands (Wilkinson 2003) and 385 (13%) born at Campbell Island. Previous estimates of pup production from Campbell Island have suggested that it comprises less than 5% of total pup production for the species and this new research has highlighted the importance of this population to the overall production for this species.

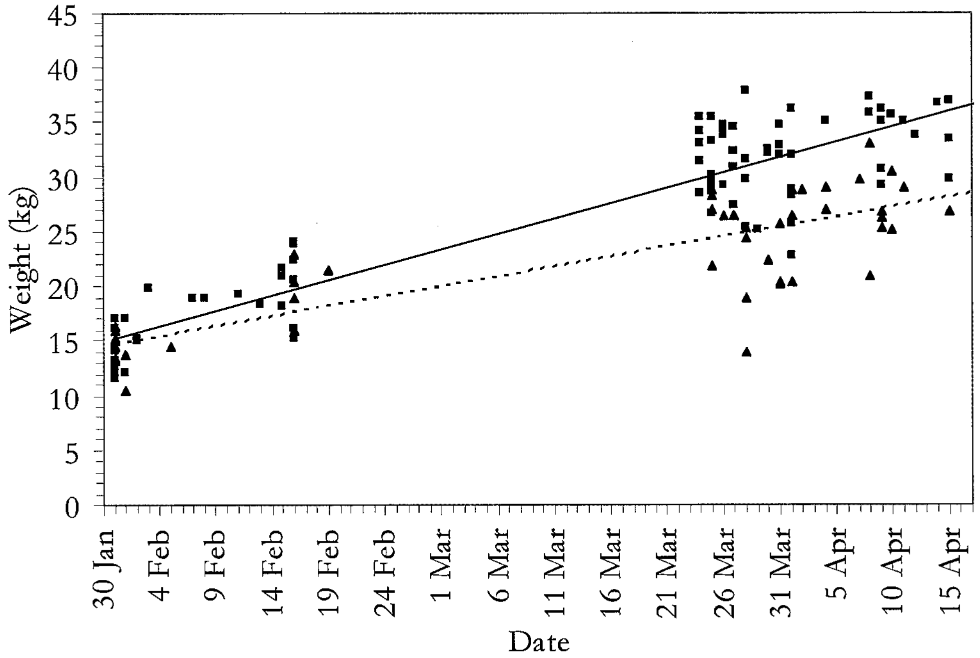

**Figure 3.3** Relationship between time and weight of tagged male (squares, solid line) and female (triangles, broken line) New Zealand sea lion (*Phocarctos hookeri*) pups at Campbell Island in 2003 (see text for regression details).

The closed population model used to estimate the number of live pups on Campbell Island has a number of assumptions associated with it. The major assumption is of population closure which means that the population is closed to births, deaths, immigration, and emigration. Research at the Auckland Islands has indicated that most pup mortality and births occur before mid January and are negligible after that (Gales & Fletcher 1999). In addition, the movement of young pups to or from Campbell Island seems unlikely as none of the 824 pups tagged at the Auckland Islands in January 2003 (comprising c. 40% of live pups born at the Auckland Islands) were recorded at Campbell Island. Conversely, no pups tagged at Campbell Island were seen at the Auckland Islands. Based on this information it is reasonable to accept the assumption of population closure for sea lion pups during the survey period at Campbell Island. If the population is in fact open when I used a closed model then both the mean and variance would have been underestimated.

The high level of pup mortality (36%) at Campbell Island is higher than the 17% reported for the Auckland Islands (Wilkinson unpubl. data) for approximately the same period in 2003 (e.g., December to late January). It is approaching the rate (44%) reported at Campbell Island in 1998 (McNally *et al.* 2001), although the 1998 survey was incomplete and occurred during an "unusual" mortality event (Baker 1998). During surveys in 1998 and 2003 almost all of the dead pups were found at Davis Point where pup carcasses are easily seen on the rock platforms. As dead pups are extremely difficult to find in the scrub, these estimates should be considered minimum estimates. They are also much higher than mortality estimates from the Auckland Islands during so-called "normal" years (c. 12% till 6 weeks of age (Gales & Fletcher 1998; Wilkinson unpubl. data)). However, rates up to 53% were recorded at the Auckland Islands during 1998 (Baker 1998) and between 20-30% for several years since then (Wilkinson unpubl. data). It was not possible to determine the cause of pup mortality at Campbell Island in either 1998 or 2003 but most dead pups appeared to be in reasonable body condition, which suggests that starvation was unlikely to be the primary factor. Bacterial agents have been implicated in years of higher than normal mortality at the Auckland Islands (Baker 1998; Duignan & Wilkinson unpubl. data).

**Table 3.4** Total number of counts of New Zealand sea lions (*Phocarctos hookeri*) including summary data on counts (number (*n*) and the mean number of individuals at each location including standard deviation (SD) and range), and the mean number of sea lions by age class for each location at Campbell Island in 2003. Age classes (pup, juvenile/sub-adult male, adult male, female) were determined following McConkey *et al.* 2002b.

| | **Summary of sea lion counts** | | | | **Mean no. of sea lions counted by age class** | | | |
|---|---|---|---|---|---|---|---|---|
| Location | *n* | Mean no. individuals | SD | Range | Adult male | Juv/sub adult male | Female | Pup |
| Davis Point | 2 | 5 | 2.1 | 3 - 6 | 0 | 0 | 5 | 0 |
| Camp Cove | 8 | 28 | 32.5 | 2 - 92 | 2 | 9 | 17 | 1 |
| Six Foot Lake | 1 | 11 | - | - | 0 | 0 | 10 | 1 |
| Middle Bay | 3 | 7 | 5.2 | 1 - 10 | 3 | 2 | 2 | 0 |
| Boyack Point | 1 | 3 | - | | 0 | 0 | 3 | 0 |
| Garden Cove | 7 | 24 | 16.4 | 3 - 45 | 2 | <1 | 21 | 1 |
| Beeman Base | 4 | 71 | 31.9 | 40 - 100 | 2 | 38 | 30 | 0 |
| Sandy Bay | 10 | 61 | 34.3 | 20 - 107 | 11 | 30 | 20 | <1 |
| Northeast Harbour | 1 | 23 | - | - | 2 | 5 | 16 | 0 |
| Tucker Cove | 6 | 3 | 2.7 | 0 - 6 | 0 | <1 | 3 | <1 |
| Penguin Bay | 1 | 6 | - | - | 1 | 0 | 5 | 0 |
| Southeast Harbour | 1 | 6 | - | - | 1 | 2 | 3 | 0 |
| Col Ridge | 1 | 1 | - | - | 0 | 0 | 1 | 0 |
| Venus Cove | 1 | 2 | - | - | 0 | 0 | 2 | 0 |

Resighting of tagged pups indicated movement of pups around the island, and highlights their mobile nature, especially those pups 3 months or older. Pups were found at lower altitudes and closer to the coast during March/April than in January/February. This is consistent with anecdotal observations by previous researchers and confirms that as pups reach 3-4 months of age they become more mobile, move away and/or are led away from birth sites in the scrub by their mothers and congregate along creeks and the coastline.

This difference in behaviour and habitat use between January/February and March/April highlights the importance of careful design for any future surveys. Both periods are required for the generation of any mark-recapture abundance estimate for pup production. Any future surveys should include a January/February survey designed to target colonial breeding and provide a marking period, and a March/April survey to target older, more mobile pups and allow for a recapture period.

The large number of both live and dead pups found at Davis Point indicates that this was a significant site of colonial breeding in 2003 and is in stark contrast to the rest of the island where births appear to be by solitary females in the scrub. The minimum estimate of 166 (43% of total pup production for Campbell Island) pups for the Davis Point Colony is likely to be an underestimate, as by the time the site was surveyed in late January all the live pups found were up in the scrub and there were none on the rock platform where all the dead pups were found. It is probable that many of the live pups born at Davis Point had either moved up into the scrub and were difficult to find or had moved away from Davis Point before our arrival.

Sea lions at Campbell Island exhibit both colonial and non-colonial breeding behaviour (McNally *et al.* 2001). The high proportion of pups apparently born away from colonies (>50%) at Campbell Island is in contrast to that observed at the Auckland Islands where breeding is almost exclusively colonial (>99%) with breeding restricted to four colonies and with little breeding occurring outside these colonies (Gales & Fletcher 1999). Although Campbell Island has a much smaller sea lion population than the Auckland Islands, there is no clear explanation for the difference in the proportion of non-colonial breeding.

Weights of individual pups over both trips were pooled to estimate the average growth rate for the study period using cross-sectional data from the population. It was not possible to determine the age of each pup and ideally it would have been preferable to re-weigh the same pups to measure specific individual growth. This was not logistically feasible and instead a random sample taken over the period was used as a representative sample. It is unlikely that the growth rate over this period is a linear function and is more likely to be a curvilinear function, with variable growth rate relative to the age and sex of the pup. However, we used a simple linear function to estimate mean growth over the period as the data would not support more sophisticated analytical methods. Not with standing this, a mean growth rate is useful for comparative purposes with other New Zealand sea lion studies (e.g., Auckland Islands, Otago) and other species. As was found in 1998 (McNally *et al.* 2001), male pups were heavier than females weighed on approximately the same date. It is probable that pups of both sexes were born at similar times, and it is therefore likely that they were of similar age. This is consistent with data for many other otariid species (Mattlin 1981; Georges & Guinet 2000; Luque & Aurioles-Gamboa 2001; Arnould & Hindell 2002). Male pups had a significantly higher growth rate (33% higher) than females which is also common in other otariids (Kovacs & Lavigne 1992; Goldsworthy 1995; Guinet *et al.* 1999).

The distribution of sightings of sea lions were broadly consistent with those reported from McNally *et al.* (2001), except that high numbers were reported at Davis Point in 1998, whereas we recorded low numbers for this location. The presence of 136 dead pups in 2003 suggests that this site was more heavily used but was abandoned by most sea lions before our first survey. Furthermore, low numbers of adult females were seen in 1998 compared with 2003. It was likely that both these differences relate to the difference in the timing of surveys (e.g., mid January in 1998 and late January–April in 2003) and also that 1998 is known to be an atypical year owing to a mortality event (Baker 1998). Sandy Bay and South East Harbour haul out sites were characterised by sandy beaches whereas all the other sites were boulder beaches or more commonly, open grass and tussock clearings.

The sighting of sea lions that had been tagged and/or bleached at the Auckland Islands indicates that there is some movement between Auckland and Campbell Islands, apparently both within and between seasons. There is only one report of a male sea lion tagged at Campbell Island (in 1992) being seen at the Auckland Islands, but this is likely to reflect the small amount of tagging on Campbell Island, rather than a lack of movement from Campbell Island to the Auckland Islands. During 2003, 18 individuals tagged at the Auckland Islands were seen on Campbell Island. Currently, Auckland and Campbell Island are treated as separate breeding locations for the purposes of management, and sea lions are listed as threatened on the basis of the small number of breeding locations (IUCN 1996). The level of interchange between Campbell and the Auckland Islands needs further investigation to explore whether these two population do in fact constitute independent breeding locations. The independence, or lack of, these locations has important management implications for the species and requires further consideration. This is especially in light of potential mortality events and the transmission of disease between the two locations.

The results of this work provide the first robust estimate of pup production for Campbell Island. Past surveys and the results from Trip 1 and 2 of this study indicate that the timing of surveys can potentially have a large impact on estimates of pup production. For example, if each trip was analysed alone, the estimates from direct counts would be c. 181 (tagged plus dead pups) and 210 pups (tagged or resighted plus dead pups) for Trip 1 and 2 respectively compared to 385 pups from both trips combined. The combination of the two trips allowed for a robust population estimate to be calculated using mark-recapture techniques. Furthermore, Trip 1 served to establish the occurrence of colonial breeding whereas the timing for Trip 2 significantly increased the detection of non-colonial breeders. Because of the changes in sea lion behaviour through the breeding season, it will be useful for the timing of future surveys to be standardised to ensure comparability between estimates.

## 3.6 ACKNOWLEDGMENTS

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# Chapter 4

# Diet of New Zealand Sea Lions at the Auckland Islands[5]

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[5] Originally published as Childerhouse, S.; Dix, B.; Gales, N. 2001. Diet of New Zealand sea lions (*Phocarctos hookeri*) at the Auckland Islands. Wildlife Research 28: 291-298.

# CHAPTER 4: DIET OF NEW ZEALAND SEA LIONS AT THE AUCKLAND ISLANDS

## 4.1 ABSTRACT

Scat and regurgitate samples *(n* = 206) from New Zealand sea lions (*Phocarctos hookeri*) were collected at the Auckland Islands between December 1994 and February 1997. Most (82%) samples were collected during three summer seasons while the remainder (18%) were collected during a single winter season. Thirty-three taxa were identified from 3523 prey items. The six most abundant prey species accounted for 90% of all prey items. The two most numerically abundant prey species, octopus (*Enteroctopus zelandicus*) and opalfish (*Hemerocoetes* species) made up almost 50% of total prey items. Other important prey species included lobster krill (*Munida gregaria*), hoki (*Macruronus novaezelandiae*), oblique-banded rattail (*Coelorhynchus aspercephalus*), and salps (*Pyrosoma atlanticum*). New Zealand fur seals (*Arctocephalus forsteri*) and seabirds were also identified in samples. New Zealand sea lions are generalist feeders utilising a wide variety of prey items, with fish comprising the most common taxa (59%) numerically and both cephalopods (21%) and crustacea (15%) forming lesser, but still important, parts of the diet. Prey taxa identified indicate that New Zealand sea lions are utilising a wide variety of benthic, demersal and pelagic species ranging from the inter-tidal zone to waters deeper than 300 m. New Zealand sea lions at the Auckland Islands target different prey species to New Zealand sea lions at other locations although they have broadly consistent prey types, with fish as the major taxa. There is only a small overlap of New Zealand sea lion prey species with commercially targeted species on the Auckland Islands Shelf in the months sampled.

## 4.2 INTRODUCTION

Over 95% of the world's population of New Zealand sea lions (*Phocarctos hookeri*) (also known as Hooker's sea lion) breed in the Auckland Islands (50°44'S, 165°36'E), approximately 500 km south of New Zealand (Gales 1995) (Figure 4.1). The total population size was estimated at between 11,100 and 14,000 individuals in 1996 and the species has a 'threatened' status from the International Union for the Conservation of Nature and under New Zealand legislation (Gales & Fletcher 1999).

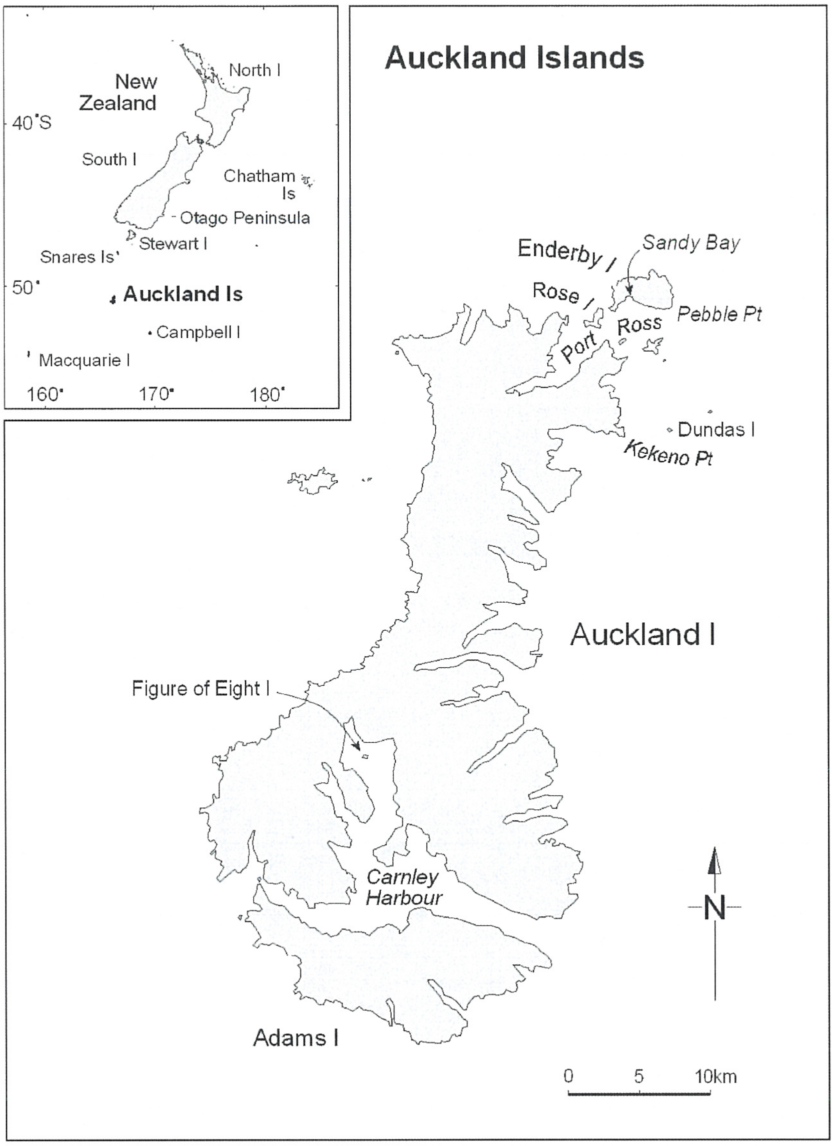

**Figure 4.1** Map showing the location of the Auckland Islands relative to New Zealand. Sites mentioned in the text are shown.

The Auckland Islands Shelf is fished annually for up to 30,000 tonnes of arrow squid (*Nototodarus sloanii*), along with several smaller fisheries for fish and crustaceans (Annala *et al.* 2000). Each year New Zealand sea lions are accidentally drowned in the squid trawl fishery that operates around the Auckland Islands and management measures aimed at protecting the sea lions have resulted in the early closure of the fishery every year since 1996 (Manly & Walshe 1999). Recent work has indicated that lactating New Zealand sea lions at the Auckland Islands may be occupying a marginal foraging environment in which diving behaviour is close to physiological limits (Gales & Mattlin 1997; Costa *et al.* 1998). It is possible that, in addition to the accidental drowning of New Zealand sea lions, fisheries on the Auckland Islands Shelf might compete directly with, and impact, the New Zealand sea lion population. Quantifying the diet of New Zealand sea lions at the Auckland Islands is an important tool in the investigation of the fisheries-marine mammal interaction.

There are no published quantitative accounts of the diet of New Zealand sea lions at the Auckland Islands although there have been some anecdotal observations of prey. Yaldwyn (1958) summarised the known prey items at the Auckland Islands as cephalopods, bivalves, fish and birds. Cawthorn *et al.* (1985) noted that New Zealand sea lions at the Auckland Islands have a seasonal feeding preference for squid and are opportunistic feeders that take fish, octopus, krill, crabs, elasmobranchs, algae, bivalves and gastropods. Lalas (1997) described the diet of New Zealand sea lions that haul out on the Otago Peninsula on the South Island of New Zealand as mostly fish, but including polychaetes, crustaceans and cephalopods, with over 70% of estimated diet biomass represented by only 5 taxa. Most of the prey taxa were demersal, although some pelagic animals were also identified (Lalas 1997). The diet of itinerant male New Zealand sea lions at Macquarie Island (650 km south-west of the Auckland Islands) comprised predominantly fish and also included cephalopods, gastropods, crustaceans and fur seals (McMahon *et al.* 1999).

Some methods of estimating the diet of marine mammals suffer from significant biases that have been widely reported (Dellinger & Trillmich 1988; Pierce & Boyle 1991). In studies where identifiable remains from scats and regurgitations are used to estimate actual proportions of prey types consumed, the biases can be large (Gales & Cheal 1992). However, Lake (1997) showed, from feeding trials with New Zealand fur seals (*Arctocephalus forsteri*), that despite these biases, scats and regurgitates can provide a reliable estimate of diet. Estimation of relative biomass of prey has been shown to be informative in some cases (Lalas 1997) but this is possible only when reliable regression equations of hard remains to biomass are available. The aim of this work is to describe the diet of New Zealand sea lions at the Auckland Islands.

## 4.3 METHODS

Scat and regurgitate samples were collected from different sites around the Auckland Islands. Collection sites were mostly breeding colonies but some haul out sites were also sampled. Fresh, intact scat and regurgitation samples were selected. Samples were collected opportunistically and were not linked to individuals. All samples were stored and labelled in individual self-sealing plastic bags prior to processing. Samples were soaked for 12–36 h in a weak detergent solution (20 : 1 ‘Simple Green’ (Sunshine Makers Inc., California)), then washed and sorted in running water through a series of sieves of decreasing mesh size (smallest 0.2 mm). All diagnostic remains from each sample were removed and stored in either 70% ethanol or 40% isopropynol.

In the laboratory, otoliths and cephalopod beaks were identified to species level by comparison with reference collections and otolith atlases (Schwarzhans 1984; Hecht 1987). Remains that could not be identified to species level were identified to the highest taxonomic level possible.

The minimum number of individuals of each fish species in each sample was estimated by dividing the total number of recovered otoliths for that species by two and rounding up. The minimum number of each cephalopod species in each sample was estimated from the total number of either upper or lower mandible present, whichever was higher. Estimates of prey size were made for some species using regression equations from measurements of uneroded beaks and otoliths. Regression equations came from published sources, personal communications, or were calculated directly from measurements of otoliths taken from known-length fish. Equations for some species were not available and equations from similar-sized and related taxa were used instead.

Crustaceans were identified by comparison of identifiable remains with reference material. Soft-shelled remains were usually floated in a Petri dish and separated, and individual animals identified and counted. It was difficult to accurately determine the total number of lobster krill (*Munida gregaria*) and salps (*Pyrosoma atlanticum*) in samples as remains were frequently found as a compact mass, preventing identification of individuals. As a result, the reported number of individuals for both these species is likely to be an underestimate. Remains of pinnipeds (i.e. fur, bone fragments, skin, nails) and seabirds (i.e. bones, feathers, feet) in samples were used to identify species. The presence of either sea bird or pinniped remains in a sample was considered as a single individual.

All remains were used to calculate the total number of prey items and overall percentage frequencies between prey groups (i.e. fish, cephalopods, crustaceans, salps, birds, seals) but only those remains identified to species or family level were used in estimating percentage frequencies within each group. Scats and regurgitates were combined to estimate total numbers and percentage frequencies of each species within each group.

The Mantel test (Mantel 1967), a multivariate, non-parametric test, was used to investigate differences in prey composition between scat and regurgitate samples and to examine possible seasonal (e.g. winter/ summer) and year effects. The programme RT (Manly 1996) was used for calculations.

## 4.4 RESULTS

Scats *(n* = 142) and regurgitations *(n* = 64) were collected. Most (83%) samples were collected on Enderby Island, with the remainder from Adams, Dundas, and Figure of Eight Islands (Figure 4.1; Table 4.1). With the exception of 26 scats and 11 regurgitations collected on Enderby Island in August 1996, all samples were collected between December and February in 1994, 1995 or 1996 (Table 4.1). Only one sample contained no identifiable remains.

**Table 4.1** Collection of samples for diet analysis of New Zealand sea lion in the Auckland Islands

| **Locality** | **Date of collection** | **Samples collected** | **Samples with Cephalopod remains** | | **Samples with fish remains** | |
|---|---|---|---|---|---|---|
| | | | *(n)* | (%) | *(n)* | (%) |
| Enderby Island | | | | | | |
| Sandy Bay | Dec. 1994 | 8 scats | 4 | 50 | 8 | 100 |
| | | 2 regurgitates | 1 | 50 | 1 | 50 |
| | Jan. 1995 | 2 scats | 2 | 100 | 1 | 50 |
| | | 5 regurgitates | 5 | 100 | 4 | 80 |
| | Feb. 1995 | 16 scats | 2 | 13 | 16 | 100 |
| | | 16 regurgitates | 11 | 69 | 5 | 31 |
| | Jan. 1996 | 20 scats | 7 | 35 | 16 | 85 |
| | | 7 regurgitates | 5 | 71 | 4 | 57 |
| | Feb. 1996 | 10 scats | 1 | 10 | 10 | 100 |
| | | 15 regurgitates | 11 | 73 | 8 | 53 |
| East Bay | Dec. 1994 | 2 scats | 1 | 50 | 2 | 100 |
| | | 1 regurgitates | 1 | 100 | | |
| Derry Castle Reef | Dec. 1994 | 3 scats | 1 | 33 | 1 | 33 |
| | Feb. 1995 | 1 regurgitates | 1 | 100 | | |
| | Jan. 1996 | 1 scat | 1 | 100 | 1 | 100 |
| Pebble Point | Dec. 1994 | 3 scats | 2 | 67 | 3 | 100 |
| | | 1 regurgitates | 1 | 100 | | |
| Enderby Island | Aug. 1996 | 26 scats | 13 | 50 | 23 | 92 |
| | | 11 regurgitates | 11 | 100 | 2 | 18 |
| | Feb. 1997 | 34 scats | 11 | 32 | 34 | 100 |
| | | 5 regurgitates | 5 | 100 | 5 | 100 |
| Other Islands | | | | | | |
| Adams Island | Dec. 1994 | 3 scats | | | 1 | 33 |
| | Jan. 1995 | 3 scats | 1 | 33 | | |
| | Feb. 1995 | 1 scat | | | | |
| Dundas Island | Jan. 1996 | 5 scats | 1 | 20 | 5 | 100 |
| Figure of Eight Island | Feb. 1995 | 5 scats | | | 0 | 0 |

In total, 3523 prey items were identified to group level (i.e. fish, cephalopod, crustacea) with 86% identified to genus level or higher. Table 4.2 shows the percentage frequency of occurrence in samples and percentage of total prey items by group and by sample type. Cephalopods were found in 48% of all samples but were more common in regurgitates than in scats, while fish were found in 73% of all samples and were more common in scats than regurgitates. There was a significant difference in the composition of scat and regurgitate samples (Mantel test; $P < 0.01$), with scats having a higher number of fish remains and regurgitates having a higher number of cephalopod remains. Fish comprised 59%, cephalopods 21%, and crustacea 15% of the total numerical abundance of prey items. Salps were found in 19% of all samples but represented only 4% of numerical abundance.

**Table 4.2** Percentages for frequency of occurrence and for number of prey taxa in samples from New Zealand sea lions

| Taxa | Total | Scats | Regurgitates |
|---|---|---|---|
| Frequency of occurrence (%) | | | |
| Cephalopoda | 48 | 30 | 77 |
| Crustacea | 16 | 15 | 17 |
| Fish | 73 | 70 | 47 |
| Salp | 19 | 21 | 14 |
| Bird | 2 | 3 | 2 |
| Seal | 4 | 1 | 9 |
| TOTAL | $n = 206$ | $n = 142$ | $n = 64$ |
| Number (%) | | | |
| Cephalopoda | 22 | 5 | 71 |
| Crustacea | 15 | 18 | 6 |
| Fish | 59 | 73 | 20 |
| Salp | 3 | 4 | 2 |
| Bird | <1 | <1 | <1 |
| Seal | <1 | <1 | 1 |
| TOTAL | $n = 3523$ | $n = 2595$ | $n = 796$ |

In all, 33 taxa were represented in the samples, comprising 19 fish, 5 cephalopod, 5 crustacean, and 4 other taxa. All taxa identified to genus level (or higher) are listed in Table 4.3. The six most abundant prey items accounted for 90% of the total prey. These species were, in decreasing order of abundance: opalfish (*Hemerocoetes species*), octopus (*Enteroctopus zelandicus*), lobster krill, hoki (*Macruronus novaezelandiae*), oblique-banded rattail (*Coelorhynchus aspercephalus*), and salps.

Of all prey species, four (oblique-banded rattail, octopus, arrow squid, and salps) were present in all seven months in which sampling was undertaken. Opalfish and red cod (*Psuedophycis* *bachus*) were found in all but one month, while hoki and warty squid (*Moroteuthis ingens*) were found in all but two. There was no difference detected in diet composition between seasons (Mantel test; $P > 0.18$) or years (Mantel test; $P > 0.35$). Estimated lengths of selected prey items are shown in Table 4.4.

Seal remains in nine samples were identified as New Zealand fur seal. Bird remains were found in five samples but only two of the remains could be identified to species, one as a black-bellied storm petrel (*Fregetta tropica*) and the other as a red-billed gull (*Larus novaehollandiae*).

## 4.5 DISCUSSION

The investigation of the diet from scats and regurgitates is commonly biased (Jobling & Breiby 1986; Dellinger & Trillmich 1988; Pierce & Boyle 1991; Pierce *et al.* 1993). Biases such as the partial or total erosion of otoliths, differential retention rates of hard remains in scats and regurgitates, and sampling biases have been reported (Gales & Cheal 1992; Lalas 1997; Tollit *et al.* 1997). It is well documented (Pierce & Boyle 1991; Gales & Cheal 1992; Lalas 1997) that fish remains are more common in scats and less common in regurgitates, while the opposite is true for cephalopods. This was also found in this study, with a significant difference in prey composition found between scats and regurgitates. In this study, fish comprised the highest proportion of prey items but over 70% of all samples collected were scats. However, both scats and regurgitates have a similar mean number of items per sample (i.e. 10 cephalopods per regurgitate, 13 fish per scat). If sample sizes had been equal, then the relative abundance of fish and cephalopods may have been similar and not highly skewed towards fish, as was found.

It has been shown in some diet studies of captive pinnipeds that cephalopod beaks may accumulate in the stomach over several meals before being regurgitated whereas otoliths tend to be digested and/or passed relatively quickly (Harvey 1989; Tollit *et al.* 1997). Even with equal sample sizes of scats and regurgitates, it is still difficult to quantify the relative importance of prey items as a single regurgitate sample may represent a significantly higher number of meals than a single scat sample. Due to these and other potential biases in using scats and regurgitates to determine diet, results should be viewed as qualitative rather than strictly quantitative. However, useful information can still be collected from scats and regurgitate sampling, which in many cases is the only way to investigate the diet of free-ranging pinnipeds.

**Table 4.3** Prey species from New Zealand sea lion (pooled totals for regurgitates and scats)

| **Group**<br>Prey species | **Common name** | **Frequency of occurrence** | | **Numerical abundance** | | | **Number per sample when present** | |
|---|---|---|---|---|---|---|---|---|
| | | *n* | % | *n* | % of group | % of all prey items | Mean | Range |
| **Fish** | | | | | | | | |
| *Hemerocoetes species* | Opalfish | 40 | 19 | 1116 | 62 | 37 | 28 | 1-167 |
| *Ceolorhynchus aspercephalus* | Oblique-banded Rattail | 33 | 16 | 169 | 9 | 6 | 5 | 1-48 |
| *Macruronus novaezelandiae* | Hoki | 22 | 11 | 343 | 19 | 11 | 16 | 1-44 |
| *Pseudophycis bachus* | Red Cod | 13 | 6 | 33 | 2 | 1 | 3 | 1-6 |
| *Paranotothenia microlepidota* | Small scaled nototheniid | 10 | 5 | 22 | 1 | 1 | 2 | 1-6 |
| *Neophrynichthys latus* | Dark Toadfish | 9 | 4 | 19 | 1 | 1 | 2 | 1-7 |
| *Sprattus antipodum* | Sprat | 8 | 4 | 12 | <1 | 0 | 2 | 1-2 |
| *Trachurus murphyi* | Jack Mackerel | 7 | 3 | 8 | <1 | 0 | 1 | 1-2 |
| *Gadiformes species* | Cods; Hakes; Grenadiers | 5 | 2 | 12 | 1 | 0 | 2 | 1-5 |
| *Micromesistius australis* | Southern Blue Whiting | 5 | 2 | 6 | <1 | 0 | 1 | 1 |
| *Electrona paucirastra* | Lanternfish | 3 | 1 | 3 | <1 | 0 | 1 | 1 |
| *Lampanyctodes hectoris* | Common Lanternfish | 3 | 1 | 3 | <1 | 0 | 1 | 1 |
| *Rajidae species* | Skate | 3 | 1 | 4 | <1 | 0 | 1 | 1 |
| *Elasmobranch species* | Cartilaginous fish | 3 | 1 | 7 | <1 | 0 | 2 | 1 |
| *Austrophycis marginatus* | Dwarf Cod | 2 | 1 | 16 | 1 | 1 | 8 | 1-15 |
| *Argentina elongata* | Silverside | 1 | <1 | 10 | 1 | 0 | 10 | 10 |
| *Thyrsites atun* | Barracouta | 1 | <1 | 5 | <1 | 0 | 5 | 5 |
| *Nototheinid species* | Antarctic Cod | 1 | <1 | 3 | <1 | 0 | 3 | 1 |
| TOTAL | | | | 1791 | 100 | 59 | | |
| **Cephalopods** | | | | | | | | |
| *Enteroctopus zealandicus* | | 51 | 25 | 580 | 89 | 19 | 10 | 1-60 |
| *Nototodarus sloanii* | Arrow squid | 18 | 9 | 38 | 6 | 1 | 2 | 1-7 |
| *Octopus campbelli* | | 9 | 4 | 17 | 3 | 1 | 2 | 1-3 |
| *Moroteuthis ingens* | Warty squid | 7 | 3 | 9 | 1 | 0 | 1 | 1-2 |
| *Todarodes fillippovae* | Antarctic flying squid | 4 | 2 | 5 | 1 | 0 | 1 | 1-2 |
| TOTAL | | | | 649 | 100 | 21 | | |
| **Crustacea** | | | | | | | | |
| *Munida gregaria* | Lobster krill | 13 | 6 | >400[1] | 91 | 13 | 41 | 1->100 |
| *Jacquinotia edwardsii* | Spider crab | 6 | 3 | 32 | 7 | 1 | 9 | 1-20 |
| *Nectocarcinus bennetti* | Swimming crab | 4 | 2 | 4 | 1 | 0 | 2 | 2 |
| *Heterosquilla tricarinata* | Mantis Shrimp | 2 | 1 | 2 | <1 | 0 | 1 | 1 |
| TOTAL | | | | 438 | 100 | 15 | | |
| **Other** | | | | | | | | |
| *Pyrosoma atlanticum* | Salps | 39 | 19 | 118[1] | - | 4 | 34 | 1-50 |
| *Arctocephalus forsteri* | New Zealand fur seal | 9 | 4 | 9 | - | 0 | 1 | 1 |
| | Bird | 5 | 2 | 5 | - | 0 | 1 | 1 |
| | Skate egg case | 5 | 2 | 9 | - | 0 | 2 | 1-3 |
| *Neothyris lenticularis* | Brachiopod | 2 | 1 | 2 | <1 | 0 | 1 | 1 |

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[1] It was not possible to accurately determine the number of individuals in each sample therefore the number in each sample reflects a minimum rather than a true estimate.

**Table 4.4** Estimated length measurements for common prey items of New Zealand sea lions. Item measured: LCL - lower crest length of mandible; LRL - lower rostral length of mandible; OL - otolith length; OW - otolith width. Length esimated: DML - dorsal mantle length; FL - fork length; SL - Standard length; TL - total length

| **Species** | **Item measured** | **Length estimated** | ***n*** | **Estimated length (mm)** | | | **Size taken in commercial fishing operations**[A] **(mm)** |
|---|---|---|---|---|---|---|---|
| | | | | **Mean (s.d.)** | **range** | **Regression reference** | |
| *Enteroctopus zealandicus*[B] | LCL | DML | 388 | 80 (16) | 26 - 126 | Smale *et al* 1993 | - |
| *Nototodarus sloanii* | LRL | DML | 15 | 109 (38) | 38 - 175 | Clarke 1986 | 100 - 340 |
| *Moroteuthis ingens* | LRL | DML | 7 | 69 (44) | 22 - 169 | Jackson 1995 | - |
| *Todarodes fillippovae*[C] | LRL | DML | 5 | 85 (31) | 38 - 121 | Clarke 1986 | - |
| *Hemerocoetes species*[D] | OL | FL | 52 | 145 (65) | 38 - 314 | S.Childerhouse unpubl. data | - |
| *Macruronus novaezelandiae* | OW | SL | 33 | 682 (151) | 38 - 849 | K.Sullivan unpubl. data | 600 - 1100 |
| *Trachurus murphyi*[E] | OL | SL | 3 | 346 (40) | 323 -392 | Fea *et al.* 1999 | 260 - 380 |
| *Electrona paucirastra* | OL | SL | 3 | 30 (2) | 29 - 33 | Fea *et al.* 1999 | - |
| *Lampanyctodes hectoris* | OL | SL | 2 | 50 (7) | 45 - 55 | Fea *et al.* 1999 | - |
| *Ceolorhynchus aspercephalus* | OL | TL | 28 | 168 (76) | 21 - 309 | S.Childerhouse unpubl. data | - |
| *Pseudophycis bachus* | OL | TL | 26 | 162 (71) | 26 - 292 | Fea *et al.* 1999 | 500 - 570 |
| *Neophrynichthys latus* | OL | TL | 11 | 180 (70) | 65 - 275 | S.Childerhouse unpubl. data | - |

[A] Estimates from Annala *et al.* (2000).

[B] Regression equation is derived for *Octopus magnificus.*

[C] Regression equation is derived for *Todarodes sagittatus.*

[D] Regression equation is derived for *Hemerocoetes* spp.

[E] Regression equation is derived for *Trachurus* sp.

It has been shown in some diet studies of captive pinnipeds that cephalopod beaks may accumulate in the stomach over several meals before being regurgitated whereas otoliths tend to be digested and/or passed relatively quickly (Harvey 1989; Tollit *et al.* 1997). Even with equal sample sizes of scats and regurgitates, it is still difficult to quantify the relative importance of prey items as a single regurgitate sample may represent a significantly higher number of meals than a single scat sample. Due to these and other potential biases in using scats and regurgitates to determine diet, results should be viewed as qualitative rather than strictly quantitative. However, useful information can still be collected from scats and regurgitate sampling, which in many cases is the only way to investigate the diet of free-ranging pinnipeds.

