

Growth and reproduction of female New Zealand sea lions

SIMON J. CHILDERHOUSE,* STEPHEN M. DAWSON, DAVID J. FLETCHER, ELISABETH SLOOTEN, AND B. LOUISE CHILVERS

Department of Marine Science, University of Otago, Dunedin, New Zealandmailto (SJC, SMD)

Department of Conservation, Wellington, New Zealand (SJC, BLC)

Department of Mathematics and Statistics, University of Otago, Dunedin, New Zealandmailto (DJF)

Department of Zoology, University of Otago, Dunedin, New Zealandmailto (ES)

Present address of SJC: Australian Marine Mammal Centre, Australian Antarctic Division, Kingston, Hobart, 7050, Tasmania, Australia (SJC)

* Correspondent: simon.childerhouse@aad.gov.au

- 1 A sample of 834 female New Zealand sea lions (*Phocarctos hookeri*), which were aged and measured, was obtained 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. 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) and weight (112.0) at ages 4 and 11 years, respectively. No significant differences were found in growth rates among years, nor between the 2 major breeding colonies in the Auckland Islands. Females reproduced between the ages of 3 and 26 years, with evidence of reproductive senescence starting at age 23 years. Although females up to age 28 years were observed, no females over 26 years were recorded as reproductive. Age-specific reproductive rate $p(x)$ increased rapidly between ages 3 and 7 years, reached a plateau between ages 7 and 23 years, and then declined rapidly after age 23 years. Mean observed reproductive rate was $p(x)_{3-28} = 0.67$ ($SE = 0.01$). This is the 1st robust estimate of reproductive rate for this species, is consistent with rates reported for other sea lions, and is considerably lower than assumed rates used in recent population modeling for this species. This calls into question the current method for estimating 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. DOI: 00.0000/00-MAMM-X-000.1.

Key words: growth, New Zealand sea lion, *Phocarctos hookeri*, reproduction

© 2010 American Society of Mammalogists

- 3 An understanding of life-history parameters is essential for appropriate conservation and management of any species, especially of a threatened species. The New Zealand sea lion (NZSL; *Phocarctos hookeri*) is endemic to New Zealand and is listed as threatened by the International Union for Conservation of Nature and Natural Resources (International Union for Conservation of Nature and Natural Resources 2009). NZSLs are caught regularly as bycatch in the New Zealand southern trawl fishery for arrow squid (*Nototodarus sloanii*). On average, >70 NZSLs, and up to 140, have been estimated as being killed each year since observations began in 1986 (Ministry of Fisheries 2005). This bycatch is managed by the New Zealand government via the application of a NZSL catch limit or fishing related mortality limit imposed on the commercial fishery. When it is estimated that either the fishing related mortality limit or the 6T squid total allowable

catch has been reached, the fishery is closed. In recent years the former has closed the fishery much more often than the latter (Ministry of Fisheries 2005).

Since 2003 fishing related mortality limits have been calculated using an age-structured Bayesian model of NZSLs developed specifically for this purpose (Breen and Kim 2006; Ministry of Fisheries 2005). A constraint of this model is that the values for most life-history parameters have been assumed or are based on limited data. One of the parameters, maximum number of pups per mature female, is presently estimated from a limited number of 317 observations of 135 marked females from a limited age range (Breen and Kim 2006). Although the

www.mammalogy.org



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. Estimates of reproductive rate generated by the model (Breen and Kim 2006) are considerably higher than rates reported for any other pinniped and are biologically unrealistic (York 1994). Sensitivity analysis has indicated that the model is particularly sensitive to input values for reproductive rate, confirming the need for better input data.

In addition to the direct removal of individuals from the population as bycatch, potential also exists for indirect competition between NZSLs and the commercial fishery via the removal of sea lion prey by the fishery (Chilvers et al. 2005). This resource competition could reduce growth rates, and comparison of inter- and intraspecific growth rates could provide an insight into potential resource competition. Mathematical models have been applied widely to describe growth in pinnipeds (Kastelein et al. 2000; Lima and Paez 1995; Rosas et al. 1993; Winship et al. 2001). Although it is generally accepted that simple growth models are unable to describe adequately the growth of pinnipeds over the entire life cycle (Aldrich and Lawler 1996; McLaren 1993; 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 and tooth-ageing of animals collected for research, during subsistence hunts, or killed incidental to fisheries operations (Dabin et al. 2004; Dickie and Dawson 2003; Lima and Paez 1995; Pitcher and Calkins 1981). Mark-recapture and other models also have been used to estimate reproductive rates of pinnipeds (Boyd et al. 1995; Hernandez-Camacho et al. 2008).

Using data gained from capture and ageing of female NZSLs, and subsequent resightings, the aims of this study were to describe growth patterns, to investigate intersite and interannual variation in growth patterns, and to estimate age-specific reproductive rates of female NZSLs at the Auckland Islands.

MATERIALS AND METHODS

Growth modeling.—Capture and sampling of lactating female NZSLs was undertaken in January and February during the austral summer in 1998, 1999, 2000, and 2001 at 2 breeding colonies approximately 9 km apart, Dundas Island and Sandy Bay on Enderby Island (50°S, 166°E). Random selection of lactating females was not possible because not all females were accessible for capture. We attempted to mitigate this 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.

Female NZSLs were captured, physically restrained, and anesthetized (Childerhouse et al., in press). All individuals were tagged on both flippers with individually numbered Allflex

cattle ear tags (1999; Allflex NZ Ltd., Palmerston North, New Zealand) or Dalton jumbo tags (2000–2001; Dalton ID Systems Ltd., Oxon, United Kingdom). Females caught at Sandy Bay in 2000 also were hot branded on the left side of the body. Females were weighed and measured (standard length). A single postcanine tooth was removed using a dental elevator. All work was conducted under a Marine Mammal and Animal Ethics Permit issued by the New Zealand Department of Conservation, and research followed guidelines of the American Society of Mammalogy (Gannon et al. 2007).

Extracted teeth were aged via readings of growth-layer groups in the cementum (Childerhouse et al. 2004). Although we found no significant difference between estimated age from tooth reading and actual age for known-age individuals (individuals tagged as pups), the fitted regression line from this relationship is used to estimate age from growth-layer group counts for all individuals of unknown age because it uses the best information available (Childerhouse et al. 2004).

The age distribution of lactating females includes only individuals of age 3 years and older because before this age females have yet to recruit into the breeding population (Childerhouse et al., in press). 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 (Ministry of Fisheries 2005). Measurements from these individuals are reported by Dickie (1999) and Duignan et al. (2003a, 2003b). In addition, measurements of 82 neonate pups were made on Sandy Bay breeding colony between 2001 and 2004 (Chilvers et al. 2006). Pup data were not used to fit growth models, because no single equation is able to describe adequately the growth of all age classes, and it is known that the growth of pups differs from that of older animals (McLaren 1993).

In all cases, length and weight data were approximately normally distributed (Fig. 1). An α -value of 0.05 was used in all statistical testing. Gompertz (Ricker 1979), von Bertalanffy (Ricker 1979; von Bertalanffy 1938), and Richards (Leberg et al. 1989; Richards 1959) growth curves were fitted to age against standard length and weight data in SPSS version 10 (SPSS Inc. 2004) following Winship et al. (2001). Parameter estimates are provided for all 3 models to allow comparisons with other sea lion species. However, the Gompertz growth model represents a standard curve that is thought to best describe mammalian growth (Heide-Jorgensen and Teilmann 1994). Growth curves for size (S : length and weight) were of the forms:

Gompertz:

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

von Bertalanffy:

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

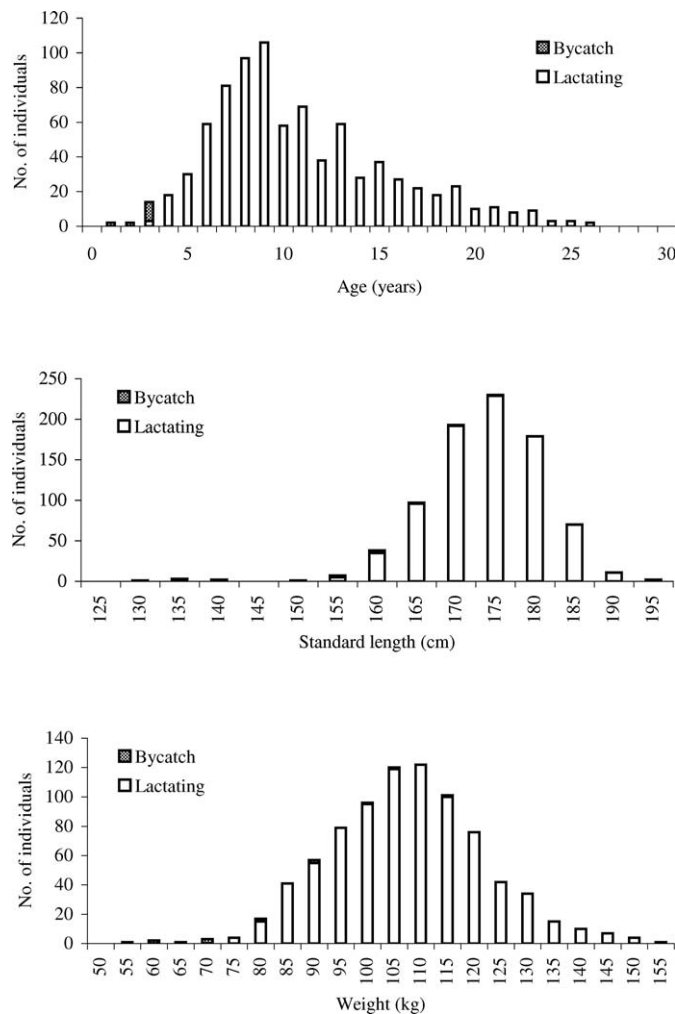


FIG. 1.—Frequency distributions of a) age, b) length, and c) weight of sampled lactating and bycaught female New Zealand sea lions ($n = 834$).

and 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_∞ is asymptotic length or weight respectively, k is the growth rate constant, t is age in years, b is the time parameter, m is Richard's shape parameter (which 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 nonlinear least-squares regression in SPSS (SPSS Inc. 2004). Goodness of fit was evaluated using the coefficient of determination (r^2) and the smallest uncertainty in parameter estimates.

