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Historical dynamics of the Australian fur seal population: evidence of regulation by man?

J.P.Y. Arnould, I.L. Boyd, and R.M. Warneke

Abstract: The Australian fur seal (Arctocephalus pusillus doriferus) was severely over-exploited in the 18th and 19th centuries and until relatively recently its population had remained steady at well below estimated pre-exloitation levels. However, the population is now increasing rapidly (6%–20% per annum) throughout its range and there is a need to understand its dynamics in order to assess the potential extent and impact of interactions with fisheries. Age distribution (n = 156) and pregnancy rate (n = 110) were determined for adult females collected at a breeding colony on Seal Rocks, southeast Australia, in 1971–1972. Mean ± SE and maximum observed ages were 9.37 ± 0.41 and 20 years (n = 1), respectively. A stochastic modelling approach was used to fit an age distribution to the observed age-structure data and calculate rates of recruitment and adult survival. Annual adult female survival and recruitment rates between 1954 and 1971 were 0.478 ± 0.029 (mean ± SE) and 0.121 ± 0.007, respectively, suggesting that the population was experiencing a decline during the 1960s. The pregnancy rate increased from 78% at 3 years of age to an average of 85% between 4–13 years of age before significantly decreasing in older females (the oldest was 19 years of age). There was no significant effect of body mass or condition on the probability of a female being pregnant (P > 0.5 in both cases) and the nutritional burden of lactation did not appear to affect pregnancy rates or gestational performance. These findings suggest that the low survivorship was due to density-independent effects such as mortality resulting from interactions with fisheries, which are known to have been common at the time. The recent increase in the population is consistent with anecdotal evidence that such interactions have decreased as fishing practices have changed.

Résumé : L’otarie à fourrure d’Australie (Arctocephalus pusillus doriferus) a été fortement surexploitée au cours des 18e et 19e siècles et, jusqu’à récemment, sa population était demeurée stable à des densités bien inférieures à celles qui prévalaient avant la chasse commerciale. Cependant, la population est actuellement en croissance rapide (6% – 20% par an) sur toute son aire de répartition; il est donc nécessaire de comprendre cette dynamique pour évaluer le potentiel de l’expansion et de l’impact des interactions avec les pêcheries commerciales. Nous avons déterminé la structure en âge (n = 156) et le taux de grossesse (n = 110) chez les femelles adultes d’une colonie reproductrice sur Seal Rocks dans le sud-est de l’Australie en 1971–1972. L’âge moyen ± erreur type observé était de 9.37 ± 0.41 ans et l’âge maximal de 20 ans (n = 1). Un modèle de type stochastique a permis d’ajuster une distribution d’âges aux données de structure d’âge et de calculer les taux de recrutement et de survie des adultes. Les taux annuels moyens (± erreur type) de survie des femelles adultes de 1954 à 1971 étaient de 0.478 ± 0.029 et les taux de recrutement, de 0.121 ± 0.007, ce qui laisse croire que la population a subi un déclin au cours des années 1960. Le taux de grossesse a augmenté de 78% à l’âge de 3 ans à une moyenne de 85% aux âges 4–13, avant de décliner significativement chez les femelles plus âgées (la plus vieille de 19 ans). Il n’y avait pas d’effet significatif de la masse ou de la condition sur la probabilité d’une femelle être enceinte (P > 0.5 dans les deux cas) et le fardeau alimentaire de l’allaitement ne semblait pas affecter les taux de grossesse ou le succès de la gestation. Ces résultats laissent croire que la faible survie était due à des facteurs indépendants de la densité, tels que la mortalité due aux interactions avec les pêcheurs, un phénomène commun à l’époque. L’accroissement récent de la population est en accord avec des indications anecdotiques que de telles interactions ont diminué, alors que les pratiques de pêche ont changé.