New Zealand sea lions in the Auckland Islands showed a reasonable diversity in prey targets, including fish, cephalopods, crustaceans and salps. Numerically, fish were the most common taxa. Overall, prey species include a wide variety of benthic, demersal and pelagic species found from the intertidal zone (i.e. crabs that occur subtidally) through to waters deeper than 300 m (i.e. hoki occur in depths >300 m). This is consistent with the reported diving behaviour, of flat bottomed dives apparently to the benthos, with most dives between 100 m and 180 m in depth (Gales & Mattlin 1997). New Zealand sea lions are commonly seen with worn patches and abrasions around their muzzle and face consistent with a benthic foraging pattern (i.e. rock grubbing). Recent research using satellite transmitters and time-depth recorders indicates that female New Zealand sea lions are foraging over most of the Auckland Islands Shelf to depths of up to of 600 m (Gales & Childerhouse, unpublished data). Video footage from 'crittercams' (video cameras attached to free-ranging animals) has shown New Zealand sea lions feeding both pelagically and benthically (Paine 1998). Females were observed catching octopus, opalfish, and arrow squid and pursuing prey into caves and holes on the sea floor in water over 200 m deep (Gales & Childerhouse, unpublished data). New Zealand sea lions at Otago appear to be foraging primarily on the continental shelf with only one deepwater prey species identified (Lalas 1997), while prey composition at Macquarie Island suggests that they are feeding in waters shallower than 500 m (McMahon *et al.* 1999).

Although there were differences in species composition in diets from the Auckland Islands, Macquarie Island and Otago Peninsula, some consistent patterns are apparent. In all three locations, New Zealand sea lions are generalist feeders utilising a wide variety of prey items, with fish as the most common taxa and both cephalopods and crustacean forming lesser, but still important, parts of the diet. There is, however, very little overlap at the species level, which is likely to be a function of local differences in prey distribution and abundance, as also proposed by McMahon *et al.* (1999). For example, octopus were very common in samples from both Otago and the Auckland Islands although they were of different species (*E. zealandicus* at the Auckland Islands and *Octopus maroum* at Otago). However, some differences are apparent, with New Zealand sea lions at the Auckland Islands taking more deepwater species than at either of the other two locations. Other potential contributing factors to a difference in diet composition between locations includes temporal variation in collection of samples and sex- and age related differences. Both the Otago and Macquarie

Island populations are almost exclusively male and samples collected there probably reflect this. Samples from the Auckland Islands are from locations occupied by both males and females of all ages. If there are sex- and age-related preferences in diet, this may influence the species composition of the samples.

The average size of most prey items was between 80 mm and 168 mm, with the only exceptions being jack mackerel (*Trachurus murphyi*) and hoki, which were substantially larger. This average size range is consistent with a diet targeting small fish (opalfish, rattails and red cod) and cephalopods, with some larger fish being taken. Hoki and red cod grow much larger than the sizes found in this study, suggesting a possible preference at this smaller size range as all age classes are present on the Auckland Islands Shelf (Annala *et al.* 2000). The prey size range found at the Auckland Islands is similar to that reported for New Zealand sea lions at Macquarie Island (McMahon *et al.* 1999) but is considerably smaller than most of the prey items reported from Otago (Lalas 1997). Any difference in prey size, as with composition, will partly reflect differences in local prey availability, which may be the case between Otago and the Auckland Islands.

Prey size was estimated from uneroded otoliths only and therefore reflects the actual size of prey without the potential bias of otolith erosion on size estimation. The use of regression equations from closely related taxa is a source of potential bias in the estimation of prey size even though surrogate taxa are similar to prey species. Consequently, size ranges generated from these surrogates should be viewed cautiously.

No significant difference in diet composition was found between seasons or years although, in some cases, sample sizes were small. However, of the six most numerous prey species, four were recorded in all months sampled and the other two in five of the seven months sampled. This suggests that these prey species comprise a regular and high proportion of the diet within the months sampled. New Zealand sea lions have been reported as having a seasonal preference for arrow squid (Cawthorn *et al.* 1985) but as no samples were collected in this study during the peak of arrow squid abundance on the Auckland Islands shelf, we were unable to confirm this. Lalas (1997) reported a seasonal difference in New Zealand sea lion diet from Otago Peninsula while McMahon *et al.* (1999) found no evidence of seasonality in the diet at Macquarie Island.

It was not possible to quantify any local variation in diet between colonies within the Auckland Islands as most of the samples were collected from Enderby Island and there were insufficient samples from other colonies to make any real comparisons. However, Dundas and Enderby Islands, where over 95% of breeding New Zealand sea lions spend summer, are only 7 km apart and local differences in diet are unlikely over this scale if individuals are foraging widely over the Auckland Islands Shelf (Gales & Childerhouse, unpublished). The only prey species for which there was some evidence of local diet differences was lobster krill, which was found almost exclusively in samples collected from Carnley Harbour, in the southern Auckland Islands. Lobster krill, which is commonly seen in large aggregations in Carnley Harbour, has not been reported from other locations around the Auckland Islands (authors' observations). This may reflect a difference in prey selection by New Zealand sea lions between the northern and southern Auckland Islands based on different prey availability.

New Zealand fur seals were found in nine samples and were identified from fur. Most remains were found in regurgitates and half were identified as having come from pups. New Zealand sea lions have previously been reported as feeding on New Zealand fur seal pups at the Snares Islands (Mattlin 1987) and Otago Peninsula (Bradshaw *et al.* 1998), and also on Antarctic and sub Antarctic fur seals (*Arctocephalus gazella* and *A. tropicalis*) on Macquarie Island (Robinson *et al.* 1999). They have also been seen killing and eating New Zealand sea lion pups on Dundas Island (Wilkinson *et al.* 2000) and southern elephant seal (*Mirounga leonina*) pups at Campbell Island (Dilks & Dunn 1978).

Birds were identified in five samples. Both species identified were small seabirds, which are commonly seen and breed in the Auckland Islands. It was not possible to determine whether the birds were scavenged or were killed by New Zealand sea lions. There are several reports of New Zealand sea lions eating yellow-eyed penguins (*Megadyptes antipodes*) at Campbell Island (Moore & Moffat 1992), Otago Peninsula (Schweigman & Darby 1998), and Enderby Island (Childerhouse, unpublished). Gentoo penguins (*Pygoscelis papua*) are also killed and eaten at Macquarie Island (Csordas 1963; McMahon *et al.* 1999). There are also several reports of penguins and fur seals being taken regularly by individual New Zealand sea lions that repeatedly hunt for them in the same location (Moore & Moffat 1992; Csordas 1963; Robinson *et al.* 1999). Predation of both birds and pinnipeds appears to be limited to sub-adult or adult males. It is unlikely that birds or pinnipeds comprise a significant component of the diet of New Zealand sea lions as they are rarely found in samples, although they may form an important component of the diet of some individuals that appear to target these species at certain times.

The only commercially targeted species in the top six prey items (by numerical abundance) was hoki, which was found in a quarter of the samples and comprised 11% of total prey abundance. Arrow squid occurred in 23% of samples but accounted for only 1% of total prey abundance. Other commercial species found include red cod, jack mackerel, barracouta (*Thysrites atun*), and southern blue whiting (*Micromesistius australis*). All commercial species combined represent 14% of total prey abundance so there appears to be only a small overlap of the prey species of the New Zealand sea lion with commercially targeted species on the Auckland Islands Shelf in the months sampled. However, stomach contents from New Zealand sea lions drowned in fishing operations during March and May 1998 were dominated by jack mackerel and southern blue whiting (Dix, unpublished) so it is possible that seasonally abundant prey, such as arrow squid, may represent a higher proportion of the diet during times when they are more abundant, and sampling at the appropriate time of year would be necessary to quantify this. There is also an overlap in the size ranges of hoki, arrow squid, and jack mackerel taken by New Zealand sea lions and commercial fisheries, although the size of New Zealand sea lion prey is generally at the lower end of the size range caught commercially. Red cod taken by New Zealand sea lions are considerably smaller than those caught commercially. Overall, the overlap in target species between New Zealand sea lions and commercial fisheries indicates that there is some resource competition between the two but, without further detailed studies, it is not possible to determine whether there are any potential impacts on either party.

## 4.6 ACKNOWLEDGEMENTS

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# Chapter 5

# Ageing Live New Zealand Sea Lions Using the First Post-canine Tooth [6]

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# CHAPTER 5: AGEING LIVE NEW ZEALAND SEA LIONS USING THE FIRST POST-CANINE TOOTH

## 5.1 ABSTRACT

Live New Zealand sea lions (*Phocarctos hookeri*) were aged from growth layer groups (GLGs) in the cementum of a lower first post-canine tooth. A single post-canine (PC1) was removed from individuals of known age *(n* = 74) between 1997 and 2001 while under a full anaesthetic. Teeth were decalcified, sectioned on a cryostat, stained and then mounted on glass slides. Age was estimated by counting GLGs in the cementum multiple times. Age estimates were calibrated with known aged individuals and confirmed the annual formation of cementum annuli in PC1 tooth. While there is some variation in assigning exact age to individuals, it was possible to age 94% of teeth to the exact year or to within 1 year of actual age. There was no significant difference in the slope of regression lines associated with actual and estimated age using this technique ($t$-test, $df = 144$, $t = 0.309$, $p > 0.05$). Accuracy in ageing was improved by discarding sets of readings with low precision and re-reading the tooth until a precise set of estimates was made. GLGs in the cementum were more accurate and robust for age estimation than using GLGs in the dentine. This paper describes a reliable method for the preparation and ageing of the first post-canine tooth (PC1) from live New Zealand sea lions.

## 5.2 INTRODUCTION

New Zealand sea lions *Phocarctos hookeri* (also known as Hooker's sea lion) are an endemic pinniped to New Zealand and are currently listed as threatened (Gales 1995; IUCN 2002). The estimated population size is approximately 11,000 -14,000 individuals and appears to be stable (Gales & Fletcher 1999). New Zealand sea lions breed almost exclusively in the New Zealand sub-Antarctic, with the present distribution being significantly reduced by sealing and subsistence harvesting from that of pre-human New Zealand (Childerhouse & Gales 1998 (Chapter 2)). There is little known about the life history parameters specific to this species and most population modelling to date has utilised parameters derived from other species (Gales & Fletcher 1999). Without specific information on New Zealand sea lion parameters it is not known how closely the modelling, and the resulting management actions, correspond to reality. This constitutes a potential risk to the management and long term survival of New Zealand sea lions. One of the first steps in obtaining specific life history information is to be able to accurately determine age.

The ageing of pinnipeds from teeth sections by reading growth layer groups is well established but methods and levels of accuracy vary between species (Scheffer 1950, Laws 1952, Payne 1978, Innes *et al.* 1981, York 1983, Arnbom *et al.* 1992, Boyd & Roberts 1993, Oosthuizen 1997). Growth layer groups (GLGs) are laid down annually or semi-annually in the dentine and cementum of teeth (Perrin & Myrick 1980, McCann 1993). The reliability of these layers in reflecting annual growth has been confirmed by tetracycline labelling in dolphins (Perrin & Myrick 1980) but in few other marine mammals.

This paper outlines a technique for the extraction and reliable ageing of the first post-canine tooth from live female New Zealand sea lions. The aims of this project were to (1) develop a method for the safe collection of teeth from live New Zealand sea lions, (2) determine if the annual formation of annuli in dentine or cementum occurs and (3) to develop a reliable method of ageing. In the context of this thesis, the accurate estimation of age is essential for estimation of age-specific demographics as will be discussed in the following Chapters.

## 5.3 METHODS

Between 1997 and 2001, lactating female New Zealand sea lions were captured as part of a wider study investigating foraging ecology and population biology. All captures took place during January and February on Enderby Island, in the Auckland Islands group (50°S 166°E). There has been an irregular tagging programme on Enderby Island since 1980 with sea lion pups being flipper tagged within a month of birth (Cawthorn 1985). This has provided a pool of known-age individuals to allow calibration and verification of ageing techniques. Tagged individuals were selected for capture to ensure that teeth from a variety of age classes were available for examination. The collection of teeth and handling of sea lions was conducted under a Marine Mammal and Animal Ethics Permit issued by the New Zealand Department of Conservation, with all captures being overseen by veterinarian.

### *5.3.1 Tooth extraction*

The sea lions were physically restrained and anaesthetised using an isoflurane gas anaesthetic machine (described in Gales & Mattlin (1998)). After physical restraint and being mildly sedated from gas anaesthesia, an intravenous injection of 2.5mL midazolam at $5mg/mL^{-1}$ concentration (Hypnoval, Roche Products Ltd., UK ) was given into the lateral gluteal vein. This was used to hasten the onset of induction and allow a reduction in the dosage of isoflurane. Once anaesthetised, sea lions were strapped to a custom made restraint frame to prevent movement if they awakened prematurely.

Once individuals were fully anaesthetised, two strips of 2.5-cm-wide webbing were used to manually hold the upper and lower jaws apart to allow removal of the tooth. The lower left first post-canine tooth (PC1) was removed using a dental elevator. If the lower left PC1 was missing then the lower right was taken. The tooth was loosened by using the elevator to work around all sides of the tooth. Once the tooth moved freely it was extracted using dental forceps. Prior to extracting, the tooth was pushed gently into the jaw and then lightly twisted from side to side to ensure that it was free. Teeth were stored in 70% ethanol in individually numbered tubes. Based on veterinary advice, sea lions were not given antibiotics or any other medication to aid recovery or prevent infection.

### *5.3.2 Tooth preparation*

Tooth preparation was based on a techniques adapted from Stewart *et al.* (1996). Teeth were soaked in distilled water for 24 hours to remove residual ethanol so that the stain was evenly taken up in the tooth. They were decalcified in 5% Nitric acid for 24 hours, rinsed in distilled water for 30 minutes, and trimmed with a scalpel to expose the plane of the section. Decalcification was then continued for a further 48-65 hours in a solution of 10 parts Formic acid to 90 parts 10% Formalin, after which the teeth were rinsed for 12 hours in water.

The teeth were then embedded in O.C.T. (Tissue-Tek) embedding compound, frozen and sectioned on a cryostat (Leica Jung Frigocut 2800E) at approximately -20°C, to produce 12µm thick longitudinal sections through the centre of the tooth. Sections were floated on distilled water for several minutes, mounted on polyvinyl alcohol (PVA) coated glass slides and air dried. The slides were stained for 35 minutes in a filtered 0.096% solution of Toluidine blue made with distilled water. They were completely air dried, soaked in xylene and mounted under a glass cover slip using DPX. Between 3 and 5 sections from a single tooth were mounted on the same slide to allow comparisons between sections.

### *5.3.3 Tooth ageing*

Slides were examined using x40-100 magnification under a transmitting light microscope (Nikon model YS2-H, Japan). Age was estimated by counting the total number of GLGs within the cementum with one year assumed as being equivalent to a GLG consisting of one dark and one light band (Perrin & Myrick 1980). New Zealand sea lion pups are born between December and February (Gales & Fletcher 1999) and therefore teeth collected during January and February would have a complete or almost complete annual growth layer from the last year of growth. Similarly, dentinal GLGs were counted in a sub-sample of prepared slides and the status of the pulp cavity (open or closed) was recorded. In addition, the number of annuli in cementum and dentine was compared to the actual age to establish if annuli were formed annually.

Three readings of each tooth were made to improve the accuracy of ageing (Doubleday & Bowen 1980, Bowen *et al.* 1983, Mansfield 1991). Teeth were read by a single person to eliminate the potential bias of inter-reader variability (Anas 1970, McLaren & Smith 1985, Oosthuizen 1997). If two of the three readings were the same, that age was assigned to the tooth. If all the estimates differed, but by no more than one year (e.g. 4, 5, 6), the mean was used. If all estimates differed by more than one year (e.g. 4, 6, 8) sections were re-read and/or re-sectioned (Dickie & Dawson 2003). All teeth were read blind without knowledge of the actual age of the individual.

### *5.3.4 Statistical analysis*

Simple linear regression (Sokal & Rohlf 1981) was used to investigate the relationship between estimated age from teeth reading and known age. Student t-tests were used to examine differences between the slope of the relationship and a slope of 1. Analysis was completed in SPSS version 10 (2004). Statistical significance was at the 0.05 level.

## 5.4 RESULTS

A single post-canine tooth was removed from 74 known-aged individuals between 1997 and 2001 (Appendix 2). The average time to remove a tooth was 2.5 minutes ($n$ = 74, s.d. = 1.3, range = 1.0-5.9). Nineteen individuals were caught between 1 and 3 years after extraction and all had completed healed wounds. There was no indication of any long term detrimental effect on individuals.

The mean cemental GLG counts as a function of actual age from post-canines (CP1) of New Zealand sea lions (Figure 5.1) indicates that while there is a close relationship, it is not perfect, with a slight tendency to overestimate the age of young individuals (e.g. ages <8) and underestimate the age of older animals (e.g. ages >12) (Appendix 2). This is also evident in the residuals (Figure 5.2a). While the slope of the regression for estimated mean age was not significantly different from actual age ($t$-test, $df$ = 144, $t$ = 0.309, $p$ > 0.05), the fitted regression line should be used for age estimation in individuals of unknown age simply because it uses the best information available. Overall, 39% of estimated mean ages agreed with the known-age and a further 55% were aged to within one year of actual age (Figure

5.2b). The remaining estimated mean ages were aged to within two (3%) or three (3%) years of actual age. The close relationship between estimated and actual age supports the conclusion that GLG counts in the cementum from first post-canines is a reliable and accurate method of ageing for New Zealand sea lions.

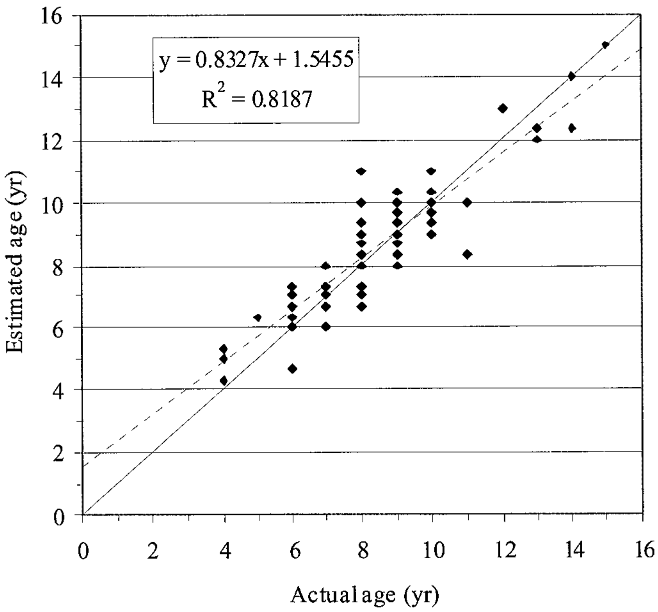

**Figure 5.1** Mean cemental GLG counts as a function of actual age from post-canines (PC1) of New Zealand sea lions (*n* = 74). Solid line shows regression line with slope of 1.0 and intercept of 0 and broken line shows the regression line of estimated age.

The ages of individuals from cementum GLGs ranged from 4 to 15 years old with most (64%) aged between 9 and 11. This partly reflects a higher tagging effort during the early 1990s that lead to a higher proportion of individuals in these age classes being available and also that these age classes appear to comprise the bulk of reproductive females (unpublished data).

GLG in both the dentine and cementum of 31 teeth were examined. Comparisons indicate that the average age at which deposition of layers in the dentine stops is at 10 years of age (s.d. = 1.8, *n* = 12). This coincides with the closure of the pulp cavity in most (83%) individuals but deposition appears to stop in some individuals prior to the closure of the cavity (Figure 5.3). Closure of the pulp cavity can be as early as 8 years old with the maximum age estimated from dentine as 13 years old (compared with an estimate of 20 years old from cementum annuli in the same tooth). The accuracy of age estimation using dentine GLGs appears similar to that achieved from cementum GLGs up to age 8 years old (Figure 5.3).

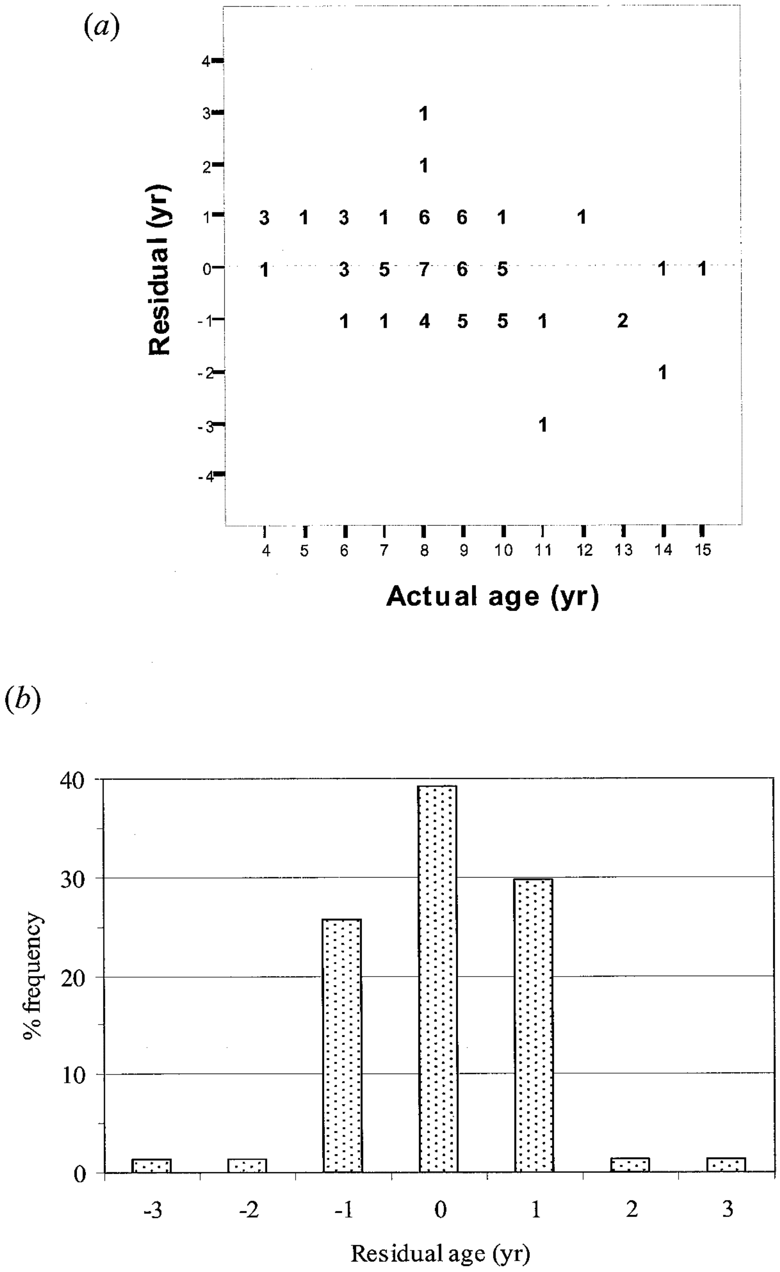

**Figure 5.2** (*a*) Residuals and (*b*) percentage frequency distribution of residuals of mean cementum GLG counts in post canines PC1 of New Zealand sea lions (*n* = 74). Numbers in (*a*) represent the frequency of observations.

Overall accuracy of ageing improved after imprecise sets of readings (e.g. those sets of readings with a range >2 years) were discarded and re-read until they were precise. In practice this meant that two or three sets of readings had to be completed for some teeth. Accuracy in the proportion of teeth aged exactly, or to within one year of known age, improved from 86% to 94% after discarding imprecise sets of readings. For clarity, accuracy is defined as the closeness of a measured or computed value to its true value and precision as the closeness of repeated measurements of the same quantity (Sokal & Rohlf 1981).

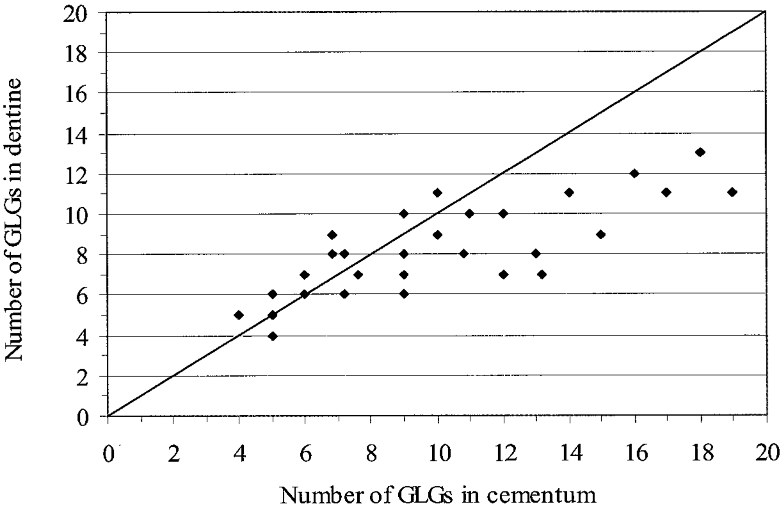

**Figure 5.3** Relationship between number of dentine growth layer groups (GLGs) and number of cementum growth layer groups in post canines of New Zealand sea lions: difference of estimated minus actual age.

## 5.5 DISCUSSION

This paper describes a reliable method for the preparation and ageing of PC1 teeth from live New Zealand sea lions. GLGs can be clearly seen in the cementum after careful sectioning and staining of decalcified teeth. It was possible to verify the deposition rate of cementum layers by examining the number of layers seen against known aged individuals. This confirms that they are deposited annually and are useful indicators of age. While there is some variation in assigning exact age to individuals, it was possible to age 94% of teeth to the exact year or to within 1 year of actual age using GLGs in the cementum. Estimated age did not significantly differ from actual age although there is evidence of bias in residuals. However, this bias is small and does not appear to effect estimated age significantly.

GLGs in the dentine of post-canines were also examined in a small number of individuals using the same sections used for cementum. In general, GLGs in the dentine were clearer and larger than those in the cementum but it was often difficult to determine the first year GLG from background, non GLG layers (an illustration of NZSL tooth section provided in Dickie 1999). Estimated age was generally consistent with actual age at ages less than 8 years old at which point the pulp cavity starts to close and the accuracy of ageing from dentine decreases considerably. Overall, using GLGs in cementum for age estimation is more accurate and robust than using GLGs in the dentine.

There was considerable variation in the location on each tooth section where the reading was made, with no single part of the tooth providing consistently good GLGs. One of the advantages of this method was the mounting of 3-5 sections from the same tooth on a single slide. This allowed for comparisons between sections to be made and the section with the clearest and most complete GLGs could be selected for ageing. In almost all sections the first year GLG could clearly be differentiated from the cementum/dentine junction due to differential staining.

A single reader and multiple readings were used in this study to eliminate the potential bias of inter-reader variability and to improve the accuracy of ageing (Bowen *et al.* 1983, McLaren & Smith 1985, Mansfield 1991, Oosthuizen 1997). Individual teeth were read until there was a high degree of precision between all three estimated ages. However, by discarding imprecise sets of readings and re-reading them, accuracy can be improved. Using this method, there appears to be a good relationship between precision and accuracy and if a set of readings has low precision, than it is likely that they also have low accuracy. This is critical when ageing teeth of unknown age it is only possible to estimate precision and not accuracy.

Canines are generally preferred to post-canines for age determination as they are larger, easier to read and therefore provide more accurate estimates of age in pinnipeds (e.g. Elephant seal (*Mirounga leonine*), Laws (1953); Crabeater seals (*Lobodon carcinophagus*), Laws (1958); Antarctic fur seals (*Arctocephalus gazella*), Arnbom *et al.* 1992; Cape fur seals (*A. pusillus pusillus),* Oosthuizen 1997). Most studies utilising canines have collected teeth from dead individuals and have not had to consider the potential impacts of a tooth removal on the individual. However, the collection of teeth from live individuals must be carefully balanced against factors such as management and conservation requirements, animal welfare, and potential impacts on the individual. The potential effects of removing a tooth from a live pinniped are unknown but could include compromising foraging efficiency or the introduction of infection. To minimise any potential impact, it is preferable to remove a small post-canine rather than a large canine as the impacts are likely to be less.

A general anaesthetic was used for all tooth removals in this study and so no local anaesthetic was required. Recaptures after tooth removal indicated that all individuals had completely healed extraction wounds after 1 year, which is consistent with a 100% healing rate reported from Antarctic fur seals and Southern elephant seals (Arnbom *et al.* 1992).

This study has demonstrated that it is possible to reliably and accurately age New Zealand sea lions from GLGs in the cementum of PC1 teeth. This provides a powerful tool for population studies, which does not rely on the collection of dead or the killing of live individuals to obtain information on age. The technique described in this Chapter is used in the following Chapters to provide accurate ages for demographic and other analysis.

## 5.6 ACKNOWLEDGEMENTS

Thanks to Nick Gales and Stephen Dawson for helpful discussions and advice. Development of the ageing technique would not have been possible without the assistance of Gerald Stokes. Thanks to the Zoology Department of the University of Otago for use of histology equipment and laboratory space. This project would not have been possible without known age individuals in the population and special thanks to Martin Cawthorn for his work tagging sea lions in the 1980s and 1990s.

# Chapter 6

# Inter-annual and Inter-site Variation in Age Distribution of Lactating New Zealand Sea Lions

# CHAPTER 6: INTER-ANNUAL AND INTER-SITE VARIATION IN AGE DISTRIBUTION OF LACTATING NEW ZEALAND SEA LIONS

## 6.1 ABSTRACT

The age distribution of 865 lactating New Zealand sea lions (*Phocarctos hookeri*) was investigated over three years (1999 - 2001) at two breeding colonies, Sandy Bay and Dundas Island, in the Auckland Island group. Most females (81%) were captured, anaesthetised and a single post-canine tooth removed for ageing. The rest were already tagged, of known-age and hence not captured. Lactating females were aged between 3 and 26, a considerably wider range than previously described for this species. Additional resightings of marked females extended the maximum observed age to 28. It is possible that maximum female age could be older if senescence is a strong feature of this species, as only reproductive females were sampled in this study. The age range of lactating New Zealand sea lions is wider than for any other sea lion species. The overall mean age of all lactating females sampled was 11.1 (SE = 0.16) years. The breeding age distribution shows a strong negative skew towards younger age classes (e.g. <10) which is consistent with a slow recruitment into the breeding pool followed by a reasonably consistent level of mortality once all females are recruited. Age distributions peaked at ages 8 and 9, likely indicative of full recruitment into the breeding population by this age. The mean age of breeding females did not change significantly through the breeding season indicating a lack of temporal structure by age. The age structure of Sandy Bay and Dundas Island breeding colonies were significantly different, with Dundas Island having an older mean and median age. Inter-annual differences in age distributions were significant at Sandy Bay, but not at Dundas Island. The two colonies are close together (i.e. less than 10 km apart) and some mixing has been recorded between the colonies. Dundas Island is a much larger colony (1,500 - 2,000 annual pup production) than Sandy Bay (~500 annual pup production). It is therefore possible that as Dundas Island is a larger colony, it is less sensitive to demographic or environmental stochasticity. These results suggest that Dundas Island has a stable population structure whereas Sandy Bay is unstable, or is at least a population with more variable population demographics. To date all demographic information for New Zealand sea lions has been estimated from the observation of individuals at Sandy Bay only. This new information showing significant differences between the two colonies indicate that demographics are unlikely to be the same at the two colonies, and that the extrapolation of demographic information from Sandy Bay to Dundas Island may not be valid. The

implications for the management and conservation of New Zealand sea lions need to be considered in light of this new information.

## 6.2 INTRODUCTION

Demographic models are widely used to study the dynamics of marine mammal populations (Payne 1977; Barlow & Boveng 1991; York 1994; Boyd *et al.* 1995; Arnould *et al.* 2003; Stolen & Barlow 2003; Evans & Hindell 2004; Dabin *et al.* 2004). A fundamental step in many of these models is the characterisation of the age structure of a population. Changes in the dynamics of populations are reflected in age-specific changes in demographics which in turn will be reflected in the age structure (Caughley 1977). Age distributions can be used to assess population stability, geographic or temporal variation, and to investigate demographic parameters such as survival, mortality, life span, and reproduction (Caughley 1977; Barlow & Boveng 199; Holmes & York 2003). An understanding of age structure is therefore essential in understanding population dynamics, especially for a threatened species.

New Zealand sea lion (NZSL) *Phocarctos hookeri* (also known as Hooker's sea lion) is endemic to New Zealand (NZ) and currently listed as threatened (Gales 1995; IUCN 2002). The most recent estimate of population size is 10,550 (CV = 0.04) individuals and annual pup production, on which these estimates are based, is declining significantly (Chilvers *et al.* 2007). Sealing and subsistence harvesting has reduced the breeding distribution of NZSLs to the NZ sub-Antarctic - fewer than ten pups are born annually outside this zone (Childerhouse & Gales 1998 (Chapter 2); Chilvers *et al.* 2007). Most (64%) of annual pup production occurs at Dundas Island, with the second largest breeding colony at Sandy Bay on Enderby Island (19% of annual pup production occurs; Chilvers *et al.* 2007) (See Figure 1.1 in Chapter 1). NZSLs are regularly caught as bycatch in the Southern 6T squid (*Nototodarus sloanii*) trawl fishery. It is estimated that on average more than 70 NZSLs have been killed each year since observations began in 1988 (Ministry of Fisheries (MFish) 2005).

Life history parameters of this species are poorly known. Most population modelling to date has either used life-history parameters derived from other species (Gales & Fletcher 1999) or has attempted to estimate them using a complex Bayesian approach (Breen & Kim 2005). Maximum ages recorded for NZSLs are 23 for males and 21 for females (Cawthorn *et al.* 1985; Dickie 1999), although these observations are based on a small number of individuals and represent estimated rather than known-ages (e.g. no individuals of known-age were used). The minimum age at first reproduction in females is reported to be 4 and age at last reproduction is 21 (Cawthorn 1993; Dickie 1999). The proportion of females that achieve maturity at these ages is not known and, to date, these values have been treated as a "knife edge" function in most models. The only estimate of the proportion of mature females giving birth to a pup is 0.75 (95% CI 66 - 84%) from resightings of branded females (Chilvers 2005). Without robust, empirical estimates of life history parameters it is difficult to assess how closely the modelling, and the resulting management actions, corresponds to reality. In the context of ongoing bycatch, this ignorance constitutes a risk to the appropriate management and long term survival of NZSLs.

From the perspective of population biology, lactating females are the most important component of the population in a polygamous breeding species. For this reason, and because it is logistically feasible to capture and handle them, lactating females are the focus of this study. I investigated the age distribution of lactating NZSLs at two breeding colonies over three years at the Auckland Islands. The aims of the study were to: (i) describe the age distribution of lactating NZSL; (ii) investigate temporal and spatial patterns of age distribution; and, (iii) make a preliminary assessment of the stability of the Auckland Islands NZSL population.

## 6.3 METHODS

### *6.3.1 Study sites*

The Auckland Island group is situated 480 km south of the NZ South Island and comprises one large main island (Auckland Island - 60 km long) and numerous smaller islands including Enderby and Dundas Islands, the sites of field work reported here (Figure 1.1 in Chapter 1). Enderby and Dundas Islands are approximately 10 km apart at the northern end of the Auckland Island group. Dundas Island is a small (c. 400 m long), low-lying island that has the largest breeding colony of the species (~2,000 pups per annum; Chilvers *et al.* 2007). A beach on the south eastern point, about 100 m long and 50 m wide, is the site of pupping and mating. Dundas Island is a challenging research site: it is ~3 km offshore in an exposed location, is surrounded by a reef, and lacks a source of fresh water. Enderby Island (4 km long by 1 km wide) has two breeding colonies, Sandy Bay (~400 pups per annum; Chilvers *et al.* 2007) and South East Point (~70 pups per annum; Chilvers *et al.* 2007). Sandy Bay is a protected sandy beach on the southern coast about 400 m long and 30 m wide where most of the pupping and mating takes place. No work was undertaken at South East Point as part of this study.

### *6.3.2 Sampling*

Capture and sampling of lactating female NZSLs were undertaken in January and February during the austral summer in 1999, 2000, and 2001 at Dundas Island and Sandy Bay. I refer to each austral breeding season, which straddles two calendar years, as the date in which sampling took place (e.g. 1989/99 season as 1999). Before sampling, to minimise disturbance to the colony and individuals, I estimated the minimum sample size required to derive an estimate of survival rate with a Coefficient of Variation of 0.10 for each site. For the purposes of estimating minimum sample size, survival rate was estimated using an expected age distribution and the technique proposed by Chapman & Robson (1960) following the general methodology utilised in Boyd *et al.* (1990). Using this technique, the minimum sample size required to achieve the desired level of precision was estimated at approximately 150 individuals per site per year.

Each year, three sampling periods, each of three to five days duration, were completed at both sites, with approximately 50 individuals sampled during each period. Sampling periods were approximately consistent between years and sites (Table 6.1). Random selection of lactating females was not possible. Some inner parts of the colonies, and therefore individual females, were not accessible for captures due to highly territorial and aggressive males. I attempted to mitigate this potential bias by spreading capture effort evenly throughout the accessible parts colony each day. Effort was spread over three periods during the season which allowed for temporal and spatial mixing of individuals between sampling days. Recent detailed observations of movements of marked females demonstrated the highly mobile nature of females within the breeding colonies over short periods suggesting that females inaccessible for sampling one day, may have been available on subsequent days (Auge 2006).