Because of significant differences in the age distribution of lactating females between Dundas Island and Sandy Bay and significant interannual variation at Sandy Bay (Childerhouse et al., in press), we constructed separate growth models for lactating females by site (Sandy Bay and Dundas Island) and year (1999, 2000, and 2001). Z-tests (Zar 1998) were used to evaluate differences among parameters. A body mass index also was used to examine differences in relative growth

between the 2 sites. Body mass index is the ratio of weight (kg) to length (cm). Age-specific growth rate was investigated by estimating the expected size (length and weight) derived from the calculated Gompertz growth model against age.

Reproductive rate.—In addition to capturing and sampling individuals for the assessment of age structure, we made regular searches for marked sea lions at the Sandy Bay colony between December and February each year. We recorded tag or brand number and breeding status (breeding [defined as seen giving birth, nursing, or seen consistently with a pup more than twice within a season] or nonbreeding) of each female of known-age seen. These observations spanned the period 1999–2005 and were combined to estimate age-specific reproductive rate $p(x)$ and investigate reproductive senescence (progressive loss of physiological function with age resulting in reduced fecundity—Abrams 1991). We defined $p(x)$ as the proportion of all tagged females of age x seen that were recorded giving birth or nursing a pup, or both. This definition is contingent on females returning to the breeding colonies so they can be resighted. Exact binomial 95% confidence intervals (95% CIs) were calculated separately for each $p(x)$.

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

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

where a is the maximum reproductive rate across all age classes, $\Phi(\cdot)$ is the cumulative distribution function for the standard normal distribution, μ_1 and σ_1 are the mean and standard deviation of the age at which females 1st give birth, and μ_2 and σ_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 $p(x)$ because 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 $\hat{p}(x)$ 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 to explore the range of age-specific $p(x)$. Data set α used all resights for which breeding status had been confirmed and is thus likely to reflect the maximum values of $p(x)$. Data set β was data set α 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 little breeding occurs away from the breeding colonies (Chilvers and Wilkinson 2008), these latter individuals were assumed to be nonbreeding in the year in which they were not seen. Data set β 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.

TABLE 1.—Sample of lactating New Zealand sea lions ($n = 819$) and female New Zealand sea lions from bycatch ($n = 15$) used for growth measurements.

Source	Year	n	Minimum age (years)	Maximum age (years)
Lactating				
Dundas Island	1998	28	4	16
	1999	134	3	25
	2000	142	4	26
	2001	138	4	23
Total		442		
Sandy Bay	1998	15	6	17
	1999	142	3	21
	2000	125	3	24
	2001	95	4	26
Total		377		
Bycatch				
	1997	3	3	3
	1998	6	1	3
	2001	4	3	3
	2002	2	2	3
Total		15		

RESULTS

Growth modeling.—A total of 819 lactating NZSLs, which were captured and measured over 4 years, comprised the bulk of the sample (Table 1). Sampling during the 1st year, 1998, was halted prematurely because of unusual mass mortality event and so the sample size was considerably smaller than in the latter 3 years. An additional 15 females aged between 1 and 3 years caught as fisheries bycatch between 1997 and 2002 also were included to increase sample sizes allowing a better fit of the growth models to the data for younger ages, which were not well represented in sampling of reproductive females. A total of 834 female NZSLs was used to calculate frequency distributions of age against length and weight (Fig. 1). The study was sampled 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, pseudoreplication is not a significant source of bias in this study.

The grand means of length and weight measurements for all females ($n = 834$) were 175.7 ($SE = 0.3$, range = 134–197) cm and 109.0 ($SE = 0.5$, range = 49–156) kg (Fig. 2). For lactating females only ($n = 819$) these measures were 176.1 ($SE = 0.2$, range = 157–197) cm and 109.6 ($SE = 0.5$, range = 75–156) kg.

The 3 growth models fit the data similarly well (Fig. 3; Appendix I). The r^2 -values were 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 because it had a similar fit to the other models but used fewer parameters than the Richards model (i.e., 3 versus 4). All further growth analysis was undertaken using only the Gompertz model.

Growth was asymptotic in both length (90% $L_\infty = 161.7$ cm at age 4 years) and weight (90% $L_\infty = 112.0$ kg at age 11 years; Fig. 3). This difference in age at the asymptotic point demonstrates that females continue to increase in weight long after achieving asymptotic length. Size-at-age models failed to predict birth length or weight accurately, with both being overestimated (Fig. 3). The allometric relationship between body length and weight was reasonably well described as the power function $\text{weight} = 0.0004 \times \text{length}^{2.4398}$ (where weight is given in kilograms and length is given in centimeters), with $r^2 = 0.60$ (Fig. 4).

The growth rate for both length and weight peaked at 10% per annum at age 1 year and steadily declined after that (Fig. 5). Growth rate declined much faster for length than weight. Annual growth rate was $<1\%$ by ages 10 and 17 years for length and weight, respectively.

Gompertz growth curves were calculated for Sandy Bay and Dundas Island samples separately (Fig. 6). Parameter estimates for length modeling were not significantly different between the 2 sites (L_∞ : $Z = 2.9$, $P = 0.84$; b : $Z = 1.6$, $P = 0.12$; k : $Z = 0.9$, $P = 0.35$). For weight, however, 2 of the 3 parameters were significantly different (L_∞ : $Z = 0.4$, $P = 0.70$; b : $Z = 2.9$, $P < 0.001$; k : $Z = 2.4$, $P = 0.02$). Although some significant differences existed in parameter values for weight, growth curves for each colony were broadly similar, as indicated by the complete overlap of the 95% CIs for length and partial overlap for weight (Fig. 6). However, the ratio of expected size calculated from fitted Gompertz growth models for each colony highlighted some differences in relative growth by age (Fig. 7a). For length, the ratio is very close to 1, with some evidence that females are slightly shorter at Sandy Bay than Dundas before age 6 years. More striking is the ratio for weight, where females less than age 6 years are considerably lighter (-12%) at Sandy Bay than Dundas. This ratio reverses after age 6 years, with females being heavier at Sandy Bay than at Dundas with the largest difference apparent at age 12 years ($+5\%$) before declining to approximately 1:1 at older ages. This difference also is seen in relative body mass index for both colonies (Fig. 7b).

Gompertz growth models were fitted separately to data from the 2 colonies for each of the 3 years (Fig. 8). To simplify the presentation of Fig. 8, only the 95% CIs for 1999 are presented. Examination of parameter estimates and the 95% CIs of growth curves provided no indication of a significant year or colony effect.