[Traduit par la Rédaction]

Introduction

During the commercial-sealing era of the 18th and 19th centuries, fur seals throughout the world were severely over-exploited and, in some cases, hunted to near extinction (Bonner 1994). However, most species have since recovered to some degree or are in the process of doing so (Bonner 1985; Wickens and York 1997). These population increases have occurred while the worldwide human exploitation of marine living resources has expanded rapidly (Alverson
1992; Shannon et al. 1992; Klaer 2001). A consequence of this has been an increase in interactions between fur seals and commercial fisheries (DeMaster et al. 1985; Wickens et al. 1992; Pemberton and Shaughnessy 1993; Arnould and Croxall 1995; Punt and Butterworth 1995; Shaughnessy and Davenport 1996; Klaer 2001). This has led to concerns being raised about the impact of commercial fishing on prey availability for fur seals and incidental mortality in fishing gear (Everson and Goss 1991; Wickens et al. 1992) and, conversely, to calls from the fishing industry for the implementation of measures to manage the fur seal population (Butterworth 1992; Pemberton and Shaughnessy 1993; Balmelli and Wickens 1994; Wickens 1996; Thomson et al. 2000). There has been considerable interest, therefore, in the population dynamics of fur seals and the modelling of their prey consumption for the purpose of developing adequate policies for managing the fisheries and the fur seal populations (Eberhardt 1990; Butterworth et al. 1995; Wickens and York 1997).

The Australian fur seal (Arctocephalus pusillus doriferus) is a temperate-latitude species with a breeding distribution restricted to Bass Strait between the southeastern tip of the Australian mainland and Tasmania, which is recognised as being of low oceanic productivity (Warneke and Shaughnessy 1985). Natal colonies are currently located on just nine islands but there is historical evidence to suggest that several other islands within Bass Strait also once hosted breeding colonies (Warneke and Shaughnessy 1985; Pemberton and Kirkwood 1994). Commercial sealing ceased in ca. 1825 and, while there have been several minor regulated culls and killings by fishers (both legal and illegal), the species has been largely protected since the 1890s (Warneke 1975). Recovery of the population was initially slow, with Warneke and Shaughnessy (1985) concluding that there had been no measurable increase between 1945 and 1975 and that the population had stabilized at well below its estimated presealing annual production level of 50 000 pups. Warneke (1988) recorded an annual production of ca. 8000 pups in 1986 and concurred with this conclusion. In stark contrast, the population of the conspecific Cape fur seal (Arctocephalus pusillus pusillus) has recovered rapidly from postsealing lows of < 100 000 animals at the end of the 19th century and presently numbers over 1.7 million individuals (Butterworth et al. 1995). The Cape fur seal, however, inhabits the nutrient-rich waters of the Benguela Current, and Warneke and Shaughnessy (1985) suggested that the lower marine productivity of the waters inhabited by the Australian fur seal may have influenced its slow population recovery and will impose a much lower limit on its ultimate size. Competition with commercial fisheries, direct interactions with fishing operations, and entanglement in man-made debris have also been suggested as factors that may have contributed to the continuing low population levels (Shaughnessy and Warneke 1987; Pemberton et al. 1992; Pemberton and Kirkwood 1994).

The Australian fur seal population is currently increasing at 6.1%–19.7% per annum throughout its range (Arnould and Littnan 2000; Littnan and Mitchell 2002; Shaughnessy et al. 2002). The reasons for the recent increases are not known. While annual pup production, presently estimated at approximately 19 000 (Arnould and Littnan 2000; Littnan and Mitchell 2002; Shaughnessy et al. 2002), is still substantially less than the estimated presealing levels (Warneke and Shaughnessy 1985; Pemberton and Kirkwood 1994), concerns have been raised about the current and future levels of interaction between Australian fur seals and commercial fisheries (Pemberton et al. 1992; Pemberton and Shaughnessy 1993; Hindell et al. 1998; Goldsworthy et al. 2003). There is a pressing need, therefore, to understand the population dynamics of Australian fur seals in order to assess the potential extent and impact of these interactions.

Crucial information necessary for modelling population dynamics in large, long-lived mammals include data on adult female survivorship and the factors influencing pregnancy rates (Harwood and Prime 1978; Eberhardt 1988; Brown and Rothery 1993). No information is currently available for these variables in Australian fur seals and previous predictions of population trends have been based on information obtained in other species (Pemberton and Kirkwood 1994; Goldsworthy et al. 2003), particularly the extensive data collected for the conspecific Cape fur seal (Rand 1955; Butterworth et al. 1995; Punt and Butterworth 1995). However, because of the markedly higher productivity of their marine environment, demographic data for Cape fur seals may not be adequate for modelling the population dynamics of Australian fur seals (Wickens and York 1997).

The aims of this study, therefore, were to (i) determine the age distribution; (ii) assess the influence of age, body condition, and lactation status on pregnancy rates; and (iii) model survivorship and recruitment in a historical sample of adult female Australian fur seals.

