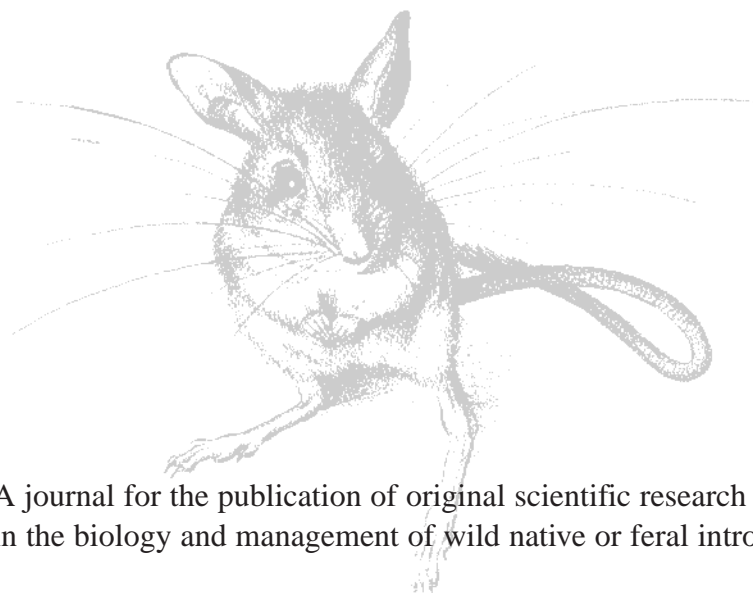

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Abundance, distribution and status of the New Zealand sea lion, *Phocarctos hookeri*

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Abstract

The abundance of the New Zealand sea lion, *Phocarctos hookeri*, was estimated using a model that incorporated estimated pup production. Pups are born at only five sites, four of which are at the sub-Antarctic Auckland Islands, which lie to the south of New Zealand. The remaining breeding site is at Campbell Island in the same region. Pup production was estimated during the 1994/95 and 1995/96 breeding seasons from mark-recapture studies at the two largest sea lion rookeries, at the Auckland Islands (Sandy Bay and Dundas Island), which account for almost 90% of total pup production for the species. Pup production for the other sites was estimated from direct counts or, in the case of Campbell Island, from recent tagging data. Total pup production estimates for all sites during the 1994/95 and 1995/96 breeding seasons are 2640 and 2807 respectively. During the four-week pupping season, pup mortality at most sites was estimated to be about 10%. The estimates of absolute abundance based on pup production for the two breeding seasons were 11 700 (95% confidence interval (CI): 10 500–13 100) and 12 500 (95% CI: 11 100–14 000) respectively. This population abundance is among the smallest reported for a species within the Otariidae. The highly localised, and historically reduced distribution make this species vulnerable to impact and warrants particular attention from conservation managers. In particular, the potential impact of the annual bycatch of *P. hookeri* in a trawl fishery requires close monitoring and, ideally, some mitigation action.

Introduction

The endemic New Zealand sea lion, *Phocarctos hookeri*, one of the world's rarest pinnipeds, breeds principally within a highly localised range to the south of New Zealand between 48°S and 53°S. Up to about 95% of pupping is reported to occur at the Auckland Islands (50°S, 166°E) and a small breeding population is also reported on Campbell Island (52°33'S, 169°09'E) (Cawthorn 1993; Gales 1995). A few pups (<10) have been observed at Snares Island (48°S, 166°20'E) and occasionally single pups are born at Stewart Island and the Otago Peninsula on the South Island of New Zealand.

Haul-out sites of *P. hookeri* are more wide-spread and extend from Macquarie Island (54°30'S, 159°E) in the south, where a few males are seen most years, to Stewart Island (47°S, 168°E), the islands of Foveaux Strait (46°30'S, 168°E) and the Otago Peninsula (46°S, 170°40'E) in the north, where haul-out sites of predominantly sub-adult males are present year-round (Lalas and McConkey 1994; Gales 1995). Sightings of single animals (usually males) have been made at various other sites around the South Island of New Zealand (Cawthorn *et al.* 1985).

Historically, commercial hunting and Maori subsistence hunting of *P. hookeri* reduced its abundance and distribution (Childerhouse and Gales 1998). The impact of these commercial and subsistence kills cannot be quantified and it is therefore not possible to predict the pristine population size.