Reproductive rate.—Data set α comprised 1,677 resights of 505 different females aged between 3 and 28 years (Fig. 9). Females were observed with pups between the ages of 3 and 25 years, but only 3 individuals older than 25 years were resighted and none was observed with a pup. Considerable variation characterized age-specific estimates of $p(x)$ (Fig. 10). Given the large variation associated with some of the point estimates, and considerably different sample sizes for different ages, a weighted mean was used (Seber 1982). The weighted mean $p(x)_{3-28}$ from data set α was 0.76 ($SE = 0.01$; Fig. 10a; Table 2). The maximum-likelihood fit of $\hat{p}(x)_{3-28}$ to

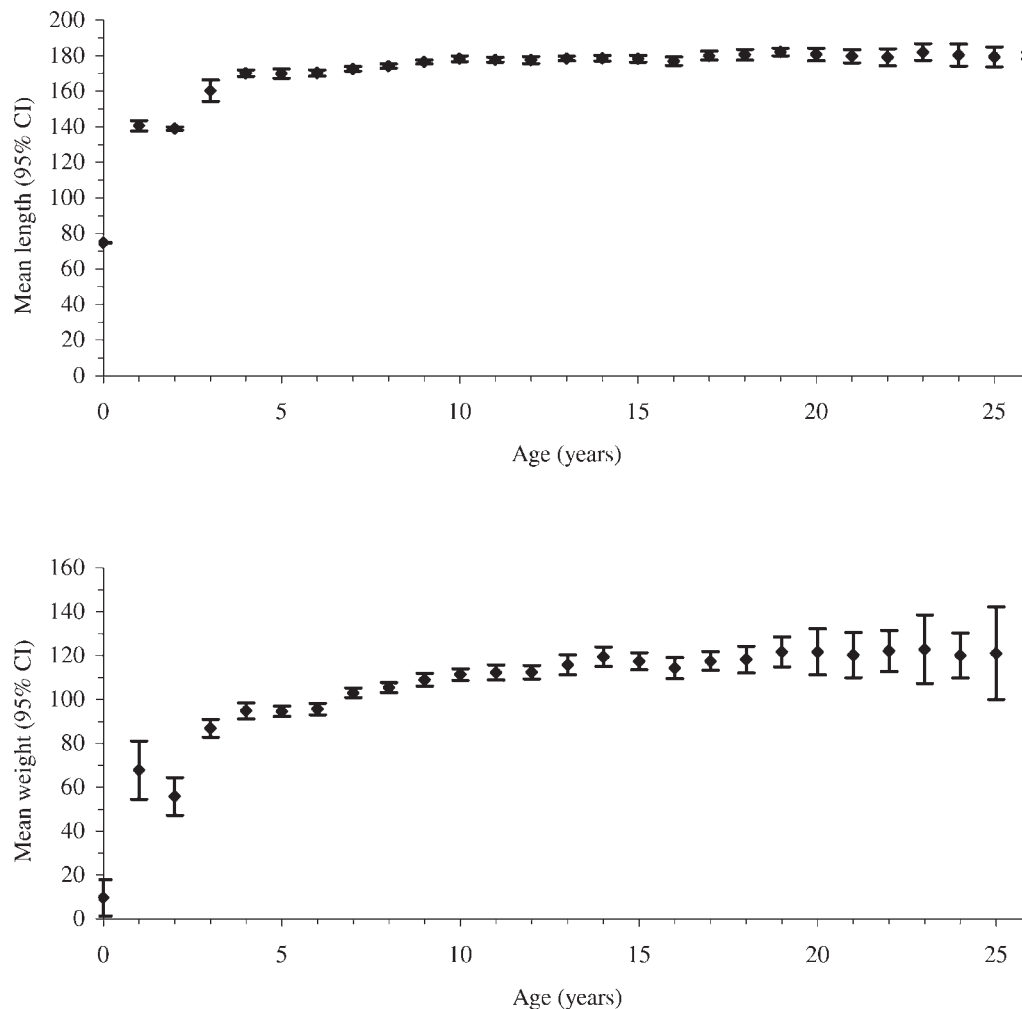


FIG. 2.—Mean (\pm 95% s CIs) a) length and b) weight by age for lactating female New Zealand sea lions ($n = 819$), bycaught females ($n = 15$), and female pups at birth ($n = 82$).

data set α showed a plateau between the ages of 7 and 23 years (Fig. 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 α and reanalyzed as the data set β (Fig. 10b). The weighted means of $p(x)_{3-28}$ and $p(x)_{7-23}$ from data set β were less than the equivalent values from data set α (Fig. 10b; Table 2).

Modeled $\hat{p}(x)$ fit the observed data well, with high r^2 -values for both data sets (Fig. 10; Table 2). No difference between the weighted means of $p(x)$ and $\hat{p}(x)$ for either data set was observed.

DISCUSSION

Growth modeling.—A potential source of bias in this study is that the reproductive females sampled may have a growth pattern different than that of females that are either not reproductive or have a lower reproductive rate. This seems unlikely because a large sample was taken over 4 years at 2 colonies, and only those females that did not produce a pup over that period would not have been available for sampling. 15 Female Steller's sea lions (*Eumetopias jubatus*) with a fetus

are significantly heavier and longer than females of the same age without a fetus (Winship et al. 2001). If this is also true for NZSLs, the growth rates reported in this study may be positively biased compared to the average growth rate for all female NZSLs. We believe that this bias is likely to be small because of the large sample size and multiyear sampling, but it will be necessary to quantify this empirically, perhaps using bycatch females.

Latitudinal data have been used widely in the estimation of growth rates in pinnipeds. Many potential sources of bias exist in the estimation of growth from latitudinal data (Winship et al. 2001), 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 (McLaren 1993; Winship et al. 2001).

Biases i–iii are related to ageing of individuals. All individuals were sampled at a similar time of year (January or February for reproductive females; February–May for bycaught females), and ageing of NZSLs from growth-layer

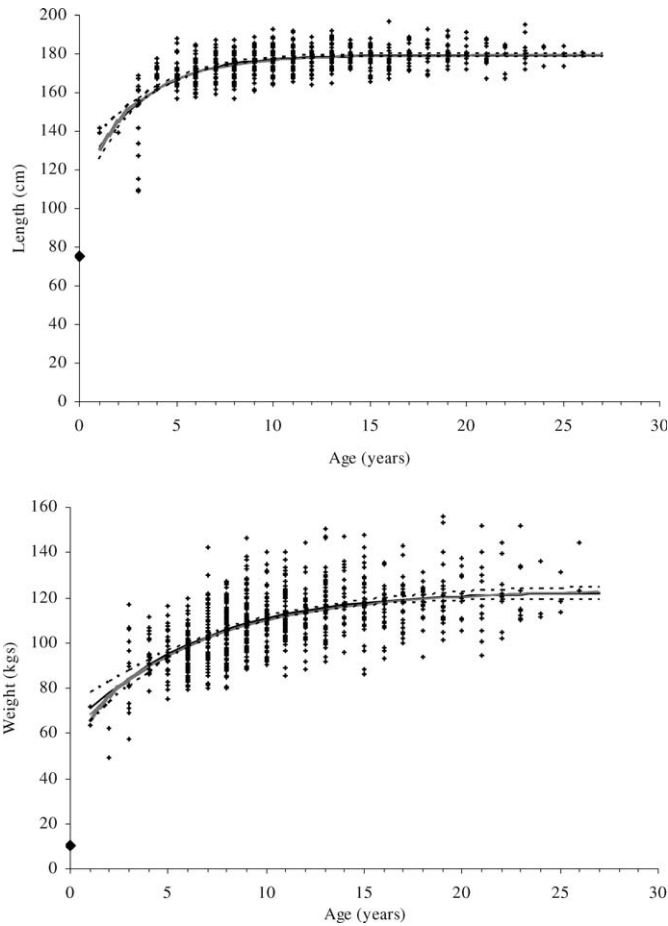


FIG. 3.—Growth curves for female New Zealand sea lions using 3 growth models (von Bertalanffy [gray line], Gompertz [black line], and Richards [hatched line]) for a) length (cm) and b) weight (kg). Dotted lines represent 95% CIs of the Gompertz growth curve. Diamonds are mean pup weight and length at birth.

groups in the cementum has no significant bias (Childerhouse et al. 2004). Biases iv and v are related to sampling selectivity within age classes, which should have been mitigated by spreading our sampling effort across colonies, across and

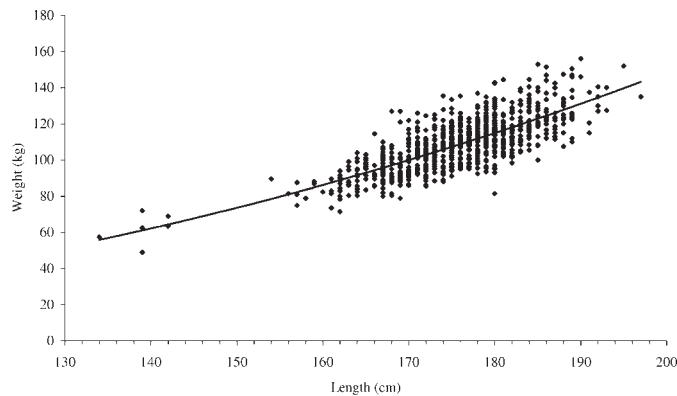


FIG. 4.—Weight-length relationship for female New Zealand sea lions following the power function $\text{weight} = 0.0004 \times \text{length}^{2.4398}$ (where weight is given in kilograms and length is given in centimeters) with $r^2 = 0.60$ and $P < 0.001$.