Materials and methods

The study was conducted at Seal Rocks (38°31'S, 145°06'E) in northern Bass Strait from February to October in 1971 and 1972. Australian fur seals give birth between mid-November and mid-December (pupping peaks on 1 December) and the lactation period normally lasts 10–11 months (Warneke and Shaughnessy 1985; Arnould and Hindell 2001). Because the species is extremely wary of humans, sampling required crawling upwind into the colony and making use of the terrain for cover. Selected individuals were killed with a 0.22 rifle shot to the head from a close range using a quiet, very low velocity cartridge. Animals constantly move around the colony and the wind direction changes frequently at the study site, so weaned females (>1 year old, identifiable from pelage characteristics) were selected at random by collecting the first individual encountered within range. Sampling was conducted over several days at monthly intervals.

Body mass (±0.1 kg) was measured on a spring scale (Salter No. 85T, Salter Pty Ltd., Melbourne, Victoria, Australia) and standard length (STDCL: straight-line nose to tail, body supine) was determined with large stainless-steel slide calipers (±0.5 cm). As body mass covaries to a large degree with body length and, hence, may not accurately reflect body lipid reserves, residual values from the mass–length relationship were used as a body-condition index (BCI) (Guinet et al. 1998; Arnould and Warneke 2002). For pregnant females, body mass was corrected by subtracting the mass of the foetus and placenta, with placentals mass as-
sumed to be 10% of foetal mass (Boyd and McCann 1989). For logistical reasons, not all measurements (body mass, length) were made on every individual sampled.

Pregnancy was determined by visual inspection of the uterus for the presence of a foetus in females collected between April and October (during the period of active gestation; Rand 1955; Boyd 1991). The sex of small foetuses was determined where possible and their STDL and body mass were measured by vernier callipers (±1 mm) and a top-loading balance (±1 g), respectively; larger foetuses were measured with a tape (±1 mm). Lactation status was determined by visual observation of a suckling pup prior to sampling, external inspection of the teats for evidence of recent suckling, manual expression of milk, and (or) inspection of dissected mammary glands for the presence of milk.

An upper canine tooth was collected from each animal and longitudinal thin sections (0.2 mm) were cut using a low-speed saw with a 0.4 mm diamond wafering blade. The thin sections were stored in a mixture of glycerol and 70% ethanol until analysis in 2001 (for details see Arnould and Warneke 2002). Age was determined by counting annual growth lines in the cementum layer under a stereomicroscope with transmitted polarized light (Payne 1978; Arbome et al. 1992). The age determined from counting annual growth lines in the cementum was adjusted for date of collection assuming a mean birth date of 1 December (Warneke and Shaughnessy 1985).

The age structure of the population was modelled to examine the underlying vital rates that could have given the observed age distribution and to examine the evidence for any historical rate of change in the size of the population. Assuming that a population has no immigration or emigration, age structure represents the combination of two processes: the initial size of each cohort and the cumulative mortality experienced by that cohort since birth. If each cohort in an age-structured population is considered independently, it would be impossible to distinguish between the effects of initial cohort size and cumulative mortality. However, initial cohort size is a function of the number of adult females in the population and is therefore constrained by the fecundity rate. Similarly, it is likely that the mortality experienced by a cohort will be correlated with the mortality experienced by all cohorts represented in the population during any time step. Therefore, the cumulative mortality experienced by a cohort will be correlated with the cumulative mortality experienced by neighbouring cohorts. Consequently, information exists within an age structure that could be used to estimate survival and reproductive rates. In this analysis we have not attempted to solve this problem analytically but have adopted a stochastic modelling approach.

For this analysis, we have combined the samples from 1971 and 1972. Our objective was to search for trends in the survival rates through time, rather than survival rates in specific years, and the advantages gained from the increase in sample sizes resulting from combining samples from the 2 years offset any increase in the temporal precision of the estimates obtained by carrying out simulations for each year separately.