**Table 6.1** Summary of sampling effort for lactating New Zealand sea lions at two breeding colonies at the Auckland Islands

| Year | Breeding colony | Start date | Finish date | *n* |
|---|---|---|---|---|
| 1999 | Sandy Bay | 19/01/1999 | 12/02/1999 | 146 |
| 2000 | Sandy Bay | 12/01/2000 | 3/02/2000 | 138 |
| 2001 | Sandy Bay | 10/01/2001 | 13/02/2001 | 143 |
| | Total | | | 427 |
| | | | | |
| 1999 | Dundas Island | 24/01/1999 | 10/02/1999 | 140 |
| 2000 | Dundas Island | 26/01/2000 | 10/02/2000 | 149 |
| 2001 | Dundas Island | 27/01/2001 | 11/02/2001 | 149 |
| | Total | | | 438 |

Selection of lactating females was initially made by identifying females nursing or calling pups. If a previously tagged or branded female (and therefore a known-age individual) was selected, it was not physically captured, but its number was recorded and it was included in the sample. Once captured, individuals were checked for milk production by expressing milk to confirm lactation. Females that were selected as part of sampling but were not captured could not be checked for lactation but were confirmed as nursing a pup before being included in the sample. Individuals were only sampled once per season. Sampling refers to both the capture of an individual for tooth ageing and the resighting of a previously aged individual that was not physically captured. It was assumed that sampled individuals reflected random sampling of the lactating female population although, in practice, it is very difficult to achieve random sampling when sampling territorial pinnipeds at breeding colonies (Boyd *et al.* 1995).

### *6.3.3 Capture, tooth extraction and ageing*

NZSLs were captured in specially designed nets (Fuhrman Diversified, Texas, USA), physically restrained, and anaesthetised using an isoflurane gas anaesthetic machine (Gales & Mattlin 1998). After physical restraint, and being mildly sedated from gas anaesthesia, an intravenous injection of 2.5 ml of midazolam at 5 mg.mL$^{-1}$ concentration (Hypnoval, Roche Products Ltd, UK) was administered. This was undertaken to hasten the onset of induction and allow a reduction in the dosage of isoflurane. Once anaesthetised, individuals were strapped to a custom-made restraint frame to prevent movement if they awakened prematurely. All individuals were tagged on both flippers with individually numbered Allflex cattle ear tags in 1999 or Dalton jumbo tags in 2000 and 2001. In addition, a PIT chip (Trovan, UK) was inserted subcutaneously dorsal and anterior to the pelvis. Females caught at Sandy Bay in 2000 were also hot branded on the left side of their body.

Once under full anaesthesia, females were weighed, measured (standard length) and a single post-canine tooth was removed, using a dental elevator. Following sampling, females were carried back into the colony and monitored until they retained consciousness. Pups were captured at the same time as the mother and reunited after sampling. A Veterinarian was present and oversaw all captures. On veterinary advice, NZSLs were not given antibiotics or any other medication to aid recovery or prevent infection. All work was conducted under a Marine Mammal and Animal Ethics Permit issued by the NZ Department of Conservation.

A single post-canine tooth was removed from all individuals of unknown-age and these were aged using readings of growth layer groups (GLGs) in the cementum. All teeth were read "blind" three times by the same person. Precision was improved via adopting the decision rules of Dickie and Dawson (2003), discarding sets of readings with low precision (i.e. range of three readings >2 years) and re-reading the tooth until a precise set of estimates was made. Methods for the removal, preparation and ageing of teeth are fully described in Childerhouse *et al.* (2004). While there was no significant difference between estimated-age from tooth reading and actual age for known-age individuals, the fitted regression line ($y = 0.8327x + 1.5455$; $r^2 = 0.8187$) from this relationship is used to estimate age from GLG counts in individuals of unknown-age as it uses the best information available (Childerhouse *et al.* 2004 (Chapter 5)).

### *6.3.4 Data analysis*

Scatterplots of individual and combined data sets were examined visually for statistical normality and using the D'Agostino-Pearson (1973) tests if required. The overall age distribution was investigated by combining all individuals of known and estimated-age by colony and year. G-tests and ANOVAs were used to investigate differences in age distributions between and within colonies and over years. Regressions and ANOVAs were used to investigate possible trends in age at capture and age at giving birth through the breeding season. Most analysis was completed in SPSS version 10 (2004) but Microsoft Excel version 11 (2003) was also used. A discussion of model assumptions and other statistical issues is included in section 6.4 Results and section 6.5 Discussion. Statistical significance was at the 0.05 level.

## 6.4 RESULTS

### *6.4.1 Sampling and ageing*

A total of 865 lactating females were sampled (e.g. captured or resighted) over the three years (Table 6.1). Most (81%) of the individuals sampled were captured and a tooth removed. Of these captured females, 91% were of unknown-age. The remaining 9% were known-age females (e.g. tagged at birth) whose teeth were used for validation of the age estimation technique. The remaining 19% of sampled individuals were not captured as they were identified from existing tags or brands and therefore of known-age.

Overall, 3435 individual tooth readings were made from 636 individuals of unknown-age with a mean number of 4.5 (SE = 0.03) readings per individual tooth. The large number of readings was necessary as sets of readings with low precision were discarded and a new set of blind readings undertaken. Most (59%) teeth had only one set of readings but some had two (39%)

and three (2%) sets of readings undertaken before a precise set was achieved. All the teeth collected were aged successfully, although in some cases, additional sections and/or re-staining was required to provide an adequate section for reading.

### *6.4.2 Estimated vs. corrected age*

Age estimated from counting GLGs was modified by the equation in Childerhouse *et al.* (2004) to derive a corrected age (Figure 6.1). In essence, this resulted in the estimated-ages of young individuals (e.g. <7 years old) being reduced and old individuals (e.g. >11 years old) being increased. The estimated mean age from GLG readings was slightly lower (mean = 10.75; SE = 0.13) after correction (mean = 11.11; SE = 0.16). While there was no significant difference between means of estimated and corrected ages (ANOVA: $F = 3.15$, $df = 1$, $p = 0.07$), the age ranges and modes were different (e.g. 4 - 23 years and 3 - 26 years; 8 and 9 years for estimated and corrected ages respectively).

### *6.4.3 Known- and estimated-age*

Overall, 20% of all sampled females in this study were of known-age. The age distribution of known-age and estimated-age females was significantly different (G-Test: $G = 26.7$, $df = 23$, $p = 0.04$) with known-age individuals having a much younger mean age (mean = 8.5 vs. 11.8) and smaller age range (6 to 15 years vs. 3 to 26 years) (Figure 6.2). Most (91%) of known-age females were recorded at Sandy Bay. This reflected a much higher tagging effort of pups at Sandy Bay than at Dundas Island in the 1980s and 1990s. Over one third (38%) of all individuals sampled at Sandy Bay were of known-age. Individuals tagged at birth between 1990 and 1993 comprised a high proportion 64% (SE = 0.04) of their respective age classes again because almost all pups born at Sandy Bay during those years were tagged at birth.

### *6.4.4 Capture date*

There was no trend in mean age at capture for either colony throughout the season (ANOVA: Dundas, $F = 0.06$, $df = 1$, $p = 0.80$; ANOVA: Sandy Bay, $F = 0.06$, $df = 1$, $p = 0.80$: (Figure 6.3a, b)). The full breeding season spans December to February but I was unable to sample in December due to the strongly territorial nature of mature males and large numbers of peripheral males. Resighting records ($n = 160$) of females of known- and estimated-age who were observed giving birth during December and January at Sandy Bay between 1999 and 2005 (Figure 6.3c) show no evidence of age varying through the breeding season (ANOVA: age, $F = 0.37$, $df = 1$, $p = 0.56$).

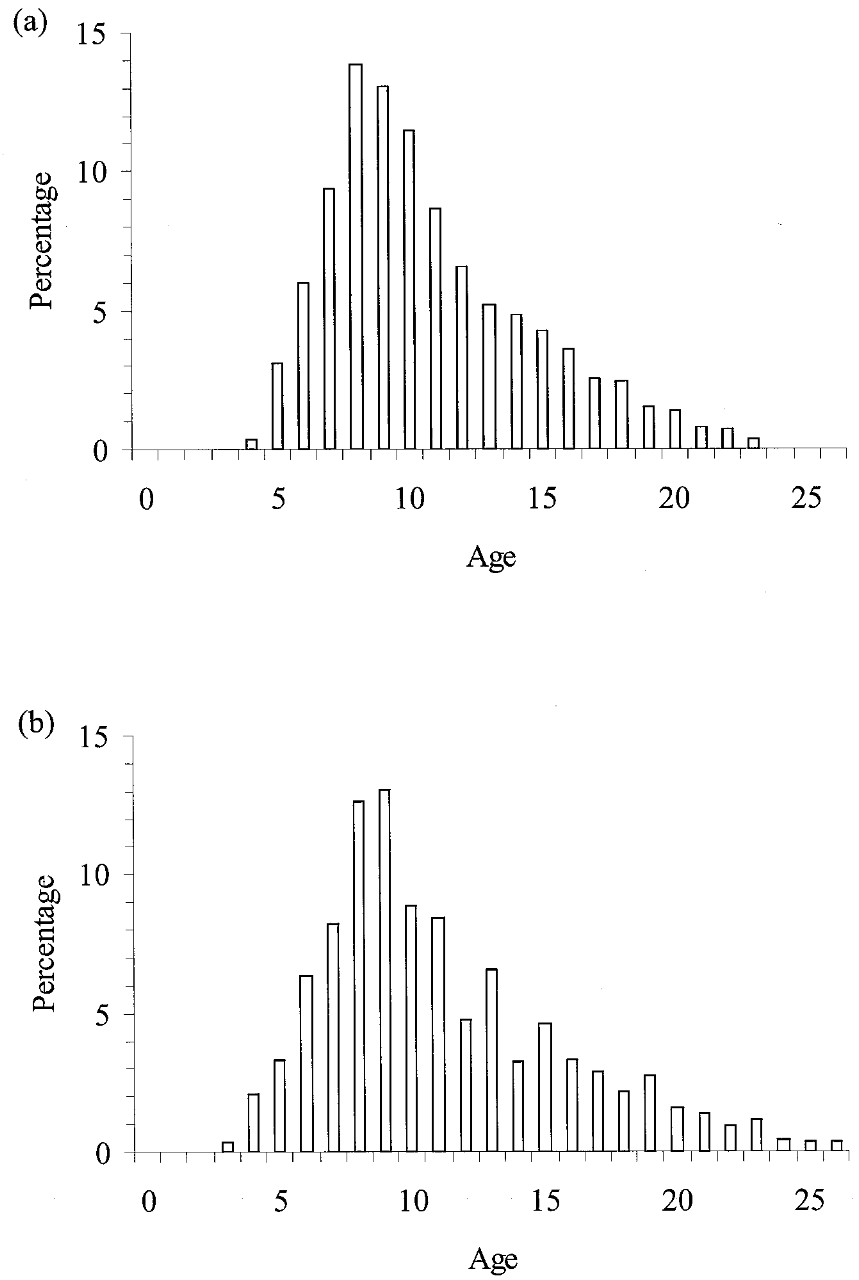

**Figure 6.1** Estimated relative age distribution of lactating New Zealand sea lions *(n* = 865) from (a) reading of growth layer groups in post-canine teeth, and (b) after adjustment of reading via application of Childerhouse *et al.* (2004) regression equation to account for minor (but not significant) ageing errors.

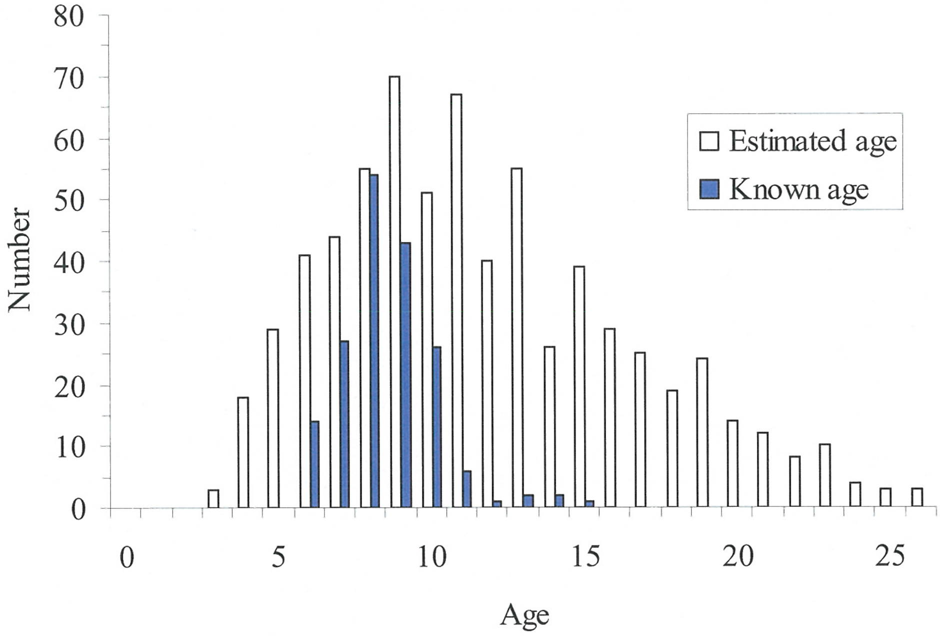

**Figure 6.2** Age distribution of known-age *(n* = 176) and estimated-age *(n* = 689) lactating New Zealand sea lions sampled between 1999 and 2001.

### *6.4.5 Inter-site and inter-annual variation*

There was a significant difference in age distribution between colonies when observations were combined over years within colonies (G-test; $G = 46.74$, $df = 23$, $p < 0.01$), characterised by Dundas Island having an older mean age (e.g. Dundas mean age of 11.7 years; Sandy Bay mean age 10.5 years) and a later peak in age distribution (Table 6.2; Figure 6.4). Age distribution was broadly similar between colonies and over years (Figure 6.5). It was not possible to use a G-test to investigate differences between years for each colony as some age classes had zero observations. Instead, a two-way ANOVA was used that confirmed the significant effect of colony and also identified a significant year effect but no interaction effect (Two-way ANOVA: colony, $F = 14.64$, $df = 1$, $p < 0.001$; year, $F = 4.64$, $df = 2$, $p < 0.01$; colony * year, $F = 0.01$, $df = 2$, $p = 0.39$). Each colony was then investigated separately for year effect and while a significant difference in mean age was found for Sandy Bay (One-way ANOVA: year, $F = 4.78$, $df = 2$, $p < 0.01$) no effect was detected for Dundas Island (One-way ANOVA: year, $F = 1.28$, $df = 2$, $p = 0.28$).

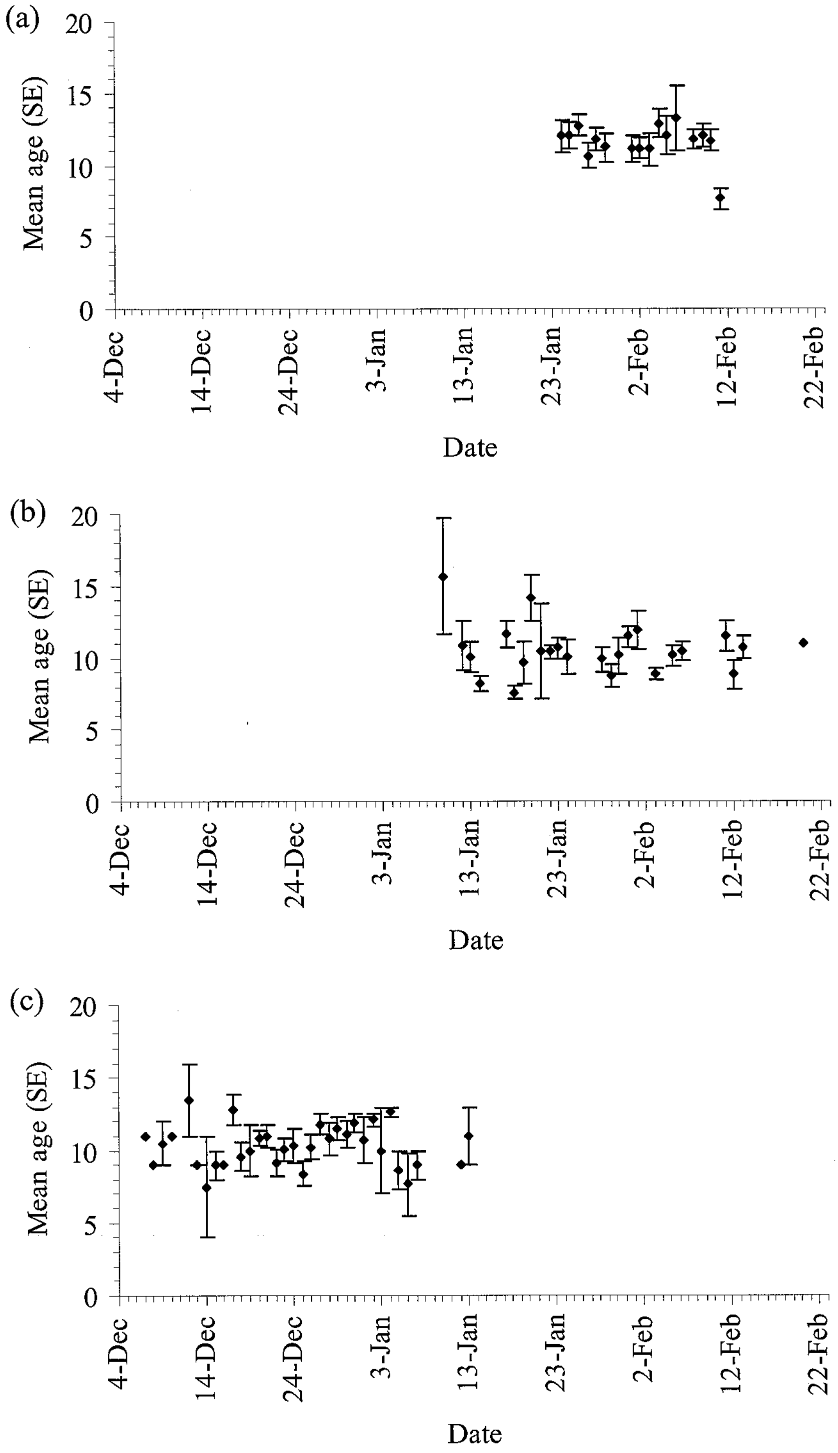

**Figure 6.3** Daily mean age (SE) of sampled females by date of capture for (a) Dundas Island (*n* = 438), (b) Sandy Bay (*n* = 427), and, (c) daily mean age of known- or estimated-age females observed giving birth at Sandy Bay (*n* = 159). Data for (c) are combined from observations between 1998 and 2005.

### 6.4.6 *Inter-site and inter-annual variation*

There was a significant difference in age distribution between colonies when observations were combined over years within colonies (G-test; $G = 46.74$, $df = 23$, $p < 0.01$), characterised by Dundas Island having an older mean age (1.2 years) and a later peak in age distribution (Table 6.2; Figure 6.4). Age distribution was broadly similar between colonies and over years (Figure 6.5). It was not possible to use a G-test to investigate differences between years for each colony as some age classes had zero observations. Instead, a two-way ANOVA was used that confirmed the significant effect of colony and also identified a significant year effect but no interaction effect (Two-way ANOVA: colony, $F = 14.64$, $df = 1$, $p < 0.001$; year, $F = 4.64$, $df = 2$, $p < 0.01$; colony * year, $F = 0.01$, $df = 2$, p = 0.39). Each colony was then investigated separately for year effect and while a significant difference in mean age was found for Sandy Bay (One-way ANOVA: year, $F = 4.78$, $df = 2$, $p < 0.01$) no effect was detected for Dundas Island (One-way ANOVA: year, $F = 1.28$, $df = 2$, $p = 0.28$).

**Table 6.2** Summary statistics for observed age distribution of lactating New Zealand sea lions at two breeding colonies (Dundas Island, Sandy Bay) for three years (1999, 2000, 2001) at the Auckland Islands. SE = standard error.

| Breeding colony | Year | *n* | mean | SE | minimum | mode | median | maximum |
|---|---|---|---|---|---|---|---|---|
| Sandy Bay | 1999 | 146 | 9.72 | 0.31 | 3 | 8 | 9 | 21 |
| Sandy Bay | 2000 | 138 | 10.59 | 0.37 | 3 | 8 | 9 | 24 |
| Sandy Bay | 2001 | 143 | 11.24 | 0.38 | 4 | 9 | 10 | 26 |
| Sandy Bay | 1999-2001 | 427 | 10.51 | 0.20 | 3 | 8 | 9 | 26 |
| | | | | | | | | |
| Dundas Island | 1999 | 140 | 11.19 | 0.40 | 3 | 8 | 10 | 25 |
| Dundas Island | 2000 | 149 | 12.07 | 0.41 | 4 | 9 | 11 | 26 |
| Dundas Island | 2001 | 149 | 11.83 | 0.38 | 4 | 9 | 11 | 23 |
| Dundas Island | 1999-2001 | 438 | 11.70 | 0.23 | 3 | 9 | 11 | 26 |
| | | | | | | | | |
| Combined | 1999-2001 | 865 | 11.11 | 0.16 | 3 | 9 | 10 | 26 |

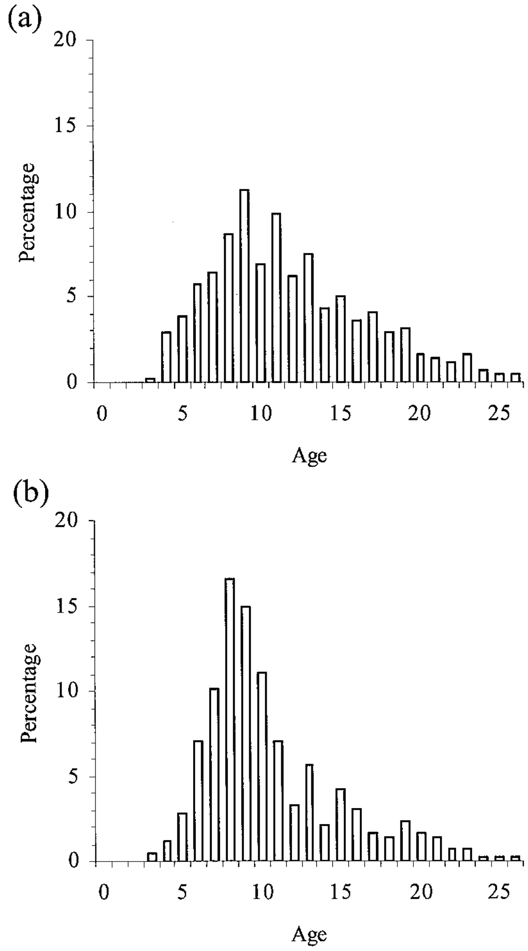

**Figure 6.4** Combined age distribution for 1999 to 2001 of lactating New Zealand sea lions for (a) Dundas Island *(n* = 438) and (b) Sandy Bay *(n* = 427) colonies.

### *6.4.7 Overall age distribution*

The overall mean age of all lactating females sampled was 11.1 (SE = 0.16) years (Table 6.2). The youngest age at first birth was at age 3. The age distribution of all females combined shows an rapid increase in the number of lactating females from age 3 to 8, peaks at age 9, then declines slowly until age 26 (Figure 6.1b). Individuals of age 8 and 9 comprised 26% of the total age distribution and those of between the ages of 7 and 11 comprised 51% of the total age distribution. The remaining ages amounted to 37% older than 11 and 12% younger than 7. The cumulative frequency distribution of sampled females shows a younger age distribution at Sandy Bay than at Dundas Island (Figure 6.6). Fifty three percent of individuals at Sandy Bay are aged 9 years (the peak of the overall age distribution) or less. At Dundas Island this same age group corresponds to only 39%. In addition to the information from sampling of lactating females, there were resightings of two known-age females of age 27 and 28 but these individuals were seen but not included in the sampling as they were not lactating.

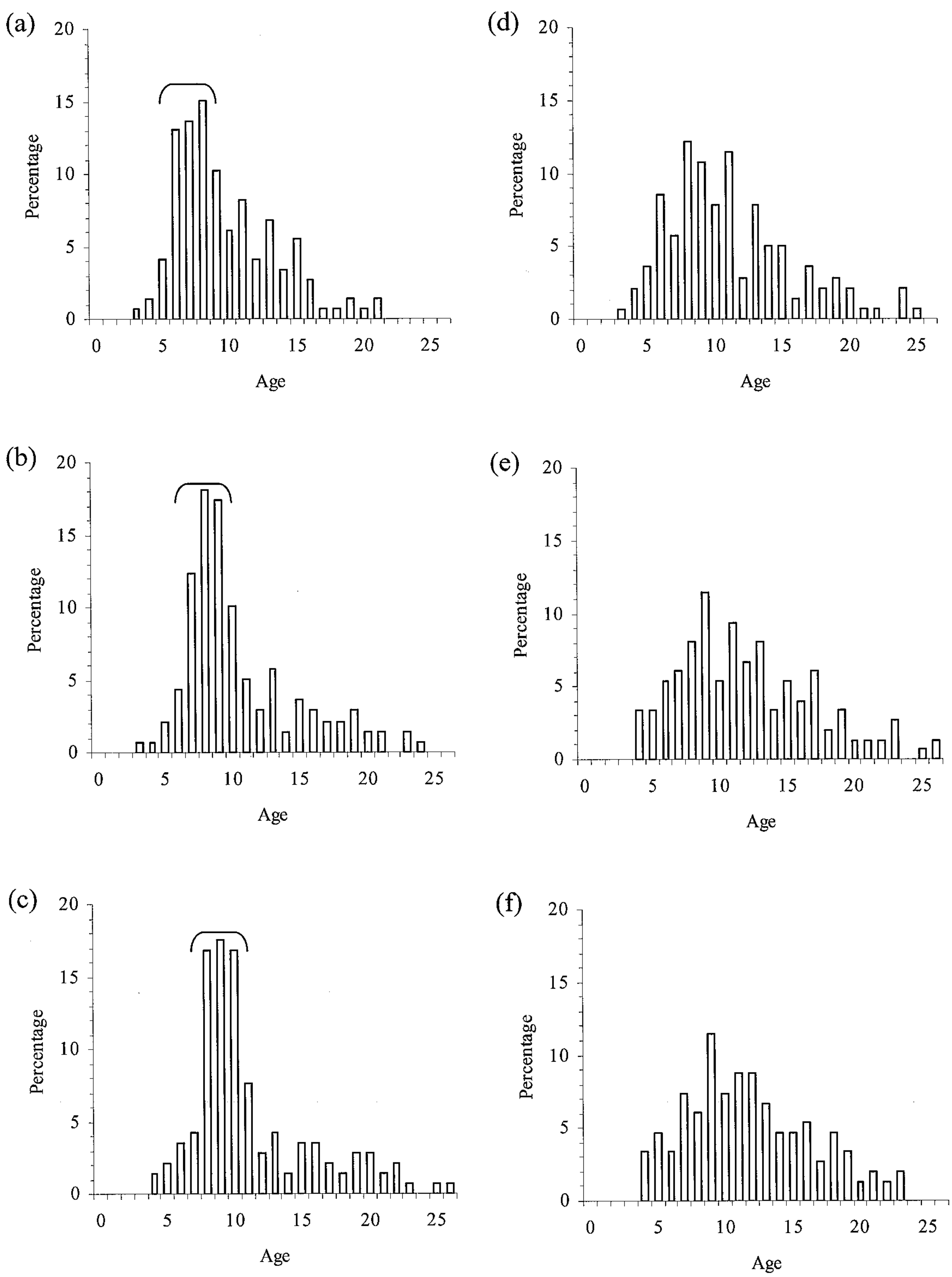

**Figure 6.5** Relative age distributions of lactating female New Zealand sea lions by breeding colony (Sandy Bay, Dundas Island) and year (1999, 2000, 2001) in the Auckland Islands. Figures are for Sandy Bay in (a) 1999 *(n* = 146), (b) 2000 *(n* = 138), and (c) 2001 *(n* = 143) and Dundas Island in (d) 1999 *(n* = 140), (e) 2000 *(n* = 149), and (f) 2001 *(n* = 149) respectively. The three strong cohorts seen at Sandy Bay are designated by the horizontal brackets.

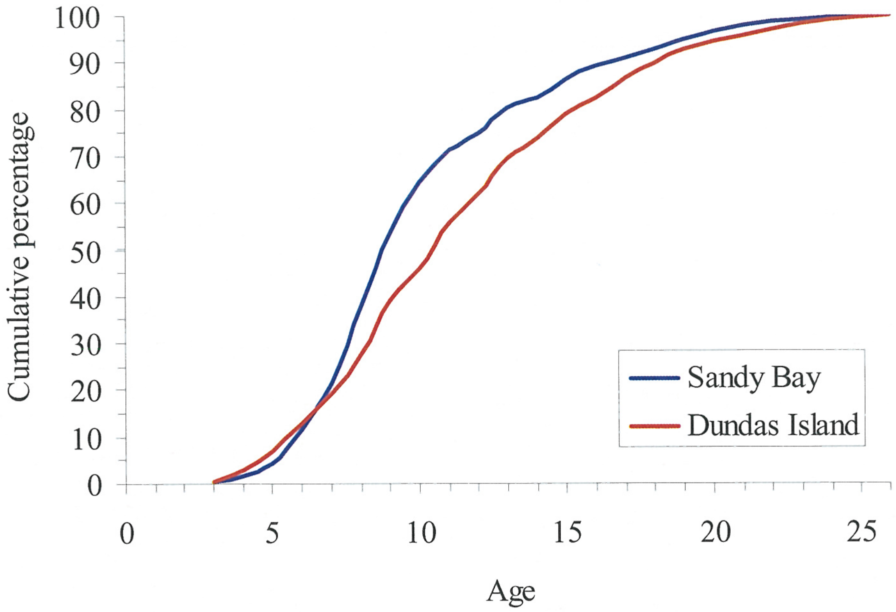

**Figure 6.6** Cumulative age frequency (%) of lactating New Zealand sea lions by breeding colony: Sandy Bay *(n* = 427) and Dundas Island *(n* = 438).

## 6.5 DISCUSSION

### *6.5.1 Overall age distribution*

This is the first description of the age distribution of lactating NZSLs. The overall age distribution combined from both colonies spans the range from 3 to 26 years of age and is considerably wider than previous estimates (i.e. 4 to 21, Dickie 1999). This is the first time that 3 year olds have been reported with pups, indicating that NZSLs can become sexually mature as early as 2 years of age. This work also extends the previous maximum age recorded from a female from 21 to 28 years, with maximum observed age at last reproduction of 26. The estimate of maximum age could be biased low if reproductive senescence is a strong feature of this species. As I sampled only breeding females, senescent females would not have been sampled. However, this potential bias is unlikely to be important for population modelling as it appears that there are few individuals older than 28 and if they are senescent, then their impact on population parameters, such as growth would be negligible.

The age range of lactating NZSLs is larger than that reported from other sea lion species (Table 6.3). While the minimum age at first reproduction is similar to that reported for other sea lion species, at consistently around ages 3 to 5, the maximum breeding age of 26 for NZSLs is considerably older than reported from most other sea lion species. Only Australian sea lions have a similar observed maximum breeding age (24): the other 3 sea lion species are observed to stop breeding before age 20 (Rosas *et al.* 1993; Pitcher & Calkins 1981; Melin 2002; R. McIntosh *unpublished data*) although these estimates may be influenced by non random and incomplete sampling. Although the maximum recorded age (30) for Steller's sea lions is older than that observed for NZSLs, females have a maximum observed breeding age of only 19 (Pitcher & Calkins 1981), although it has been suggested that they may continue to breed into their early 20s (Loughlin 2002). It is possible that the large difference between maximum age and maximum breeding age could indicate reproductive senescence, or be due to low sampling, tagging or resighting effort. As only reproductive females were sampled in this study of age distribution, it is difficult to determine the effect of senescence in NZSLs. However, preliminary analysis of age-specific natality rates indicates that reproductive senescence is likely to be a strong feature of NZSLs (this is discussed in detail in Chapter 6).

The age distribution of breeding females shows a strong negative skew towards younger age classes (i.e. <10). This is consistent with a slow recruitment into the breeding pool followed by a reasonably consistent level of mortality once all females are recruited, although it is not possible to confirm this pattern from the age distribution information alone. A striking feature of the distribution is the peak at 8 and 9 year classes. This suggests full recruitment into the breeding population by about this age, as individuals younger than 8 or 9 were less frequently sampled and therefore likely to be immature. The majority of breeding females are aged between 7 and 11 years of age. All females older than this, despite spanning 15 year classes, contribute only slightly more than a third of total pup production.

Any age distribution is sensitive to fluctuations in demographic parameters. A good example is from the 1998 breeding season when it is estimated that up to 60% of pups died before two months of age from an unusual mortality event (Baker 1999; Gales & Childerhouse 1999). The impact of this event has significant implications for this species. However, it was expected that the full effect of the loss of this cohort would not be seen until 2006 and 2007, when the 1998 cohort are age 8 and 9 respectively. Pup production in these years was expected to be approximately 8% less than normal: a significant decline for an already threatened population. However, surveys in 2006 and 2007 have confirmed that pup production at the Auckland Islands was 27% and 28% less than 1998 respectively (L. Chilvers *pers. comm.*). This is considerably higher than can be explained from the loss of the 1998 cohort alone. These observed declines also include the effect of lesser, but still significant, pup mortality events seen in 2001 and 2002 (Wilkinson *et al.* 2006), and the bycatch of an estimated 898 adult sea lions in the southern squid fishery over the last 11 years (Chilvers *et al.* 2007).

The age distribution of breeding NZSLs is consistent with a generalised otariid and mammalian life history pattern characterised by large size, long lived, delayed sexual maturity, low fecundity, high survival, and slow reproductive rate (Renouf 1991, Boness 2002). These traits define NZSLs as *K*-selected animals, although not as an extreme *K*-selected species (e.g. sperm whales) (Boyce 1984). The evolution of these characteristics is related to their semi-aquatic lifestyle, the high temporal and spatial variability in the distribution of resources in the marine environment (Lunn *et al.* 1994; Boyd *et al.* 1995), and their evolution from a terrestrial carnivore ancestor (Berta & Wyss 1995; Berta & Sumich 1998).

### *6.5.2 Sampling strategy*

It was assumed that the age distributions reflect random sampling of the breeding population although, in practice, it is very difficult to achieve this as there is not equal access to all females at all times (see Boyd *et al.* 1995). A consistent selection methodology was used over years and colonies with sampling effort spread throughout the breeding season to minimise any possible bias. One of the features of the sampling design was the consistent selection criteria applied to both marked (e.g. known-age) and unmarked females in both colonies. This ensured that there was no bias from capture probability, which was especially important at Sandy Bay where a high proportion of marked females were sampled each year. While sample size was the same between colonies, a significantly higher proportion of marked females were sampled at Sandy Bay (mean ~28%) than Dundas Island (mean ~7%) each year. As the selection criterion for known- and unknown-age individuals in the sample was consistent, there is no reason to suspect that this would be a source of bias. Given the robust sampling strategy, the sampling methodology is assumed to be unbiased

The ageing technique used here is validated by blind reading of teeth of known-age individuals. Age estimates are precise and while there is no significant bias in the accuracy of ageing, estimated-ages were modified to account for minor (but not significant) identified biases in ageing to improve accuracy (Childerhouse *et al.* 2004 (Chapter 5)). While there was a significant difference in the age distribution of known- and unknown-age individuals, this reflects varied tagging effort over time (e.g. tagging was undertaken up until 1993 when it was halted and so no individual younger than age 6 was marked and available in the population for sampling) rather than any differential selection. There was no evidence of the mean age changing through the season, as has been reported in some other species which, if present, could have biased the age distributions I report here (Boyd & McCann 1989; Lunn & Boyd 1993).

### *6.5.3 Differences in colonies*

The two colonies had significantly different breeding female age distributions, with Dundas Island having an older mean (1.2 years older) and median (2 years older) than Sandy Bay, although the age range was the same for both colonies. Sandy Bay had a more skewed age distribution with a higher proportion of individuals in younger age classes. The explanation for this difference is not clear but is somewhat surprising given that the colonies are less than 10 km apart. While males are known to move between the colonies regularly, females are highly philopatric and are rarely recorded breeding away from their natal colony (Chilvers *et al.* 2005a; Robertson *et al.* 2006). This would tend to point to an intrinsic factor such as density dependence or some other behavioural mechanism which may be impacting differentially on the two colonies.

Pup production at both colonies has been reasonably constant since at least the 1980s until the 1998 when both colonies started to decline (Childerhouse & Gales 1998 (Chapter 2); Wilkinson *et al.* 2003; Chilvers *et al.* 2007). The rate of decline from 1998 to 2006 at Dundas Island (-4.8% per annum) is significantly higher than at Sandy Bay (-1.2% per annum) for the same period ($t$-test, $t = 0.001$, $df = 18$, $p < 0.01$). It likely that differential rates of decline will be expressed in differences in age distributions as has been demonstrated here, although the exact mechanism for the difference remains unclear. Some plausible explanations for the difference in age distributions between the two colonies include differences in colony sizes leading to different population pressures (e.g. density dependence), differences in individual female foraging strategies, or even differential levels of fisheries bycatch. These issues are further considered below.