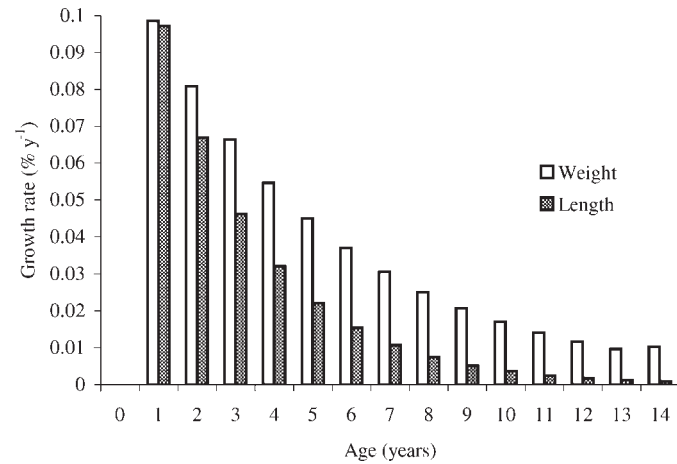


FIG. 5.—Estimated age-specific growth rate for length (cm) and weight (kg) for female New Zealand sea lions (NZSLs) modeled from a Gompertz growth curve. Growth rate is defined as percent annual increase in length or weight from time t_i to time t_{i+1} .

within years, and by using a large sample size. The number of individuals in each age class was generally large ($\bar{X} = 32$; $SE = 1.1$), although smaller sample sizes characterized older and younger age classes. Leberg et al. (1989) noted that biased sampling of a population with respect to age can bias the asymptotic size parameter of growth models, but this is unlikely in this study because there was a wide range of ages with samples available for all known age classes.

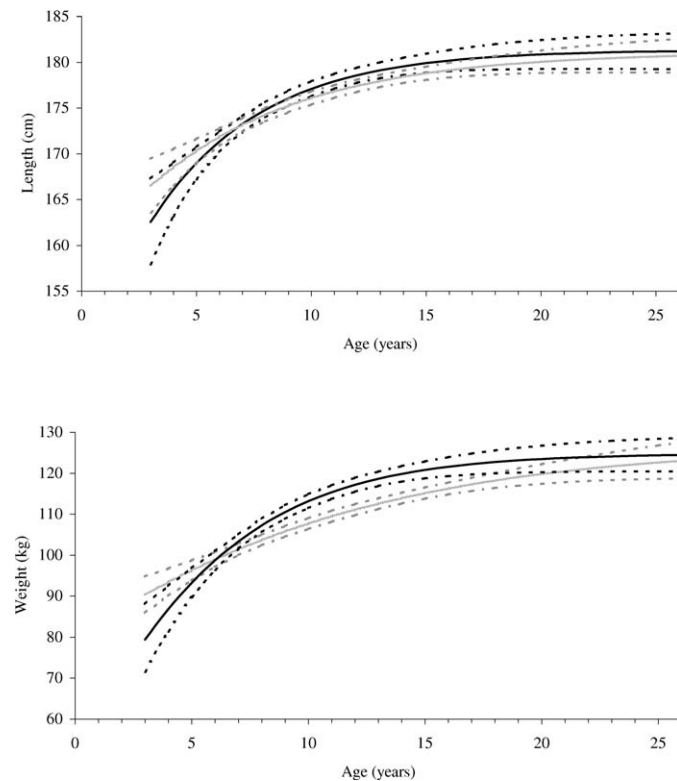


FIG. 6.—Fitted Gompertz growth models for a) length and b) weight for lactating New Zealand sea lions for Sandy Bay (solid black line) and Dundas Island (dashed gray line), with 95% CIs indicated by dotted lines for each.

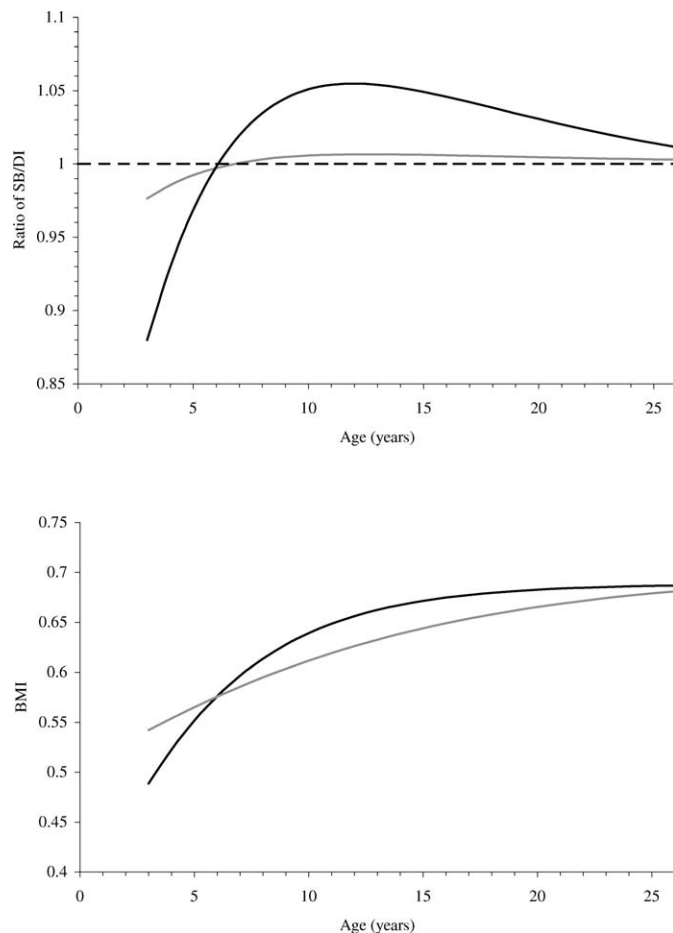


FIG. 7.—Body size of lactating New Zealand sea lions (NZSLs) from 2 breeding colonies, Sandy Bay (SB) and Dundas Island (DI): a) ratio (expected size at Sandy Bay divided by expected size at Dundas Island) of expected length (black line) and mass (gray line) by age for all NZSLs ($n = 834$), and b) body mass index (BMI) by age of lactating NZSLs calculated from fitted Gompertz growth models for Sandy Bay (black line) and Dundas Island (gray line) colonies. Body mass index is the expected weight (kg) divided by expected length (cm).

Biases vi and vii relate to differential survival between different-sized individuals and are more difficult to assess. It is likely that some interaction exists between size and survival, with the simple example of faster-growing juveniles or subadults 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 also could be 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 nonbreeding 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 nonbreeding females. No evidence of any interannual variation in growth rate was observed in the study, nor is there any environmental variation

evident over this period, making it unlikely that bias vi would be an effect in this study.

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 ages 3 and 4 years, which also corresponds with the earliest evidence of sexual maturity suggested by Laws (1956). Mass did not reach 90% of asymptotic weight until age 8 years, demonstrating that females continue to increase in weight long after achieving asymptotic length, which is consistent with body mass index increasing with age. Similar growth patterns also are seen in female Steller's sea lions (Winship et al. 2001) and female California sea lions (*Zalophus californianus*—Kastelein et al. 2000). Female NZSL and Steller's and California sea lions attain 90% of asymptotic length at or around age 4 years, but southern sea lions (*Otaria flavescens*) reach this point slightly later, at around age 6 years (Kastelein et al. 2000; Rosas et al. 1993; 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 (Winship et al. 2001). This may be simply a species-specific difference but also could be the effect of NZSLs occupying a marginal foraging environment as proposed previously by Chilvers et al. (2005). 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. 2005). A suboptimal growth rate is consistent with an individual that is occupying a marginal foraging environment, but it is not possible to assess this from the available data. Present research on growth of NZSLs at other locations (e.g., Otago Peninsula) will help determine if the rates reported here are suboptimal for the species.

Although we observed no significant colony effect for length, evidence was found for an effect for weight. Females at Sandy Bay were in poorer condition than those at Dundas Island until age 6 years when the situation reversed itself, with Sandy Bay females being in better condition. This result is surprising given that the 2 colonies are only 9 km apart, have some interchange, share foraging areas, and weights of female pups at 6 weeks of age are not significantly different between the 2 sites (Chilvers et al. 2005, L. Chilvers, pers. obs.). However, if juvenile–young adult females at Sandy Bay are nutritionally stressed compared to Dundas Island individuals, this could be reflected in reduced survival. This is consistent with the finding that the 2 colonies have significantly different age distributions of lactating females, with Sandy Bay having a lower proportion of older individuals (Childerhouse et al., in press), as would be expected if the survival of younger individuals is reduced. The mechanism that drives the differing body conditions between the 2 colonies is unclear given the apparent similarities between the 2 colonies.