The initial conditions for the simulation assumed that the observed age structure was stable, but this was not an assumption of the simulations. The initial mean annual survival rate was 8, estimated by fitting an exponential regression model to the age structure of adult females. Only females ≥3 years of age were included in the analysis (these age groups are sexually mature and are therefore most likely to be an unbiased sample of the population age structure of adults; Arnould and Warneke 2002), but the regression also provided an estimate of the initial cohort size required to produce this age structure. These variables were then used as the starting values within a stochastic model of the population. During each simulation, the population was projected forward using a Leslie matrix. We assumed that there was no age-specific component to the survival rate because we reasoned that, on average, all adult females were likely to be exposed to the same extrinsic factors affecting their survival in any calendar year. In this case, the matrix used at each time step was structured by selecting potential values for the adult female survival rate by assuming that it was normally distributed, with a mean equal to the slope of the exponential regression. The same method was used to provide values for the rate of recruitment to the adult female population, but this was centred around recruitment at 3 years of age estimated from the exponential model. This stochastic approach allowed us to investigate the parameter space that could have produced the observed age structure while relaxing the assumption of a stable age structure that accompanies classical cohort analysis. The pregnancy rate in the model was fixed at 0.78 (see below). Model simulations in which the pregnancy rate was allowed to vary, however, did not significantly alter the population age structure or the projected recruitment and adult survival rates.

Each modelled population was projected forward for 10 000 time steps, and the population age structure, expressed in terms of the proportion of adult females in each cohort ≥3 years of age, was compared with the observed age structure using minimum least squares weighted for sample size in each age class. This was repeated 100 times to obtain an estimate of the variance associated with the results.

Statistical analyses were performed using Statistica™ (Version 5.1, Statsoft Inc.) and the 9-population model was developed in C++. The Kolmogorov–Smirnov test was used to determine whether the data were normally distributed and a F test to confirm homogeneity of variances. Unless otherwise stated, data are presented as the mean ± SE and results considered significant at the P < 0.05 level.

Results

Female age distribution and survivorship

A total of 156 weaned females were collected. There was no correlation between sampling date (Julian) and female age (r = 0.07, n = 156, P > 0.3). Nine individuals were younger than the earliest age of first pregnancy (3 years; see below) and were excluded from further analyses. The age distribution of breeding-age females is presented in Fig. 1 together with the mean age structure derived from the population model. The most common age class was 4 years (15%) but a large proportion of animals were ≥10 years of age (42%), with secondary peaks in frequency evident at 14 years and, to a lesser extent, 8 years of age. The model was able to simulate these features of the observed age structure.

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Table 1. Observed and modelled age structures of female Australian fur seals (Arctocephalus pusillus doriferus) from Seal Rocks, 1971–1972, and calculated recruitment and adult survival rates.

<table>
<thead>
<tr>
<th>Age (years)</th>
<th>Frequency (%)</th>
<th>Year</th>
<th>Recruitment rate (mean ± SE)</th>
<th>Adult survival rate (mean ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>1970–1971</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>9.52</td>
<td>10.01±1.87</td>
<td>0.159±0.034</td>
<td>0.630±0.137</td>
</tr>
<tr>
<td>4</td>
<td>15.65</td>
<td>15.41±1.75</td>
<td>0.158±0.033</td>
<td>0.630±0.130</td>
</tr>
<tr>
<td>5</td>
<td>8.84</td>
<td>9.13±1.51</td>
<td>0.106±0.026</td>
<td>0.420±0.105</td>
</tr>
<tr>
<td>6</td>
<td>5.44</td>
<td>6.87±1.21</td>
<td>0.106±0.024</td>
<td>0.423±0.093</td>
</tr>
<tr>
<td>7</td>
<td>4.08</td>
<td>5.80±1.01</td>
<td>0.123±0.031</td>
<td>0.491±0.120</td>
</tr>
<tr>
<td>8</td>
<td>6.80</td>
<td>6.97±1.22</td>
<td>0.110±0.036</td>
<td>0.435±0.140</td>
</tr>
<tr>
<td>9</td>
<td>5.44</td>
<td>5.68±1.0</td>
<td>0.082±0.029</td>
<td>0.322±0.114</td>
</tr>
<tr>
<td>10</td>
<td>2.72</td>
<td>4.16±1.0</td>
<td>0.079±0.027</td>
<td>0.312±0.105</td>
</tr>
<tr>
<td>11</td>
<td>3.40</td>
<td>3.66±1.04</td>
<td>0.064±0.022</td>
<td>0.251±0.084</td>
</tr>
<tr>
<td>12</td>
<td>5.44</td>
<td>4.88±1.14</td>
<td>0.143±0.037</td>
<td>0.567±0.146</td>
</tr>
<tr>
<td>13</td>
<td>5.44</td>
<td>4.61±1.24</td>
<td>0.082±0.028</td>
<td>0.317±0.109</td>
</tr>
<tr>
<td>14</td>
<td>7.48</td>
<td>5.88±1.14</td>
<td>0.146±0.037</td>
<td>0.576±0.150</td>
</tr>
<tr>
<td>15</td>
<td>3.40</td>
<td>3.01±0.75</td>
<td>0.128±0.037</td>
<td>0.507±0.149</td>
</tr>
<tr>
<td>16</td>
<td>6.80</td>
<td>4.85±1.13</td>
<td>0.170±0.040</td>
<td>0.674±0.155</td>
</tr>
<tr>
<td>17</td>
<td>3.40</td>
<td>2.85±0.69</td>
<td>0.146±0.039</td>
<td>0.578±0.152</td>
</tr>
<tr>
<td>18</td>
<td>4.08</td>
<td>2.76±0.70</td>
<td>0.133±0.045</td>
<td>0.526±0.180</td>
</tr>
<tr>
<td>19</td>
<td>1.36</td>
<td>1.79±0.45</td>
<td>0.117±0.048</td>
<td>0.464±0.191</td>
</tr>
<tr>
<td>20</td>
<td>0.68</td>
<td>1.68±0.41</td>
<td>0.121±0.048</td>
<td>0.479±0.189</td>
</tr>
</tbody>
</table>