The two colonies have considerably different pup production: Dundas Island with approximately 2,000 annually and Sandy Bay with approximately 500 annually (Chilvers *et al.* 2007). Given this difference in size it is possible that density-dependent factors (e.g. availability of pupping space) are less at Sandy Bay than Dundas Island. If this was the case, it could result in Sandy Bay having higher recruitment when conditions were favourable, as is seen with the 1991 to 1993 cohorts. Another possible scenario is that females from Dundas

**Table 6.3** Estimates of reproductive parameters of breeding female sea lions, including age at first reproduction (AFR), and maximum observed female age

| | Breeding age females | | | | | | Max female age | |
|---|---|---|---|---|---|---|---|---|
| Species | AFR | Min | Max | Mean (SE) | Median | Mode | | Reference |
| New Zealand sea lion | | 3 | 26 | 11.1 (0.16) | 8 | 9 | 28 | This study |
| Steller's sea lion | 3-8 | 3 | 19 | | | | 30 | Pitcher & Calkins 1981 |
| | | 3 | 19 | 8.8 (0.44) | 8 | 4, 7 | 29 | Winship *et al.* 2001 |
| Californian sea lion | | 4 | 18 | | | | 18 | S. Melin 2002 |
| | 5-9 | | | | | | | Peterson & Bartholomew 1967;<br>Odell 1975;<br>Atkinson 1997 |
| Australian sea lion | 4.5-6 | 4.5 | 24 | | | | 24 | Higgins 1993;<br>McIntosh *unpublished data* |
| Southern sea lion | 3-4 | 3 | 15 | | | | 15 | Rosas *et al.* 1993; Atkinson 1997 |

[1] This age frequency refers to females with foetus rather than females with a pup or pregnant

Island and Sandy Bay have different foraging strategies and/or feeding grounds and that Sandy Bay females had several above average years of foraging in relation to Dundas Island. This seems unlikely given that foraging studies which suggest lactating females from Sandy Bay forage widely over the Auckland Island's shelf and recent work at Dundas Island has documented similar patterns (Chilvers *et al.* 2005b; L. Chilvers *pers. comm.*).

Sandy Bay also had significant inter-annual variation in age structure, characterised by three strong cohorts seen moving through each year. These strong cohorts were first seen as individuals of age 6 to 8 in 1999, corresponding to individuals born between 1991 and 1993. These three cohorts can be seen increasing in age each year of sampling. By contrast, no such strong cohorts are evident at Dundas Island. These three cohorts appear to be driving the inter-colony differences in age distribution and most likely reflect higher than normal recruitment of these cohorts into the breeding population.

Inter-annual differences in age distributions were not apparent from Dundas Island, which suggests that Dundas Island has a stable population structure. Sandy Bay, on the other hand, shows signs of strong cohorts moving through the age distribution, indicative of an unstable population, or at least a population with more variable population demographics. The three strong cohorts (i.e. females born from 1991 to 1993) seen at Sandy Bay derive from years of slightly lower than average pup production (Wilkinson *et al.* 2003) suggesting that subsequent recruitment and survival may have been higher than normal rather than reflecting an increase in pup production.

There are several potential factors that may be influencing differential age distributions. It has been suggested that Sandy Bay is a younger colony than Dundas Island, however this is not consistent with the reports stretching as far back as the 1940s in which both colonies were known to exist with reasonable numbers of NZSL present (Pollock 1941; Falla 1965; Childerhouse & Gales 1998 (Chapter 2)). Before observed declines post 1998 (Chilvers *et al.* 2007), annual pup production at both colonies had remained reasonably consistent over the last 30 years, although monitoring at Dundas Island has been less regular and robust (Childerhouse & Gales 1998 (Chapter 2); Wilkinson *et al.* 2003). Male harassment resulting in injury and mortality of breeding females has been shown to be a significant issue and the observed rates are higher at Sandy Bay than Dundas Island (Chilvers *et al.* 2005a). Southern sea lion females benefit from group breeding through increased survival of their pups (Campagna *et al.* 1992) and also through reduced male-female agonistic interactions (Cassini

& Fernandez-Juricic 2003), both factors leading to an increased net reproductive performance in larger colonies. Any or several of these factors could influence the differential age distributions between the two colonies but the exact mechanism, or combination of mechanisms, remains unclear.

### *6.5.4 Implications for management*

The number of sea lions killed in the 6T squid fishery is managed via a bycatch limit of sea lions. Total sea lion catch is estimated from observer coverage, which is typically around 25% (MFish 2005). The catch limit itself is estimated using an age-structured Bayesian model (Breen & Kim 2005) which, despite substantial criticism of its structure and performance (Goodman 2004; Slooten 2004), has been adopted as the basis for management by the MFish (MFish 2005). The present version of the model uses a breeding age distribution of females between 4 and 19 with a maximum age of 21. This work has extended both these estimates considerably and any future models should incorporate these new estimates. The impact of these new data will result in reduced estimates of survival, reproductive and population growth rate from those reported from the Breen & Kim model at present, which will therefore lead to reduced levels of sustainable bycatch. Another critical issue is that all of the biological data presently used in the model are derived from observations at Sandy Bay. This study has demonstrated that the age distribution of Sandy Bay is significantly different from Dundas Island. It is therefore probable that female demographics from both sites are also different and the application of rates from one site to the other is inappropriate.

## 6.6 ACKNOWLEDGEMENTS

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# Chapter 7

# Growth and Reproduction of Female New Zealand Sea Lions

# CHAPTER 7: GROWTH AND REPRODUCTION OF FEMALE NEW ZEALAND SEA LIONS

## 7.1 ABSTRACT

A sample of 834 female New Zealand sea lion (*Phocarctos hookeri*) were aged and measured between 1998 and 2001. In addition, the reproductive histories of 505 marked females from the Auckland Islands were recorded from 1998 to 2005. These data sets were used to investigate growth and reproductive rates of female New Zealand sea lions. Length and weight ranged from 134 to 197 cm and 49 to 156 kg respectively. A Gompertz growth model best described growth and predicted that females attained 90% of asymptotic length (161.7 cm) at age 4 and weight (112.0 kg) at age 11. Age-specific growth rates for both length and weight peaked at 10% per annum at age one and steadily declined after that. Overall, relative age-specific growth was 5% and 30% lower for New Zealand sea lions than Steller's sea lion (*Eumetropia jubatus*) for length and weight respectively. There were no significant differences in growth rates among years, nor between the two major breeding colonies in the Auckland Islands. Females reproduced between the ages of 3 and 26, with evidence of reproductive senescence starting at age 23. While females up to age 28 were observed, no females over 26 were recorded as reproductive. Age-specific reproductive rate $p(x)$ increased rapidly between ages 3 and 7, reached a plateau between ages 7 and 23, and then rapidly declined after age 23. Mean observed reproductive rate was $p(x)_{3\text{-}28} = 0.67$ (SE = 0.01). This is the first robust estimate of reproductive rate for this species, and is among the lowest reported for any sea lion species. This new estimate is considerably lower than assumed rates used in recent population modelling for this species, calling into question the current estimation of levels of sustainable bycatch. Low growth and reproductive rates are consistent with a population that is occupying a marginal foraging environment. These factors, along with a recent significant decline in pup production, suggest that current management is insufficient to ensure population stasis, let alone meet the statutory goal of recovery.

## 7.2 INTRODUCTION

An understanding of demographic parameters is essential to the appropriate conservation and management of any species, especially for a threatened species. The New Zealand sea lion (NZSL) (*Phocarctos hookeri*) is a pinniped endemic to New Zealand (NZ) (Gales 1995) and is listed as threatened by the IUCN (IUCN 2002). NZSLs are regularly caught as bycatch in the NZ 6T squid (*Nototodarus sloanii*) trawl fishery. On average over 70 NZSLs, and up to

140, have been estimated as being killed each year since observations began in 1986 (Ministry of Fisheries (MFish) 2005). This interaction is managed by the NZ Government via the application of a NZSL catch-limit or Fishing Related Mortality Limit (FRML) imposed on the commercial fishery. When it is estimated that either the FRML or the 6T squid quota has been reached, the fishery is closed although in recent years the fishery has predominantly been closed upon reaching the FRML (Wilkinson *et al.* 2000; MFish 2005).

Since 2003 FRMLs have been calculated using an age-structured Bayesian model developed specifically for this purpose (Breen & Kim 2005; MFish 2005). One of the constraints of this model is that the values for most demographic parameters are assumed or based on limited data. One of the key parameters, female reproductive rate, is presently estimated from a limited number of observations of marked females from a limited age range (Breen & Kim 2005). While the Bayesian framework allows for flexibility in fitting the model to the limited amount of observed data, it is essential that reliable and robust estimates of reproductive rates are available for use in the model. A problem with the current model is that the estimates of reproductive rate generated by the model (between 0.98 and 1.00; Breen & Kim 2005) are considerably higher than rates reported for any other pinniped, and are biologically unrealistic (York 1994; Wickens & York 1997). Sensitivity analysis has indicated that the model is particularly sensitive to input values for reproductive rate, confirming the need for better input data (Slooten 2004).

In addition to the direct removal of individuals from the population, there is also potential for indirect competition between NZSLs and the commercial fishery via the removal of sea lion prey by the fishery (Gales 1995; Chilvers *et al.* 2005b). This resource competition could reduce growth rates and therefore comparison of growth rates among similar species might indicate the likelihood of competition. Mathematical models have been widely applied to describe growth in pinnipeds (Rosas *et al.* 1993; Boyd *et al.* 1994; Lima & Paez 1995; Kastelein *et al.* 2000; Winship *et al.* 2001; Dickie & Dawson 2003; Dabin *et al.* 2004). While it is generally accepted that simple growth models are unable to adequately describe the growth of pinnipeds over the entire life cycle (McLaren 1993; Aldrich & Lawler 1996; Winship *et al.* 2001), such models do allow for comparison between sexes, and among populations and species (McLaren 1993).

Estimation of reproductive rates for pinnipeds has relied largely on the autopsy of reproductive organs and tooth-ageing of animals collected for research, during subsistence hunts, or killed incidental to fisheries operations (Lander 1981; Pitcher & Calkins 1981; Boyd 1985; York 1994; Bester 1995; Hammill & Gosselin 1995; Lima & Paez 1995; Dickie & Dawson 2003; Dabin *et al.* 2004). Mark-recapture models have also been used to estimate reproductive rates (Boyd *et al.* 1995; Melin 2002). Reproductive rate is a generic term and has been applied in different ways including ovulation, pregnancy, birth, and weaning rate, leading to difficulties when making comparisons among studies. In this study reproductive rate is defined as the proportion of females of age $x$ seen giving birth and/or nursing a pup out of the total number of tagged females of age $x$ seen.

This study was part of a larger project investigating age structure and demographics of NZSLs. The aims of this study were to (i) describe growth patterns, (ii) investigate inter-site and inter-annual variation in growth patterns, and (iii) estimate age-specific reproductive rates of female NZSLs at the Auckland Islands.

## 7.3 METHODS

The general methods are the same as those presented in Chapter 5 and only a brief summary is presented here. Please refer to Chapter 5 for a more detailed description of the general methods.

### *7.3.1 Growth modelling*

*Sampling*

Capture and sampling of lactating female NZSLs was undertaken in January and February during the austral summer in 1998, 1999, 2000, and 2001 at Dundas Island and Sandy Bay. Random selection of lactating females was not possible as not all females were accessible for capture. I attempted to mitigate this potential bias by spreading capture effort evenly throughout the accessible parts of the colony and throughout the season. Females seen nursing or calling pups were selected for capture. Once captured, individuals were checked for milk production by expressing milk to confirm lactation.

*Capture, tooth extraction and ageing*

Female NZSLs were captured, physically restrained and anaesthetised. All individuals were tagged on both flippers with individually numbered Allflex cattle ear tags (1999) or Dalton jumbo tags (2000 - 2001). Females caught at Sandy Bay in 2000 were also hot branded on the left side of their body. Females were weighed and measured (standard length). A single post-canine tooth was removed using a dental elevator. All work was conducted under a Marine Mammal and Animal Ethics Permit issued by the NZ Department of Conservation (DOC).

Extracted teeth were aged via readings of growth layer groups (GLGs) in the cementum (Childerhouse *et al.* 2004 (Chapter 5)). While there was no significant difference between estimated-age from tooth reading and actual age for known-age individuals (i.e. individuals tagged as pups), the fitted regression line ($y = 0.8327x + 1.5455$; $r^2 = 0.82$) from this relationship is used to estimate age from GLG counts as it uses the best information available (Childerhouse *et al.* 2004 (Chapter 5)).

### *Additional data*

The age distribution of lactating females includes only individuals of age 3 and older, as before this age females are reproductively immature and have yet to recruit into the breeding population (Chapter 5). To allow the model to fit to younger age classes it was advantageous to include measurements for these younger females. This information was available from several other sources. NZSLs caught and killed in the 6T squid fishery on the Auckland Islands shelf are routinely returned and autopsied (Wilkinson *et al.* 2003). Measurements from these individuals are reported in Dickie (1999) and Duignan *et al.* (2003a, b). In addition, measurements of 82 neonate pups were made on Sandy Bay breeding colony between 2001 and 2004 (Chilvers *et al.* 2006a). Pup data were not used to fit growth models and were only used as an additional reference point in growth models to provide some information about how well the models fitted the younger age classes. Consistent measurements were taken from bycaught individuals, pups and lactating females.

### *Growth models*

All measurement data were aggregated into a single data set for overall analysis of growth. In all cases, length and weight data were approximately normally distributed (Figure 7.1). For statistical testing, *p*-values of 0.05 or less were considered to represent a significant difference. Gompertz (Ricker 1979), von Bertalanffy (von Bertanlanffy 1938; Ricker 1979), and Richards (Richards 1959; Leberg 1989) growth curves were fitted to age against standard length and weight data in SPSS version 10 (2004) following Winship *et al.* (2001). Parameter estimates are provided for all three models to allow comparisons with other sea lion species. Growth curves for size (S: length and weight) were of the form:

Gompertz: $$S_t = L_\infty \exp^{-e^{-k(t-b)}} \quad (1)$$

von Bertalanffy: $$S_t = L_\infty(1-\exp^{-k(t-b)})^3 \text{ and,} \quad (2)$$

Richards: $$S_t = [L_\infty^{1-m} - (L_\infty^{1-m} - S_0^{1-m})\exp^{[-2t(1+m)]/T}]^{1/(1-m)} \quad (3)$$

where $L_\infty$ is asymptotic length or weight respectively, $k$ is the growth rate constant, $t$ is age in years, $b$ is the time parameter, $m$ is the Richard's shape parameter (i.e. a parameter that specifies the relative position of the asymptote), $S_0$ is size at $t = 0$, and T is the growth period indicative of growth rate. Growth models were fitted using non-linear least squares regression in SPSS. Goodness of fit was evaluated using the coefficient of determination ($r^2$) and the smallest uncertainty in parameter estimates.

### *Inter-annual and inter-site variation in growth*

There is a significant difference in the age distribution of lactating females between Dundas Island and Sandy Bay and also significant inter-annual variation at Sandy Bay (Chapter 5). Inter-annual and inter-site variation was therefore investigated by estimating separate growth models for lactating females by site (Sandy Bay and Dundas Island) and year (1999, 2000, 2001). Differences were investigated by testing for significance between parameters using $Z$ tests (Zar 1998), comparing 95% confidence intervals for each parameter and investigating overlaps among curves. A body mass index (BMI) was also used to examine differences in relative growth between the two sites. BMI is the ratio of weight (kg) to length (cm).

### *Growth rate*

Age-specific growth rate was investigated by estimating the expected size (length and weight) derived from the calculated Gompertz growth model against age. Data on growth rate for NZSL was compared with equivalent data from a Richards growth model for Steller's sea lions (*Eumetropia jubatus*) (Winship *et al.* 2001) with relative age-specific growth rate investigated using the ratio of NZSL growth rate divided by Steller's sea lion growth rate for each given age. The comparison with Steller's sea lion allows for an assessment of the growth rate of NZSL relative to the only other well studied sea lion species and potentially provides an insight into the status of the NZSL population (e.g. is it likely to be occupying a marginal foraging environment?).

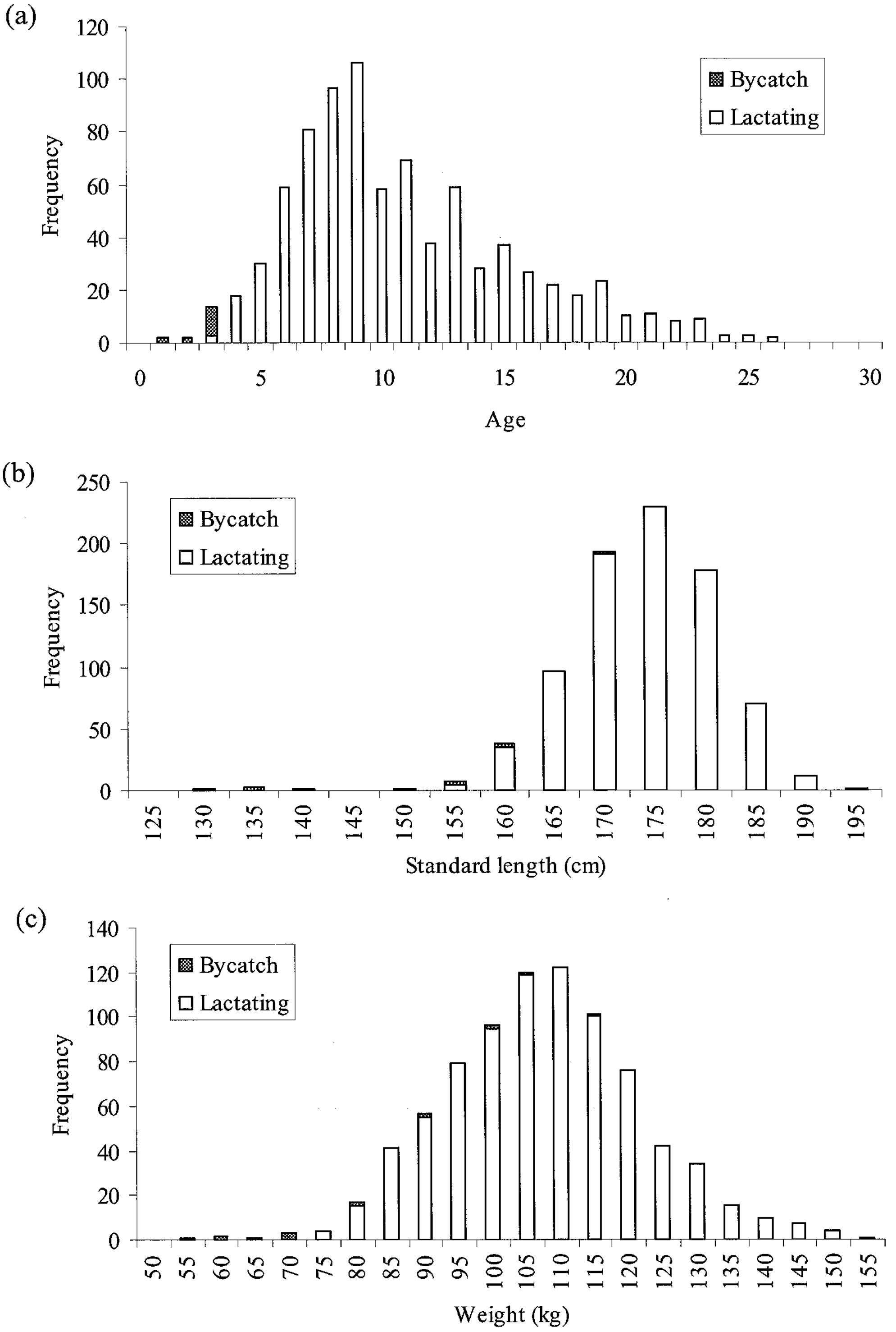

**Figure 7.1** Overall frequency distribution of (a) age (years), (b) length (binned by 5 cm) and (c) weight (binned by 5 kg) of sampled lactating and bycaught female New Zealand sea lions *(n* = 834)

### *7.3.2 Reproduction*

*Reproductive rate p(x)*

In addition to the capture and sampling of individuals for the assessment of age structure, regular searches were made for marked sea lions at the Sandy Bay colony between December and February each year. I recorded tag or brand number and breeding status (i.e. seen giving birth, nursing or seen consistently with a pup more than twice within a season, non-breeding) of each female of known-age seen. These observations spanned the period 1999 to 2005 and were combined to estimate age-specific reproductive rate $p(x)$. I defined $p(x)$ as the proportion of females of age $x$ seen giving birth and/or nursing a pup out of the total number of tagged females of age $x$ seen. This definition is also contingent on females returning to the breeding colonies so they can be resighted. Exact binomial 95% confidence intervals were calculated separately for each $p(x)$.

I fitted the following model to the data using maximum likelihood to generate a quantitative and predictive description of reproductive rate:

$$\hat{p}_1(x) = a\Phi\left(\frac{x-\mu_1}{\sigma_1}\right)\left\{1-\Phi\left(\frac{x-\mu_2}{\sigma_2}\right)\right\} \qquad (4)$$

where $a$ is the maximum reproductive rate across all age classes; $\Phi(.)$ is the cumulative distribution function for the standard normal distribution; $\mu_1$ and $\sigma_1$ are the mean and standard deviation of the age at which females first give birth; $\mu_2$ and $\sigma_2$ are the mean and standard deviation of the age at which females last give birth. Individuals caught in the fishery were not used in the estimation of $p(x)$ as females were caught during early pregnancy and at this stage it is difficult to determine pregnancy status. By definition, the estimation of $p(x)$ is related to the birth of a pup and it was not possible to determine if these females would have given birth if they had not been killed. For clarification, $p(x)$ is the observed value of reproductive rate and $\hat{p}_1(x)$ is the estimated value of reproductive rate from the maximum likelihood fit of equation 4 to the observed data.

Two sets of the data were used in exploring the range of age-specific $p(x)$. Data set 1 used all resights for which breeding status had been confirmed and is thus likely to reflect the maximum values of $p(x)$. Data set 2 was Data set 1 plus individuals that were known to be alive but were not seen in a particular year (e.g. they were seen in $t_i$, not seen in $t_{i+1}$, but seen again in $t_{i+2}$). Given that NZSLs are highly philopatric and there is little breeding away from the breeding colonies (Chilvers *et al.* 2005a), these latter individuals were assumed to be non breeding in the year in which they were not seen. Data set 2 is likely to reflect the minimum plausible value of $p(x)$. Females seen, but whose breeding status was not confirmed, were excluded from both data sets.

## 7.4 RESULTS

### *7.4.1 Growth modelling*

*Sampling*

A total of 819 lactating NZSLs were captured and measured over the four years of sampling (Table 7.1). Sampling during the first year, 1998, was halted prematurely due an unusual mass mortality event (Baker 1998) and so the sample size was considerably less than the latter three years. An additional 15 females aged between ages 1 and 3 caught as fisheries bycatch between 1997 and 2002 were included in the sample to investigate overall growth rate. A total of 834 female NZSLs were used to calculate frequency distributions of age against length and weight (Figure 7.1). The study was undertaken using random sampling of individuals and sampling with replacement between seasons (i.e. no individual was sampled more than once during a season but may have been resampled during a subsequent season). Given the large sample size (n = 819), the very low rate of resampling of the same individual (n = 38 individuals, <5% of total captures) and the random sampling of individuals, pseudo-replication will not be a significant source of bias in this study.

*Overall summary*

The overall mean measurements of all females *(n* = 834) were 175.7 (SE = 0.3) cm and 109.0 (SE = 0.5) kg with length and weight ranging from 134 to 197 cm and from 49 to 156 kg respectively (Figure 7.2). The mean length and weight of lactating females *(n* = 819) were 176.1 (SE = 0.2) cm and 109.6 (SE = 0.5) kg with length and weight ranging from 157 to 197 cm and 75 to 156 kg respectively.

*Overall growth curves*

The three growth models fitted the data similarly well (Figure 7.3; Appendix 3). The $r^2$ values were reasonably low (~0.35) due to the large sample size and the wide variation in size among individuals of the same age. The Gompertz growth model was selected as the best model to describe growth in female NZSLs as it uses fewer parameters than the Richards model (i.e. 3

vs. 4). Also, the Gompertz growth model represents a standard curve that is thought to best describe mammalian growth (Laird 1966; Heide-Jorgensen & Teilmann 1994). All further growth analysis was undertaken using only the Gompertz model.

**Table 7.1** Summary of sampling of (a) lactating New Zealand sea lions (*n* = 819) and (b) female New Zealand sea lions from bycatch (*n* = 15) used for growth measurements

(a)

| Breeding colony | Year | *n* | Min age | Max age |
|---|---|---|---|---|
| Dundas Island | 1998 | 28 | 4 | 16 |
| Dundas Island | 1999 | 134 | 3 | 25 |
| Dundas Island | 2000 | 142 | 4 | 26 |
| Dundas Island | 2001 | 138 | 4 | 23 |
| Total | | 442 | | |
| | | | | |
| Sandy Bay | 1998 | 15 | 6 | 17 |
| Sandy Bay | 1999 | 142 | 3 | 21 |
| Sandy Bay | 2000 | 125 | 3 | 24 |
| Sandy Bay | 2001 | 95 | 4 | 26 |
| Total | | 377 | | |

(b)

| Year | *n* | Min age | Max age |
|---|---|---|---|
| 1997 | 3 | 3 | 3 |
| 1998 | 6 | 1 | 3 |
| 2001 | 4 | 3 | 3 |
| 2002 | 2 | 2 | 3 |
| Total | 15 | | |

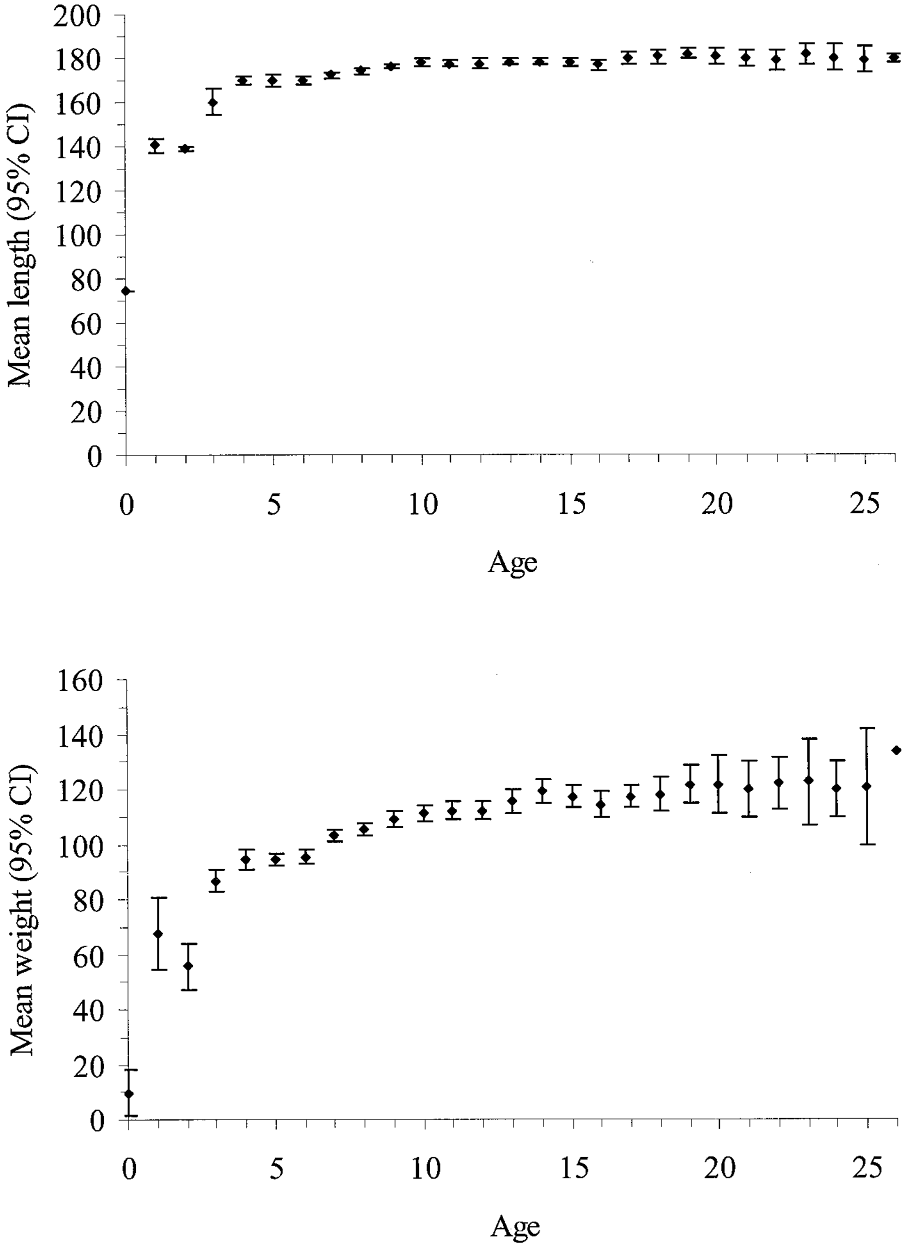

**Figure 7.2** Mean measurements (± 95% confidence intervals) by age for lactating female New Zealand sea lions *(n* = 819), bycaught females *(n* = 15), and female pups at birth *(n* = 82): Panel (a) length (cm) and (b) weight (kg)

Growth was asymptotic in both length and weight (Figure 7.3). Ninety percent of asymptotic growth was achieved at age 4 for length (90% $L_\infty = 161.7$ cm) and age 11 for weight (90% $L_\infty = 112.0$ kg). This difference in age demonstrates that females continue to increase in weight long after achieving asymptotic length. Size-at-age models failed to accurately predict birth length or weight accurately with both being overestimated (Figure 7.3). The allometric relationship between body length and weight was reasonably well described as the power function $Weight\ (kg) = 0.0004\ Length\ (cm)^{2.4398}$ with an $r^2 = 0.60$ (Figure 7.4).

### *Growth rate*

The growth rate for both length and weight peaked at 10% per annum at age one and steadily declined after that (Figure 7.5a). Growth rate declined much faster for length than weight. Annual growth rate was less than 1% by ages 10 and 17 for length and weight respectively. I did not extrapolate the Gompertz model to include the zero age class as no single equation is able to adequately describe the growth of all age classes and it is known that the growth of pups differs from that of older animals (McLaren 1993).

Relative age-specific growth of weight was consistently lower for NZSLs than for Steller's sea lions, whereas relative growth in length varied by age between the two species, with NZSLs having higher relative growth between the ages of 3 and 9. Age-specific growth was lower for NZSLs than Steller's sea lions of equivalent age until reaching asymptotic age (Figure 7.5b). Overall, relative age-specific growth was 5% and 30% lower for length and weight respectively between the two species.

### *Inter-site variation in growth*

Gompertz growth curves were calculated for Sandy Bay and Dundas Islands samples separately (Figure 7.6; Appendix 4). Parameter estimates for length modelling were not significantly different between the two sites ($L_\infty : Z = 2.9, p = 0.84$; $b : Z = 1.6, p = 0.12$; $k : Z = 0.9, p = 0.35$). For weight, however, two of the three parameters were significantly different ($L_\infty : Z = 0.4, p = 0.70$; $b : Z = 2.9, p < 0.001$; $k : Z = 2.4, p = 0.02$). Although there were some significant differences in parameter values for weight, the growth curves for each colony were broadly similar, as indicated by the clear overlap of the 95% confidence intervals (Figure 7.6). However, the ratio of expected size calculated from fitted Gompertz growth models for each colony highlighted some differences in relative growth by age (Figure 7.7a). For length, the ratio is very close to one with some evidence that females are slightly shorter at Sandy Bay than Dundas prior to age 6. More striking is the ratio for weight, where females less than age

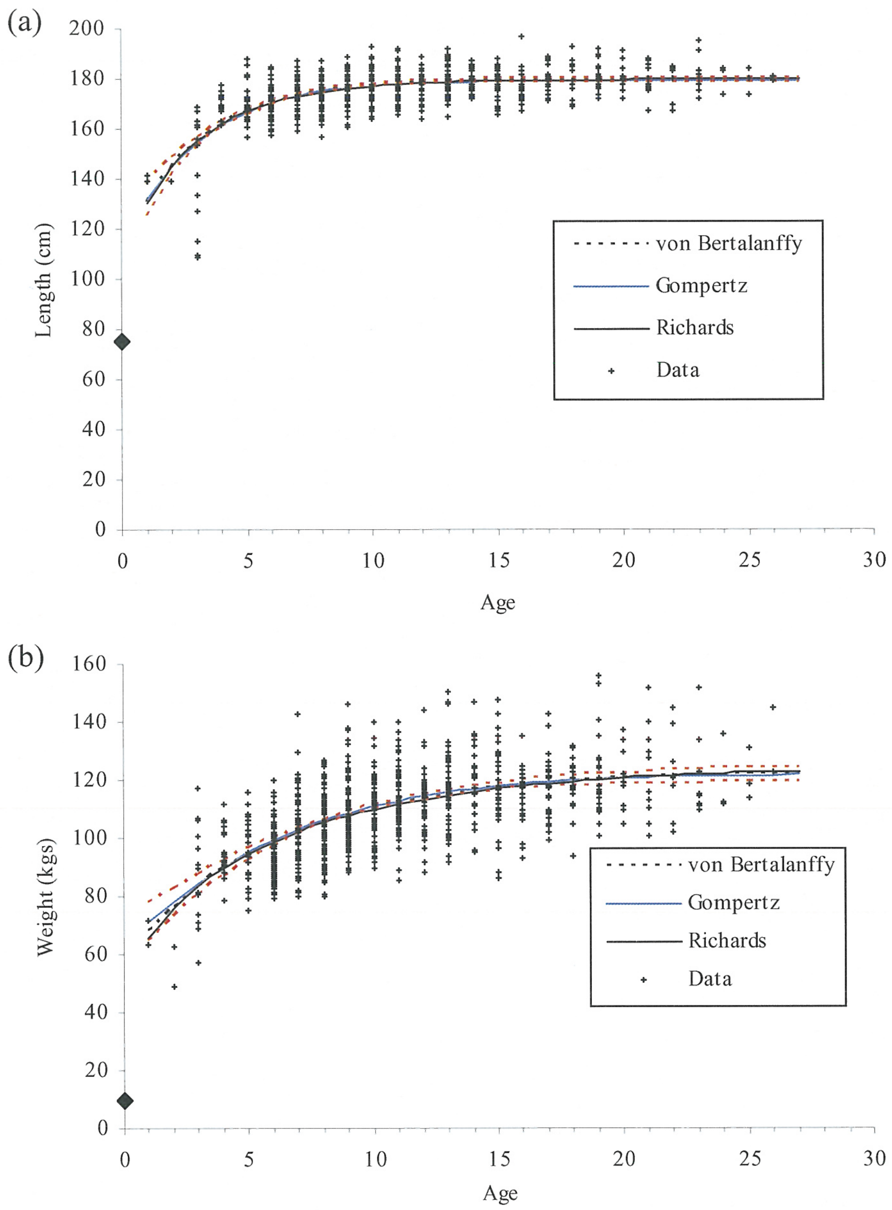

**Figure 7.3** Growth curves for female New Zealand sea lions using three growth models (von Bertalanffy, Gompertz, Richards) for (a) length (cm) and (b) weight (kg). The red dotted lines represent 95% confidence intervals of the Gompertz growth curve and the diamond is mean pup weight at birth.

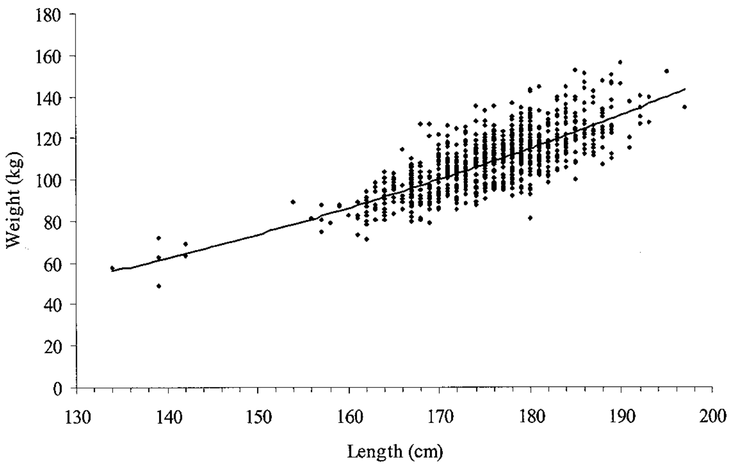

**Figure 7.4** Weight-length relationship for female New Zealand sea lions following the power function *Weight (kg) = 0.0004 Length (cm)* $^{2.4398}$ with an $r^2 = 0.60$ and $p < 0.001$.

six are considerably lighter (-12%) at Sandy Bay than Dundas. This ratio reverses after age six with females being heavier at Sandy Bay than Dundas with the largest difference apparent at age 12 (+5%) before declining to approximately 1:1 at older ages. This difference is also seen in relative BMI for both colonies (Figure 7.7b).

### *Inter-annual variation in growth*

Gompertz growth models were fitted separately to data from the two colonies for each of the three years (Figure 7.8). To simplify the presentation of Figure 7.8, only the 95% confidence intervals for 1999 are presented. Examination of parameter estimates (Appendix 5) and the 95% confidence intervals of growth curves provided no indication of a significant year or colony effect.