Recent estimates of the population size of *P. hookeri* have been between 4000 and 14 083 (Falla *et al.* 1979; Cawthorn *et al.* 1985; Anon 1991; Cawthorn 1993). Most of these measurements did not include pup counts from Dundas Island.

The only breeding colony for which reasonable time-series data on pup production are available is that at Sandy Bay, Enderby Island. At this site 350–500 pups have been born each year for the last 25 years (Falla 1965; Taylor 1971; Best 1974; Marlow 1975).

During the 1970s a trawl fishery for arrow squid (*Nototodarus sloanii*) was established on the shelf waters around the Auckland Islands and the Snares Island (Fig. 1) and has led to an estimated, annual, incidental catch of 17–140 sea lions between 1988 and 1995 inclusive (Baird 1996). The impact of the bycatch on the population size of *P. hookeri* is unknown as there are no accurate temporal data on population size nor any survival curves or life history parameters for this species. Woodley and Lavigne (1993) used life history tables for northern fur seals (*Callorhinus ursinus*) and Himalayan thar (*Hemitragus jemlahicus*) to model the impact of the bycatch on the population size of *P. hookeri*. They concluded that both models would result in *P. hookeri* having a limited capacity for population increase. If data from *C. ursinus* are used, a bycatch of over 1% of mature females would result in a population decline; in the case of modelling using *H. jemlahicus* as a type animal, *P. hookeri* populations would decrease with any level of bycatch. By contrast, Anon. (1991) used some life history parameters from Steller sea lions (*Eumetopias jubatus*) to predict that an incidental take of 80 females per season represented a removal of less than 2.5% of females of all ages from the population. On the basis of draft guidelines from the United States National Marine Fisheries Service (NMFS) to govern incidental catch in marine mammal populations, and the assumption that the New Zealand sea lion population is not less than 20% of its pre-exploitation size, the authors argued that a bycatch of up to 80 females each year is probably insufficient to cause a population decline.

A catch limit of sea lions was determined by the New Zealand Department of Conservation in 1993 based on the NMFS draft guidelines. The resulting limit for incidental catch of sea lions was 63 of any age/sex class, or 32 females per annum; for this calculation, 10 500 was used as the best estimate of minimum stock abundance. These bycatch limits were used for the fishing seasons in 1993–96 inclusive. In 1995 the estimated bycatch of sea lions exceeded the catch limit, but the fishery was not closed as a delay in processing the data resulted in the situation not being recognised until after the fishing season was over. In 1996, 1997 and 1998 the fishery was closed early as estimated bycatch exceeded the catch limit.

Considerable debate has ensued on the robustness of the data used to establish population size and status. The objectives of this study were to address these concerns and: (1) document breeding sites; (2) document the pupping season and changes in the pup numbers during the season (a pupping curve) for the major breeding sites; (3) estimate pup production and establish a methodology whereby pup production at key sites can be used to monitor population status; (4) estimate the total population size on the basis of pup production; and (5) examine recent trends in population size.

Methods

Age and sex classes

Four age and sex categories were recognised during surveys: non-juvenile males (bulls and subadult males), adult females (cows), juveniles and pups. Females were differentiated from non-juvenile males by their smaller size, lack of a mane, and creamy coloured pelage with darker pigmentation around the muzzle and flippers. By contrast, non-juvenile males are blackish-brown with the development of black manes reaching the shoulder in older animals.

Pups of the year were clearly distinguishable by their small size. Their pelage is a thick coat of dark brown hair that becomes dark grey with cream markings on the top of the head, the nose, tail and at the base of the flippers during the first few weeks of life.

Juveniles are distinguishable from the older categories by their small size. They resemble females in coloration for the first two years of life, after which males become a little darker.