Note: Values are presented as the mean ± SE. The years involved in each estimate are given as split years because the samples from 1971 to 1972 were combined, so the estimated recruitment and survival rates will be mean values for the split years.

Fig. 1. Observed (shaded bars) and modelled (●) age distributions of breeding-age female Australian fur seals (Arctocephalus pusillus doriferus) from Seal Rocks, 1971–1972.

Mean ± SE and maximum observed ages were 9.37 ± 0.41 and 20 years (n = 1), respectively. The calculated annual rates of adult female survival and recruitment between 1954 and 1971 (Table 1) were 0.478 ± 0.029 (mean ± SE) and 0.121 ± 0.007, respectively.

Pregnancy rates

Pregnancy status was determined in a total of 110 females. The youngest and oldest pregnant females were 3 and 19 years of age, respectively, the overall pregnancy rate in breeding-age females being 78%. Stepwise logistic regression analysis using date, body mass, STDL, BCI, and age as continuous variables and pregnancy as the binomial response showed significant negative and positive relationships for date and age (P < 0.001 in both cases) and STDL (P < 0.02), respectively. The pregnancy rate varied with age, increasing from 78% at 3 years to an average of 85% between 4 and 13 years of age before decreasing in older females, this relationship being best described by a second-order polynomial (Fig. 2). The probability that a female was pregnant decreased from 86 ± 7% in early gestation (May–April, n = 28) to 55 ± 9% in late gestation (September–October, n = 28). Stepwise logistic regression analyses also indicated that there was no significant effect of body mass or BCI (or age or STDL) on the probability of a female being pregnant when the analysis was carried out just within early and late gestation (P > 0.06 in all cases) or within lactating and nonlactating females (P > 0.1 in all cases). However, the proportions of seals that were pregnant and lactating and seals not pregnant and nonlactating were both higher than

Fig. 2. Age-specific pregnancy rates for Australian fur seals from Seal Rocks, 1971–1972. To reduce variability, sample sizes were increased by grouping animals into 2-year age classes (regression equation: y = −0.53x² + 8.65x + 53.93; r² = 0.90).
Table 2. Chi-square contingency table with observed and expected (in parentheses) frequencies of adult female Australian fur seals from Seal Rocks, 1971–1972 (*n* = 107).

<table>
<thead>
<tr>
<th></th>
<th>Lactating</th>
<th>Nonlactating</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pregnant</td>
<td>60 (54)</td>
<td>23 (29)</td>
</tr>
<tr>
<td>Nonpregnant</td>
<td>10 (16)</td>
<td>14 (8)</td>
</tr>
</tbody>
</table>

Note: *χ²* = 7.72, df = 1, *P* < 0.01.

expected (*χ²* test, *χ²* = 7.72, df = 1, *P* < 0.01; Table 2), suggesting that females were reproducitively either “very good” or “very poor”. In addition, the results suggest that the energetic cost of lactation did not affect pregnancy rates.