Reproductive rate.—Resighting records of individually identified and known-age female NZSLs demonstrate that NZSL females produce pups between the ages of 3 and 25

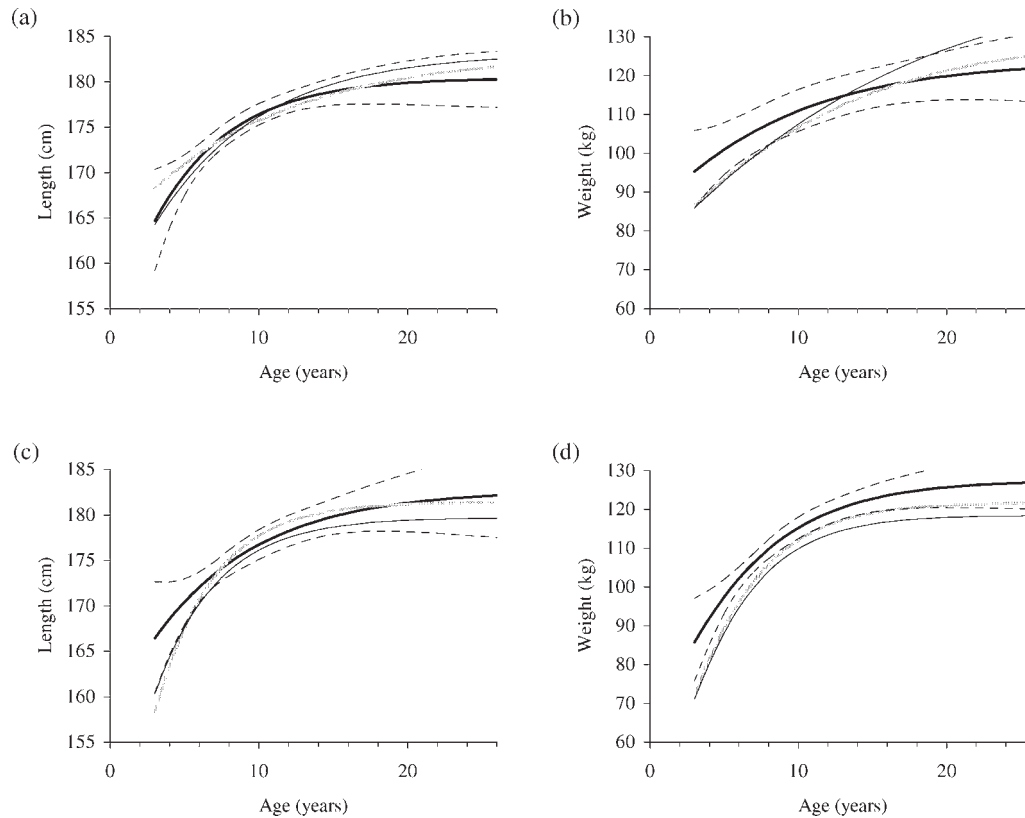


FIG. 8.—Interannual and intersite variation in Gompertz growth models for lactating New Zealand sea lions at the Auckland Islands. Shown are: Dundas Island (DI) a) length (cm) and b) weight (kg), and Sandy Bay (SB) c) length (cm) and d) weight (kg). Years are 1999 (thick black line), 2000 (gray line), and 2001 (thin black line). 95% CIs are shown for 1999 only.

years. This is very similar to the age distribution of lactating NZSLs found from sampling (3–26 years—Childerhouse et al., in press). Only 1 individual was recorded pupping as early as age 3 years. This is again consistent with the observed age structure of lactating females where only 3 (0.3%) of 865 sampled lactating females were observed to give birth at age 3 years (Childerhouse et al., in press). Females up to age 28

years have been resighted, but no females older than 25 years were seen with pups. Reproductive senescence appears to start at approximately age 23 years, although this is based on a relatively small sample size ($n = 30$ females > 20 years).

Examination of autopsy data indicates that NZSLs ovulate as early as age 3 years and suggests that all females are ovulating by age 4 years (Dickie 1999; Duignan et al. 2003a,

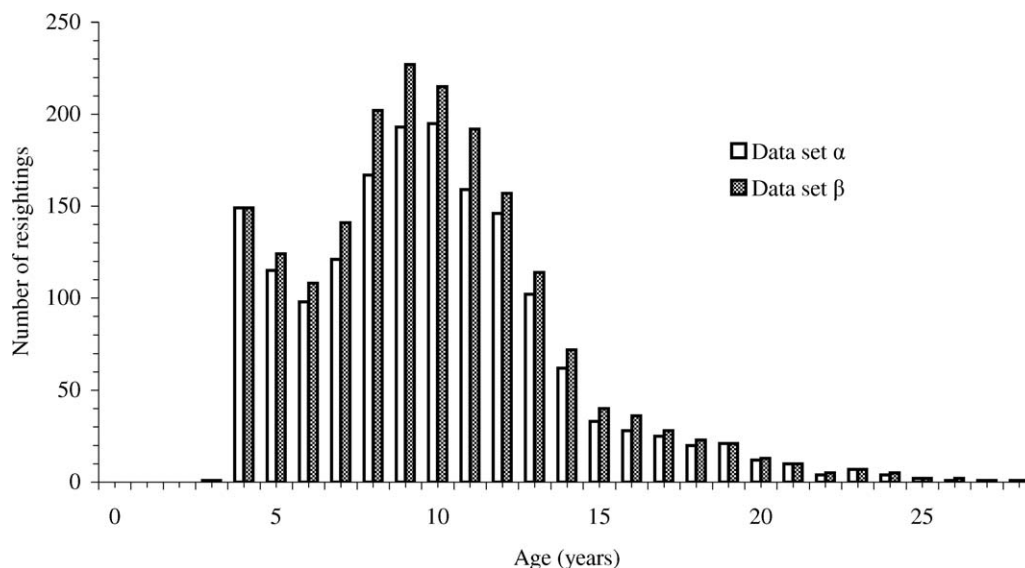


FIG. 9.—Total number of resightings of known-age female New Zealand sea lions for data set α ($n = 1,677$) and data set β ($n = 1,896$).

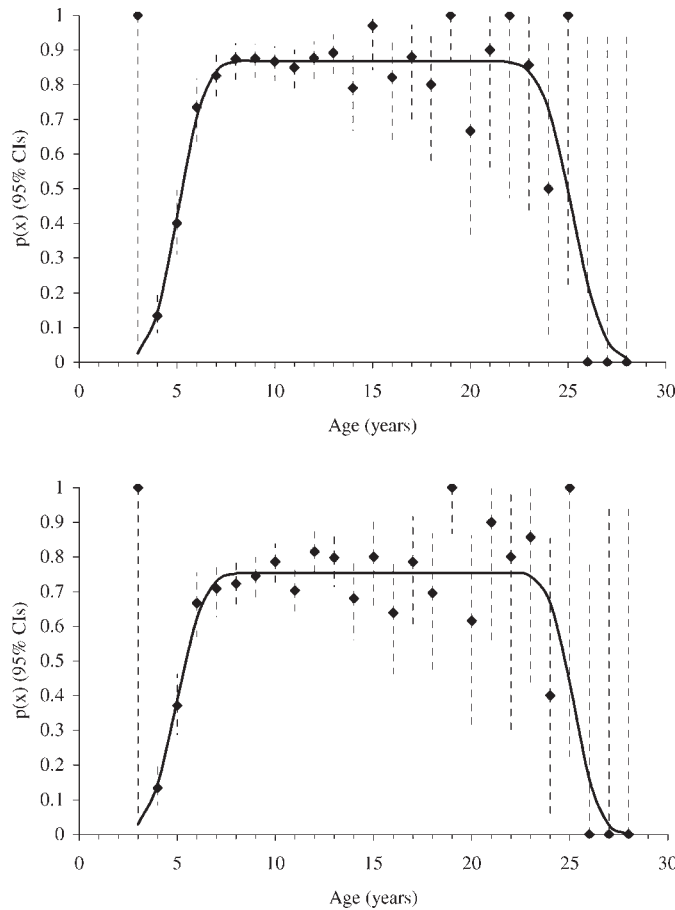


FIG. 10.—Observed $p(x)$ and modeled $\hat{p}(x)$ age-specific reproductive rate for female New Zealand sea lions at Sandy Bay, Auckland Islands, obtained from tag and brand resightings over 1998–2005: a) data set α ($n = 1,677$) and b) data set β ($n = 1,896$). Diamonds are the observed age-specific reproductive rate $p(x)$, and the fitted line is the estimated age-specific reproductive rate $\hat{p}(x)$. Dotted lines are exact 95% CIs.

2003b). However, this is based on a limited sample of only 22 females less than age 5 years. Three females of estimated age 3 years have been recorded as giving birth, indicating that females can ovulate as early as age 2 years. This proportion is likely to be very small given that only 0.3% of breeding

females were age 3 years (Childerhouse et al., in press).^[19] Therefore, females can ovulate as early as age 2 years, and most are ovulating by age 4 years. These findings are similar to that reported from autopsy records of Steller’s sea lions that indicate age at 1st ovulation is 3 years with an estimated 100% of females ovulating by age 6 years (Pitcher and Calkins 1981).

Young (<4 years) and old (>21 years) age classes are represented by few individuals in the sample, resulting in large CIs for $p(x)$. For example, the sample contained only 1 individual of age 3 years and 1 individual of age 25 years, 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; however, note that the exact 95% CIs span from approximately 0 to 1. Given these large CIs, estimates of reproductive rate for these ages are strongly influenced by the shape of the equation that was fit. The choice of model was made after 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 because it has considerably flexibility in shape and it best fit the observed data. Although the model fit is generally consistent with the data (given the large variability), the reproductive rates for young and old individuals should be viewed with caution.