Assessment of pup mortality

Dead pups were recorded separately from live pups. Pup carcasses deteriorate rapidly as they are scavenged by skuas (*Catharacta skua lonnbergi*) and trampled by sea lions. During the 1994/95 season on

Enderby Island each observer recorded only dead pups that were judged, on the basis of the degree of decomposition, to have died since the previous census. For the following breeding season dead pups were collected daily and removed from the colony to avoid the possibility of counting a carcass twice. At Dundas Island it was not possible to remove dead pups from the colony because of the relatively large number of animals and the aggressive territoriality of the bulls. Consequently, mortality was estimated from a thorough count of all pup carcasses at the time of the mark-recapture study when access to the breeding area was possible following the departure of most territorial males. On Figure of Eight Island all dead pups were counted, regardless of their condition. The largest single count on each season was used as the mortality estimate.

Direct multiple counting

Sandy Bay, Enderby Island

Daily counts were conducted at Sandy Bay, Enderby Island from 4 December 1994 to 17 January 1995, after which counts were conducted on a less frequent basis until 30 January 1995. Direct counts of animals were not conducted during the 1995/96 season. The Sandy Bay area was sub-divided into zones: three beach areas (A, B and C), which were demarcated by small streams; the sward, which is an open grass and herb field immediately behind the beach; and the rata forest, which surrounds the sward. Each area was counted separately. Almost all pupping occurs on the beach, and it is here that sea lions form large aggregations. On the beach, the large, darker non-juvenile males were conspicuous and easy to count; a single count was made of males by one observer. Adult females and pups were the most numerous age/sex classes on the beach and formed aggregations that made them difficult to count. On most days three observers counted these animals, each observer conducting three separate counts. On some occasions only two observers were available to conduct the triple counts. Separate counts were recorded in the three beach zones (A, B and C), as well as smaller groupings within the zones that were defined on the day by the observers and demarcated by features such as gaps between aggregations of animals. The observers always remained in a single group during the count so that the same aggregations were counted. All beach counts were conducted from the sward/beach margin, which offered a height advantage of about 3 m above beach level. Furthermore, the beach/sward margin represented the inshore margin of the beach territories maintained by bulls, allowing the observers reasonable access. All counts were made using hand tally counters. Later in the season when animals move to the sward and into the rata forest they are more widespread and were counted once, observers spreading out to cover the whole area as effectively as possible.

All individual counts were recorded. The estimate of live pups or cows for that day was derived when all counts of pups or cows were summed and means and standard errors calculated. Estimates for the two other age and sex classes were derived from the sum of the single counts in each area.

Pebble Point, Enderby Island

Sea lions at Pebble Point were counted everyday from 4 December 1994 until 12 January 1995, after which less frequent counts were conducted until the end of January 1995. Less frequent counts were conducted during the 1995/96 breeding season, when only pup numbers were recorded. Whilst cows and pups formed large aggregations, the counting procedure at this site was the same as that for Sandy Bay. When they were more widespread, single counts were conducted.

Dundas Island

Sea lions on Dundas Island were not censused as frequently as those on Enderby Island as access to the island was difficult and our stays relatively short. The counting methods were the same as those used on Sandy Bay, but the task itself was more difficult as the sea lions are more numerous at this site, form very large aggregations, and there are no convenient vantage points of sufficient height offering a good view over the sea lions. Furthermore, the grassland surrounding the beach area was occupied by territorial bulls through most of the pupping season. Points from which counts were conducted varied between visits. On occasions when time limited our work on Dundas Island, our priority for counts was pups and cows, then non-juvenile males.

Figure of Eight Island

Figure of Eight Island at the south of the main Auckland Island was visited by small craft when weather permitted. The island is heavily vegetated and counts were made by three counters walking under the forest canopy in transects taking direct counts of pups and other age and sex classes.

Campbell Island and Snares Island

Sea lions have been reported to breed on Campbell Island and Snares Island in small numbers. Estimates of pup production at these two sites were based on results of a pup-tagging effort on Campbell Island within the past ten years and *ad hoc* observations made at appropriate times of year on Snares Island.

Pup production curves

Pup production curves were fitted to the data at each site for which frequent pup counts were conducted during the 1994/95 season, using a fourth-order polynomial. In order to test for differences in the dates of mean, maximum pup numbers at Sandy Bay, Pebble Point and Dundas Island, the standard errors associated with the estimated dates (determined from the optimisation routine in Microsoft Excel) were found using parametric bootstrapping (Efron and Tibshirani 1993). In comparing two sites, the difference between any two estimated dates of peak pup production was assessed as significantly different if it was greater than twice the standard error of this difference (SED) where:

$$SED = \sqrt{SE_1^2 + SE_2^2}$$

and SE_1 and SE_2 are the individual standard errors.