A total of 70 individuals were recorded as lactating when sampled during the gestation period. There was no relationship between sampling date and the probability that a female was lactating (logistic regression, *χ²* = 0.41, df = 1, *P* > 0.5). A significant positive relationship (logistic regression, *χ²* = 14.72, df = 1, *P* = 0.0001), however, was found between the probability that a female was lactating and her BCI. Lactating animals had a higher BCI than nonlactating ones within both the pregnant (*t*₂⁹ = 4.87, *P* < 0.0001) and nonpregnant groups of females (*t*₂ = 2.35, *P* < 0.03). Furthermore, foetal BCI (derived from residuals of the sex-specific foetal STDL and body mass relationship, *n* = 65) did not differ significantly between lactating and nonlactating females (*t*₂¹ = 0.165, *P* > 0.33), indicating that the nutritional burden of lactation did not affect gestational performance in those seals that were pregnant. Maternal age, body mass, and BCI had no effect on foetal size (stepwise logistic regression, *P* > 0.2 in all cases). Foetal BCI was also not correlated with maternal age, length, body mass, or BCI (*P* > 0.1 in all cases).

**Discussion**

**Female survivorship**

The mean age (9.4 years) and modal age (4 years) observed in the present study are similar to those reported for other fur seal and sea lion species (Boyd et al. 1990; Rosas et al. 1993; Butterworth et al. 1995; Wickens and York 1997). The annual survival rates estimated using the population model fitted to the age structure, however, are lower than those reported for most fur seal species (Wickens and York 1997).

The results of the modelled age structure suggest that age classes 5–11 years had previously experienced survival rates considerably lower than those experienced by the older age classes. The reasons for this are not known but the results suggest either that the sample was biased toward older age classes or that this population experienced a change in conditions during the decade before this sample was obtained. If the adult age structure in the sample was unbiased, then the estimated recruitment and survival rates suggest that, at the time of sampling, this population was experiencing a rapid decline. Based on the mean estimated recruitment and survival rates between 1954 and 1971, the population growth rate was 0.763 (i.e., the population was declining at a rate of about 24% per annum). Using the estimated adult female survival rate and the recruitment rate in 1971, the rate of population growth would be 0.924 and the population was declining at a rate of about 8% per annum. These results suggest that both adult survival and recruitment were generally well below the level required to sustain the population during the 1950s and 1960s and that there was a particular dip during the early–mid 1960s.

Following a range-wide aerial census of pup production in 1986 (14 years after the present study), Warneke (1988) concluded that there had been no measurable increase in the Australian fur seal population since a census carried out in 1945, which is consistent with the results of the present study. Results of mark–recapture estimates, however, indicate that annual pup production at the study colony has increased substantially since the present sample was obtained (from 2100–2200 in 1966–1974 to ca. 4024 in 1997). Between 1968 and 1991, pup production increased 2.4% per annum (Shaughnessy et al. 1995) and then 6.1% per annum until 1997, when the most recent census was conducted (Shaughnessy et al. 2000). Pup production has also been increasing at several other large colonies and total production for the population is estimated to have doubled since the present study (Arnold and Littnan 2000; Littnan and Arnold 2002; Shaughnessy et al. 2002). These observations suggest increases in fecundity or adult survival, or a combination of these, since the present sample was obtained.

Changes in prey availability could theoretically be responsible for the calculated rates of population decline during the 1960s and the observed increases since the present study. There is little evidence, however, for major shifts in the marine productivity in Bass Strait and surrounding waters over the last century (Klaer 2001; N.L. Klaer, unpublished data). Records from steam trawlers in southeastern Australia during 1915–1961 indicate decreases in total fish catches, but these appear to be more likely due to overfishing than to environmental fluctuations (Klaer 2001; N.L. Klaer, unpublished data). Competition with commercial fisheries, therefore, could have had an impact on the Australian fur seal population. However, while Australian fur seals are known to consume some commercial target species (Gales and Pemberton 1994; Goldsworthy et al. 2003), the degree of competition with fisheries is difficult to assess because of a lack of detailed information regarding the level of temporal and spatial overlap between their foraging areas and the activities of the fishing fleet.