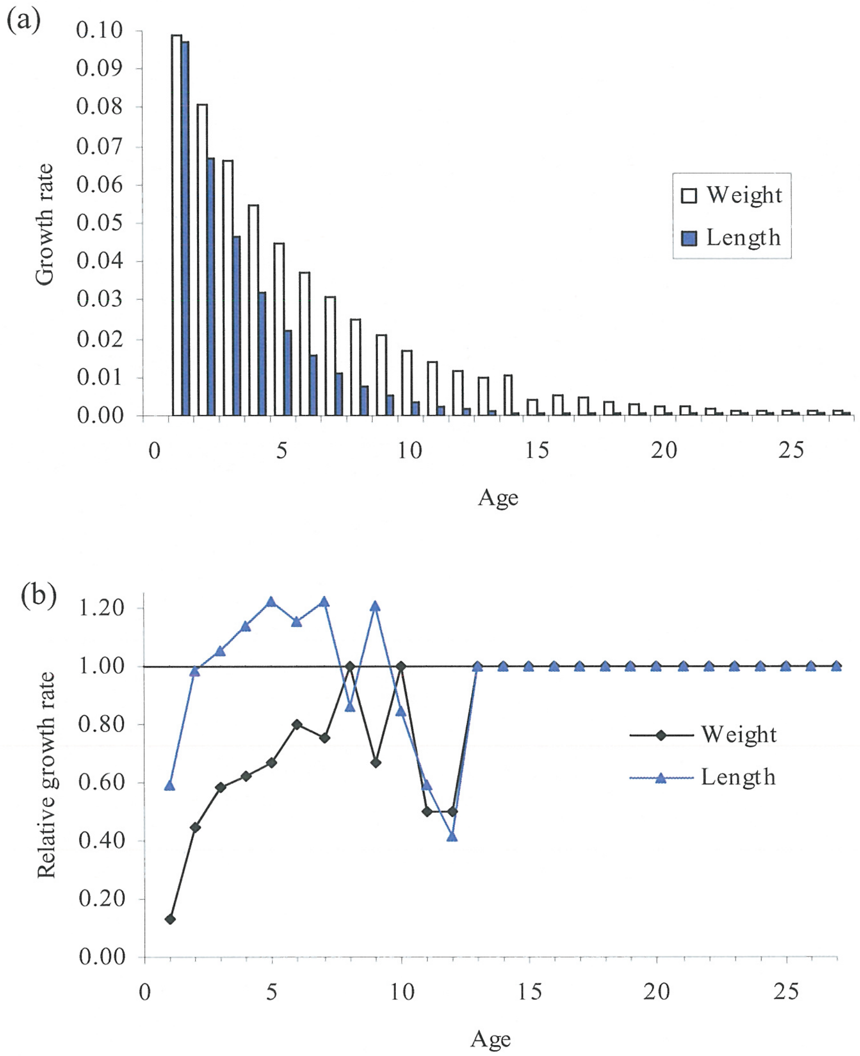

**Figure 7.5** (a) Estimated age-specific growth rate for length (cm) and weight (kg) for female New Zealand sea lions (NZSL) modelled from a Gompertz growth curve, and (b) Relative age-specific growth rates estimated from predicted weight of female NZSLs and Steller's sea lions (Winship *et al.* 2001). Weight is predicted from a Gompertz growth model for NZSL and from a Richards growth model for Steller's sea lions. Relative growth rate (GR) is calculated from predicted GR of NZSL divided by predicted GR of Steller's sea lion for each age

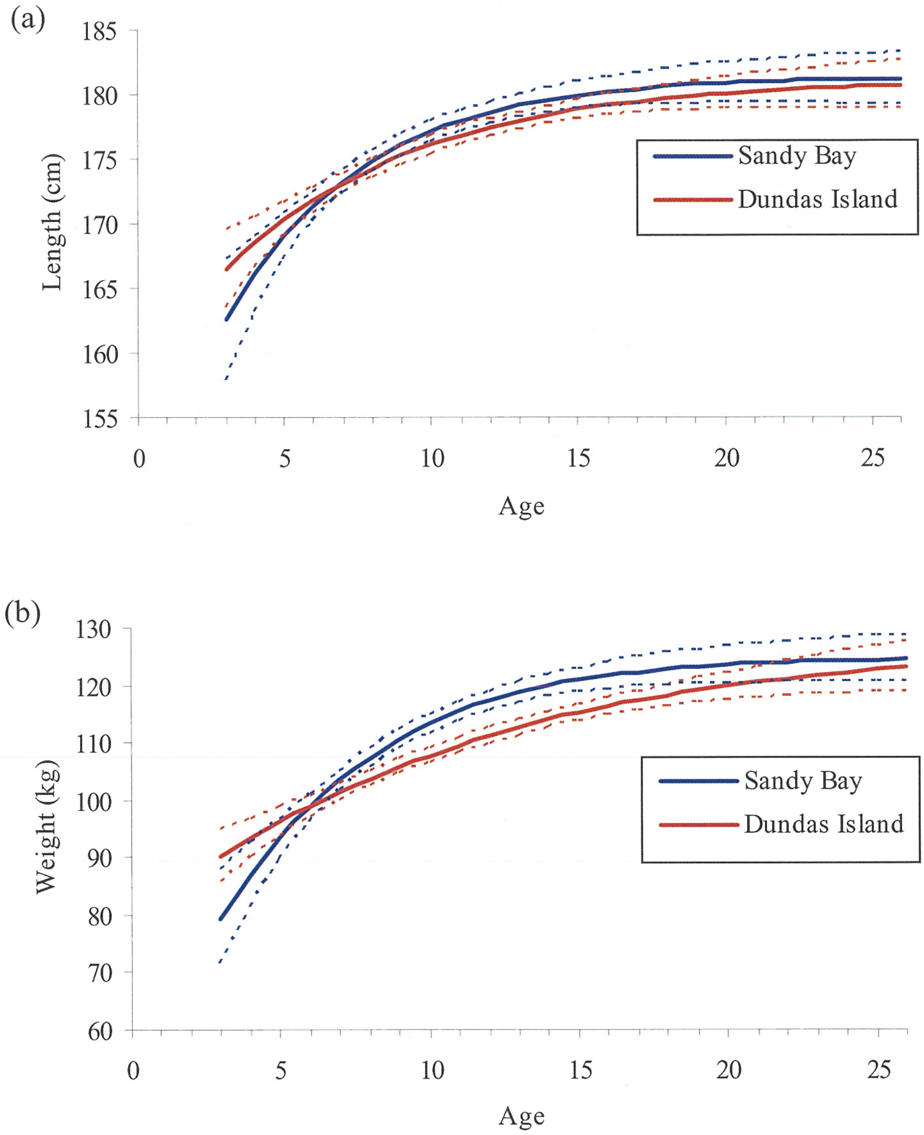

**Figure 7.6** Fitted Gompertz growth models for (a) length and (b) weight for lactating New Zealand sea lions by colony (Sandy Bay and Dundas Island) with 95% confidence intervals indicated by dotted lines

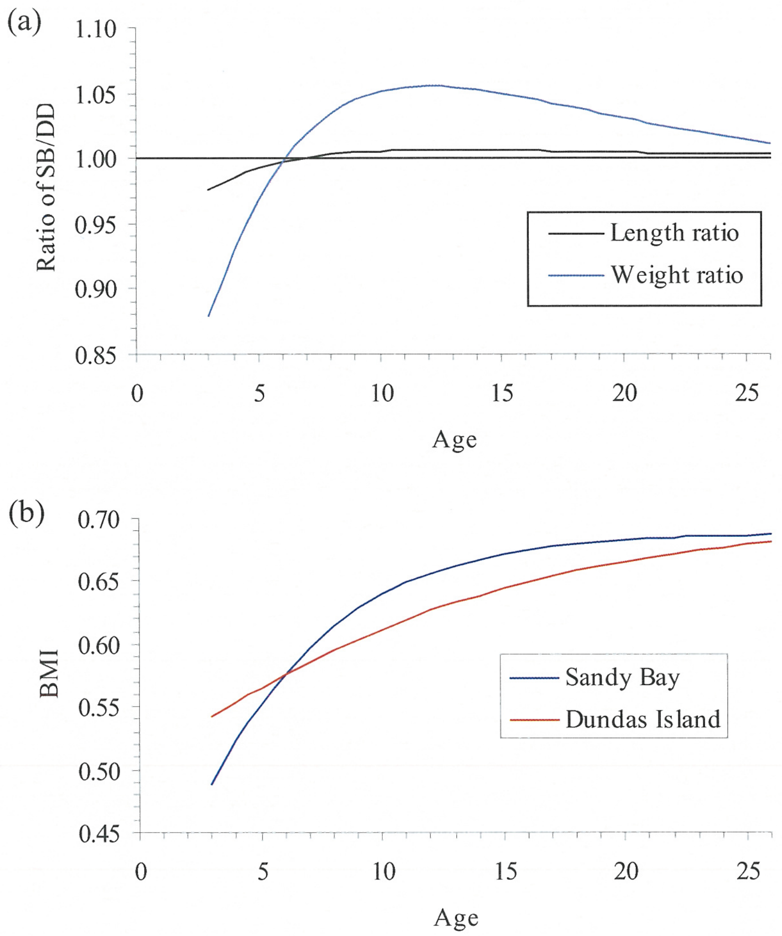

**Figure 7.7** Variation in body size of lactating New Zealand sea lions (NZSLs) from two breeding colonies: Sandy Bay and Dundas Island. Panel: (a) Ratio of expected size by age for all NZSLs *(n* = 834), and (b) Body Mass Index (BMI) by age of lactating NZSLs calculated from fitted Gompertz growth models for Sandy Bay and Dundas Island colonies. Ratio is expected size at Sandy Bay divided by expected size at Dundas Island. BMI is the expected weight (kg) divided by expected length (cm).

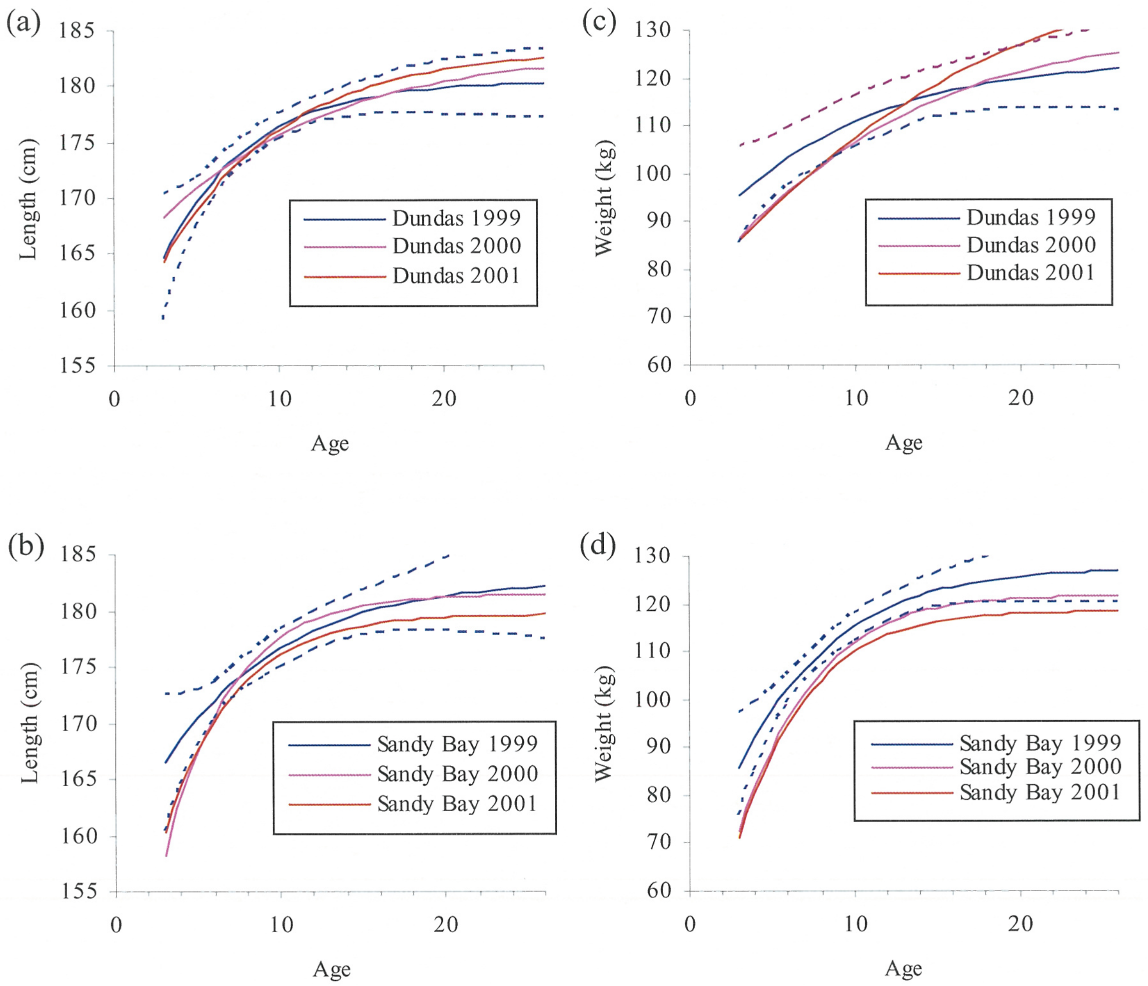

**Figure 7.8** Inter-annual and inter-site variation in Gompertz growth models for lactating New Zealand sea lions at the Auckland Islands. Length (cm) for (a) Dundas Island and (b) Sandy Bay; and weight (kg) for (c) Dundas Island and (d) Sandy Bay. 95% confidence intervals are shown for 1999 only.

### *7.4.2 Reproduction*

*Observed reproductive rate p(x)*

Data set 1 comprised 1677 resights of 505 different females aged between 3 and 28 years old (Figure 7.9). Females were observed with pups between the ages of 3 and 25 but only three individuals older than 25 were resighted and none were observed with a pup. There was considerable variation in age-specific estimates of $p(x)$ (Appendix 6). Given the large variation associated with some of the point estimates, and considerably difference sample sizes for different ages, a weighted mean was used (Seber 1982). The weighted mean $p(x)_{all}$ from Data set 1 for all females aged 3 and over was 0.76 (SE = 0.01) (Figure 7.10a; Table 7.2). The maximum likelihood fit of $\hat{p}_1(x)_{all}$ to Data set 1 showed a plateau between the ages of 7 and 23 years old (Figure 7.10a).

An additional 219 resights of females that were known to be alive but were not resighted in a season were added to Data set 1 and re-analysed as the Data set 2 (Figure 7.10b). The weighted means of $p(x)_{all}$ and $p(x)_{7\text{-}23}$ from Data set 2 were less than the equivalent values from Data set 1 (Figure 7.10b; Table 7.2).

*Modelled reproductive rate* $\hat{p}_1(x)$

Modelled $\hat{p}_1(x)$ fitted the observed data well with high $r^2$ values for both data sets (Figure 7.10; Table 7.2). There was no difference between the weighted means of $p(x)$ and $\hat{p}_1(x)$ for either data set.

## 7.5 DISCUSSION

### *7.5.1 Growth modelling*

*Sampling*

A potential source of bias is that the reproductive females sampled may have a different growth pattern to females that are either not reproductive or have a lower reproductive rate. This seems unlikely as a large sample was taken over four years at two colonies and only those females that did not produce a pup at all over that period would not have been available for sampling. Female Steller's sea lions with a foetus are significantly heavier and longer than females of the same age without a foetus (Winship *et al.* 2001). If this is also true for NZSLs, the growth rates reported in this study may be biased higher than the average growth rate for all female NZSLs. I believe that this bias is likely to be small due to the large sample size and multi-year sampling. The addition of 15 younger individuals that had been caught as bycatch in the trawl fishery provided increased sample sizes allowing a better fit of the growth models to the data for younger ages.

*Growth model assumptions*

Latitudinal data have been widely used in the estimation of growth rates in pinnipeds (Bryden 1972; Boyd *et al.* 1994; Hammill *et al.* 1995; Lima & Paez 1995; McLaren 1993; Rosas *et al.* 1993; Trites & Bigg 1996; Kastelein *et al.* 2000; Winship *et al.* 2001; Dickie & Dawson 2003; Dabin *et al.* 2004). There are many potential sources of bias in the estimation of growth from latitudinal data including (i) precision of assigned age, (ii) variation in birth date, (iii) accuracy of the ageing technique, (iv) unequal body size representation within age classes, (v) unequal representation of ages, (vi) differential mortality related to size, and (vii) differential growth and survival rates related to environmental conditions (Innes *et al.* 1981; Leberg *et al.* 1989; McLaren 1993; Winship *et al.* 2001).

The first three potential sources of bias (i - iii) are related to ageing of individuals. All individuals were sampled at a similar time of year (i.e. January or February for reproductive females; February to May for bycaught females) and ageing of NZSLs from GLGs in the cementum has been shown to have no significant bias (Childerhouse *et al.* 2004 (Chapter 5)). The next two potential sources of bias (iv - v) are related to sampling selectivity within age classes, which should be mitigated by our efforts of spreading sampling effort across colonies, across and within years, and by using a large sample size *(n* = 834 individuals). The number of individuals in each age class was generally large (mean = 32; SE = 1.1) although there were smaller sample sizes for older and younger age class. Leberg *et al.* (1989) noted that biased sampling of a population with respect to age may bias the asymptotic size parameter of growth models but this is also unlikely in this study as there was a good spread of ages with samples available for all age classes.

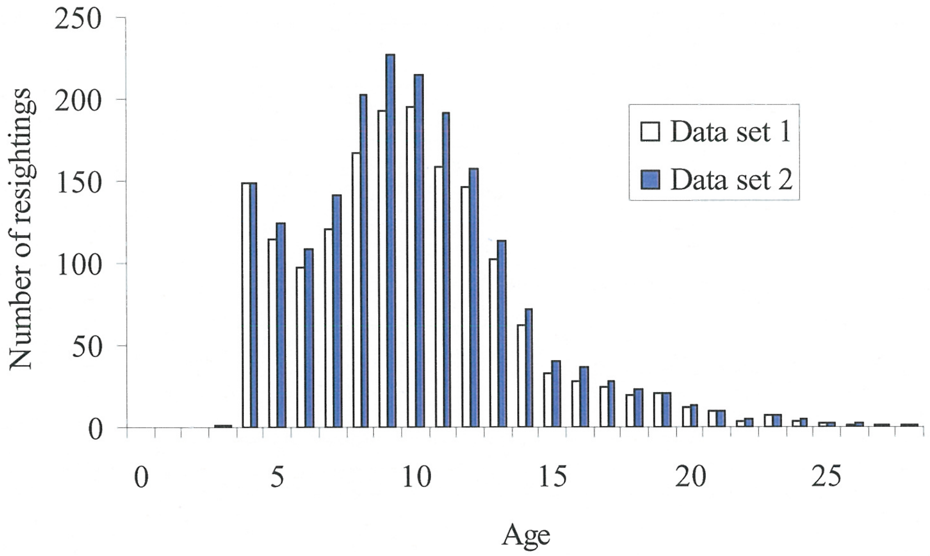

**Figure 7.9** Total number of resightings of known-age female New Zealand sea lions for the Data set 1 *(n* = 1677) and Data set 2 *(n* = 1896).

**Table 7.2** Estimates of weighted means of observed *p(x)* and modelled $\hat{p}_1(x)$ reproductive rates for female New Zealand sea lions at the Auckland Islands using Data set 1 (confirmed reproductive histories of known-age females) and Data set 2 (Data set 1 plus individuals that were not seen but known to be alive). Model parameters are the fit of the $\hat{p}_1(x)$ model to the observed data. See text for notation descriptions.

| | | 3-28 ages | | 7-23 ages | | Model parameters | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | $n$ | $p(x)$ | SE | $p(x)$ | SE | $\varphi$ | $\mu_1$ | $\delta_1$ | $\mu_2$ | $\delta_2$ | $r^2$ |
| *Observed* | | | | | | | | | | | |
| Data set 1 | 1677 | 0.76 | 0.01 | 0.86 | <0.01 | | | | | | |
| Data set 2 | 1896 | 0.67 | 0.01 | 0.75 | <0.01 | | | | | | |
| *Modelled* | | $\hat{p}_1(x)$ | SE | $\hat{p}_1(x)$ | SE | | | | | | |
| Data set 1 | | 0.76 | 0.01 | 0.86 | <0.01 | 1.89 | 5.05 | 1.08 | 25.21 | 1.22 | 0.93 |
| Data set 2 | | 0.67 | 0.01 | 0.75 | <0.01 | 1.12 | 4.97 | 1.11 | 25.20 | 1.00 | 0.85 |

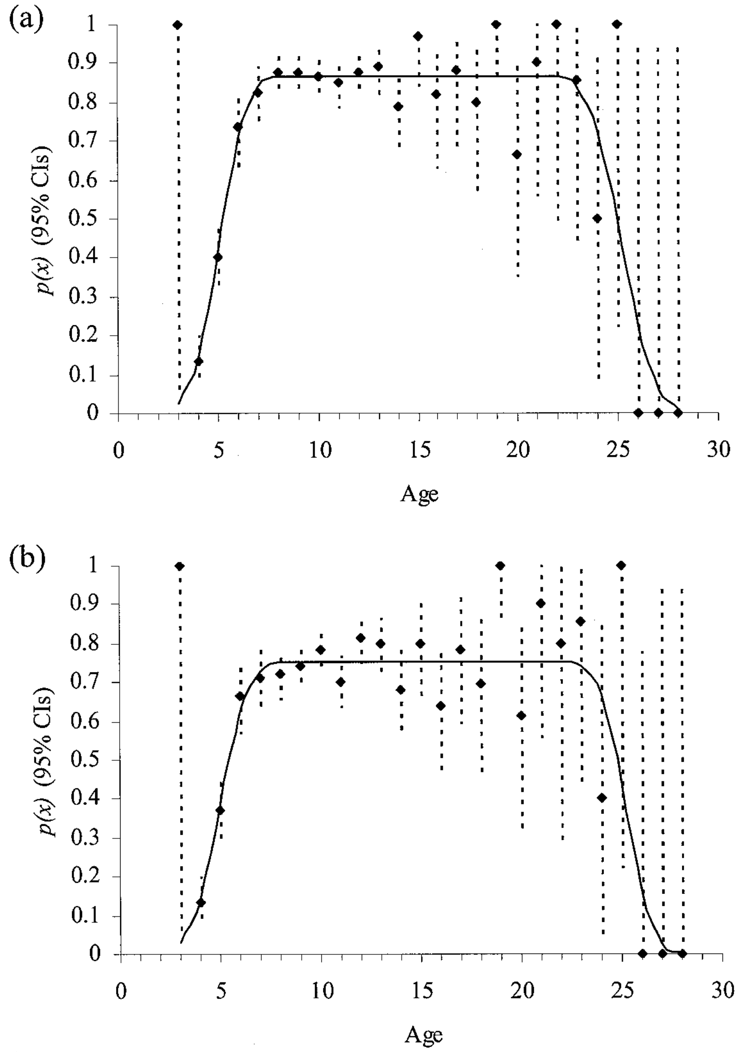

**Figure 7.10** Observed *p(x)* and modelled $\hat{p}_1(x)$ age-specific reproductive rate for female New Zealand sea lions at Sandy Bay, Auckland Islands obtained from tag and brand resightings over 1998 to 2005. Panel: (a) Data set 1 *(n* = 1677) and (b) Data set 2 *(n* = 1896). The diamonds are the observed age-specific reproductive rate *p(x)* and the fitted line is the estimated age-specific reproductive rate $\hat{p}_1(x)$. Dotted lines are exact 95% confidence intervals.

The last two sources of bias (vi - vii) relate to differential survival between different sized individuals and are more difficult to assess. It is quite likely that there is some interaction between size and survival, with the simple example of faster growing juveniles or sub-adults possibly having a higher survival rate than slower growing individuals (Winship *et al.* 2001). This would result in a preponderance of large individuals among young adults (McLaren 1993). This bias may also be further complicated by the almost exclusive sampling of breeding females in this study which, in other studies, have been shown to be generally larger and in better condition than non breeding females of the same age (Winship *et al.* 2001). Hence it is possible that the growth at age models presented here are positively biased, resulting in higher growth rate estimates than would be estimated from a data set including both breeding and non breeding females. There is no evidence of any inter-annual variation in growth rate observed in the study nor is there any environmental variation evident over this period making it unlikely that bias (v) would be an effect in this study.

### *Overall growth curves*

Mathematical growth models have been used widely in biology to describe growth in a range of species. The fitting of a single relatively simple equation to describe growth over the entire life cycle is problematic; no single model can adequately describe such a dynamic and non-linear process (Zach 1988; McLaren 1993; Aldrich & Lawler 1996). The fundamental problem is that pup growth appears to be qualitatively and quantitatively different to growth of sub-adults and adults. However, modelling of this latter phase of growth is straightforward, and allows direct comparisons to be made between sexes, among populations and species (Brown *et al.* 1976; McLaren 1993; Pruitt *et al.* 1979; Trites & Bigg 1996).

All three models used here have been routinely used to describe growth in pinnipeds. Some authors have suggested that simpler models such as the von Bertalanffy and Gompertz models should be preferred as they are easier to interpret, do not have problems with parameter correlation, and often describe the data just as well as more complicated models (e.g. the Richards model; Zach 1988, Hammill *et al.* 1995). In contrast, others argue that the Richards model should be preferred as it is more flexible than the 3 parameter models, is better at detecting growth patterns due to environmental conditions, and produces less biased estimates of growth when the true growth pattern does not conform to a 3 parameter model (Brisbin *et al.* 1987; Leberg *et al.* 1989).

In this study, the choice of growth model matters little. The three growth models tested fitted the data well and had 95% confidence intervals that overlapped. As there was no real difference between the fit of the models or the parameter estimates, the von Bertalanffy and Gompertz models are preferred over the Richards model on the basis of parsimony (i.e. they use fewer parameters; i.e. 3 vs. 4). Furthermore, the Gompertz growth curve represents a standard curve that is thought to best describe mammalian growth (Laird 1966; Heide-Jorgensen & Teilmann 1994), especially that in pinnipeds (York 1983; Hammill *et al.* 1995). As such it was selected as the best model to describe growth in female NZSLs.

### *Individual growth*

Length and weight exhibited asymptotic growth. Laws (1956) found that length at puberty, as a percentage of final size, was remarkably consistent among pinnipeds at 87%. Female NZSLs reached 90% of asymptotic length at between age 3 and 4, which also corresponds with the earliest evidence of sexual maturity, as suggested by Laws (1956). Mass did not reach 90% of asymptotic weight until age 8, demonstrating that females continue to increase in weight long after achieving asymptotic length which is consistent with BMI increasing with age. Similar growth patterns are also seen in female Steller's sea lions (Winship *et al.* 2001) and female California sea lions (*Zalophus californianus*) (Kastelein *et al.* 2000). Female NZSL, Steller's and Californian sea lions attain 90% of asymptotic length at or around age 4 while Southern sea lions (*Otaria flavescens*) reach this point slightly later, at around age 6 (Rosas *et al.* 1993; Kastelein *et al.* 2000; Winship *et al.* 2001).

The estimated age-specific growth rate for weight in NZSLs was considerably lower than that reported for Steller's sea lions for all ages. This may be simply a species specific difference but could also be the effect of an individual occupying a marginal foraging environment as has been proposed previously (Gales & Mattlin 1997; Chilvers *et al.* 2005b). NZSLs regularly exceed their theoretical aerobic dive limit, with the implication that they have to work harder to obtain sufficient energy for thermoregulation, growth and reproduction (Chilvers *et al.* 2005b). Reduced growth rate is consistent with an individual that is occupying a marginal foraging environment. Further research on growth of NZSLs at other locations (e.g. Otago Peninsula), would help in determining if the rates reported here are sub-optimal for the species.

### *Inter-site and inter-annual variation in growth*

Although some of the parameter values for growth rate in weight between Sandy Bay and Dundas Island, were significantly different, overall there was no significant difference between growth curves for either length or weight between the sites as evidenced by almost completely overlapping confidence intervals. Despite the lack of statistical significance, there are some small differences in growth patterns that may be biologically important. In particular, females appear both shorter and lighter at Sandy Bay than Dundas Island prior to age 6 but after this age females at Sandy Bay are larger. The pattern is more marked for weight than length with Sandy Bay females being 12% lighter at age 3 but peaking at 5% heavier at age 12. While this may be a true effect of colony, it is more likely to be an artefact of the small sample sizes for younger females as there is no significant difference in weight of female pups at 6 weeks of age between the 2 sites (L. Chilvers *unpublished data*). There was no evidence of an inter-annual variation in growth for either site over the 3 year study.

### *Species comparisons*

There are six sea lion species that show considerable variation in body size. Mature female NZSLs and Californian sea lions are about the same size (~1.8 m, ~100-110 kg, Heath 2002). By comparison, mature female Australian (*Neophoca cinera*) and Galapagos (*Z. wollebacki*) sea lions are smaller (~1.5 m, ~80 kg (Heath 2002; Campbell *et al.* 2006) while Southern sea lions are slightly larger (~2.0 m, ~150 kg; Cappozzo 2002). Mature female Steller's sea lions are the largest (~2.3 m and ~260 kg; Winship *et al.* 2001). Little is known about the physical characteristics of the presumed extinct Japanese sea lion (*Z. japonicus*) but is likely to have been similar in size to Californian and Galapagos sea lions which share the same genus (Heath 2002). While there is limited information available on other sea lion species, NZSLs have the same general pattern of growth as other sea lions characterised by rapid juvenile growth that slows and reaches a plateau around the age of sexual maturity (Laws 1956; Rosas *et al.* 1993; Kastelein *et al.* 2000; Winship *et al.* 2001).

## *7.5.2* ***Reproduction***

### *Reproductive age*

Resighting records of individually identified and known-age female NZSLs demonstrate that NZSL females produce pups between the ages of 3 and 25. This is very similar to the age distribution of lactating NZSLs found from sampling (3 to 26; Chapter 5). Only one individual was recorded pupping as early as age 3. This is again consistent with the observed age structure of lactating females where only 3 (0.3%) out of 865 sampled lactating females were observed to give birth at age 3 (Chapter 5). Females up to age 28 have been resighted but no females older than 25 were seen with pups. Reproductive senescence appears to start at approximately age 23, although this is based on a relatively small sample size (*n* = 30 females >20 years),

Autopsy data indicate that NZSLs ovulate as early as age 3 and suggest that all females are ovulating by age 4. However, this is based on a limited sample of only 22 females less than age 5 (Dickie 1999; Duignan *et al.* 2003a, b). Three females of estimated-age 3 have been recorded as giving birth, indicating that females can ovulate as early as age 2. This proportion is likely to be very small given that only 0.3% of breeding females were age 3 (Chapter 5). Therefore, females may ovulate as early as age 2, and most are ovulating by age 4. These findings are similar to that reported from autopsy records of Steller's sea lions that indicate that age at first ovulation is 3 with estimated 100% of females ovulating by age 6 (Pitcher & Calkins 1981).

### *Reproductive rate p(x)*

Young (<4 years) and old (>21) age classes are represented by few individuals, resulting in large confidence intervals for *p(x)*. For example, the sample contained only one individual of age and one individual of age 25, and both were observed with a pup. The resulting high estimate of reproductive rate of 1.00 for these ages is simply the result of a small sample size but this is reflected in the exact 95% confidence intervals that span the range from approximately 0 to 1. Given these large confidence intervals, estimates of reproductive rate for these ages are influenced by the shape of the equation that was fitted. The choice of this model shape was determined from consideration of the reproductive patterns of other otariid species. Several other curves were explored in fitting the observed reproductive data, but the *p(x)* model was selected as it has considerably flexibility in shape and it best fitted the observed data. While the model fit is generally consistent with the data (given the large variability) the reproductive rates for younger and older individuals should be viewed with caution and may represent over estimates.

Reproductive rate increased rapidly between ages 3 and 7, reached a plateau between ages 7 and 23, and then rapidly declined after age 23. A similar pattern has been reported from Steller's sea lions in which reproductive rate declined to zero after age 20 (although small sample sizes for older individuals was also a constraint of this study; Pitcher & Calkins 1981).

An observed peak in reproductive rate at intermediate ages followed by a decline in reproductive rate for older individuals is well described in fur seals (Northern fur seals *Callorhinus ursinus*, Lander 1981; South American fur seals *Arctocephalus australis*, Lima & Paez 1995; sub-Antarctic fur seal *A. tropicalis*, Bester 1995, Dabin *et al.* 2004) but is not a feature of all fur seals (e.g. Antarctic fur seals *A. gazella*, Boyd *et al.* 1995). The large decline in reproductive rate in NZSLs occurs at approximately 0.89 of maximum age while in Steller's sea lions, Antarctic and South American fur seals it occurs at approximately 0.56, 0.58 and 0.72 respectively of maximum estimated-age (Pitcher & Calkins 1981; Boyd *et al.* 1995; Lima & Paez 1995). NZSLs appear to have higher reproductive productivity in the latter stages of their life than other pinniped species although the overall mean reproductive rate is lower.

As was expected, the value of $p(x)$ varied depending on the choice of data set. Data set 1 is the most optimistic case but is positively biased as females known to be alive but not seen at the breeding colony, and therefore likely to be not breeding, are excluded from analysis. The effect of expanding Data set 1 by adding these females was to lower the overall reproductive rate by 0.09. The observed variation in the estimation of reproductive rate is particularly important as population models used to estimate sustainable removals are likely to be sensitive to this parameter. Therefore, the more conservative value of $p(x)$ (e.g. derived from Data set 2) should be used when considering population modelling to ensure that reproductive rate is not positively biased.

### *Modelling of Reproductive rate* $\hat{p}_1(x)$

The model $\hat{p}_1(x)$ fitted the data well and delineated the increase, stability and then decline in reproductive rate with increasing age. The mean value of $\hat{p}_1(x)_{all}$ was the same as $p(x)_{all}$ and was within the observed range of reproductive rates for other sea lion species. Due to small sample sizes of ages less than 5 and over 20 and the resulting large confidence intervals associated with these point estimates, the fit of $\hat{p}_1(x)$ to these older ages is less informative and driven to a certain extent by the shape of the model. This is apparent in the lack of observed breeding of females over age 25 but with estimated $\hat{p}_1(x)$ rates of 0.23 and 0.06 for ages 26 and 27 respectively. While the impact of this discrepancy is likely to be small, as the proportion of breeding females aged 25 or over is estimated to be less than 1% (Chapter 5), it is important to improve sample sizes for these older individuals for future analysis.

To date, most modelling on this species has focussed on abundance estimation (Gales and Fletcher 1999), likely population trend (Woodley & Lavigne 1993; Manly & Walshe 1999; Lalas & Bradshaw 2003), or estimating sustainable levels of bycatch (Breen & Kim 2005). There has been little focus on empirical parameter estimation. Most modelling has simply relied on parameter estimates for other species. Most models have estimated reproductive rate at between 0.60 and 0.90 for NZSLs. There are only two estimates using observed data from NZSLs: Lalas & Bradshaw (2003) used reproductive rate estimates of 0.75 and 1.0 that were based on observed breeding histories of female NZSLs at Otago; and Breen & Kim (2005) who used a uniform prior of 0.2 - 1.0 in their Bayesian population model and reported a posterior estimate of 0.99 (0.98 – 1.00) using some data from the Auckland Islands NZSL population. This study shows that these estimates were excessively optimistic. My overall estimate of reproductive rate for NZSLs of age 3 and over from this study is 0.67 (SE = 0.01). This is the first robust estimate of reproductive rate for this species. Despite this, it should be treated with some caution, since it is calculated from observations of females at the Sandy Bay breeding colony where only 19% of NZSLs breed (Chilvers *et al.* 2007). The largest breeding colony at Dundas Island, where 64% breed, has a different age structure of breeding females (Chapter 5) and therefore could also have a different reproductive rate. It is essential that similar observations are made at Dundas Island to investigate if there is a difference in reproductive rate between the colonies. If there is, it could have significant implications for the present modelling approach and the bycatch limits based upon it.

Pitcher *et al.* (1998) reported a 0.97 pregnancy rate for mature female Steller's sea lions in early gestation which declined to 0.67 in late gestation, resulting in a birth rate of 0.63. If there is similar difference between early pregnancy rate and birth rate in NZSLs, this would indicate that pregnancy rates early in gestation would be close to 1.00. The mean observed birth rate of 0.67 for NZSL is within the range reported for other sea lions (c.f. Steller's sea lion, 0.63, Pitcher & Calkins 1981; Australian sea lion, 0.71, Higgins & Gass 1993; California sea lion, 0.77 for ages 6 to 12, Melin 2002). This would place NZSLs among the slowest reproducing of sea lions.

### *7.5.3 Management Implications*

This is the first robust estimate of reproductive rate for this species, and is among the lowest reported for any sea lion species. This new estimate is considerably lower than assumed rates used in recent population modelling for this species, calling into question the current estimation of levels of sustainable bycatch that are driven in a large part by reproductive rate.

NZSLs have the lowest growth rate reported for any sea lion species and this, combined with low reproductive rates, is consistent with a population that is occupying a marginal foraging environment as has been previously proposed (Gales & Mattlin 1997; Chilvers *et al.* 2005b). These factors, along with a recent significant decline in pup production, suggest that current management is insufficient to ensure population stasis, let alone meet the statutory goal of recovery.

## 7.6 ACKNOWLEDGEMENTS

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# Chapter 8

# Modelling Demographic Parameters of Female New Zealand Sea Lions

# CHAPTER 8: MODELLING DEMOGRAPHIC PARAMETERS OF FEMALE NEW ZEALAND SEA LIONS

## 8.1 ABSTRACT

The age-distribution of 865 lactating New Zealand sea lions (*Phocarctos hookeri*) was investigated over three years (1999 - 2001) at two breeding colonies, Sandy Bay and Dundas Island, in the Auckland Island group. In addition, the reproductive histories of 505 marked females from the Auckland Islands were recorded from 1998 to 2005. These datasets were used to investigate mean and age-specific demographic rates (survival, maturity, reproductive) of female New Zealand sea lions. Based on an observed decline in pup production over the period 1998 to 2006, the population was assumed to be in decline and therefore non-stationary. Two different models were used to estimate and investigate female New Zealand sea lions demographic rates. Mean annual adult survival rate was estimated at 0.81 (SE = 0.04) using a multi-parameter (i.e. survival, maturity, reproductive rate) model fitted using maximum likelihood and adjusted for a non-stationary population with a known rate of change using the method developed by Eberhardt (1988). Age-specific demographic values were also estimated including adjustment for a non-stationary population and the incorporation of Siler's (1979) competing risk model for the estimation of age-specific survival. Age-specific survival followed a simple linear relationship, with a general decline from 0.84 at age 0 to 0.78 at age 28. This linear relationship was unexpected given that mortality patterns in mammals generally follow a "U" shaped curve. This result probably reflects a lack of data at young and old ages, that prevents the model from fitting higher levels of mortality to these age classes. Notwithstanding these issues, the model produces plausible estimates of survivorship that are consistent with the expected pattern characteristic of otariid life histories. Mean reproductive rate was estimated at 0.67 (SE = 0.05) for ages 3 to 28. This is among the lowest reproductive value reported for a sea lion species. There was no evidence of any inter-site or inter-annual effect on any demographic parameter, except for maturity rate, which indicates that Dundas Island has a later age when 90% of females are mature. The major implications of this work are in the application of these vital rates to modelling the effect of fisheries bycatch on New Zealand sea lions. Existing models have used unrealistic demographic values and therefore do not represent the best available information. The application of this new demographic information from this study has the potential to revise existing management advice about the impact of the fishery on the New Zealand sea lion population.