Reproductive rate increased rapidly between ages 3 and 7 years, reached a plateau between ages 7 and 23 years, and then declined rapidly after age 23 years. Chilvers et al. (in press)^[20] reported a similar convex relationship for reproductive rate for NZSL starting at 4 years, peaking between 8 and 13 years, and then declining with age. A similar pattern has been reported from Steller’s sea lions in which reproductive rate declined to 0 after age 20 years (although small sample sizes for older individuals also were a constraint of this study—Pitcher and Calkins 1981) and California sea lions (Hernandez-Camacho et al. 2008; Holmes et al. 2007; Melin 2002). An observed peak in reproductive rate at intermediate ages followed by a decline in reproductive rate for older individuals is well described in some fur seals (e.g., northern fur seals [*Callorhinus ursinus*—Lander 1981], South American fur seals [*Arctocephalus australis*—Lima and Paez 1995], and

TABLE 2.—Estimates of weighted means of observed $p(x)$ and modeled $\hat{p}(x)$ reproductive rates for female New Zealand sea lions at the Auckland Islands using data set α (confirmed reproductive histories of known-age females) and data set β (data set α plus individuals that were not seen but known to be alive). Model parameters are the fit of the $\hat{p}(x)$ model to the observed data. See text for notation descriptions.^[14]

	n	$p(x)_{3-28}$	SE	$p(x)_{7-23}$	SE	Model parameters					
						ϕ	μ_1	δ_1	μ_2	δ_2	r^2
Observed											
Data set α	1677	0.76	0.01	0.86	<0.01						
Data set β	1896	0.67	0.01	0.75	<0.01						
		$\hat{p}(x)_{3-28}$	SE	$\hat{p}(x)_{7-23}$	SE						
Modeled											
Data set α		0.76	0.01	0.86	<0.01	1.89	5.05	1.08	25.21	1.22	0.93
Data set β		0.67	0.01	0.75	<0.01	1.12	4.97	1.11	25.20	1.00	0.85

[22] subantarctic fur seals [*A. tropicalis*—Bester 1995; Dabin et al. 2004]) but is not a feature of all fur seals (e.g., Antarctic fur seals [*A. gazelle*—Boyd et al. 1995]). The large decline in reproductive rate in NZSLs occurs at approximately 0.89 of maximum age, but in Steller's sea lions and Antarctic and South American fur seals it occurs at approximately 0.56, 0.58, and 0.72, respectively, of maximum estimated age (Boyd et al. 1995; Lima and Paez 1995; Pitcher and Calkins 1981). 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 expected, $p(x)$ varied depending on the choice of data set. Data set α is positively biased because females known to be alive, but not seen at the breeding colony and therefore unlikely to be breeding, are excluded from analysis. The effect of expanding data set α by adding these females to create data set β was to lower the overall reproductive rate by 0.09 (Table 2). Population models used to estimate sustainable removals are likely to be highly sensitive to this parameter given that it is a critical measure of productivity. Therefore, we suggest that the estimate from data set β is preferred in such modeling because it is less biased.

The model $\hat{p}(x)$ fit the data well and described the increase, stability, and then decline in reproductive rate with increasing age. The mean value of $\hat{p}(x)_{3-28}$ was the same as $p(x)_{3-28}$ and was within the observed range of reproductive rates for other species of sea lions. Because of small sample sizes of ages <5 and >20 years and the resulting large CIs associated with these point estimates, the fit of $\hat{p}(x)$ 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 older than age 25 years but with estimated $\hat{p}(x)$ rates of 0.23 and 0.06 for ages 26 and 27 years, respectively. Although the impact of this discrepancy is likely to be small, because the proportion of breeding females aged ≥ 25 years is estimated to be $<1\%$ (Childerhouse et al., in press), it is important to improve sample sizes for these older individuals for future analysis to improve the fit of the model and provide more information on senescence.

To date, most modeling on this species has focused on estimation of abundance (Gales and Fletcher 1999), likely population trend (Lalas and Bradshaw 2003; Manly and Walshe 1999; Woodley and Lavigne 1993), or estimating sustainable levels of bycatch (Breen and Kim 2006). Little attention had been afforded estimation of empirical parameters, except for Chilvers et al. (in press), who modeled reproductive rate from multistate mark-recapture data from branded females. This produced similar estimates to this study. Most modeling has relied simply on parameter estimates for other species, using values between 0.60 and 0.90. Three estimates of reproductive rate use observed data from NZSLs. Lalas and Bradshaw (2003) used reproductive rate estimates of 0.75 and 1.0 that were based on observed breeding histories of female NZSLs at Otago Peninsula. Breen and Kim (2006) made the peculiar choice not to estimate reproductive rate but rather R_0 , maximum number of pups per

mature female, estimating a Bayesian posterior of 0.99 (0.98–1.00) using a limited data set from the Auckland Islands NZSL population. Their estimate is not directly comparable to the reproductive rates estimated here. Nevertheless, an R_0 of 0.99 seems excessively optimistic. Chilvers et al. (in press) modeled reproductive rate from multistate mark-recapture data from branded females, which produced similar estimates to this study. Our overall estimate of reproductive rate for NZSLs of age ≥ 3 years from this study is 0.67 ($SE = 0.01$). This is the 1st robust estimate of mean reproductive rate for this species. Despite this, it should be treated with caution because 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 (Childerhouse et al., in press) and therefore also could have a different reproductive rate. Similar observations are needed at Dundas Island to investigate whether a difference in reproductive rate exists between the colonies. If so, this reproductive rate could have significant implications for the present modeling approach and the bycatch limits based upon it.

The mean observed birth rate of 0.67 between ages 3 and 28 years for NZSL is within the range reported for other sea lions (0.63 for Steller's sea lions [Pitcher and Calkins 1981], 0.59 for Steller's sea lions aged 4–21 years [Holmes et al. 2007], 0.71 for Australian sea lions [Higgins and Gass 1993], 0.77 for California sea lions aged 6–12 years [Melin 2002], and 0.49 for California sea lions aged 10–25 years [Hernandez-Camacho et al. 2008]). A comparison of age-specific reproductive rates for several sea lion species is shown in Fig. 11.

Management implications.—Our estimate of reproductive rate is based on a large sample of known-age females and is among the lowest reported for any sea lion species. The new estimate is considerably lower than assumed rates used in recent population modeling for this species. The model used to estimate sustainable levels of bycatch in the 6T squid fishery is highly sensitive to reproductive rate. For this and other reasons, including the implausibility of key results (e.g., estimates of R_{\max} and maximum pupping rate) and lack of fit to the observed decline in pup production (Chilvers et al. 2007), the Breen–Kim modeling approach must be seen as highly questionable. NZSLs have the lowest growth rate reported for any sea lion species and this, combined with a low reproductive rate, is consistent with a population that is occupying a marginal foraging environment (Chilvers et al. 2005). 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.

ACKNOWLEDGMENTS

This research was funded by the Department of Conservation, with part of the costs recovered through Conservation Services Levies on the New Zealand fishing industry. The work was conducted with

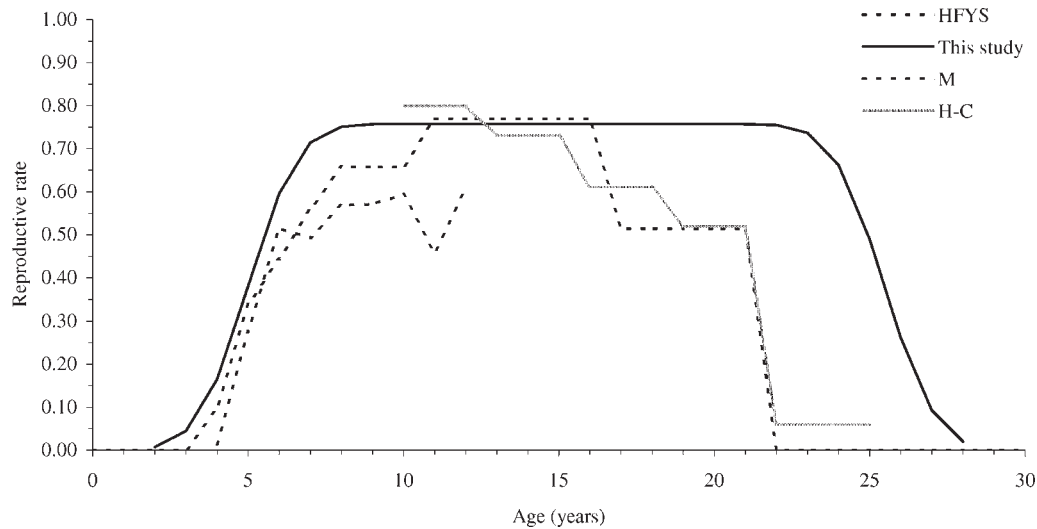


FIG. 11.—Estimates of age-specific reproductive rates from New Zealand sea lions (this study), Steller's sea lions (Holmes et al. 2007 [HFYS]), and California sea lions (Melin 2002 [M]; Hernandez-Camacho et al. 2008 [H-C]).

Animal Ethics and Marine Mammal Permits from the Department of Conservation. We are grateful to members of the Department of Conservation NZSL research team over the period of the study for their assistance in the field, in particular I. Wilkinson, W. Hockly, and P. Duignan. Thanks go to N. Gales, R. Mattlin, and I. West for discussions in developing this study and providing useful feedback and guidance. L. Douglas provided useful comments on an earlier draft.