An alternative explanation for the age structure observed in the present sample and the subsequent population growth is that through the 1960s there was a relatively high level of harvest of this population, which has since subsided. Between 1923 and 1983, fishers in Victoria could legally shoot “nuisance seals” interfering with fishing operations (Warneke 1966; R.M. Warneke, unpublished data) and anecdotal evidence suggests that this was common practice, with at least 8% (17% where the cause of death was known) of tagged individuals retrieved showing signs of having died from gunshot wounds (Warneke 1975). Furthermore, mortality due to operational interactions with fisheries (e.g., drowning in nets and lobster pots and entanglement in manmade debris) at the time the present sample was collected accounted for an additional 23% (49% where the cause of death was known) of tag retrievals.

The attitudes and practices of fishers, their perception of seals as competitors, and the size of the fishing fleet have
Table 3. Relationship between the adult survival rate and the rate of population increase derived from model predictions based on the age structure observed in the present study and a constant rate of recruitment (0.159).

<table>
<thead>
<tr>
<th>Adult survival rate</th>
<th>Annual rate of population increase</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.63</td>
<td>0.925</td>
</tr>
<tr>
<td>0.65</td>
<td>0.942</td>
</tr>
<tr>
<td>0.69</td>
<td>0.977</td>
</tr>
<tr>
<td>0.73</td>
<td>1.012</td>
</tr>
<tr>
<td>0.77</td>
<td>1.048</td>
</tr>
<tr>
<td>0.81</td>
<td>1.084</td>
</tr>
<tr>
<td>0.85</td>
<td>1.119</td>
</tr>
</tbody>
</table>

changed over the last 20 years (Kailola et al. 1993; Hickman 1999; Hume 2000; Norman 2000) and this is likely to have substantially reduced the non-natural mortality of Australian fur seals and contributed to the population growth. Indeed, using the observed age structure and recruitment rates from the early 1970s and varying the adult survival rate in the model predictions indicate that a 20% increase in adult survival would result in a 12% per annum increase in population (Table 3). Furthermore, as there is likely to be a positive correlation between adult and juvenile survival, the real change in adult survival required to account for the population increase is likely to be considerably smaller. A rate of increase in the population of between 1.2% and 4.8% would be sufficient to account for the observed change in population size between the present study and 1997. If the estimated mortality rate due to shooting and (or) operational interaction with fisheries is considered to be a minimum (because of under-reporting by fishers and low recovery of tags), the relaxation of this source of mortality could account for the recent history of the population.

Pregnancy rates

Age at first pregnancy (3 years) was the same as that reported for Cape fur seals (Butterworth et al. 1995) and similar to that in other otariids (Wickens and York 1997). The pregnancy rate at the age at first pregnancy in Cape fur seals (37%), however, was less than half that in Australian fur seals (78%), with comparable rates not being reached until females were 2–3 years older. In the present study, maximal pregnancy rates were observed at 4–13 years of age before decreasing significantly in older females, which suggests the existence of reproductive senescence in these animals. Similar declines in the reproductive performance of older females have been documented in South American (Arctocephalus australis), Cape, Antarctic (Arctocephalus gazella), and northern (Callorhinus ursinus) fur seals (Trites 1991; Boyd et al. 1995; Butterworth et al. 1995; Lima and Paez 1995).

The decline in the proportion of females that were pregnant throughout the course of gestation suggested that some foetuses were aborted as pregnancy progressed, potentially in response to nutritional stress. Indeed, numerous aborted foetuses are observed around Australian fur seal natal colonies in September (personal observation), which coincides with the onset of the third (and most nutritionally expensive) trimester (Widdowson 1981; Bronson and Manning 1991). Similar observations of abortions and declining pregnancy rates during gestation have been reported for Steller sea lions (Eumetopias jubatus) and Cape fur seals (Guinet et al. 1998; Pitcher et al. 1998). In view of this decline in pregnancy rates, a potential bias in the present study could result from no samples having been collected in the month prior to the breeding season (November). However, as most females wean their pup during October and are able to forage extensively thereafter (Cane 1995; Arnould and Hindell 2001), the further incidence of abortion due to nutritional stress during this period is likely to have been low. Conversely, as females who abort may continue to suckle their pup through to a second year (Arnould and Hindell 2001; Hume et al. 2001), and therefore may be more likely to be ashore during October, the observed pregnancy rate in late gestation could be negatively biased.