## 8.2 INTRODUCTION

Demographic modelling has been widely used to investigate the dynamics of marine mammal populations (Caughley 1977; Slooten & Lad 1991; Brault & Caswell 1993; York 1994; Wickens & York 1994; Barlow & Calpham 1997; Caswell *et al.* 1999; Caswell 2001). At their simplest, population dynamics are characterised by the interaction of births and deaths, immigration and emigration but are also subject to both intrinsic (e.g. senescence, varying fecundity with age) and extrinsic effects (e.g. density-dependent mortality from limited food resources) (Caughley 1977; Boyd *et al.* 1995). Demographic modelling has frequently relied on a specified age structure and age-specific birth and survival rates (Barlow & Boveng 1991; Evans & Hindell 2004). While this information is available for some marine mammal populations, it is partially or completely lacking for most. Statistical models that estimate demographic parameters can be used to explore and understand population dynamics (Caswell 2001). An understanding of demographic parameters and population dynamics is essential to the appropriate conservation and management of any species, especially a threatened species.

The New Zealand sea lion (NZSL) (*Phocarctos hookeri*) is a pinniped endemic to New Zealand (NZ) (Gales 1995) and is listed as threatened by the IUCN (IUCN 2002). NZSLs are regularly caught as bycatch in the NZ 6T squid (*Nototodarus sloanii*) trawl fishery. On average over 70, and up to 140 NZSL, have been killed each year since observations began in 1986 (Ministry of Fisheries (MFish) 2005). This interaction is managed by the NZ Government via the application of a Fishing Related Mortality Limit (FRML) imposed on the commercial fishery. When it is estimated that either the FRML or the 6T squid Total Allowable Commercial Catch (TACC) has been reached, the fishery is closed. In recent years the fishery has been closed more often for reaching the FRML rather than the squid TACC (Wilkinson *et al.* 2003; MFish 2005).

Since 2003, FRMLs have been calculated using an age-structured Bayesian model that has been developed to model the effects of bycatch on the population (Breen *et al.* 2003; Breen & Kim 2005; Ministry of Fisheries 2005). The model is complex (i.e. it has >40 parameters) and is compromised by the fact that most demographic parameters are estimated from limited or no empirical data. Most of the key biological parameters, including female reproductive and survival rates, are presently estimated from a small sample of observations of marked females (Breen & Kim 2005). Furthermore, estimates for some of the vital rates generated by the model do not fit the observed data (e.g. mean adult female reproductive rate >0.98, first year survival ~80%; Breen & Kim 2005), and are biologically implausible given what is known about other better studied pinnipeds (York 1994; York & Wickens 1997). In addition, the lack of model fit to the observed population trend data (i.e. significant declines in annual pup production) is another cause for concern. While the Bayesian framework does allow for flexibility in fitting the model to the observed data, it is essential that reliable and robust biological data sets and estimates of vital rates are available for use in the model. The model (or another variant) could then utilise more informative priors, leading to more biologically realistic values of posteriors and overall model outputs. These improvements are essential when investigating levels of NZSL bycatch that are sustainable and will not impede population recovery.

There are no robust published estimates of either reproductive or survival rates for NZSL based on NZSL data. There have been attempts to explore what rates are plausible, via modelling using limited NZSL datasets or, more commonly, using rates derived from other pinniped species (Woodley & Lavigne 1993; Gales & Fletcher 1999; Manly & Walshe 1999; Lalas & Bradshaw 2003; Breen *et al.* 2003; Breen & Kim 2005). While these models have been useful preliminary steps for investigating potential population dynamics of NZSL, they have had little biological grounding with data from NZSLs and therefore it is not known how well the models and results correspond to biological reality.

This study was part of a larger project investigating age structure and demographics of NZSL. The aims of this part of the study were to: (i) estimate average adult and age-specific survival rates using age-distribution data from lactating females; (ii) investigate the feasibility of estimating juvenile female survival rates using age-distribution data from lactating females; (iii) estimate age-specific reproductive rates from resightings of marked females; and (iv) investigate inter-site and inter-annual variation in vital rates of female NZSL at the Auckland Islands.

## 8.3 METHODS

### *8.3.1 General field work*

The sampling design for estimating the age-distribution of lactating females and the ageing methodology is provided in Chapter 5. A full description of methodology underpinning the collection and use of individual female resighting histories is provided in Chapter 6.

### 8.3.2 *Modelling of biological parameters*

Two approaches were taken in estimating biological parameters. The first was to use a Chapman-Robson (1960) catch curve to estimate mean adult female survival from age-distribution data of lactating females. The second was a more complex modelling approach to estimate age-specific survival, maturity and reproductive rates from the age-distribution of lactating females and observed reproductive rates.

Given that the age-distributions are significantly different between Dundas Island and Sandy Bay breeding colonies, they were analysed separately (Chapter 5). Furthermore, while there was no evidence of inter-annual variation in age-distribution at Dundas Island, there was at Sandy Bay, so estimates of mean annual survival were also made for each year independently (Chapter 5). For comparisons, composite data sets were made comprising all individuals sampled at Sandy Bay and Dundas Island respectively, and all individuals from both sites and all years combined.

### 8.3.3 *CR modelling from a stationary population*

If the annual survival rate is constant, the number of animals in successive age-classes should follow a negative exponential model. In a stationary population, the exponent of the expression describing this curve represents the instantaneous mortality rate, and the natural logarithm of this value will be the annual survival rate (Chapman & Robson 1960). A stationary population is defined as a state in which the rates of mortality and recruitment are relatively constant with respect to time and age (Chapman & Robson 1960). In a non-stationary (i.e. changing) population the intrinsic rate of increase can be added to the instantaneous mortality rate, and the natural logarithm of this will give the true annual survival.

Exponential models were fitted by the method of Chapman & Robson (1960) to age-distributions for samples collected between 1999 and 2001 at Sandy Bay and Dundas Island to estimate mean annual survival. The Chapman & Robson (1960) model assumes that there is some age $X_0$, such that for all ages $X \geq X_0$, the probability of selection (i.e. sampling) is the same, and the annual survival rate is the same. In this study, $X_0$ was taken as the peak of the age-distribution. $X_0$ varied by site and year and therefore mean survival is estimated for all ages $\geq X_0$ for each data set independently. All cohorts younger than $X_0$ were excluded from the analysis, as recommended by Robson & Chapman (1961) for samples where younger individuals are under-represented. In this study, younger females were not available for sampling, as only lactating females were included in the study and a high proportion of young females are not lactating. An assumption of this method is that the sampled population is stationary and that the age distribution is stable. This model is referred to as the Chapman-Robson Stationary population (CR-S) model.

### *8.3.4 SLP modelling from a stationary population*

*Modelling framework*

A multi-parameter model was also developed to explore the interaction of life history parameters and to potentially investigate juvenile female survival. As for the CR-S model, this model assumed that the population was stationary and is referred to as the Sea Lion Stationary Population (SLP-S) model. It involved the following parameters:

Maturity rate
$b(x) = \Pr(\text{an individual returns to the colony} \mid \text{individual is of age } x)$

Reproductive rate
$p(x) = \Pr(\text{an individual breeds} \mid \text{individual has returned to the colony and is of age } x)$

Survivorship
$l(x) = \Pr(\text{an individual survives to age } x)$

The model was fitted to the following two data sets:

1. $n(x)$ : number of females of age $x$ in a random sample of lactating females (plus their pups)
2. $r(x)$ : number of marked females of age $x$ with a pup (out of $m(x)$ marked females of age $x$)

I now describe the details of the model-fitting:

1. Assuming a 1:1 sex ratio in the pups, the number of female pups associated with the lactating females is

$$n(0) = 0.5\sum_{x>0} n(x)$$

2. The log-likelihood for $n(x)$ was specified as

$$log\, L_1 = \sum_x n(x) log\, \pi(x)$$

where $\pi(x)$ = Pr(an individual that is in $n(x)$ is of age *x*).

3. The log-likelihood for $r(x)$ was specified as

$$log\, L_2 = \sum_x \{r(x) log\, p(x) + (m(x) - r(x)) log(1 - p(x))\}$$

4. You can write

$$\pi(x) = \frac{\alpha(x)\beta(x)}{\sum_x \alpha(x)\beta(x)}$$

Where $\alpha(x)$ = Pr(an individual is in $n(x)$ | individual is of age *x*) and $\beta(x)$ = Pr(an individual is of age *x*).

5. As there are no 1-year olds at the colony, we have $\alpha(1) = 0$. For $x \neq 1$ $\alpha(x) = b(x)p(x)$, where for the convenience of notation we define $b(0) = p(0) = 1$ (as all pups are included in $n(x)$, $\alpha(0) = 1$).

6. Assuming a stable age distribution we can write *exp*

$$\beta(x) = \frac{\exp(-rx)l(x)}{\sum_x \exp(-rx)l(x)}$$

where *r* is the logarithm of the population growth rate.

7. Steps 4 and 5 imply that $\pi(1) = 0$ and for $x \neq 1$

$$\pi(x) = \frac{b(x)p(x)\exp(-rx)l(x)}{\sum_x b(x)p(x)\exp(-rx)l(x)}$$

8. I modelled survivorship using the model proposed by Siler (1979), setting $l(x)=l_1(x)l_2(x)l_3(x)$ where

$$l_j(x)=exp\left(-\frac{a_1}{b_1}(1-exp(-b_1x))\right), \quad l_c(x)=exp(-a_2x) \quad \text{and} \quad l_s(x)=exp\left(\frac{a_3}{b_3}(1-exp(b_3x))\right)$$

where $l_c$ represents the constant risk of mortality experienced by all age classes; $l_j$ and $l_s$ represent the risks of mortality during the juvenile and senescent stages of life respectively. The use of five parameters ($a_1$, $a_2$, $a_3$, $b_1$, $b_3$) allows considerable flexibility in the shape of this function.

9. I modelled maturity rate by setting

$$\hat{b}(x)=\Phi\left(\frac{x-\mu_b}{\sigma_b}\right)$$

where $\Phi(\cdot)$ is the cumulative distribution function for the standard normal distribution. The parameters $\mu_b$ and $\sigma_b$ are the true mean and standard deviation of the age at which individuals first return to the colony. The assumption underlying *b(x)* is that all individuals return to the colony when they are mature and are therefore available for sampling and resighting.

10. I modelled reproductive rate by setting

$$\hat{p}_2(x)=\left(\frac{x-\mu_1}{\sigma_1}\right)\left\{1-\phi\left(\frac{x-\mu_2}{\sigma_2}\right)\right\}$$

where $a$ is the maximum reproductive rate across all age classes; $\mu_1$ and $\sigma_1$ are the mean and standard deviation of the age at which individuals give birth for the first time; $\mu_2$ and $\sigma_2$ are the mean and standard deviation of the age at which individuals give birth for the last time. The choice of this model shape was determined from consideration of the reproductive patterns of other otariid species and the fit of the model to the observed data. For clarification, *p(x)* is the observed value of reproductive rate and $\hat{p}_1(x)$ is the estimated value of reproductive rate from the maximum likelihood fit of equation 4 to the observed data in

Chapter 6, and $\hat{p}_1(x)$ is the estimated value of reproductive rate from the maximum likelihood fit of the SLP model to the observed data undertaken in this Chapter.

11. The parameters were estimated by maximising the total log-likelihood $log\,L_1 + log\,L_2$.

Mean annual survival and reproductive rates were estimated for all SPL models using weighted means (Seber 1982) of age-specific values. This facilitates direct comparison between mean annual rates estimated from the CR and SPL models. Means were weighted by the number of observations for each age.

### *8.3.5 Modelling vital rates from non-stationary populations*

*Assessing population status*

One of the key assumptions of these modelling approaches is that of a stationary population. I investigated whether the Sandy Bay and Dundas Island colonies were stable over the study period using estimates of pup production as an indicator of population status. Estimates of pup production have been made using the same methodology since 1995 (methods described in Chapter 2; see also Gales & Fletcher 1999; Chilvers *et al.* 2007).

*Adjusting mean survival for non-stationary populations*

Adult survival rates $s$ estimated from age-distribution data are likely to be biased when the population is non-stationary and no adjustments are made to account for this (Caughley 1977). I explored the extent of this bias on the resulting model fits and parameter estimates by also modelling a non-stationary population with a known rate of change. I used the method of Eberhardt (1988) to adjust the CR-S survival rate estimates using $r$, the exponential rate of population change that was estimated from the pup production data series. This modification alters the assumption of a stationary population to the assumption of a non stationary one. This model is referred to as the Chapman-Robson Non-stationary population (CR-N) model. In addition, I also modified the SLP-S model by adjusting parameter $r$ to be consistent with a non stationary population and re-ran the model fitting. Specifically, parameter $r$ was set to 0 for a stationary population but was replaced with values estimated from the pup production data series to adjust for a non-stationary population. This model is referred to as the Sea Lion Non-stationary population (SLP-N) model. Survival estimates from these models adjusted to account for a non-stationary population are referred to as $\tilde{s}_i$.

### *8.3.6 Statistical robustness and comparisons*

One of the aims of this work was to investigate inter-site and inter-annual variation in vital rates of female NZSL at the Auckland Islands. This is not necessarily straightforward. In particular, standard error estimates of means for age-specific survival, while useful for comparing models and estimates, are only approximations of the true variance and it is not known how accurate these approximations are. To accurately estimate standard errors for these means would require development of very detailed statistical models, most likely involving the use of bootstrapping, that are more appropriate for a statistical thesis than a biological one. Investigation of differences between the functions of the demographic parameters would most likely require AIC model comparison methods that are outside the scope of this thesis. An alternative approach is to estimate 95% confidence intervals for functions, and then examine the curves for differences. This approach is also statistically complex. As a result, in some cases, the reported comparisons lack confidence intervals, and therefore the comparisons do not account for the full uncertainty associated with the estimates. While I am aware of these issues, I have undertaken the work on the assumption that, even though the estimates of variance I have used are approximations of the true variance, they are still useful in exploring model and parameter differences. Further extensions for this work could focus on the development of accurate variance estimators and the exploration of model differences using AIC methods.

## 8.4 RESULTS

### *8.4.1 Data summary*

A total of 865 individuals were sampled (captured or resighted) for the age structure investigation over the three years at the two study sites (Figure 8.1). In addition, 1896 resightings were made of 505 different females aged between 3 and 28 years old, as part of the reproductive rate study. This is the same as Data set 2 described in Chapter 6, and includes resights of females that were known to be alive but were not resighted in a season.

### *8.4.2 Assessing population status*

Over the period 1995 until 2005, pup production at Sandy Bay was reasonably consistent (Figure 8.2). Pup production at Dundas Island increased until a peak in 1998 and has declined since, showing an overall decline for the whole study period. The mean annual change in pup production between 1998 and 2005 was -0.012 for Sandy Bay, -0.047 for Dundas Island, and was -0.041 for Sandy Bay and Dundas combined. While the two colonies have different population trajectories over the ten-year study period, they both show reasonably stable pup production over the three-year sampling period, 1999 to 2001.

### *8.4.3 CR modelling*

Mean annual survival rates $s$ from the CR-S and CR-N models are shown in Table 8.1 by site, year and for the combined data sets. Adjusting the CR-S model to account for a non-stationary population with observed rates of population decline (i.e. CR-N) resulted in lower estimates of mean survival rate $\tilde{s}$ for all sites and years. There was no clear evidence of inter-annual, inter-site or model effects (Figure 8.3a).

### *8.4.4 SLP modelling*

#### *Simulation testing and model fitting*

Performance testing was undertaken to check that model fitting was providing sensible results. Testing was undertaken by fitting the SLP-S model to simulated data sets. Estimates of model-derived parameters were very close to the parameter values used in generating the simulated data sets. The mean error between estimated and actual age-specific parameter values was only 0.003 for all of the parameters with a maximum error of 0.008. Generally, there is some bias associated with the calculation of parameters using maximum likelihood estimation procedures but the SLP-S model appeared to provide a good to fit to the simulated data. On this basis, performance was considered satisfactory.

#### *Parameter estimation*

In general, model fit was similar for both models (i.e. SLP-N and SLP-S) for the two sites and three years but some differences were evident (Figure 8.4). A description of the results for each parameter follows.

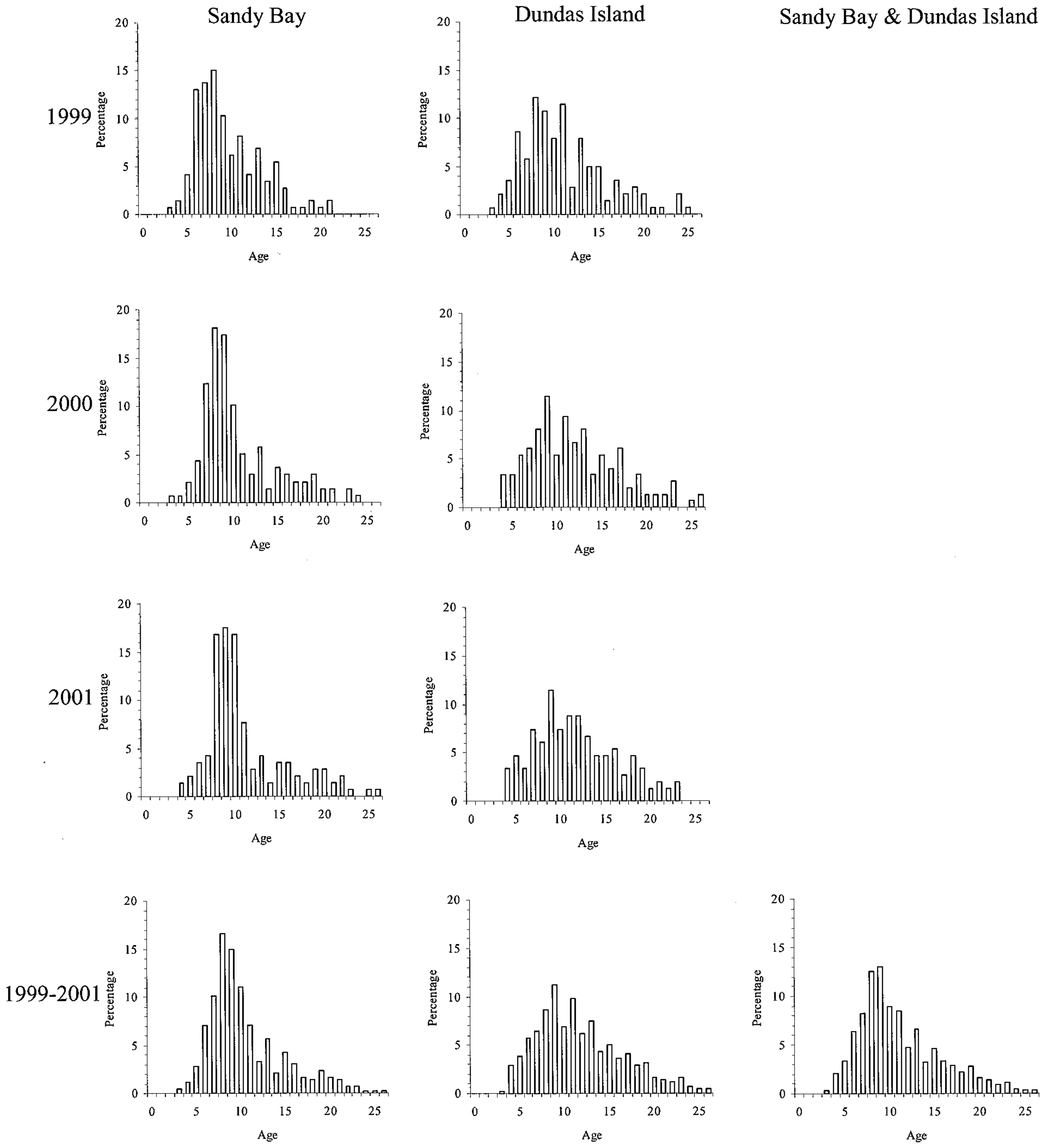


**Figure 8.1** Relative age-distributions of lactating female New Zealand sea lions by breeding colony and year in the Auckland Islands.

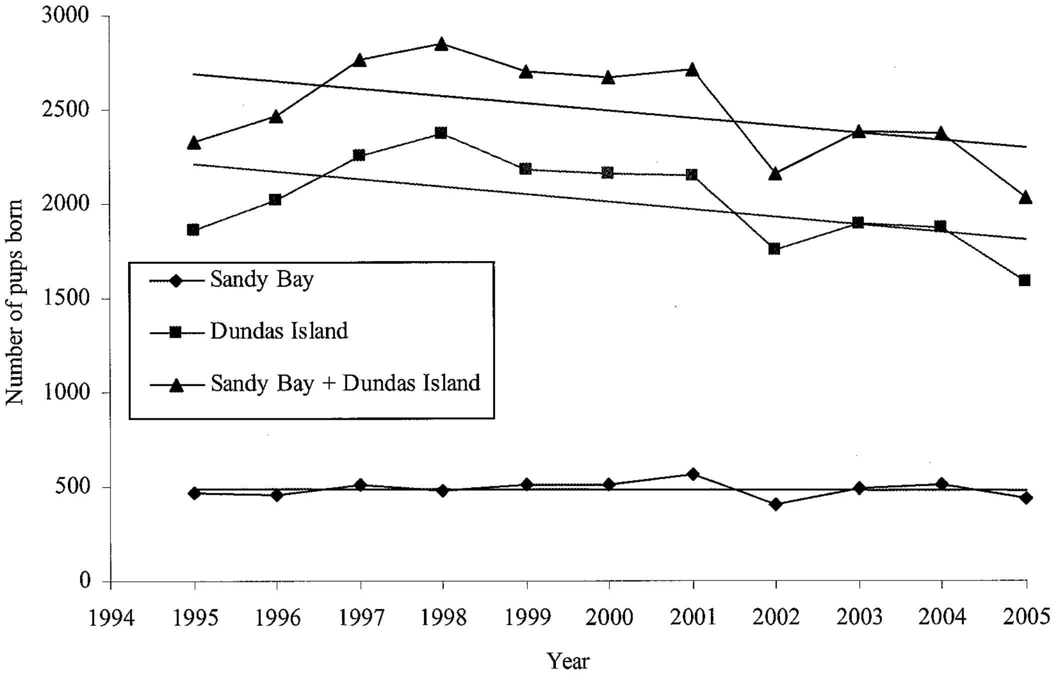


**Figure 8.2** Estimates of annual pup production for Sandy Bay, Dundas Island and the Auckland Islands for 1995 to 2005 with simple linear regressions for each data set. Shading denotes the 1999 to 2001 sampling period for age structure. Source: Chilvers *et al.* (2007).

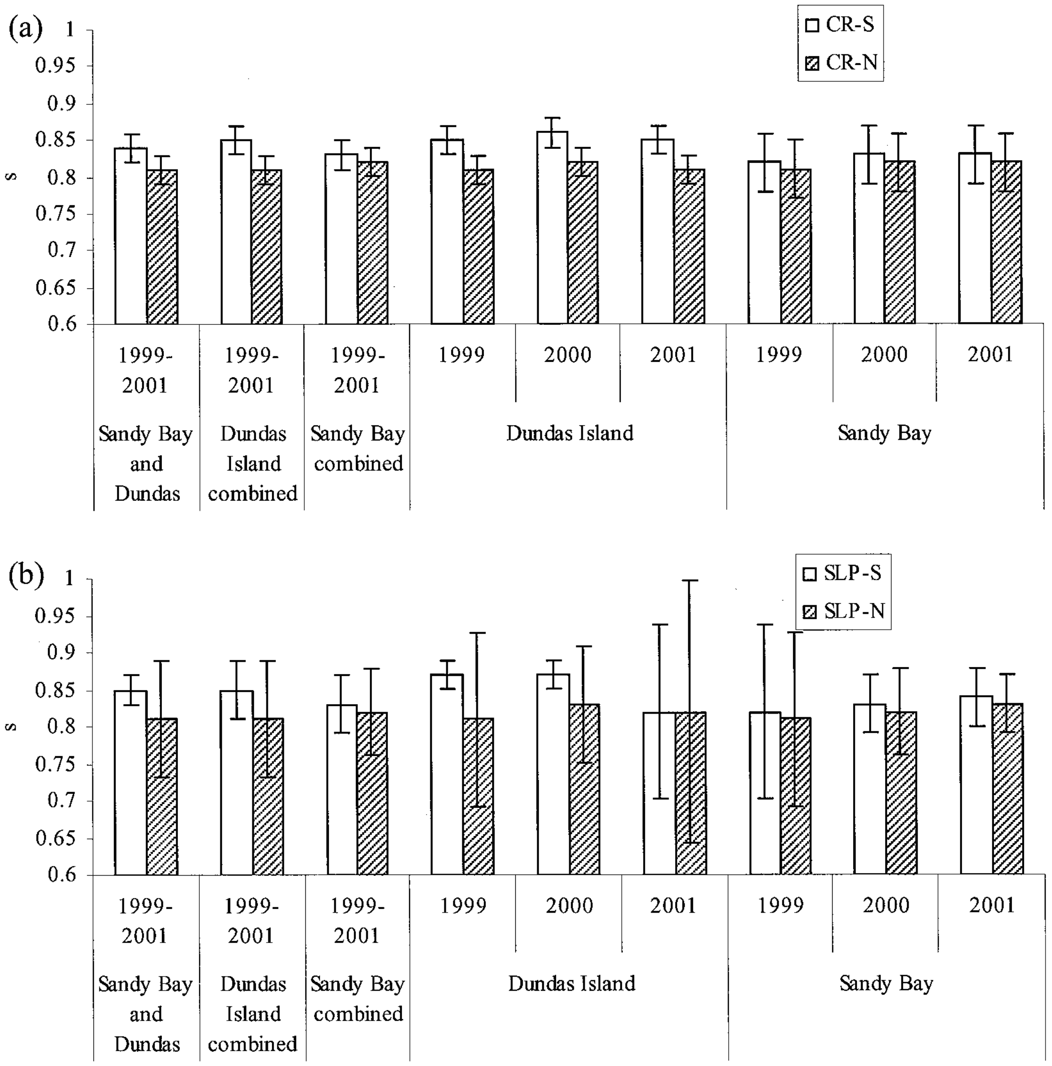


**Figure 8.3** Estimates of mean annual adult survival rate ($s$ and $\tilde{s}$) for the (a) Chapman-Robson Stationary (CR-S) and Chapman-Robson Non-stationary (CR-N) models and the (b) Sea lion Stationary (SLP-S) and Sea lion Non-stationary (SLP-N) population models for lactating New Zealand sea lions. Means from the SLP models are weighted means and 95% confidence intervals.

**Table 8.1** Estimates of mean annual survival rate using Chapman-Robson catch curves and Siler-based (Siler 1979) population modelling for lactating New Zealand sea lions at the Auckland Islands for stationary and non-stationary populations. Notation: $s$ = estimated mean survival post peak in age-distribution; $\tilde{s}$ = estimated mean survival post peak in age-distribution accounting for population change; $n$ = number of lactating sea lions in the sample post the peak at age; $r$ = exponential rate of population change; SE = standard error; CR = Chapman-Robson model; SLP = Sea lion Population model; -S = Stationary population; -N = Non-stationary population

| | | | | $s$ (SE) | | | $\tilde{s}$ (SE) | |
|---|---|---|---|---|---|---|---|---|
| Breeding colony | Year | Peak at age | $n$ | CR-S | SLP-S [1] | $r$ | CR-N[2,3] | SLP-N[1,2,3] |
| Sandy Bay and Dundas Island | 1999-2001 | 9 | 580 | 0.84 (0.01) | 0.85 (0.01) | -0.041 | 0.81 (0.01) | 0.81 (0.04) |
| Dundas Island combined | 1999-2001 | 9 | 316 | 0.85 (0.01) | 0.85 (0.02) | -0.048 | 0.81 (0.01) | 0.81 (0.04) |
| Sandy Bay combined | 1999-2001 | 8 | 336 | 0.83 (0.01) | 0.83 (0.02) | -0.012 | 0.82 (0.01) | 0.82 (0.03) |
| Dundas Island | 1999 | 8 | 111 | 0.85 (0.01) | 0.87 (0.01) | -0.048 | 0.81 (0.01) | 0.81 (0.06) |
| | 2000 | 9 | 110 | 0.86 (0.01) | 0.87 (0.01) | -0.048 | 0.82 (0.01) | 0.83 (0.04) |
| | 2001 | 9 | 112 | 0.85 (0.01) | 0.82 (0.06) | -0.048 | 0.81 (0.01) | 0.82 (0.09) |
| Sandy Bay | 1999 | 8 | 98 | 0.82 (0.02) | 0.82 (0.06) | -0.012 | 0.81 (0.02) | 0.81 (0.06) |
| | 2000 | 8 | 110 | 0.83 (0.02) | 0.83 (0.02) | -0.012 | 0.82 (0.02) | 0.82 (0.03) |
| | 2001 | 9 | 103 | 0.83 (0.02) | 0.84 (0.02) | -0.012 | 0.82 (0.02) | 0.83 (0.02) |

[1] Weighted means and SE as described by Seber (1982) section 1.3.2

[2] Eberhardt (1988) method used to adjust the survival estimate in a non-stationary population

[3] Parameter $r$ allowed the model fit to adjust to a non-stationary population

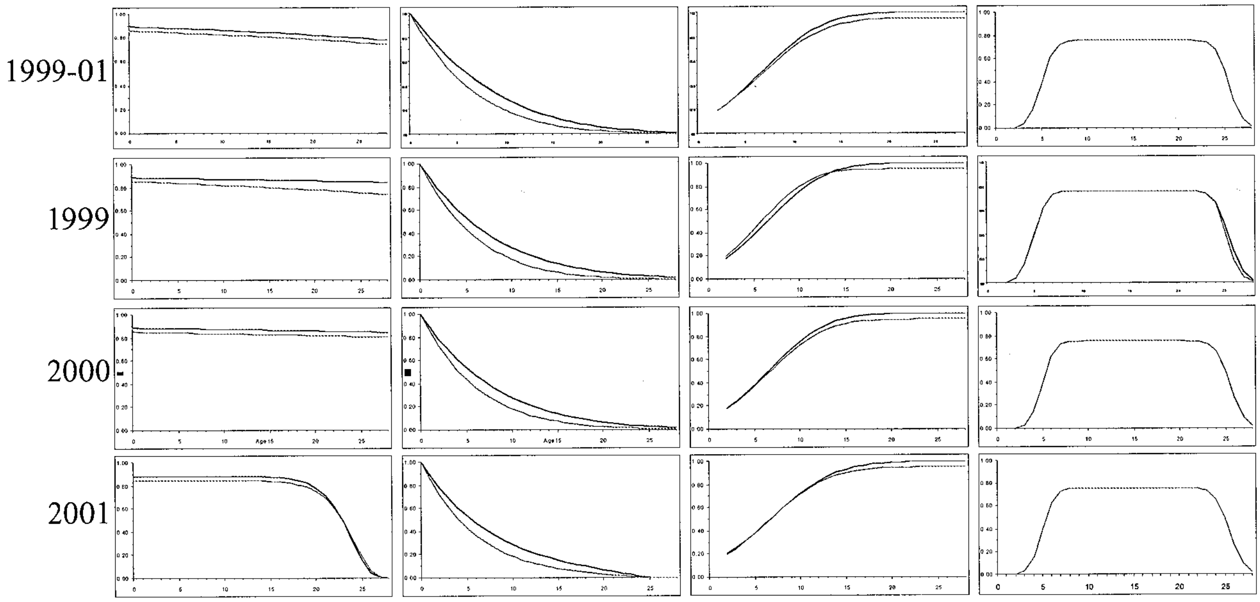
### *Reproductive rate* $\hat{p}_2(x)$

Model-based estimates of $\hat{p}_2(x)$ were almost identical for the two sites, all years and both models (Figure 8.4, 8.5). This result was expected, given that all model runs were fitting to the same observed data set and suggests that the age distribution data is not providing any information on $\hat{p}_2(x)$. There was a consistent pattern of recruitment into the breeding population starting at age 3, peaking and reaching a plateau at age 7, and then declining at age 23. All of the data sets had a plateau of *p(x)* equal to 0.75 or 0.76. There was a small amount of variability in estimates of $\hat{p}_2(x)$ between sites and years for ages >21 (Figure 8.5). This most likely reflects the small sample sizes for these ages rather than any real differences among sites or years. Sample sizes for each age class in the data set used to fit $\hat{p}_2(x)$ are listed in Appendix 6. Overall, the weighted mean for $\hat{p}_2(x)_{3-28}$ was 0.67 (SE = 0.18) and for $\hat{p}_2(x)_{7-23}$ was 0.75 (SE = 0.01) estimated from the SLP-N model for all sites and years combined. Both of these values were the same between models, sites and years.

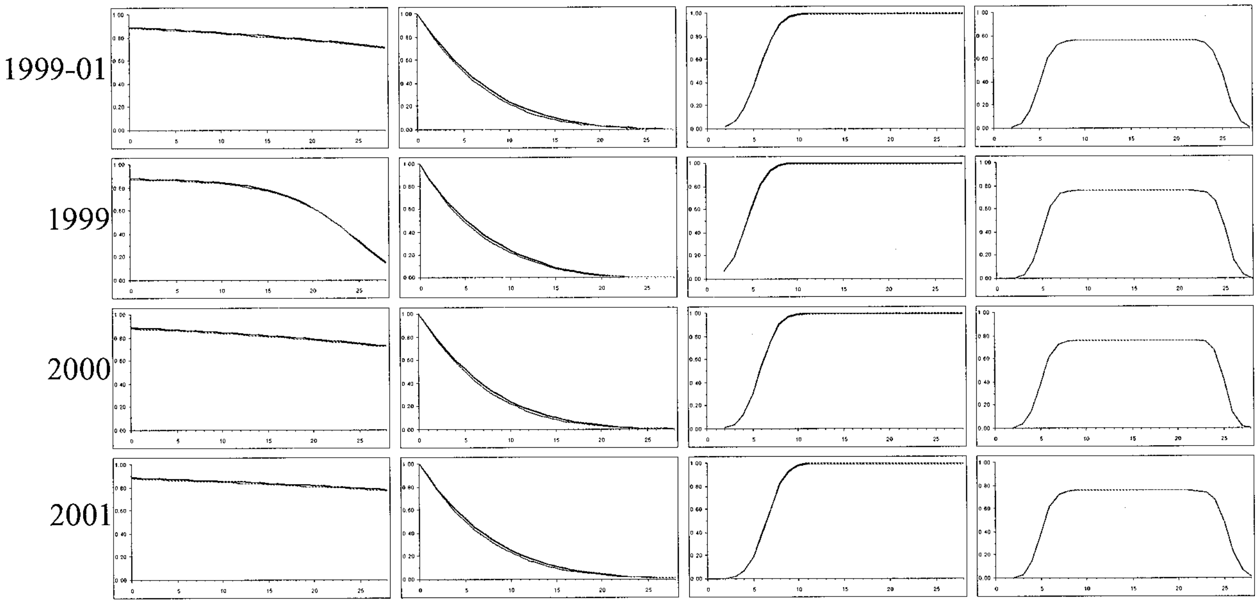
### *Maturity rate b(x)*

There was some variation in estimates of *b(x)* evident between the two sites, over years, and between the SLP-S and SLP-N models (Figure 8.6). The only consistent pattern was for the earliest age of sexual maturity (EASM) at age 2, although this is most likely an artefact of the model structure as the model was constrained to this age. Sandy Bay showed some evidence of inter-annual variation but little inter-model variation. Age when 50% of females are sexually mature ($ASM_{50}$) was 5 or 6 at Sandy Bay and age when 95% of females are sexually mature ($ASM_{95}$) was 8 or 9 (Figure 8.6, Table 8.2). These values were the same for both models. Dundas Island also showed little evidence of inter-annual variation or model differences except for a small difference for $ASM_{95}$ with SLP-N estimates being 2 to 3 years younger than SLP-S estimates. At Dundas Island there was a consistent pattern for $ASM_{50}$ at age 6 or 7 but $ASM_{95}$ varied between ages 15 and 18 for the two models (Table 8.2).

(a) Dundas Island



(b) Sandy Bay



(c) Dundas Island and Sandy Bay combined

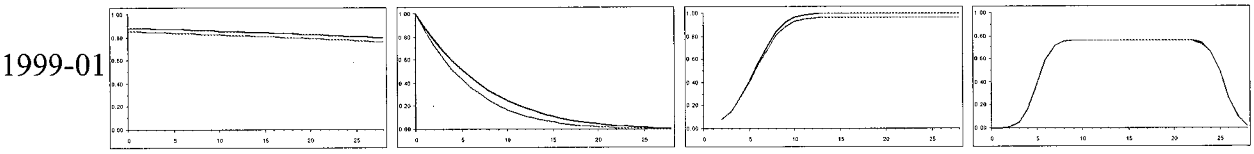


**Figure 8.4** Parameter estimates from the Sea Lion Population (SLP) modelling for two sites and three years including composite data by site and for both sites combined. Blue lines are for stationary (SPL-S) and pink lines for non-stationary (SPL-N) models. Y axis is 0.00-1.00 and x axis is age 0-28 years old.