Historic pup production at Sandy Bay

Counts of pups on several occasions during the breeding season have been made frequently at Sandy Bay since 1972. Counts in 1972/73 were conducted by Best (1974); all other data are from M. Cawthorn (unpublished data).

Data from eight of these seasons were selected, these being the ones for which counts spanned most of the breeding season. They were combined with those from the 1994/95 season to determine whether there had been a temporal shift in the pupping season. An estimate and standard error for the date of mean maximum pup numbers in each season was calculated using the method described above for the 1994/95 data. Similarly, estimates of the peak number of pups and their standard errors were calculated to determine whether changes in pup production had occurred over time. Weighted regressions were used to test for linear trends, with each weight being the reciprocal of the square of the standard error of the estimate.

Marking and recapturing

Mark–recapture estimates were used only for pups at Sandy Bay and Dundas Island. The size of the pup population was first estimated from the mean of the direct counts conducted immediately before the mark–recapture study. The number of pups marked was approximately 25–50% of this count estimate. Marking was spread as evenly as possible through the colony (based on pup density). The mark–recapture study was timed to occur when pupping had ceased, but before the pups had started to disperse from their natal site. A satisfactory mark–recapture study could not have been conducted any earlier as bulls were still territorial and did not allow access to most pups.

In 1994/95 pups were marked with circular, 10-cm-diameter, flexible vinyl discs that were glued to the crown of their heads with a fast-setting cyanoacrylic glue (Loctite 454). The size of the discs was reduced to about 6 cm for the pups on Dundas Island during the 1995/96 experiment. White discs were used during both years at Sandy Bay, orange discs used at Dundas Island in 1994/95 and yellow discs in 1995/96. Discs were clearly visible from a distance and pups in most postures could be visually categorised as marked or unmarked. Most discs were shed through normal wear and tear a few days to a few weeks after the experiment.

Recaptures involved moving systematically through the entire sea lion colony counting pups. Two or three observers were used for each experiment. Each pup was classified as either marked or unmarked and a tally of each was maintained by each observer using two hand-tally counters. Any pups that could not be definitely categorised as marked or unmarked were excluded from the count. Observations of pups were made over the entire range of the pups' distribution. All recapture operations were conducted the day following the marking operation in order to allow even mixing of marked and unmarked individuals. Each counter conducted 3–5 replicate counts. The total number of replicates (Q) was the sum of replicates for each counter.

Calculation of mark–recapture estimates

Results of each recapture were used to calculate a modified Petersen estimate of pup production P_i (Chapman 1952), namely

$$P_i = \left[\frac{(M+1)(C_i+1)}{(R_i+1)} \right] - 1$$

where, for replicate i , M is the number of previously marked sea lion pups, C_i is the number of pups examined in the recapture sample, and R_i is the number of marked pups in the recapture sample. The overall estimate of pup production, P , is the mean of the Q individual estimates, i.e.

$$P = \frac{\sum_{i=1}^Q P_i}{Q}$$

The standard error, SE , of P was calculated directly from the individual estimates (Chapman 1952), as

$$SE = \sqrt{\frac{1}{Q(Q-1)} \sum_{i=1}^Q (P_i - P)^2}$$

The power of estimates of pup production to detect change

An analysis was undertaken to determine the power of future mark-recapture estimates of pup production to detect a trend over time. Potential trends were assumed to be log-linear. Variables used in the analysis were: the coefficient of variation ($CV = SE/Estimate \times 100$) of the mark-recapture estimates (estimated at 2%); the standard deviation of log-production about a log-linear trend (estimated to be 0.09 using the data from 1994/95 and 1995/96); the true percentage change in pup production (D); and the probability of wrongly detecting a change (α , set at 10%).