LITERATURE CITED

- ABRAMS, P. A. 1991. The fitness costs of senescence: the evolutionary importance of events in early adult life. *Evolutionary Ecology* 5:343–360.
- ALDRICH, J. C., AND I. F. LAWLER. 1996. The model free analysis of growth curves. *Marine Ecology* 17:491–500.
- BESTER, M. N. 1995. Reproduction in the female subantarctic fur seal, *Arctocephalus tropicalis*. *Marine Mammal Science* 11:362–375.
- BOYD, I., J. CROXALL, N. LUNN, AND K. REID. 1995. Population demography of Antarctic fur seals: the cost of reproduction and implications for life-histories. *Journal of Animal Ecology* 64:505–518.
- BREEN, P. A., AND S. W. KIM. 2006. Exploring alternative management procedures for controlling bycatch of Hooker's sea lion in the 6T arrow squid fishery. NIWA, Wellington, New Zealand, Final Research Report for Ministry of Fisheries Research Project MOF2002/03L Objective 3 Revision 5:1–60.
- CAMPBELL, R., L. CHILVERS, S. CHILDERHOUSE, AND N. GALES. 2006. Conservation management issues and status of the New Zealand (*Phocarctos hookeri*) and Australian (*Neophoca cinerea*) sea lion. Pp. 58–74 in *Sea lions of the world* (A. Trites, et al., eds.). Alaska Sea Grant College Program, University of Alaska, Fairbanks.
- CAPPOZZO, H. L. 2002. South American sea lion. Pp. 1143–1146 in *Encyclopedia of marine mammals* (W. F. Perrin, B. Würsig, and J. G. M. Thewissen, eds.). Academic Press, San Diego, California.
- CHILDERHOUSE, S., G. DICKIE, AND G. HESSEL. 2004. Ageing live New Zealand sea lions *Phocarctos hookeri* using post canine teeth. *Wildlife Research* 28:177–181.

- CHILDERHOUSE, S. J., S. M. DAWSON, E. SLOOTEN, D. J. FLETCHER, AND I. S. WILKINSON. In press. Age distribution of lactating New Zealand sea lions: inter-annual and inter-site variation. *Marine Mammal Science*.
- CHILVERS, L., B. ROBERTSON, I. WILKINSON, AND P. DUIGNAN. 2006. Growth and survival of New Zealand sea lions *Phocarctos hookeri*: birth to 3 months. *Polar Biology* 30:459–469.
- CHILVERS, L., AND I. WILKINSON. 2008. Philopatry and site fidelity of New Zealand sea lions (*Phocarctos hookeri*). *Wildlife Research* 35:463–470.
- CHILVERS, L., I. WILKINSON, AND S. CHILDERHOUSE. 2007. New Zealand sea lion, *Phocarctos hookeri*, pup production 1995–2005. *Wildlife Research* 41:205–213.
- CHILVERS, L., I. WILKINSON, P. DUIGNAN, AND N. GEMMELL. 2005. Summer foraging areas for lactating New Zealand sea lions, *Phocarctos hookeri*. *Marine Ecology Progress Series* 304:235–247.
- CHILVERS, L., I. WILKINSON, AND D. I. MACKENZIE. In press. Predicting life-history traits for female New Zealand sea lions, *Phocarctos hookeri*: integrating short-term mark–recapture data and population modelling. *Journal of Agricultural, Biological, and Environmental Statistics*.
- DABIN, W., G. BEAUPLÉ, E. A. CRESPO, AND C. GUINET. 2004. Age structure, growth, and demographic parameters in breeding-age female subantarctic fur seals, *Arctocephalus tropicalis*. *Canadian Journal of Zoology* 82:1043–1050.
- DICKIE, G. 1999. Population dynamics of New Zealand fur seals (*Arctocephalus forsteri*) and New Zealand sea lions (*Phocarctos hookeri*). M.S. thesis, University of Otago, Dunedin, New Zealand.
- DICKIE, G., AND S. M. DAWSON. 2003. Age, growth, and reproduction in New Zealand fur seals. *Marine Mammal Science* 19:173–185.
- DUIGNAN, P., N. GIBBS, AND G. JONES. 2003a. Autopsy of pinnipeds incidentally caught in fishing operations 1997/98, 1999/2000, and 2000/01. Department of Conservation, Wellington, New Zealand, Department of Conservation Science Internal Series 118:1–106.
- DUIGNAN, P., N. GIBBS, AND G. JONES. 2003b. Autopsy of pinnipeds incidentally caught in commercial fisheries, 2001/02. Department of Conservation, Wellington, New Zealand, Department of Conservation Science Internal Series 131:1–41.

- GALES, N. J., AND D. FLETCHER. 1999. Abundance, distribution and status of the New Zealand sea lion *Phocarcctos hookeri*. *Wildlife Research* 36:35–52.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- HEATH, C. B. 2002. California, Galapagos, and Japanese sea lions. Pp. 783–787 in *Encyclopedia of marine mammals* (W. F. Perrin, B. Wursig, and J. G. M. Thewissen, eds.). Academic Press, San Diego, California.
- HEIDE-JORGENSEN, M. P., AND J. TEILMANN. 1994. Growth reproduction, age structure and feeding habits of white whales (*Delphinapterus leucas*) in west Greenland waters. *Meddelelser om Gronland, Bioscience* 39:195–212.
- HERNANDEZ-CAMACHO, C. J., D. AURIOLES-GAMBOA, J. LAAKE, AND L. R. GERBER. 2008. Age-specific birth rates of California sea lions (*Zalophus californianus*) in the Gulf of California, Mexico. *Marine Mammal Science* 24:664–676.
- HIGGINS, L. V., AND L. GASS. 1993. Birth to weaning: parturition, duration of lactation, and attendance cycles of Australian sea lions (*Neophoca cinerea*). *Canadian Journal of Zoology* 71:2047–2055.
- HOLMES, E. E., L. W. FRITZ, A. E. YORK, AND K. SWEENEY. 2007. Age-structured modelling reveals long-term declines in the natality of western Steller sea lions. *Ecological Applications* 17:2214–2232.
- INTERNATIONAL UNION FOR CONSERVATION OF NATURE AND NATURAL RESOURCES. 2009. IUCN Red list of threatened species. www.iucnredlist.org. Accessed 28 September 2009.
- KASTELEIN, R. A., N. M. SCHOONEMAN, N. VAUGHAN, AND P. R. WIEPKEMA. 2000. Food consumption and growth of California sea lions (*Zalophus californianus californianus*). *Zoo Biology* 19:143–159.
- LALAS, C., AND C. BRADSHAW. 2003. Expectations for population growth at new breeding colonies for the vulnerable New Zealand sea lion (*Phocarcctos hookeri*) using a simulation model. *Biological Conservation* 114:67–78.
- LANDER, R. H. 1981. A life table and biomass estimate for Alaskan fur seals. *Fisheries Research* 1:55–70.
- LAWS, R. M. 1956. Growth and sexual maturity in aquatic mammals. *Nature* 178:193–194.
- LEBERG, P. L., I. L. BRISBIN, JR., M. H. SMITH, AND G. C. WHITE. 1989. Factors affecting the analysis of growth patterns of large mammals. *Journal of Mammalogy* 70:275–283.
- LIMA, M., AND E. PAEZ. 1995. Growth and reproduction patterns in South American fur seals. *Journal of Mammalogy* 76:1249–1255.
- MANLY, B. F. J., AND K. WALSHE. 1999. The population management plan for the New Zealand sea lion. Pp. 271–283 in *Marine mammal survey and assessment methods* (D. G. Robertson, ed.). Balkema, Rotterdam, Netherlands.
- MCLAREN, I. A. 1993. Growth in pinnipeds. *Biological Reviews* 68:1–79.
- MELIN, S. R. 2002. Foraging ecology and reproduction of the California sea lion (*Zalophus californianus californianus*). Ph.D. dissertation, University of Minnesota, Minneapolis–St. Paul.
- MINISTRY OF FISHERIES. 2005. Operational plan to manage the incidental capture of New Zealand sea lions in the squid (SQU) 6T trawl fishery for the 2005–06 fishing year. Ministry of Fisheries, Wellington, New Zealand, Unpublished Report.
- PITCHER, K. W., AND D. G. CALKINS. 1981. Reproductive biology of Steller's sea lions in the Gulf of Alaska. *Journal of Mammalogy* 62:599–605.
- RICHARDS, F. J. 1959. A flexible growth function for empirical use. *Journal of Experimental Botany* 10:290–300.
- RICKER, W. E. 1979. Growth rates and models. Pp. 677–743 in *Fish physiology: bioenergetics and growth* (W. S. Hoar, D. J. Randall, and J. R. Brett, eds.). Academic Press Inc., Orlando, Florida.
- ROSAS, R., M. HAIMOVICI, AND M. PINEDO. 1993. Age and growth of the South American sea lion *Otaria flavescens* (Shaw, 1800), in southern Brazil. *Journal of Mammalogy* 74:141–147.
- SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Blackburn Press, Caldwell, New Jersey.
- SPSS INC. 2004. SPSS version 10. SPSS Inc., Chicago, Illinois.
- VON BERTALANFFY. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology* 10:181–213.
- WINSHIP, A. J., A. W. TRITES, AND D. G. CALKINS. 2001. Growth in body size of the Steller's sea lion (*Eumetropia jubatus*). *Journal of Mammalogy* 82:500–519.
- WOODLEY, T. H., AND D. M. LAVIGNE. 1993. Potential effects of incidental mortalities on the Hooker's sea lion (*Phocarcctos hookeri*) population. *Aquatic Conservation: Marine and Freshwater Ecosystems* 3:139–148.
- YORK, A. 1994. The population dynamics of northern sea lions, 1975–1985. *Marine Mammal Science* 11:38–50.
- ZAR, J. H. 1998. *Biostatistical analysis*. 4th ed. Prentice Hall, London, United Kingdom.