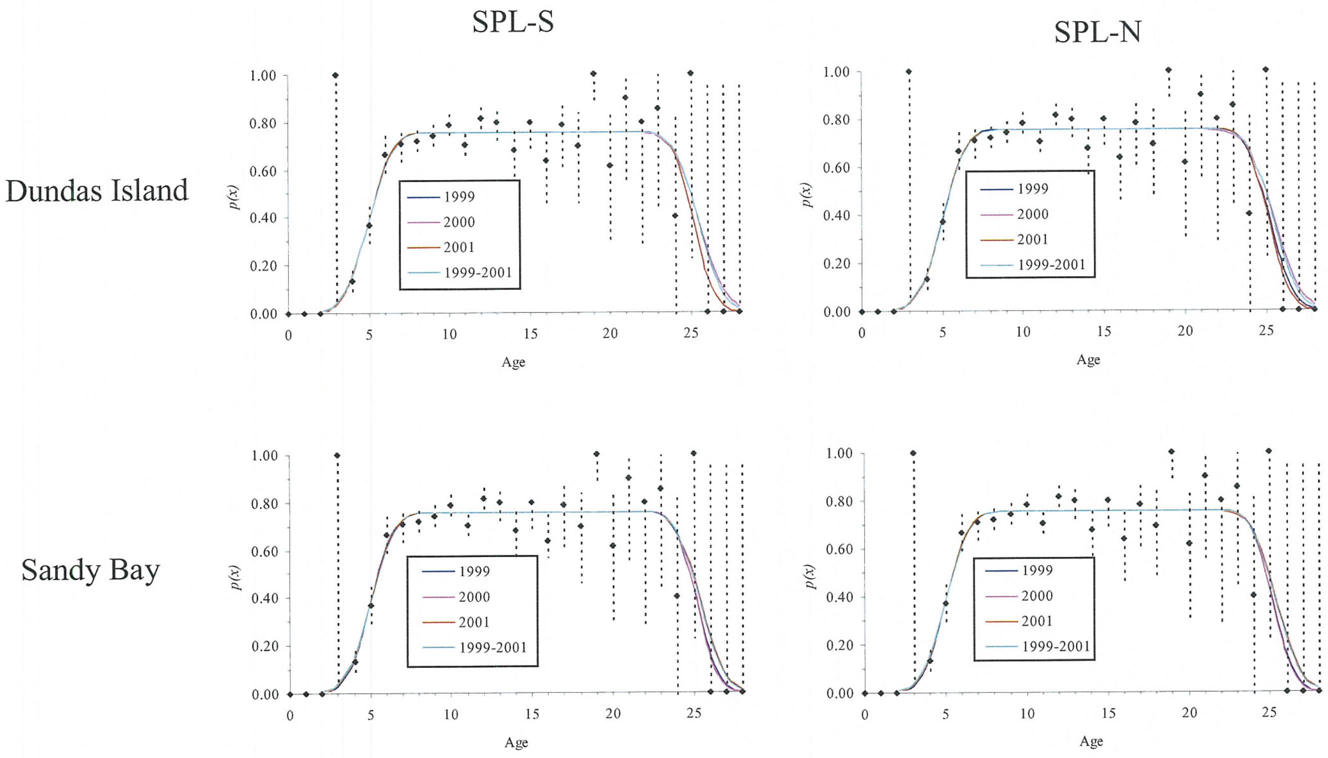


**Figure 8.5** Comparisons of estimates of reproductive rate $\hat{p}_2(x)$ from Sea Lion Population (SLP) modelling by site (Dundas Island, Sandy Bay, Dundas Island + Sandy Bay combined) and year (1999, 2000, 2001, 1999 - 2001 combined) for stationary (SLP-S) and non-stationary (SLP-N) populations. Diamonds are observed values of reproductive rate *p(x)* with are exact 95% confidence intervals (dashed lines). Note: in most cases the curves overlap considerably with each other and therefore it is not possible to see the individual curves.

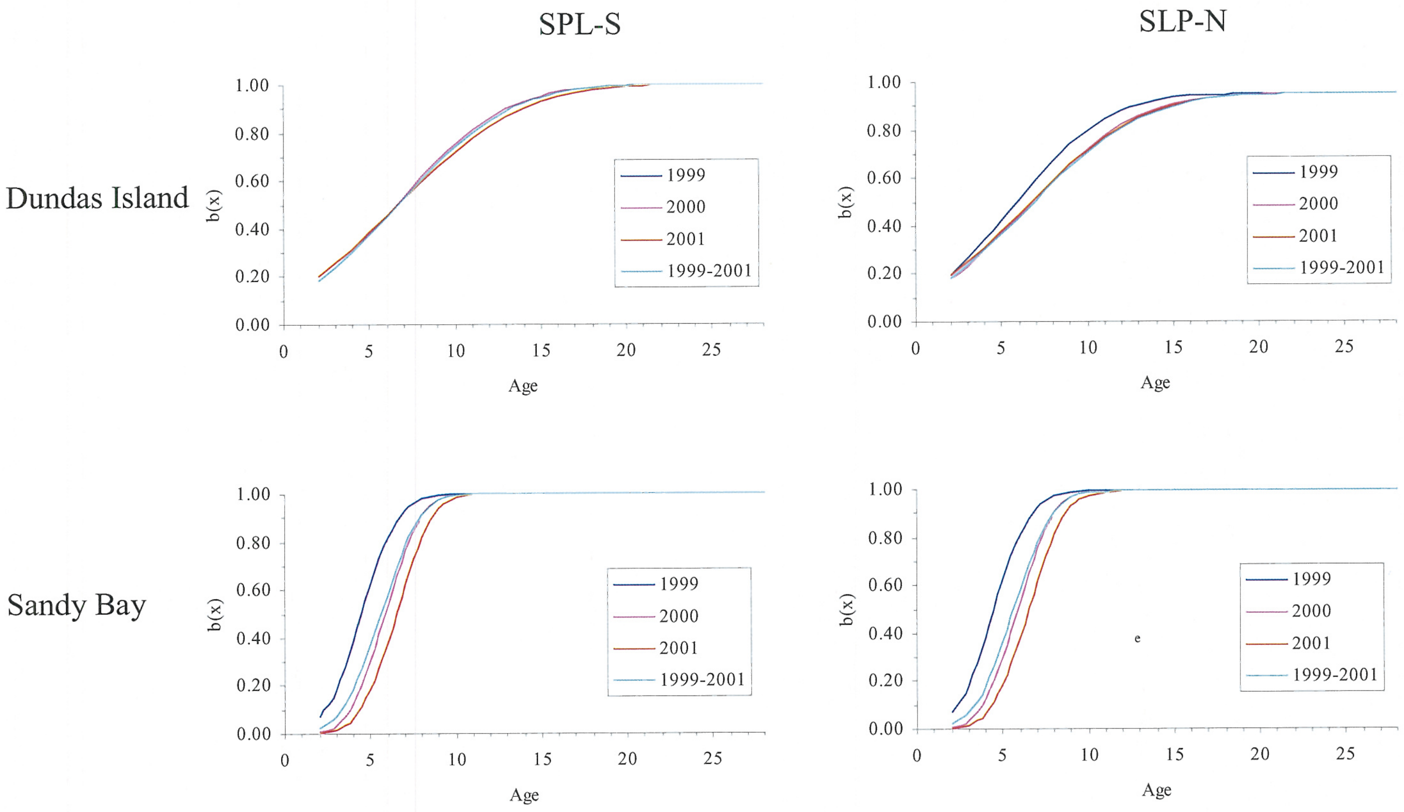


**Figure 8.6** Comparisons of estimates of maturity rate *b(x)* from Sea Lion Population (SLP) modelling by site (Dundas Island, Sandy Bay, Dundas Island + Sandy Bay combined) and year (1999, 2000, 2001, 1999 - 2001 combined) for stationary (SLP-S) and non-stationary (SLP-N) populations

*Age-specific survival rate s*

In general, the models estimated *s* as following an approximately simple linear relationship, with a general decline with increasing age (Figure 8.7). However, at Sandy Bay in 1999 and at Dundas Island in 2001, *s* showed a rapid decline at ages greater than 15 and 20 respectively. This is most likely due to the lack of older individuals sampled at those sites in those years and provided no data for the model to fit to at these ages (no individuals >21 at Sandy Bay in 1999; no individuals >23 at Dundas Island in 2001). There was no evidence of any inter-annual trend in *s* for either model or at either site (Figure 8.7). However, there was some evidence of an inter-site effect for *s* with Dundas Island having higher estimates than Sandy Bay for the SLP-S model although this difference was not evident for the SLP-N model (Figure 8.7). There was also a model effect for Dundas Island with SLP-S having higher estimates than SLP-N, although this effect was not apparent at Sandy Bay (Figure 8.7). Survivorship *l(x)* is a direct function of *s*, and therefore followed a similar pattern to that reported for *s* (Figure 8.8). For comparable years, estimates of *l(x)* were higher for Dundas Island than for Sandy Bay for the SLP-S model, but Sandy Bay was generally slightly higher than Dundas Island for the SLP-N model (Figure 8.9).

**Table 8.2** Estimates of age at sexual maturity calculated from the Sea Lion Population model (SLP) for lactating New Zealand sea lions for stationary (SPL-S) and non-stationary (SLP-N) populations. Notation: EASM = Earliest age at sexual maturity; $ASM_{50}$ = Age when 50% of females are sexually mature; $ASM_{95}$ = Age when 95% of females are sexually mature.

| | | SLP-S | | | SLP-N | | |
|---|---|---|---|---|---|---|---|
| Colony | Year | EASM | $ASM_{50}$ | $ASM_{95}$ | EASM | $ASM_{50}$ | $ASM_{95}$ |
| Dundas Island | 1999 | 2 | 7 | 15 | 2 | 6 | 17 |
| | 2000 | 2 | 7 | 15 | 2 | 7 | 17 |
| | 2001 | 2 | 7 | 16 | 2 | 7 | 18 |
| | 1999-2001 | 2 | 7 | 15 | 2 | 7 | 18 |
| Sandy Bay | 1999 | 2 | 5 | 8 | 2 | 5 | 8 |
| | 2000 | 2 | 6 | 9 | 2 | 6 | 9 |
| | 2001 | 3 | 6 | 9 | 2 | 6 | 9 |
| | 1999-2001 | 2 | 5 | 9 | 2 | 6 | 9 |
| Both | 1999-2001 | 2 | 6 | 10 | 2 | 6 | 11 |

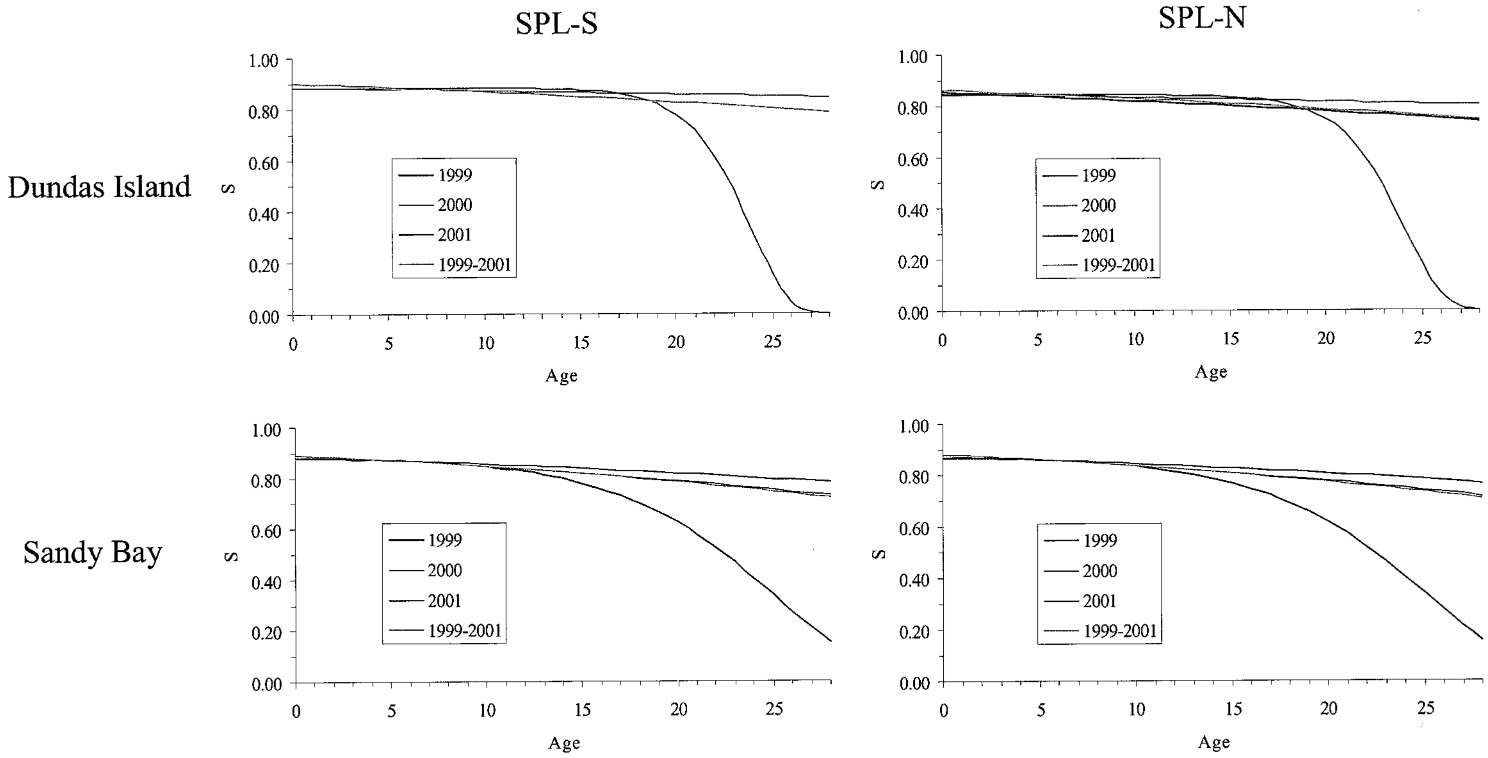


**Figure 8.7** Comparisons of estimates of age-specific survival rate ($s$ and $\tilde{s}$) from Sea Lion Population (SLP) modelling by site (Dundas Island, Sandy Bay, Dundas Island + Sandy Bay combined) and year (1999, 2000, 2001, 1999 - 2001 combined) for stationary (SLP-S) and non-stationary (SLP-N) populations.

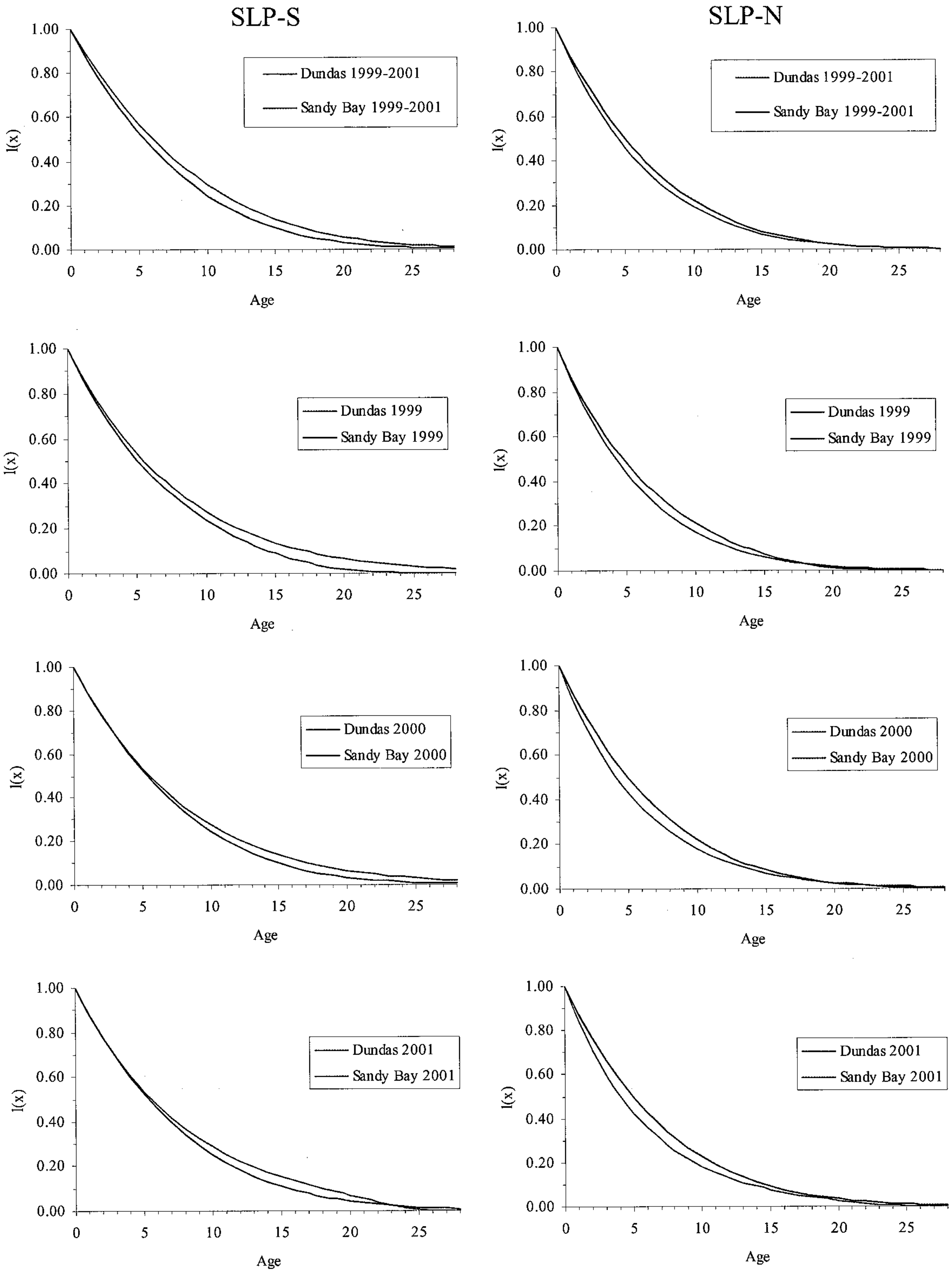


**Figure 8.9** Estimates of survivorship *l(x)* from Sea Lion population (SLP) modelling by site (Dundas Island, Sandy Bay, Dundas Island + Sandy Bay combined) and year (1999, 2000, 2001, 1999 - 2001 combined) for stationary (SLP-S) and non-stationary (SLP-N) populations, with a focus on inter-site effect.

*Mean survival rate*

Mean annual survival rates from the SLP-S and SLP-N models are shown in Table 8.1 by site, year and for combined data sets. Adjusting the SLP-S model to account for a non-stationary population with observed rates of population decline (i.e. SLP-N) resulted in lower estimates of mean survival rate for all sites and years (Figure 8.3b). There was no clear evidence of an inter-annual or inter-site or model effect given the overlapping 95% confidence intervals (Figure 8.3b).

## 8.5 DISCUSSION

### *8.5.1 Selection of the "best" models*

*Population status*

Two hypotheses result from the interpretation of the pup production estimates: (i) given that pup production estimates were stable across the three-year study period; the population was also stable over that period and is therefore stationary; and (ii) while pup production was stable over the study period, over the longer term there is a consistent downward trend for both sites, albeit with considerably different population trajectories for each site (i.e. Dundas Island -0.048, Sandy Bay -0.012). Given the extensive data series demonstrating a decline in pup production at both breeding colonies, the first hypothesis is illogical, and therefore I have assumed that the population is in decline and the models must be adjusted accordingly. Therefore the CR-N and SLP-N models are likely to be more realistic and more robust than the CR-S and SLP-S models.

The underlying assumption behind this conclusion is that pup production is a reliable indicator of population status. Pup production is regarded as the best index of relative population size in pinnipeds (Berkson & DeMaster 1985). It has been used as an indicator of population status for many pinniped species, including for the estimation of the rate of population change (e.g. Antarctic fur seal *Arctocephalus gazella*, Boyd *et al.* 1990; Steller's sea lion *Eumetopias jubatus*, York 1994; South American fur seal *A. australis*, Lima & Paez 1997; NZSL, Gales & Fletcher 1999). Pup production estimates are, however, potentially biased indicators of population status. It is possible, for example, that certain combinations of life history parameters can lead to the appearance of a stable population when in fact there is a change occurring in the age-distribution (Caughley 1974; Eberhardt 1988). For example, a decline in reproductive rate in an increasing population could falsely imply population stability, and vice versa. Either of these situations would be difficult to detect without concurrent monitoring of other life history parameters in addition to pup production. For NZSL, pup production is the only available long-term indicator of population and therefore is the most efficient method of adjusting for a non-stationary population in the absence of data on absolute population status.

The age-distribution of Sandy Bay showed significant inter-annual variation, although this same pattern was not seen at Dundas Island (Chapter 5). Inter-annual variation in age-distribution is a potential indicator of population change and could be related to the declines seen in pup production. However, this remains equivocal, given the larger reduction in pup production seen at Dundas Island and the lack of any inter-annual variation in age-distribution there. Another potential source of differences in age distributions could be higher levels of bycatch at one of the colonies. This potential effect would be difficult to quantify given it is not possible to determine which colony bycaught sea lions come from.

### *Model choice: CR or SLP?*

Estimates of mean annual adult survival rate from the CR-N and SLP-N models were similar. Precision for the CR model was considerably better than for the SLP-N model, as would be expected given that it is a simpler model. However, a key issue for both models is whether their underlying assumptions are met. How well the models meet these assumptions, will influence the degree of bias associated with the estimates. The data sets used in each model appear to be generally consistent with the assumptions, with a key exception being that the age distribution data is representative of breeding females and not all females. Therefore changes seen in the distribution by age are a function of both survival and reproductive rate. From the analysis of reproductive rate in the SLP model, it is evident that reproductive rate is not constant over all age classes. Therefore to accurately estimate survival from the age distribution, it is necessary to account for variation in reproductive rate. This cannot be done in the CR-N model and therefore the SLP-N model is to be preferred as it addresses this source of bias in the data set.

As a general rule of thumb, simpler models are likely to have higher precision but higher bias, whereas more complex models will have less precision and lower bias. Selecting a "best" model is therefore likely to involve tradeoffs between precision and bias. This is evident in the comparison with the CR-N model having a higher level of precision that the SLP-N model, although somewhat surprisingly the mean estimates of survival are very similar.

Overall, for the estimation of mean adult survival rate the SLP-N model is to be preferred as although it has a lower level of precision it better meets the assumptions and is therefore less likely to be biased. It addition, SLP-N model provides age-specific estimates of survival, reproductive and maturity rates which are essential in investigating NZSL demographics.

*Inter-annual and inter-site variation*

There was no evidence of any inter-site or inter-annual effect for either the CR-N or the SLP-N models. This suggests that the most robust estimate of mean adult survival rate and age-specific survival rates would come from the data set combining both sites and all years. In addition, it has been suggested that pooling age-distributions over several years acts to smooth any deviations from a stable age-distributions owing to observed annual variation in births (Chapman 1964).

In summary, the most robust estimates of mean adult survival and age-specific demographics will come from the SLP-N model using the combined data set.

### 8.5.2 Estimation of "best" survival rates

I considered using life tables for the estimation of survival but these were not able to be constructed from these data for two reasons: (i) Life tables require cohort size to decrease with age but in this study cohort size increased until age 8 or 9 and declined after that so estimates could not be used for individuals younger than this, and (ii) the observed decrease in cohorts older than age 8 or 9 was a combination of survival and reproductive rates and it was not possible to tease apart the relative influence of these two rates. Both of these factors result from the exclusive sampling of reproductive females. Instead, I utilised demographic modelling that included parameters for both survival and reproductive rates that could separately account for these parameters.

The best estimate of $\tilde{s}$ between the ages of 9 and 28 for lactating NZSL is 0.81 (SE = 0.04). This estimate is very close to an unpublished estimate for NZSL of 0.80 (SE = 0.02) produced by Breen & Kim (2006). The Breen & Kim estimate, however, spans the ages 9 to 21 rather than 9 to 28 as in this study. Other authors have estimated $s$ for NZSL at between 0.75 and 0.95 but most estimates have been little more than inferred guesses based on reports from other species with few NZSL observations (Doonan & Cawthorn 1984; Woodley & Lavigne 1993; Gales & Fletcher 1999; Manly & Walshe 1999; Lalas & Bradshaw 2003). Lalas & Bradshaw (2003) used simulation modelling to suggest that the most realistic values for mean

$s$ for NZSL between the ages of 1 and 24 is 0.85. York (1994) estimates mean $s$ as 0.80 (SE = 0.01) between the ages of 9 and 28 for Steller's sea lions that have a similar longevity as NZSL. In comparison to other otariids, the value of 0.81 estimated in this study is within the range of estimates reported for fur seals (Wickens & York 1997). This estimate of survival has been derived for female NZSL and, based on considerably different life history patterns, it is not reasonable to assume an equivalent rate for males. Therefore, there is an urgent need to investigate male survival to determine if there is any differential mortality between the sexes.

The best estimate from the SPL-N model of age-specific $\tilde{s}$ for lactating NZSL followed a simple linear relationship, with a general decline from 0.84 at age 0 to 0.78 at age 28. Siler's (1979) competing risk model was used to estimate age-specific survival in the SPL-N model. It was expected that NZSL mortality follows a typical "U"-shaped mammalian pattern, with an initial period of high juvenile mortality, followed by a period of relatively low mortality, and concluding with a period of rapidly increasing senescent mortality (Caughley 1977; Barlow & Boveng 1991; Sibly *et al.* 1997). This pattern has been confirmed in other otariid seals for which full age-mortality models are available (e.g. Northern fur seal *Callorhinus ursinus*, Chapman 1964; Antarctic fur seal, Boyd *et al.* 1995; Steller's sea lion, York 1994; South American fur seal, Lima & Paez 1997). Despite this, the best fit from the SPL-N model for age-specific $s$ was a simple linear relationship with little evidence of conformity to the expected pattern. This result was unexpected given what is known about other otariid species as it seems unlikely that NZSL does not show a "U"-shaped mortality curve. If this is the case, then the model has appeared to estimate a mean value of $\tilde{s}$ over all the ages, rather than estimating true age-specific $s$. The most likely explanation for this is the lack of younger (e.g. ages 1 to 3) and paucity of older (e.g. ages greater than 21) individuals in the samples, providing insufficient data for the model to fit to. In addition, it is possible that the parameterisation of the model involved tradeoffs between survival and the other parameters, reducing the fit for age-specific survival. Notwithstanding these issues, the model produces plausible estimates of adult survivorship that are consistent with other otariids (Figure 8.10).

### *8.5.3 Juvenile survival rates*

One of the aims of this work was to investigate the feasibility of estimating juvenile survival rates from age-distribution data. While the model successfully generated estimates of juvenile survival, it is not clear just how accurate these are. For instance, NZSL pup survival to 60 days-old has been estimated reliably from mark-recapture data at Sandy Bay, having a mean of 0.78 (SE = 0.06) (Chilvers *et al.* 2006a) whereas age-specific survival for age 0 is estimated at 0.85 from the SLP-N model. Steller's sea lions have a mean survival for ages 0 to 2 of 0.78 (York 1994) compared with 0.85 for NZSL from the SLP-N model (Figure 8.10). These results indicate that the age-specific survival estimates for young NZLS are biased high and are probably unrealistic. However, while age-specific estimates for young age classes may appear biased, the estimates of survivorship may be more useful as the general pattern of survivorship maybe more realistic. For example, survivorship to the age at the peak of the distribution (e.g. age 9) may be a useful estimate of recruitment and reflect mean annual survival to this age. The value from the model for NZSL is 0.21, very similar to that estimated for SSL of 0.24 (York 1994). Additional data would be required to estimate juvenile age-specific survival robustly. Such data are difficult to obtain because young individuals are rarely seen at breeding colonies but pup tagging and resighting studies are underway at Sandy Bay to address this issue over the long term.

### *8.5.4 Estimates of other biological parameters*

Estimates of $\hat{p}_2(x)$ followed a consistent pattern of recruitment into the breeding population starting at age 3, peaking and reaching a plateau at age 7, and then declining around age 23. The maximum estimate of $\hat{p}_2(x)$ was 0.75 for the plateau that spanned the range from age 9 until age 21. Overall, mean $\hat{p}_2(x)_{3-28}$ was 0.67 from SLP-N model and was consistent with the value of 0.67 estimated both directly from the data *p(x)* and from the fitted model $\hat{p}_1(x)$ in Chapter 6. From simulation modelling and observations of breeding females, Lalas & Bradshaw (2003) suggested that the most realistic values for reproductive rate for NZSL is 0.50 for age 4 and 0.75 for ages 5 to 25. My estimate is lower than the Lalas & Bradshaw estimate, but theirs is based on observations of NZSLs around Otago whereas mine is from the Auckland Islands individuals. These finding are consistent with preliminary investigation of the two data sets that supports a difference in reproductive rate between the two sites, with Otago NZSLs appearing to reach sexual maturity earlier and maintaining a higher reproductive rate. This also consistent with the idea that Auckland Islands may be affected by density dependence.

As discussed in Chapter 6, the choice of the model shape for $\hat{p}_2(x)$ was determined from consideration of the reproductive patterns of other otariid species. The generally observed pattern is a rapid increase following age at first reproduction, flattening off for mature individuals, and then rapidly decreasing at older ages. This pattern has been reported from many other otariid species including Steller's sea lions (Pitcher & Calkins 1981); Northern fur

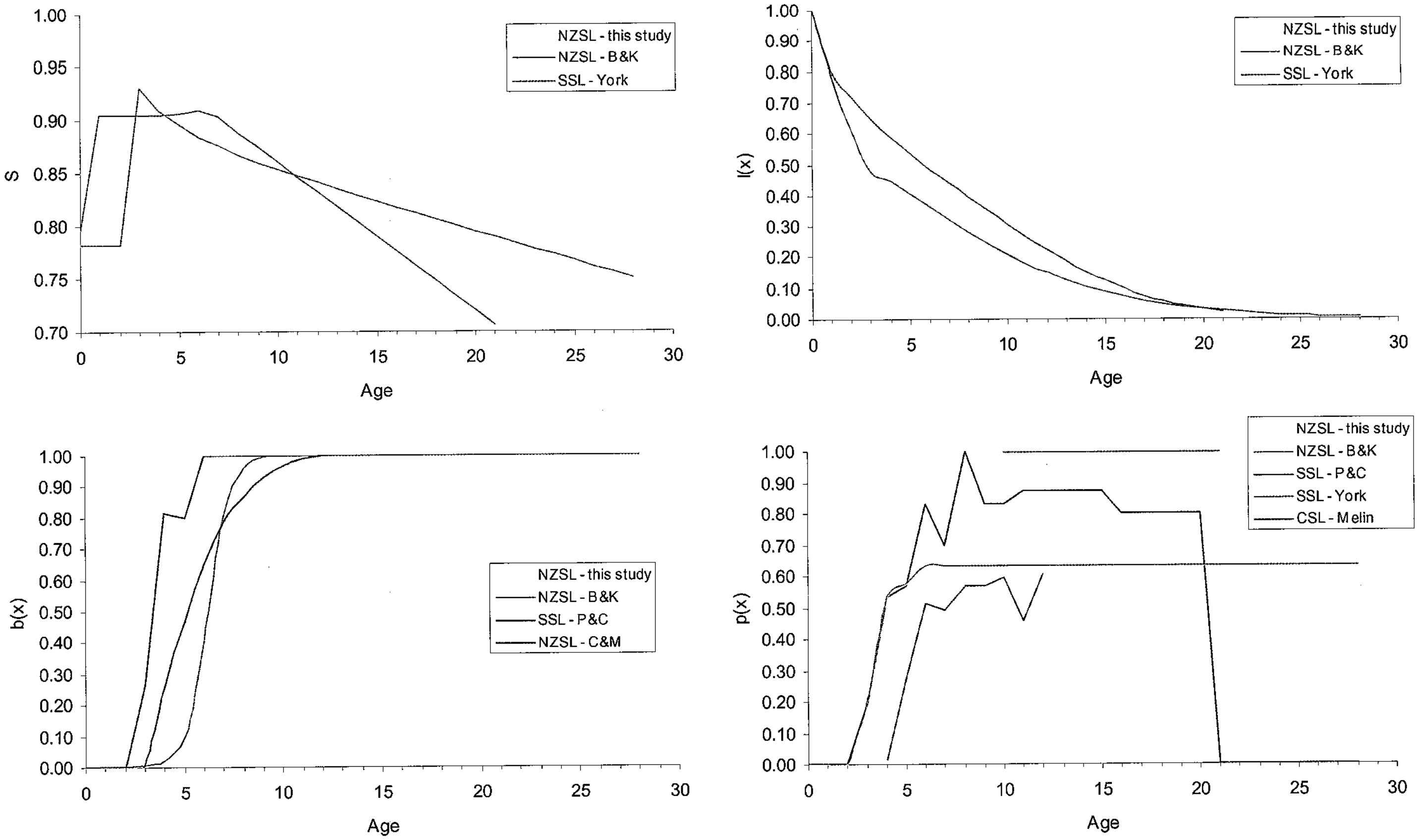


**Figure 8.10** Estimates of life history parameters using the SLP-N model for New Zealand sea lions (NZSL) compared with estimates from other sea lions. Data sets include: *NZSL - this study*: NZSL Dundas Island and Sandy Bay 1999 - 2001 (this study); *NZSL - B&K*: NZSL Dundas Island and Sandy Bay 1999 - 2001 (Breen & Kim 2006); *SSL - York*: Steller's sea lion (York 1994); *SSL - P&C*: Steller's sea lion (Pitcher & Calkins 1981), *NZSL - C&M*: NZSL Sandy Bay (Chilvers & McKenzie *unpublished data*); *CSL - Melin*: Californian sea lion (Melin 2002). Notation: $s$ age-specific survival rate; $l(x)$ survivorship rate; $\hat{p}_2(x)$ age-specific reproductive rate; $b(x)$ age-specific maturity rate

seals (Lander 1981); South American fur seals (Lima & Paez 1995); sub-Antarctic fur seal *A. tropicalis* (Bester 1995, Dabin *et al.* 2004) but is not a feature of all fur seals (Antarctic fur seals, Boyd *et al.* 1995). Several other curves were explored in fitting the observed reproductive data, but the $\hat{p}_2(x)$ model was selected as it has considerable flexibility in shape and it best fitted the observed data.

L. Chilvers (*unpublished data* in Breen & Kim 2005) reported a mean reproductive rate of 0.77 (SE = 0.13) from resightings of branded females at Sandy Bay. The data set used by Chilvers was a subset of the data set used in this study. It does not include many young individuals, and so is likely to be biased high. However Chilver's estimate is similar to the plateau level of 0.76 reported in this study. Breen & Kim (2006) provide an estimate of reproductive rate of 0.99 for mature females. This value is not realistic given the observed breeding behaviour of NZSL reported in this paper. The mean observed mean reproductive rate of 0.67 for NZSL is among the lowest recorded from any sea lion (e.g. Steller's sea lion, 0.63, Pitcher & Calkins 1981; Australian sea lion, 0.71, Higgins & Gass 1993; California sea lion *Zalophus californianus*, 0.77 for ages 6 to 12, Melin 2002) (Figure 8.10) and would place NZSL among the slowest reproducing sea lion.

The observations that were used to model reproductive rate were all made at Sandy Bay. There is no equivalent set of observations from Dundas Island. If there is a difference in reproductive rate between the colonies, it is unlikely to be reflected in the modelling, and hence the accuracy of estimates for other parameters at Dundas Island is also likely to be less reliable. While there is no evidence to suggest a difference in reproductive rate between the colonies, there is an urgent need to collect site-specific estimates of reproductive rate. In the absence of site-specific values, assuming that the Sandy Bay data are representative of both sites is the most reasonable approach.

Overall estimates of *b(x)* for the total data set were age 6 for $ASM_{50}$ and 11 for $ASM_{95}$. These values and the general shape of the function were similar to other estimates from NZSL (Chilvers & McKenzie *unpublished data*; Breen & Kim 2006) and other species (Pitcher & Calkins 1981) (Figure 8.10). There was evidence of an inter-site effect in *b(x)* with $ASM_{95}$ considerably later (i.e. age 9 vs. age 18) for Dundas Island although $ASM_{50}$ for both sites were comparable. The apparent difference in $ASM_{95}$ between colonies is consistent with the observed difference in age distribution (Chapter 5) but the actual mechanism for this difference remains unclear.

### *8.5.5 What does this mean for NZSL?*

NZSL have vital rates comparable to other closely related species. This study has provided robust estimates of mean survival and reproductive rate. The latter is the first robust estimate for this species and among the lowest reported for any sea lion species. There is no evidence of any inter-annual or inter-site differences in vital rates except for evidence of a difference in maturity rate between sites. The major implications of this work are in the application of these vital rates to the investigation of the effect of fisheries bycatch on NZSL. To date, the Bayesian population model developed for this purpose (Breen *et al.* 2003, Breen & Kim 2006) has generated some biologically unrealistic values (e.g. mean adult female reproductive rate >0.98, first year survival ~80%) and has been fitted to scant and out-of-date information (e.g. maximum age of 22). While there remain some fundamental flaws with the basic model structure (Goodman 2003; Slooten 2005), the reliability of the model's outputs would nevertheless be improved by updated and accurate inputs. Given the complexity of the Breen & Kim model it is difficult to assess how this new information will impact on the results, but changes could be large and significant. However, the impact of these new data will result in reduced estimates of survival, reproductive and population growth rate from those reported from the Breen & Kim model at present, which will therefore lead to reduced levels of sustainable bycatch. The estimate of mean adult survival rate from the Breen & Kim model is very close to the estimate from this study but spans a much narrower age range (i.e. ages 9 to 21 vs. 9 to 28).