Assessment of population size from pup production estimates

A model was used to estimate the absolute abundance of *P. hookeri*. The inputs of the model are reproductive rates of the adult females and survival of the juvenile cohorts. Age at first reproduction was estimated as 4 years (Cawthorn 1993; N. Gales, unpublished data), which means that females are sexually mature at 3 years and there were three female juvenile cohorts. The following assumptions were made for the model:

- the population is stable,
- the sex ratio of male and female pups is 1 : 1,
- there was no differential mortality between sexes at any age class,
- there was no density dependence,
- the parameters were consistent between colonies, and
- the population estimate N and the age/sex categories refer to the end of a season, which ended when the subsequent pupping season began.

As pup production (P) was used as the basis for the total population estimate, all equations were expressed in terms of P . Hence:

$$P_f = 0.5P$$

where P_f is the number of female pups born, and

$$F = P_f/R$$

where F is the number of mature females and R is the female reproductive rate, and

$$J_f = J_1 + J_2 + J_3 = P_f(S_1 + S_1S_2 + S_1S_2S_3)$$

where J_1, J_2, J_3 are the total number of juvenile females (J_f) in the three age cohorts, and S_1, S_2, S_3 are the survival rates in the first, second and third years of life. Also

$$N_f = J_f + F$$

where N_f is the total number of females, and

$$N = 2N_f$$

where N is the total population size.

As the model has assumed that the sea lion population is stable we can assess how reasonable the survival estimates for juveniles are by calculating the predicted adult female mortality (which must equal the

number of females entering the mature age class) and comparing this with values reported for other pinnipeds. Thus

$$F_m = F(1 - S_f) = J_3$$

where F_m is annual female mortality and S_f is the annual survival of adult females.

As $F = P/R$ and $P_f = 0.5P$, it follows that

$$S_f = 1 - (J_3/F) = 1 - 0.5R S_1 S_2 S_3$$

The risk analysis programme @Risk (Palisade Corporation, Newfield, USA) was used as an add-in to the model which was run on a Microsoft Excel spreadsheet. @Risk allows the user to tailor a probability distribution and its parameters for the model inputs, run a predetermined number of evaluations of the model, drawing from the input probability ranges, and produce a probability distribution of the outcome(s) of interest (in this case, absolute abundance). We chose to use ten thousand evaluations.

Female reproductive rate (R) was assigned a triangular distribution with a minimum of 0.6, a most-likely value of 0.75 and a maximum of 0.9. The mean of R from this distribution is 0.75. The parameters for juvenile survival were selected to ensure that the chance of a pup reaching adulthood ($S_1 S_2 S_3$) was close to 50%. S_1 was estimated to have a triangular distribution with a minimum value of 0.58, a most-likely value of 0.68 and a maximum value of 0.78. S_2 and S_3 were assumed to be independent and both had a triangular distribution with a minimum of 0.75, a most-likely value of 0.85 and a maximum of 0.95.

A normal distribution was used to represent the uncertainty associated with pup production. The mean of this distribution was the estimate of P , taken to be the total of all counts in that season (Table 1). The standard deviation of the distribution was the standard error associated with this estimate. In order to calculate this standard error, we first estimated those constituent standard errors that were not directly available from the data. For this purpose it was assumed that for counts of live pups the ratio SE/estimate would be the same at Figure of Eight Island and Campbell Island as at Pebble Point. Similarly, it was assumed that this ratio would be the same for counts of dead pups as for live pups at the same site, and that it would be the same in 1995/96 as it was at the same site in 1994/95. The standard error of the total count was then taken as the square root of the sum of squares of all constituent standard errors.

Table 1. Estimates of live and dead pups at all New Zealand sea lion colonies

Site		Method	1994/95	1995/96
Sandy Bay	Live pups	Mark-recapture	421 ± 4	417 ± 3
	Dead pups	Direct count	46	38
Pebble Point	Live pups	Multiple counts	59 ± 1	49
	Dead pups	Direct count	12	20
Dundas Island	Live pups	Mark-recapture	1603 ± 20	1810 ± 22
	Dead pups	Direct count	234	207
Figure of Eight Island	Live pups	Direct count	123	113
	Dead pups	Direct count	19 ^A	31
Campbell Island	Live pups	Historic count	98	98
	Dead pups	Historic count	24	24

^AEstimated from mean mortality at Sandy Bay, Pebble Point and Dundas Island

Results

Breeding sites

The New Zealand sea lion breeds at four sites at the Auckland Islands: (1) Pebble Point, Enderby Island, (2) Sandy Bay, Enderby Island, (3) Dundas Island, and (4) Figure of Eight Island (Fig. 1). Occasional sightings of single pups in various bays on the north-east of Auckland Island have been made in previous years (P. Moore, personal communication), but no such sightings were made during this study, despite periodic searches.