Submitted 26 March 2009. Accepted 8 July 2009.

Associate Editor was William F. Perrin.

APPENDIX I. Parameter estimates (SE) for different models describing the growth of female New Zealand sea lions ≥ 1 year of age (e.g., standard length and weight at age in years). Model notation: L_{∞} = asymptotic length or weight respectively; b = constant of integration; k = growth rate constant; t = age in years; m = Richards shape parameter (e.g., a parameter that specifies the relative position of the asymptote); S_0 = size at $t = 0$; T = growth period indicative of growth rate; r^2 = coefficient of determination.

Model	L_{∞}	b	k	S_0	T	m	r^2
Length (cm)							
von Bertalanffy	179.50 (0.43)	0.38 (0.03)	0.34 (0.02)				0.382
Gompertz	179.24 (0.42)	-0.82 (0.09)	0.36 (0.02)				0.383
Richards	179.70 (0.36)			106.55 (12.85)	-0.26 (-0.01)	-1.04 (-0.03)	0.380
Weight (kg)							
von Bertalanffy	123.09 (1.70)	0.52 (0.04)	0.16 (0.02)				0.350
Gompertz	122.29 (1.53)	-0.42 (0.09)	0.19 (0.02)				0.350
Richards	124.43 (1.64)			51.29 (1.54)	-2.48 (-0.32)	-1.16 (-0.15)	0.350

Authors QueriesJournal: **Journal of Mammalogy**Paper: **mamm-91-01-16**Title: **Growth and reproduction of female New Zealand sea lions**

Dear Author

During the preparation of your manuscript for publication, the questions listed below have arisen. Please attend to these matters and return this form with your proof. Many thanks for your assistance

Query Reference	Query	Remarks
1	Author: This article has been lightly edited for grammar, style, and usage. Please compare it with your original document and make any corrections on these pages. Please limit your corrections to substantive changes that affect meaning. If no change is required in response to a question, please write "OK as set" in the margin. Please expand addresses with any street numbers and names and any numerical postal codes if necessary. Copy editor	
2	Author: Should "weight" be changed to "mass" or "body mass" here and throughout? Copy editor	
3	Author: Is "International Union for Conservation of Nature and Natural Resources" correct as spelled out for "IUCN" here in text and in parentheses? Copy editor	
4	Author: Please update Childerhouse et al., in press, with year if now published. Copy editor	
5	Author: Is "NZ" correct in "Allflex NZ Ltd.", or should it be spelled out New Zealand? Copy editor	
6	Author: Please update Childerhouse et al., in press, with year if now published. Copy editor	

7	Author: Should scientific name "(Phocarctos hookeri)" be added after common name in each figure caption? Copy editor	
8	Author: Is "von Bertalanffy" rather than "von Bertanlanffy" correct as changed in von Bertalanffy 1938, as in Lit. Cit.? Copy editor	
9	Author: Please update Childerhouse et al., in press, with year if now published. Copy editor	
10	Author: Correct to omit (a) in Table 1 caption and before table itself (there is no (b) or other parts to compare it to)? Should scientific name "(Phocarctos hookeri)" be added after common name in caption for Table 1? Is 1st column of Table 1 correct as modified to insert "Lactating"? Copy editor	
11	Author: Please omit "(NZSLs)" in Fig. 5 caption unless it appears in the figure itself. Copy editor	
12	Author: Please omit "(SB)", "(DI)", and "(BMI)" in Fig. 7 caption unless they appear in the figure itself. Copy editor	
13	Author: Please omit "(DI)" and "(SB)" in Fig. 8 caption unless they appear in the figure itself. Copy editor	
14	Author: Should scientific name "(Phocarctos hookeri)" be added after common name in caption for Table 2? Copy editor	
15	Author: Is scientific name "(Eumetopias jubatus)" correct as added here at 1st mention of Steller's sea lions, as scientific names are given for other species throughout the "Discussion"? Copy editor	

16	Author: Please update Childerhouse et al., in press, with year if now published. Copy editor	
17	Author: Please update Childerhouse et al., in press, with year if now published. Copy editor	
18	Author: Please update Childerhouse et al., in press, with year if now published. Copy editor	
19	Author: Please update Childerhouse et al., in press, with year if now published. Copy editor	
20	Author: Please update Chilvers et al., in press, with year if now published. Copy editor	
21	Author: Is “Hernandez-Camacho” rather than “Hernandez-Comacho” correct as changed in Hernandez-Camacho et al. 2008, as in Lit. Cit.? Copy editor	
22	Author: Is “subantarctic fur seals” rather than “sub-Antarctic fur seals” correct as changed as in Wilson and Reeder’s Mammal Species of the World, 3rd. ed., as in Merriam Webster’s Collegiate Dictionary, and as in titles of Bester 1995 and Dabin et al. 2004 in the Lit. Cit.? Copy editor	
23	Author: Should “e.g., Antarctic fur seals” be changed to “e.g., antarctic fur seals”? Copy editor	
24	Author: Should “and Antarctic and South American fur seals” be changed to “and antarctic and South American fur seals”? Copy editor	
25	Author: Please update Childerhouse et al., in press, with year if now published. Copy editor	

26	Author: Please update Chilvers et al., in press, with year if now published. Copy editor	
27	Author: Should "R0" be changed to "R0"? Copy editor	
28	Author: Should "R0" be changed to "R0"? Copy editor	
29	Author: Please update Chilvers et al., in press, with year if now published. Copy editor	
30	Author: Please update Childerhouse et al., in press, with year if now published. Copy editor	
31	Author: Is "this reproductive rate" rather than "it" correct as changed in "If so, this reproductive rate could have" for clarity (or please indicate what "it" is)? Copy editor	
32	Author: Is "Hernandez-Camacho" rather than "Hernandez-Comacho" correct as changed in Hernandez-Camacho et al. 2008, as in Lit. Cit.? Copy editor	
33	Author: Is "Steller's sea lions" rather than "Steller sea lions" correct as changed in Fig. 11 caption, as throughout the text; please make correct and consistent throughout)? Copy editor	
34	Author: Should scientific name "(Phocarctos hookeri)" be added after common name in caption for Appendix I? Copy editor	
35	Author: Should "Antarctic" be changed to "Antarctic" in title of Boyd et al. 1995? Copy editor	

36	Author: Please ensure that Campbell et al. 2006 is mentioned in text or omit here in Lit. Cit. Copy editor	
37	Author: Please ensure that Capozzo 2002 is mentioned in text or omit here in Lit. Cit. Copy editor	
38	Author: Please update Childerhouse et al., in press, with year, volume, and page range if now published. Copy editor	
39	Author: Correct to omit issue number (5) in Chilvers and Wilkinson 2008 (please only retain issue number if each issue is paged separately)? Copy editor	
40	Author: Please update Chilvers et al., in press, with year, volume, and page range if now published. Copy editor	
41	Author: Should “200/01” be changed to “2000/01” in title of Duignan et al. 2003a (please follow original title)? Copy editor	
42	Author: Please ensure that Heath 2002 is mentioned in text or omit here in Lit. Cit. Copy editor	
43	Author: Is “International Union for Conservation of Nature and Natural Resources” correct as spelled out for “IUCN” (correct to omit “the”)? Copy editor	
44	Author: Is “South American” rather than “South Amercian” correct as changed in title of Lima and Paez 1995 (please follow original title)? Copy editor	
45	Author: Please provide report number, if any, and total page range of report for Ministry of Fisheries 2005. Copy editor	

46	Author: Please provide initial(s), if any, for von Bertalanffy in von Bertalanffy 1938. Copy editor	
47	Author: Is "T. H." rather than "T." correct as changed for initials for Woodley in Woodley and Lavigne 1993, as often seen (please follow original article)? Is "D. M." rather than "D." correct as changed for initials for Lavigne in Woodley and Lavigne 1993, as often seen (please follow original article)? Is "Hooker's sea lion" rather than "Hooker's NZSL" correct as changed in title of Woodley and Lavigne 1993 (please follow original title)? Copy editor	