Whereas Boyd (1991) suggested that implantation is the point where nutritional factors have their greatest influence on pinniped reproduction, Pitcher et al. (1998) postulated that otariid species with extended lactation may abandon pregnancy later in gestation when the energetic costs increase and future reproductive success can be better assessed. Indeed, the rate of abortion in Steller sea lions and Cape fur seals was found to be negatively related to body condition, suggesting a need for adequate lipid stores to maintain pregnancy (Guinet et al. 1998; Pitcher et al. 1998). In the present study, however, the pregnancy rate was not related to BCI at any stage of gestation.

The overall pregnancy rate (78%) in Australian fur seals is the same as that reported in Cape fur seals (78%–79%; Butterworth et al. 1995; Guinet et al. 1998) and within the range found in other otariid species (Wickens and York 1997). It is also consistent with reports of some female Australian fur seals not producing a pup every year and suckling offspring for a second or even third year (Hume et al. 2001). Recent studies (Coulson et al. 2000, 2001) have shown that density-dependent effects on large mammals tend to lower fecundity rates before influencing adult survival. The comparatively normal pregnancy rates observed in the present study, therefore, support the notion that the apparently low survival rates were due to a density-independent process (e.g., shooting, drowning in nets) rather than to any effect of the food supply. Comparisons between species, however, must be interpreted with caution, as sampling times in relation to stage of gestation differed markedly between studies. In addition, the present study encompassed only 2 years, whereas longer term studies have documented significant interannual differences in pregnancy rate due to environmental variability (Boyd et al. 1995; Lima and Paez 1995; Guinet et al. 1998; Pitcher et al. 1998).

In the present study, there was no difference in pregnancy rate or foetal BCI between lactating and nonlactating females, suggesting that lactation did not impinge on gesta-

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tional performance. In contrast, Pitcher et al. (1998) found that lactation had a negative impact on pregnancy rates in Steller sea lions, especially in younger animals, and Lima and Paez (1995) found foetal mass to be significantly lower in lactating than in nonlactating South American fur seals. In the present study, there was also a positive relationship between BCI and the probability that a female was lactating, as has been observed in Cape fur seals and Steller sea lions (Guinet et al. 1998; Pitcher et al. 1998). This is not surprising, as most of the milk delivered to pups is produced on land from stored body reserves (Arnould and Boyd 1995), so lactating females might be expected a priori to have larger adipose stores than nonlactating ones, as a result of milk-production patterns rather than superior foraging abilities in lactating females. Consequently, the differences in BCI between lactating and nonlactating females are likely to have been the consequence rather than the cause of lactation.

Compared with the conspecific Cape fur seal population, which inhabits the nutrient-rich productive waters of the Benguela Current and has experienced a rapid increase (Warneke and Shaughnessy 1985; Butterworth et al. 1995), the Australian fur seal population has experienced comparatively slow growth since the end of commercial harvesting (Warneke and Shaughnessy 1985; Warneke 1988). Warneke and Shaughnessy (1985) proposed that the low marine productivity of Bass Strait might be limiting the rate of recovery of the Australian fur seal population through effects on female fecundity. Contrary to what might be expected if this was the case (Caughley 1980; Fowler 1990), however, the age at first pregnancy and overall pregnancy rates in the present study were comparable to those found in Cape fur seals. Indeed, the proportion of 3-year-old female Australian fur seals that were pregnant was double that of Cape fur seals. Furthermore, the apparent lack of influence of body condition and lactation on pregnancy rates suggests that nutritional resources were not limiting for Australian fur seals at the time of the present study. However, if the population was experiencing a substantial level of harvesting (as suggested above), it is possible that any potential effects of the nutrient-poor nature of Bass Strait on fecundity may have been masked by a reduction in density-dependent effects. Indeed, Arnould and Warneke (2002) found that the body condition of Australian fur seal females decreased between the present sample and the late 1990s and suggested that this may be indicative of increased competition for resources as the population has recovered. It will be of interest to monitor changes in pregnancy rates of Australian fur seals as the population continues to grow and approach historical levels.

In summary, the model predictions based on the age structure of Australian fur seals at Seal Rocks in 1971–1972 suggest that survivorship was sufficiently low for the population to be experiencing a decline. However, the relatively high pregnancy rate, especially in younger females, and the apparent lack of any effect of body mass or condition on pregnancy suggest that food was not limiting and that the low survivorship was due to density-independent effects. Mortality resulting from interactions with fishers is known to have been common at this time and could account for the low survivorship. The recent increase in the population is consistent with anecdotal evidence that fatal interactions with fishers have decreased as fishing practices have changed.

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**References**


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