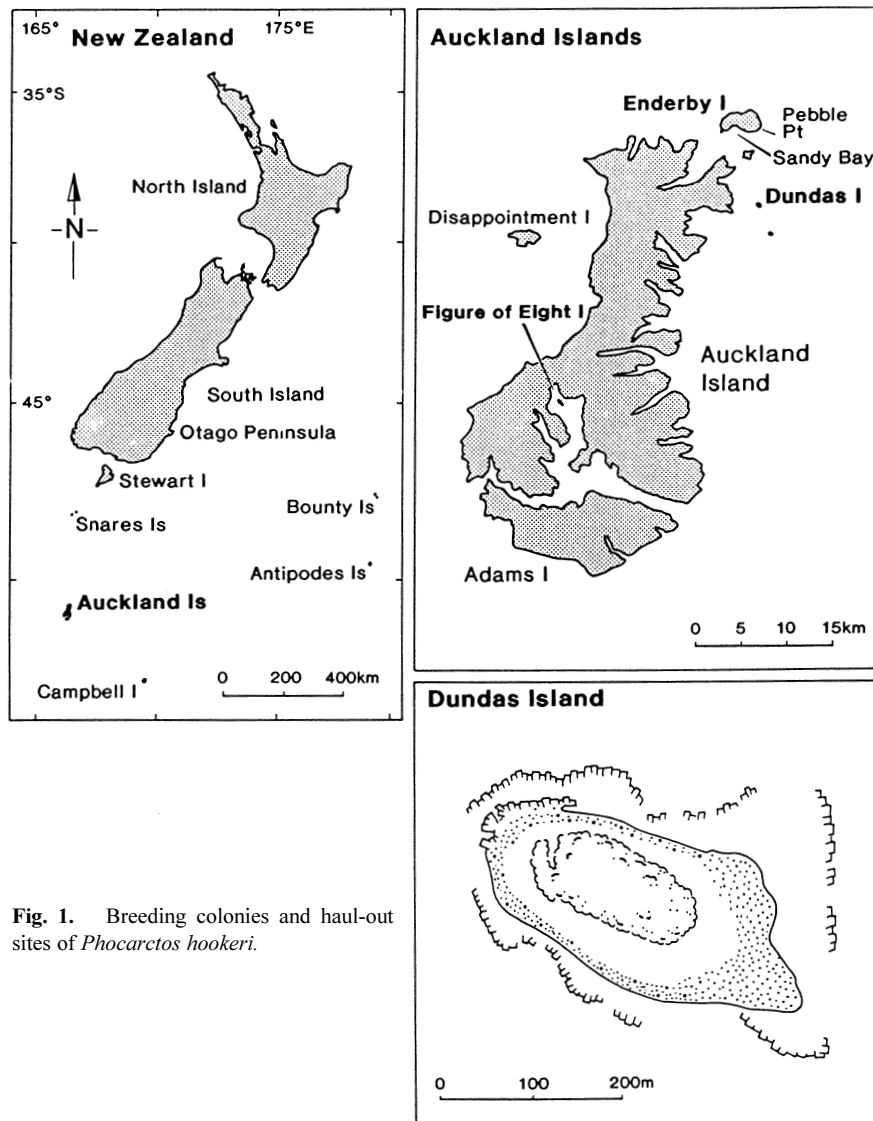


Fig. 1. Breeding colonies and haul-out sites of *Phocarctos hookeri*.

Sandy Bay, is a small, south-facing bay on the mid South coast of Enderby Island (Fig. 1). It is well protected from the predominantly westerly air flow that occurs year-round at these latitudes. A curved beach of about 400 m long and 20–30 m wide at mean high water is the site of virtually all pupping and mating. Behind the beach is an open area of grassland up to 400 m wide that extends to the edge of the rata forest which is the dominant vegetation over the centre of the island.