Low population growth and reproductive rates are consistent with a population that is occupying a marginal foraging environment. This conclusion has been proposed by other researchers on the basis of other information such as (i) NZSLs dive deeper and longer than any other otariid (Gales & Mattlin 1997; Chilvers *et al.* 2006b), (ii) NZSLs have the longest foraging trips and largest foraging areas of any otariid (Chilvers *et al.* 2005b), (iii) NZSLs have both physiological (e.g. increased blood volume; Costa *et al.* 1998) and behavioural (e.g. increased swimming performance; Crocker *et al.* 2001) adaptations but do not appear to have achieved their high level of diving performance through metabolic adaptations (Costa & Gales 2000), and (iv) The NZ sub-Antarctic ecosystem around Campbell and the Auckland Islands where NZSLs forage is known to be resource limited and have low primary production (Bradford-Grieve *et al.* 2001). These findings, along with recent significant declines in pup production, suggest that current management of the NZSL population is insufficient to ensure population stability, let alone meet the statutory goal of recovery.

The Auckland Islands squid fishery is worth up to $49 million annually (Ministry of Fisheries 2005). As a matter of routine, it is closed not due to scarcity of squid by rather the bycatch of NZSLs. A sustainable limit for the latter is estimated via the Breen & Kim model, and therefore the accuracy of this model is not only important for NZSL conservation and recovery but also for the management of the fishery. The new parameter estimates developed in this study can be used to develop more informative priors and the inclusion of the new NZSL biological data should considerably improve the model's robustness.

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# Chapter 9

# Conservation Biology of New Zealand Sea Lions: General Discussion and Conclusions

# CHAPTER 9: CONSERVATION BIOLOGY OF NEW ZEALAND SEA LIONS: GENERAL DISCUSSION AND CONCLUSIONS

## 9.1 INTRODUCTION

The research in this thesis was developed to meet identified research needs relating to the interaction between New Zealand sea lions (NZSL) (*Phocarctos hookeri*) and the 6T commercial squid fishery. These research needs were originally identified in the NZSL Recovery Plan (Gales 1995) and refined in subsequent discussions on management (Department of Conservation 1996). The aim of this thesis was for its outcomes to be directly applied to understanding and improving the management of this interaction to ensure that any impacts from the commercial fishery are minimised. Some of the results of this thesis have already been used in management. The most recent research will be presented to Department of Conservation (DOC) and Ministry of Fisheries (MFish) technical groups for review and inclusion in future management decisions.

The thesis was broken into three independent but related sections that focus on different aspects of this interaction: (i) NZSL population status, (ii) investigation of the potential indirect effects of fishing on NZSLs, and (iii) life history characteristics and demographics of the Auckland Island NZSL population. This Chapter summarises and synthesises the results of this thesis, puts them in the context of existing management and evaluates whether the existing management is appropriate. It also highlights areas for future research and potential directions for future management.

## 9.2 POPULATION STATUS

Prior to this study, the historical distribution and abundance of NZSLs was poorly understood. Archaeological and other historical records demonstrate that NZSLs were substantially more widespread before the arrival of humans in New Zealand than they are today (Childerhouse & Gales 1998 (Chapter 2)). The species used to range along the whole length of the coast, from the north of the North Island through to Stewart Island and the sub-Antarctic islands. Although there is no direct estimate of pristine abundance, the present population size is clearly reduced. Distribution has contracted, and large colonies existed on the mainland (e.g. Gill 1998) and on Stewart Island (Starke 1986), where now the species is absent or rare. Subsistence and commercial killing is the most likely cause of historical changes in distribution and abundance.

Before humans arrived, the breeding range of NZSL spanned the entire country including documented pupping sites at the northern end of both main islands: near Nelson in the South Island (Worthy 1992, 1994) and at North Cape in the North Island (Gill 1998). The present breeding range is almost entirely restricted to the Auckland Islands and Campbell Island. Within the last decade a few individuals have bred on mainland New Zealand and Stewart Island; this may reflect a slow recolonisation of earlier breeding grounds.

The present population status has been recently summarised in Chilvers *et al.* (2007) and I am a co-author. This work documents a 31% decline in pup production at the Auckland Islands between 1998 and 2006. This is a major concern for a species that is already listed as threatened. Campbell Island, the only significant breeding site outside the Auckland Islands, was thoroughly surveyed for the first time in 2003 (Childerhouse *et al.* 2005 (Chapter 3)). Using mark-recapture methodology, I estimated that 385 pups were born at Campbell Island, comprising 13 % of the total pup production for the species for 2003. This is the first robust estimate of pup production for NZSLs at Campbell Island. The figure of 385 pups is considerably higher than any of the previous estimates reported from Campbell Island, but given that previous estimates were based on incomplete or non systematic surveys, it is not possible to determine whether breeding has increased or decreased. Another survey is planned for 2008 using a comparable methodology to the 2003 survey that will allow for an assessment of whether pup production at Campbell Island is declining as has been seen at the Auckland Islands.

This research has provided a solid understanding of NZSL historical distribution and abundance which supports and underpins present management decisions. The key conclusion from my work is that the present NZSLs population is a remnant population that is slowly recolonising its former breeding range. This is in stark contrast to previously stated beliefs (mainly by representatives of the fishing industry) that the NZSL population was actually expanding and increasing their traditional range rather than recovering from past exploitation. This shift in perception is subtle but critical when considering appropriate management; a population that is seen as expanding outside its historic range would warrant a lower level of protection and conservation to a population that remains at a fraction of its former range and is slowly recovering.

## 9.3 INDIRECT EFFECTS OF FISHING

The 6T Squid fishery in the Auckland Islands catches and kills significant numbers of NZSL during fishing operations (Ministry of Fisheries 2006). This bycatch has a direct impact on the NZSL population but there is also other potential indirect effects from fisheries that may impact on the population (Chilvers et al. 2005b). I found that NZSLs are generalist feeders utilising a wide variety of prey items including fish, cephalopods, and crustaceans (Chapter 8). Prey taxa indicate that New Zealand sea lions utilise a wide variety of benthic, demersal and pelagic species ranging from the inter-tidal zone to waters deeper than 300 m. Based on this research there appears to be only a small overlap of NZSL prey species with commercially targeted species on the Auckland Islands Shelf in the months sampled. Access to the Auckland Islands is difficult and expensive, and so studies to date have concentrated on the period when NZSLs breed. The diet component of this study is limited by the lack of sampling between February and May, the time of the squid-spawning and squid fishery, and therefore the dietary overlap over this period remains unresolved. It is possible that despite being generalist feeders, squid form a seasonally important part of the diet. The timing of the squid spawning and of the fishery coincides with the period when reproductive females are likely to be in their poorest condition immediately following birth and post-partum fasting. As a result, the commercial removal of significant quantities of squid (~35,000 Tonnes annually, MFish 2005) at this time of year may have a significant impact over and above the direct impact of bycatch. So, while resource competition is possible, quantifying its nature and importance requires further detailed work.

## 9.4 POPULATION DEMOGRAPHICS AND MODELLING

An essential component of understanding demographics is the accurate estimation of age of an individual. The ageing of pinnipeds from teeth sections by reading growth layer groups is well established but methods and levels of accuracy vary between species (Scheffer 1950, Laws 1952, Payne 1978, Innes *et al.* 1981, York 1983, Arnbom *et al.* 1992, Boyd & Roberts 1993, Oosthuizen 1997). Growth layer groups (GLGs) are laid down annually or semi-annually in the dentine and cementum of teeth (Perrin & Myrick 1980, McCann 1993). The reliability of these layers in reflecting annual growth has been confirmed by tetracycline labelling in dolphins (Perrin & Myrick 1980) but in few other marine mammals. A novel method for the ageing of live NZSLs was developed (Childerhouse *et al.* 2004 (Chapter 5); Chapter 4) and demonstrated that NZSLs can be reliably aged from growth layer groups in the cementum of the lower first post-canine tooth. Although there was no significant difference between estimated and actual ages as determined from the blind ageing of known-age individuals, some bias in the ageing of younger and older individuals was evident, and corrected for via regression analysis. Accuracy in ageing was improved by discarding sets of readings with low precision and re-reading the tooth until a precise set of estimates was made. This technique is particularly important when ageing teeth from unknown individuals when precision, but not accuracy, can be estimated. This accurate and robust ageing methodology extended the sample size of aged individuals that could be used in this demographic study far beyond the small numbers of known-age and marked individuals already present in the population.

The major focus of the demographics study was the investigation of the age distribution of 865 lactating NZSLs over three years (1999 - 2001) at two breeding colonies, Sandy Bay and Dundas Island, in the Auckland Island group (Chapter 5). In addition to the sampling of age distribution, the reproductive histories of 505 marked females from the Auckland Islands were recorded from 1998 to 2005. These two data sets were used to investigate female NZSL growth, reproduction (Chapter 6) and demographics (Chapter 7).

The age distribution of reproductive females shows a strong negative skew towards younger age classes (i.e. ages <10) that is consistent with slow recruitment into the breeding pool followed by a reasonably consistent level of mortality once all females are recruited (Chapter 5). Age distribution peaked at ages 8 - 9, indicating full recruitment into the breeding population by about this age. This research demonstrated a considerably wider age range of reproductive females (between 3 and 26) than had previously been reported or estimated for this species. There was also evidence of reproductive senescence. While females up to age 28 were observed, no females over 26 were recorded as reproductive. If senescence is a strong feature of this species, it is possible that maximum female age could be older than 28 years. This is because only reproductive females were sampled during the age distribution study and few older individuals were marked (and therefore available for resighting in the second part of the study).

The age range of lactating NZSLs (Chapter 6) is wider than that reported for any other sea lion species. Age-specific reproductive rate followed a standard pinniped pattern, increasing rapidly between ages 3 and 7, reached a plateau between ages 7 and 23, and then rapidly declined after age 23. Mean observed reproductive rate for females between the ages of 3 and 26 was 0.67 (SE = 0.01). This is the first robust estimate of reproductive rate for this species, and places them among the slowest breeding of any sea lion species (e.g. 0.63 for Steller's sea lion *Eumetropia jubatus* (Pitcher & Calkins 1981); 0.71 for Australian sea lion (*Neophoca cinerea*), Higgins & Gass 1993; 0.77 for ages 6 to 12 for California sea lion *Zalophus californianus* (Melin 2002)). The estimate of reproductive rate was identical when modelled alone $\hat{p}_1(x)$ or as part of a more complex population model $\hat{p}_2(x)$.

A Gompertz model best described growth and predicted that females attained 90% of asymptotic length (161.7 cm) at age 4 and weight (112.0 kg) at age 11 (Chapter 6). These ages are similar to that reported for female Steller's sea lions at age 4 and 13 respectively (Winship *et al.* 2001). Age-specific growth rates, for both length and weight, peaked at 10% per annum at age one and declined steadily after that. While mature female Steller's sea lions are considerably larger than NZSLs (e.g. mean length and weight: 2.32 m and 273 kg; 1.79 m and 120 kg). The mean relative growth rates were 5% and 30% lower for NZSLs than Steller's sea lion for length and weight respectively. NZSLs appear to be the slowest growing sea lion species, although comparable data are only available for Steller's sea lions. Two potential limitations of this research included a focus on lactating females that may have resulted in positively biased growth (i.e. as reproductive females have been shown to have higher growth rates than non reproductive females (Winship *et al.* 2001)). Additionally, as these estimates are for Auckland Island females, they may not be indicative of growth for females in other parts of their range (e.g. Campbell Island ~200 km south; Otago Peninsula ~600 km north).

Population modelling was used to further explore demographic rates of female NZSL in Chapter 7. Based on an observed decline in pup production over the period 1998 to 2006 (Chilvers *et al.* 2007), the population was assumed to be in decline and therefore non-stationary. The decline in pup production is assumed to reflect a real decline in population abundance, as no independent data are available on population abundance (and it is difficult to see how they could be obtained). Two different models were used to estimate and investigate female NZSL demographic rates. Mean annual adult survival rate was estimated at 0.81 (SE = 0.04) using a multi-parameter (i.e. survival, maturity, reproductive rate) model fitted using maximum likelihood and adjusted for a non-stationary population with a known rate of change using the method developed by Eberhardt (1988). This is the first robust estimate of mean survival for this species. Age-specific demographic values were also estimated including adjustment for a non-stationary population and the incorporation of Siler's (1979) competing risk model for the estimation of age-specific survival. Estimated age-specific survival followed a simple linear relationship, with a general decline from 0.84 at age 0 to

0.78 at age 28. Independent research has confirmed that some of these values are biologically implausible (e.g. survival at age 0, Chilvers *et al.* 2006a). This linear relationship was unexpected given that mortality in mammals generally follows a "U" shaped curve (Caughley 1977). The linear relationship estimated in this study most likely reflect a lack of young and individuals in the sample (because only reproductive females were sampled) and a paucity of old individuals. Hence insufficient data were available to fit the true pattern. Notwithstanding these issues, the model produces plausible estimates of adult survivorship that are consistent with that reported for other otariids (York 1994; Boyd *et al.* 1995; Wickens & York 1997).

There was no evidence of any inter-site effect for either survival, reproductive or growth rate but there was an inter-site effect evident for maturity rate, with Dundas Island having an older mean and median age (Chapter 7). This result was reinforced by the significantly older age distribution observed at Dundas Island. However, it is important to note that these analyses are based on the same data set and therefore are not independent. Inter-site differences in age distribution are mostly likely driven by different demographics. A difference in the proportion of females that are mature could explain the observed inter-site difference, even if reproductive and survival rates are similar. However, a substantial limitation on the population modelling was that there was no reproductive data available from Dundas Island, and therefore data from Sandy Bay were used to model reproductive rate at both sites.

The large sample sizes for age distribution make the significant observed difference between the colonies more robust than results from the modelling. This is because the maximum likelihood fit will generally lead to trade offs among parameters unless there is a strong signal in the data. The conclusion of an inter-site difference in age distribution and maturity rate is strongly suggestive of real demographic differences but without site-specific estimates of reproductive rate, it is unlikely that any difference in survival (if it exists) will be found.

There are other data that provide further support for inter-site differences, including significantly different levels of decline in annual pup production (e.g. Dundas -4.8%; Sandy Bay -1.2%) and higher rates of male harassment of females at Sandy Bay (Chilvers *et al.* 2005a). Females are highly philopatric to the natal colony (Chilvers *et al.* 2005a; Robertson *et al.* 2006), and therefore the female components of the two colonies are effectively isolated from each other, allowing the potential for the development of site-specific differences. Even so, the observed inter-site differences seem surprising given that the two colonies are less than 10 km apart and breeding females from both colonies appear to forage in similar areas (L.

Chilvers *pers. comm.*). This suggests that females at both colonies are subject to similar environmental pressures and constraints. If external pressures are truly equivalent between the colonies, then an intrinsic factor (e.g. density dependence) is the most likely cause of differences between the two colonies.

There is no obvious explanation for the differences between the two colonies; the data do not point to any single factor. It has been shown that larger colonies have an increased net reproductive performance (e.g. Southern sea lions (*Otaria flavescens*), Campagna *et al.* 1992). Dundas has four times the annual pup production of Sandy Bay but has a higher rate of decline in pup production - the opposite of what would be expected if this was factor was important. Given that the colony at Dundas Island is considerably larger, density-dependent factors could be higher there. Availability of space for pupping does not appear to be a factor at either colony as both sites offer room for expansion although it is not clear what constitutes acceptable breeding and birthing habitat for NZSLs. Natural erosion has reduced the amount of sandy beach at Dundas Island, requiring more females to give birth on hard substrates, and this may increase pup mortality. Sandy Bay has higher rates of male harassment of females (Chilvers *et al.* 2005a) but again the impact of this on demographics is unknown. However, without site-specific demographic information from both colonies, density-dependent factors will remain unresolved. Other factors could include differential bycatch effecting mortality or different prey preferences related to different foraging strategies but preliminary analysis suggests that both colonies share common feeding grounds (Chilvers *et* al. 2005b, L. Chilvers *pers. comm.*) and so this seems unlikely.

There are insufficient data to determine the cause(s) of site-specific differences. The key conclusion is that the colonies have different demographics, and therefore need to be treated independently in any modelling exercise. Ideally this would include the estimation of separate demographic values based on site-specific data sets. Furthermore, observed inter-annual variation in age distribution at Sandy Bay, indicates a need for temporal as well as spatial structuring of any model.

## 9.5 FUTURE RESEARCH IDEAS

The research described in this thesis has highlighted several topics for further work, including:

- Collection of site specific data on demographics at Dundas Island and Figure of 8 Island as both colonies are showing large declines;
- Development of new population models with spatial and temporal structuring, potentially using Bayesian methods;
- Investigation of demographic and individual growth parameters on populations other than the Auckland Islands (e.g. Campbell Island, Otago Peninsula) as these may provide evidence of whether the Auckland Islands actually represents a marginal foraging environment for NZSLs;
- Further investigation of potential resource competition via better understanding of NZSL spatial and temporal partitioning of diet at the Auckland Islands, including ecological and energetic modelling. It would be advantageous if spatial and temporal data on squid catch rates could be included in this analysis;
- Development of accurate variance estimators and the exploration of model differences using AIC methods; and,
- Integration of the new information from this thesis into existing population and management models.

## 9.6 SYNTHESIS AND CONCLUDING REMARKS

This research has shown that NZSLs broadly fit within the generalised otariid and mammalian life history pattern characterised by large size, long lived, delayed sexual maturity, low fecundity, high survival, and slow reproductive rate (Renouf 1991; Boness 2002). These traits define NZSLs as *K*-selected animals, although not as an extreme *K*-selected species (e.g. sperm whales) (Boyce 1984). The evolution of these characteristics is related to their semi-aquatic lifestyle, the high temporal and spatial variability in the distribution of resources in the marine environment (Lunn *et al.* 1994; Boyd *et al.* 1995), and their evolution from a terrestrial carnivore ancestor (Berta & Wyss 1995; Berta & Sumich 1998).

The main focus of this thesis was the estimation of new demographic information to support the management of the NZSL – Squid fishery interaction. The major implications of this work will become apparent with the integration of these new demographic estimates into the modelling of fisheries bycatch effects on NZSL. Regrettably, this has not yet been possible as the Breen & Kim model is not publicly available but data from this thesis have been made available to the model developers for integration into future model runs. To date all demographic information for NZSLs has been derived from the observation of individuals at

Sandy Bay only. This thesis documents significant differences between the two colonies and indicates that demographics are not the same at the two colonies. The extrapolation of demographic information from Sandy Bay to Dundas Island is therefore neither appropriate nor acceptable in the management of a threatened species. As a matter of some urgency, the new information should be incorporated into the existing process for setting sustainable levels of NZSL bycatch. In addition, existing models for managing this interaction currently use unrealistic demographic values and therefore cannot provide robust guidance. The application of this new demographic information has the potential to significantly alter the existing management advice on the impact of the 6T squid fishery on the NZSL population.

This thesis has demonstrated that NZSL is among the longest lived, slowest growing and slowest reproducing sea lion species. Taken alone, these results suggest a dim outlook for an already threatened species. In the context that pup production is known to be in significant decline, and the species' foraging environment is thought to be marginal, and that resource competition may also be having an impact, the picture darkens further. Taken as a whole, these data suggest that current management is insufficient to ensure population stasis, let alone meet the Government's statutory goal of recovery. With respect to NZSL bycatch, perhaps we should be asking ourselves not how can we better estimate a sustainable level of bycatch, but rather should we using a catch limit at all? Allowable levels of bycatch have steadily increased since a catch limit was imposed in 1993, despite a population that is declining significantly. To date the evidence of decline in this population has had little influence on allowable levels of bycatch. Alternative management techniques such as area closures and/or gear restrictions would likely lead to significant reductions in NZSL bycatch and reduce or eliminate any potential resource competition between the fishery and NZSLs. The NZSL is clearly in need of urgent and effective management action. Despite active management intervention over the last decade, this threatened species is clearly at a critical point in its "recovery". Without improved management and some real leadership by DOC and MFish, this species is likely to achieve a higher threat classification, and will fail to reach the stated Government objective of, "achieving non threatened status within 20 years" (DOC 1996).

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# Appendices

# APPENDIX 1:

Citations for scientific publications on other aspects of New Zealand sea lion research that I have lead- or co-authored are show below. These do not appear in my thesis as they are not directly relevant to the topic of my thesis or I was not the primary author of these papers:

Chilvers, L., Wilkinson, I., **Childerhouse**, S. 2007. New Zealand sea lion, *Phocarctos hookeri*, pup production - 1995 to 2006. New Zealand Journal of Marine and Freshwater Research 41: 205-213.

Campbell, R.; Chilvers, L.; **Childerhouse**, S.; Gales, N. 2006. Conservation Management Issues and Status of the New Zealand (*Phocarctos hookeri*) and Australian (*Neophoca cinerea*) Sea Lion. *In*: Trites, A.; Atkinson, S.; DeMaster, D.; Fritz, L.; Gelatt, T.; Rea, L.; Wynne, K. (eds.). Sea lions of the world. Alaska Sea Grant College Program, University of Alaska Fairbanks. p. 58-74.

Bradford-Grieve, J., Probert, K., Nodder, S., Thompson, D., Hall, J., Hanchet, S., Boyd, P., Zeldis, J., Baker, A., Best, H., Broekhuizen, N., **Childerhouse**, S., Clarke, M., Hadfield, M., Safi, K., Wilkinson, I. 2003. Pilot trophic model for subantarctic water over the Southern Plateau, New Zealand: a low biomass, high transfer system. Journal of Experimental Marine Biology and Ecology 289: 223-262.

**Childerhouse**, S.; Gales, N. 2001b. Fostering behaviour in the New Zealand sea lion *Phocarctos hookeri*. New Zealand Journal of Zoology 28: 189-195.

NcNally, N., Heinrich, S., **Childerhouse**, S. 2001. Distribution and breeding of New Zealand sea lions *Phocarctos hookeri* on Campbell Island. New Zealand Journal of Zoology 28: 79-87.

Wilkinson, I., **Childerhouse**, S., Duignan, P., Gulland, F. 2000. Observations of cannibalism in New Zealand sea lion. Marine Mammal Science 16(2): 494-500.

Gales, N., **Childerhouse**, S. 1999. Field observations and sampling regime. *In*: Baker, A. (ed.). Unusual mortality of the New Zealand sea lion, *Phocarctos hookeri*, Auckland Islands, January-February 1998. Report of a workshop held 8-9 June 1998, Wellington, and a contingency plan for future events. DOC, Wellington, NZ. 84 p.

# APPENDIX 2:

Details of known-age female New Zealand sea lions used in the estimation of ageing bias from Growth Layer Groups (GLGs) in the cementum of post canine tooth (PCI) including the estimated mean age from tooth readings.

| Original tag # | New tag # | Date of capture | Age (yr) | Estimated mean age from GLG readings (yr) |
|---|---|---|---|---|
| UK | NT | 20/02/1987 | 4 | 4.33 |
| UK | NT | 20/02/1987 | 4 | 5.00 |
| UK | NT | 20/02/1987 | 4 | 5.00 |
| UK | NT | 20/02/1987 | 4 | 5.33 |
| UK | NT | 20/02/1987 | 5 | 6.33 |
| UK | NT | 20/02/1987 | 6 | 4.67 |
| UK | NT | 20/02/1987 | 6 | 6.00 |
| 4264 | B1026 | 22/01/1999 | 6 | 6.33 |
| 4391 | B1031 | 28/01/1999 | 6 | 6.33 |
| 4495 | B1034 | 28/01/1999 | 6 | 6.67 |
| 4420 | B1048 | 29/01/1999 | 6 | 7.00 |
| 4517 | B1050 | 29/01/1999 | 6 | 7.33 |
| 3653 | B1005 | 19/01/1999 | 7 | 6.00 |
| 3822 | B1013 | 22/01/1999 | 7 | 6.67 |
| 3859 | B1015 | 22/01/1999 | 7 | 7.00 |
| 3592 | B1020 | 22/01/1999 | 7 | 7.33 |
| 3749 | B1022 | 22/01/1999 | 7 | 7.33 |
| 3752 | B1033 | 28/01/1999 | 7 | 7.33 |
| 3997 | B1216 | 26/01/1999 | 7 | 8.00 |
| 2776 | B1010 | 22/01/1999 | 8 | 6.67 |
| 2571 | B1016 | 22/01/1999 | 8 | 7.00 |
| 2652 | B1040 | 28/01/1999 | 8 | 7.33 |
| 2747 | B1044 | 28/01/1999 | 8 | 7.33 |
| 2716 | B1057 | 29/01/1999 | 8 | 8.00 |
| 2588 | B1105 | 6/02/1999 | 8 | 8.00 |
| 2919 | B1186 | 24/01/1999 | 8 | 8.33 |
| 2940 | B1224 | 26/01/1999 | 8 | 8.33 |
| 4231 | 0946 | 14/01/2001 | 8 | 8.33 |
| 4373 | 0964 | 22/01/2001 | 8 | 8.33 |
| 4513 | 0966 | 22/01/2001 | 8 | 8.67 |
| 4538 | 0971 | 22/01/2001 | 8 | 9.00 |
| 4425 | 0983 | 23/01/2001 | 8 | 9.00 |
| 4524 | 1473 | 24/01/2001 | 8 | 9.00 |
| 4246 | 0997 | 31/01/2001 | 8 | 9.00 |
| 4184 | 0999 | 31/01/2001 | 8 | 9.00 |
| 4290 | 1019 | 6/02/2001 | 8 | 9.33 |
| 4190 | 1028 | 6/02/2001 | 8 | 10.33 |
| 4376 | 1029 | 13/02/2001 | 8 | 10.67 |
| 2529 | B1024 | 22/01/1999 | 9 | 8.00 |
| 3107 | B1039 | 28/01/1999 | 9 | 8.00 |
| 3074 | B1054 | 29/01/1999 | 9 | 8.33 |
| 3206 | B1061 | 29/01/1999 | 9 | 8.33 |
| 3528 | 0947 | 14/01/2001 | 9 | 8.33 |
| 3577 | 0949 | 20/01/2001 | 9 | 8.67 |
| 3646 | 0955 | 20/01/2001 | 9 | 8.67 |
| 3529 | 0963 | 22/01/2001 | 9 | 8.67 |
| 3434 | 0974 | 22/01/2001 | 9 | 9.00 |
| 3835 | 0994 | 31/01/2001 | 9 | 9.00 |
| 3700 | 1002 | 31/01/2001 | 9 | 9.33 |
| 3573 | 1005 | 31/01/2001 | 9 | 9.67 |
| 3726 | 1006 | 31/01/2001 | 9 | 10.00 |
| 3469 | 1014 | 5/02/2001 | 9 | 10.00 |
| 3492 | 1023 | 6/02/2001 | 9 | 10.00 |
| 3457 | 1037 | 13/02/2001 | 9 | 10.00 |
| 3945 | 1136 | 28/01/2001 | 9 | 10.33 |
| UK | NT | 20/02/1987 | 10 | 9.00 |
| UK | NT | 20/02/1987 | 10 | 9.00 |
| UK | NT | 20/02/1987 | 10 | 9.00 |
| 2730 | 1490 | 14/01/2001 | 10 | 9.33 |
| 2744 | 1371 | 14/01/2001 | 10 | 9.33 |
| 2839 | 0975 | 22/01/2001 | 10 | 9.67 |
| 2723 | 1034 | 13/02/2001 | 10 | 9.67 |
| 3279 | 1139 | 28/01/2001 | 10 | 10.00 |
| 3373 | 1096 | 2/02/2001 | 10 | 10.33 |
| UK | NT | 20/02/1987 | 10 | 10.33 |
| UK | NT | 20/02/1987 | 10 | 11.00 |
| UK | NT | 20/02/1987 | 11 | 8.33 |
| 2536 | 0953 | 20/01/2001 | 11 | 10.00 |
| 2381 | B1090 | 5/02/1999 | 12 | 12.67 |
| 1465 | NR | 17/01/2000 | 13 | 12.00 |
| 2318 | 1405 | 30/01/2000 | 13 | 12.33 |
| 2288 | 0998 | 31/01/2001 | 14 | 12.33 |
| 2074 | 1143 | 28/01/2001 | 14 | 14.00 |
| B1003 | NR | 19/01/1999 | 15 | 15.00 |

Notation: NT Not tagged; NR Not recorded

# APPENDIX 4:

Parameter estimates for Gompertz models describing the growth of lactating New Zealand sea lions combined and by colony Sandy Bay (SB) and Dundas Island (DD). Notation: $n$ = sample size; $L_\infty$ = asymptotic length or weight respectively; $b$ = constant of integration; $k$ = growth rate constant; SE = standard error; $r^2$ = coefficient of determination.

| *Length* | $n$ | $L_\infty$ (SE) | $b$ (SE) | $k$ (SE) | $r^2$ |
|---|---|---|---|---|---|
| Sandy Bay + Dundas Island | 819 | 179.24 (0.42) | -0.82 (0.09) | 0.36 (0.02) | 0.383 |
| Sandy Bay | 377 | 181.33 (1.10) | -1.56 (0.23) | 0.22 (0.05) | 0.231 |
| Dundas Island | 442 | 181.10 (0.26) | -2.00 (0.16) | 0.16 (0.04) | 0.225 |
| | | | | | |
| *Weight* | | | | | |
| Sandy Bay + Dundas Island | 819 | 122.29 (1.53) | -0.42 (0.09) | 0.19 (0.02) | 0.350 |
| Sandy Bay | 377 | 124.81 (2.31) | -0.14 (0.20) | 0.22 (0.04) | 0.329 |
| Dundas Island | 442 | 126.90 (4.88) | -0.76 (0.08) | 0.10 (0.03) | 0.322 |

# APPENDIX 5:

Parameter estimates for Gompertz models describing the growth of lactating New Zealand sea lions by colony Sandy Bay and Dundas Island and by year (1999 - 2001). Notation: $n$ = sample size; $L_\infty$ = asymptotic length or weight respectively; $b$ = constant of integration; $k$ = growth rate constant; SE = standard error; $r^2$ = coefficient of determination.

| *Length* | $n$ | $L_\infty$ (SE) | $b$ (SE) | $k$ (SE) | $r^2$ |
|---|---|---|---|---|---|
| Sandy Bay 1999 | 142 | 182.73 (3.36) | -1.93 (0.290 | 0.15 (0.08) | 0.213 |
| Sandy Bay 2000 | 125 | 181.45 (1.53) | -1.19 (0.33) | 0.27 (0.07) | 0.314 |
| Sandy Bay 2001 | 95 | 179.71 (1.31) | -1.43 (0.53) | 0.25 (0.09) | 0.208 |
| Dundas Island 1999 | 134 | 180.42 (1.79) | -1.79 (0.31) | 0.20 (0.07) | 0.259 |
| Dundas Island 2000 | 142 | 183.12 (6.39) | -2.16 (0.22) | 0.10 (0.09) | 0.158 |
| Dundas Island 2001 | 138 | 183.19 (3.12) | -1.78 (0.21) | 0.15 (0.06) | 0.310 |
| *Weight* | | | | | |
| Sandy Bay 1999 | 142 | 127.51 (4.14) | -0.34 (0.27) | 0.20 (0.06) | 0.387 |
| Sandy Bay 2000 | 125 | 121.77 (3.54) | -0.14 (0.36) | 0.26 (0.07) | 0.340 |
| Sandy Bay 2001 | 95 | 118.50 (2.61) | 0.15 (0.51) | 0.27 (0.08) | 0.269 |
| Dundas Island 1999 | 134 | 123.73 (7.26) | -0.97 (0.23) | 0.12 (0.07) | 0.218 |
| Dundas Island 2000 | 142 | 130.35 (11.51) | -0.58 (0.12) | 0.10 (0.05) | 0.384 |
| Dundas Island 2001 | 138 | 145.88 (19.11) | -0.40 (0.12) | 0.08 (0.04) | 0.475 |

# APPENDIX 6:

Estimates of observed $p(x)$ and modelled age-specific reproductive rate $\hat{p}_1(x)$ for female New Zealand sea lions at the Auckland Islands using Data set 1 (confirmed reproductive histories of known-age females) and Data set 2 (Data set 1 plus individuals that were not seen but known to be alive). Notation: $p(x)$ observed proportion of females of age $x$ seen giving birth and/or nursing a pup out of the total number of tagged females of age $x$ seen 95%; $\hat{p}_1(x)$ model fitted to the observed values of $p(x)$; 95% CIs are exact upper and lower 95% confidence intervals.

| Data set 1 | | | | | | | Data set 2 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| age | *n* seen | *n* with pup | $p(x)$ | 95% CIs | | $\hat{p}_1(x)$ | age | *n* seen | *n* with pup | $p(x)$ | 95% CIs | | $\hat{p}_1(x)$ |
| 3 | 1 | 1 | 1.00 | 0.05 | 1.00 | 0.02 | 3 | 1 | 1 | 1.00 | 0.05 | 1.00 | 0.03 |
| 4 | 149 | 20 | 0.13 | 0.08 | 0.20 | 0.14 | 4 | 149 | 20 | 0.13 | 0.08 | 0.20 | 0.14 |
| 5 | 115 | 46 | 0.40 | 0.31 | 0.50 | 0.42 | 5 | 124 | 46 | 0.37 | 0.29 | 0.46 | 0.39 |
| 6 | 98 | 72 | 0.73 | 0.64 | 0.82 | 0.70 | 6 | 108 | 72 | 0.67 | 0.57 | 0.75 | 0.62 |
| 7 | 121 | 100 | 0.83 | 0.75 | 0.89 | 0.84 | 7 | 141 | 100 | 0.71 | 0.63 | 0.78 | 0.73 |
| 8 | 167 | 146 | 0.87 | 0.81 | 0.92 | 0.87 | 8 | 202 | 146 | 0.72 | 0.66 | 0.78 | 0.75 |
| 9 | 193 | 169 | 0.88 | 0.82 | 0.92 | 0.87 | 9 | 227 | 169 | 0.74 | 0.68 | 0.80 | 0.75 |
| 10 | 195 | 169 | 0.87 | 0.81 | 0.91 | 0.87 | 10 | 215 | 169 | 0.79 | 0.73 | 0.84 | 0.75 |
| 11 | 159 | 135 | 0.85 | 0.78 | 0.90 | 0.87 | 11 | 192 | 135 | 0.70 | 0.63 | 0.77 | 0.75 |
| 12 | 146 | 128 | 0.88 | 0.81 | 0.93 | 0.87 | 12 | 157 | 128 | 0.82 | 0.75 | 0.87 | 0.75 |
| 13 | 102 | 91 | 0.89 | 0.82 | 0.94 | 0.87 | 13 | 114 | 91 | 0.80 | 0.71 | 0.87 | 0.75 |
| 14 | 62 | 49 | 0.79 | 0.67 | 0.88 | 0.87 | 14 | 72 | 49 | 0.68 | 0.56 | 0.79 | 0.75 |
| 15 | 33 | 32 | 0.97 | 0.84 | 1.00 | 0.87 | 15 | 40 | 32 | 0.80 | 0.64 | 0.91 | 0.75 |
| 16 | 28 | 23 | 0.82 | 0.63 | 0.94 | 0.87 | 16 | 36 | 23 | 0.64 | 0.46 | 0.79 | 0.75 |
| 17 | 25 | 22 | 0.88 | 0.69 | 0.97 | 0.87 | 17 | 28 | 22 | 0.79 | 0.59 | 0.92 | 0.75 |
| 18 | 20 | 16 | 0.80 | 0.56 | 0.94 | 0.87 | 18 | 23 | 16 | 0.70 | 0.47 | 0.87 | 0.75 |
| 19 | 21 | 21 | 1.00 | 0.87 | 1.00 | 0.87 | 19 | 21 | 21 | 1.00 | 0.87 | 1.00 | 0.75 |
| 20 | 12 | 8 | 0.67 | 0.35 | 0.90 | 0.87 | 20 | 13 | 8 | 0.62 | 0.32 | 0.86 | 0.75 |
| 21 | 10 | 9 | 0.90 | 0.56 | 1.00 | 0.87 | 21 | 10 | 9 | 0.90 | 0.56 | 1.00 | 0.75 |
| 22 | 4 | 4 | 1.00 | 0.47 | 1.00 | 0.86 | 22 | 5 | 4 | 0.80 | 0.28 | 0.99 | 0.75 |
| 23 | 7 | 6 | 0.86 | 0.42 | 1.00 | 0.84 | 23 | 7 | 6 | 0.86 | 0.42 | 1.00 | 0.74 |
| 24 | 4 | 2 | 0.50 | 0.07 | 0.93 | 0.73 | 24 | 5 | 2 | 0.40 | 0.05 | 0.85 | 0.67 |
| 25 | 2 | 2 | 1.00 | 0.22 | 1.00 | 0.49 | 25 | 2 | 2 | 1.00 | 0.22 | 1.00 | 0.44 |
| 26 | 1 | 0 | 0.00 | 0.00 | 0.95 | 0.23 | 26 | 2 | 0 | 0.00 | 0.00 | 0.78 | 0.16 |
| 27 | 1 | 0 | 0.00 | 0.00 | 0.95 | 0.06 | 27 | 1 | 0 | 0.00 | 0.00 | 0.95 | 0.03 |
| 28 | 1 | 0 | 0.00 | 0.00 | 0.95 | 0.01 | 28 | 1 | 0 | 0.00 | 0.00 | 0.95 | 0.00 |
| Total | 1677 | 1271 | | | | | | 1896 | 1271 | | | | |