Pebble Point is on the south-eastern corner of Enderby Island (Fig. 1) and is more open to ocean swells than Sandy Bay. Pupping and mating occurs on a flat area of hard-packed sand immediately inshore of a rocky point. Behind this area a grassland extends to the edge of rata forest.

Dundas Island is a small island to the south of Enderby Island (Fig. 1). A beach on the south-eastern point about 100 m long and up to 50 m wide is the site of pupping and mating. The remainder of the island is fringed by a low grassland of predominantly *Poa* tussock that is separated by a muddy ditch from a slightly raised centre of grasses, megaherbs and *Hebe elliptica*

bushes. The island is fairly well protected from the eastern-setting swells and experiences strong tidal flows. It is fringed by a reef.

Figure of Eight Island in Carnley Harbour (Fig. 1) is completely protected from the ocean swells. It is a small island almost completely covered by a mixed forest of *Metrosideros umbellata*, *Coprosma* and *Dracophyllum*. The sea lions breed beneath the forest canopy at the north-western point of the island where they form muddy wallows.

Campbell Island is situated 280 km south-east of the Auckland Islands. The sea lion population on this island is widely dispersed. Cow, pup and bull groups are often found on the side and even the tops of the island hills at heights of up to 800 m. The habitat utilised varies from coastal sand and rock to dense low scrub in which the sea lions tunnel for access.

Snares Island, situated 270 km north of the Auckland Islands, does not appear to be a current breeding site for *P. hookeri* as no pups retaining their natal pelage have been seen there for the past four years despite annual visits to the island by biologists each February. Even post-moult under-yearlings, which would have been capable of swimming to the Snares from the Auckland Islands, are sighted only occasionally at the Snares (J. Molloy, personal communication).

The weather in the region to the south of New Zealand is most strongly influenced by the strong circum-polar westerly air flow. These winds blow throughout the year, but are strongest during the winter months when the low-pressure systems have their most northerly influence. Temperatures are mild and rarely fall below freezing.

Pup-production curve

The days (after 30 November) at which the estimated maximum number of pups occurred for Sandy Bay, Dundas Island and Pebble Point in 1994/95 pupping season were 43.7 ± 0.5 (estimate \pm s.e.) (i.e. 13 January), 45.3 ± 1.8 (14 January), and 33.8 ± 0.8 (3 January) respectively (Fig. 2). These dates represent the end of pup production. Consequently, the duration of pupping was 33 days for Sandy Bay, 35 days for Dundas Island and 24 days for Pebble Point. After this time no births or new-born pups were observed, the dominant bulls left their harems to younger males and mating activity declined rapidly. By about ten days after the cessation of pupping most animals had dispersed from the beach. Cows and pups moved into the surrounding rata forests and grasslands at the two Enderby Island colonies (Fig. 3) and those on Dundas Island moved more widely over the entire island.

The peak pupping dates at Dundas Island and Sandy Bay were not significantly different (difference, 1.7 days; SE of difference 1.8), but that at Pebble Point was significantly earlier than at the other two sites (Dundas Island v. Pebble Point: difference, 11.5 days, SE of difference 1.9; Sandy Bay v. Pebble Point: difference, 9.8 days, SE of difference 0.9).

Historic pup production at Sandy Bay

Counts of pups at Sandy Bay for 8 selected years between 1972 and 1993 are shown in Fig. 4. The estimates of the date of maximum pup numbers from these years and 1994/95 ranged from 9 to 16 January, with a mean of 13 January. There was no evidence of a linear trend in this date ($t_7 = -0.7$, $P = 0.5$). Power analysis showed that there was a 74% chance of detecting a trend of one day in three years (using $\alpha = 10\%$).

There was no evidence of a trend in pup production in estimates from Sandy Bay between 1972 and 1995 (log-linear trend = -0.74 , $t = -0.54$, $P = 0.6$, residual s.d. = 0.07). Power analysis showed there to be an 83% chance of detecting a linear trend in pup production of 1% per year (with $\alpha = 10\%$).

Pup-production estimates

Sandy Bay, Enderby Island

The maximum mean number of live pups counted at Sandy Bay during the 1994/95 breeding season was 411 ± 2.6 (estimate \pm SE), on 13 January 1995. The following day a mark-recapture

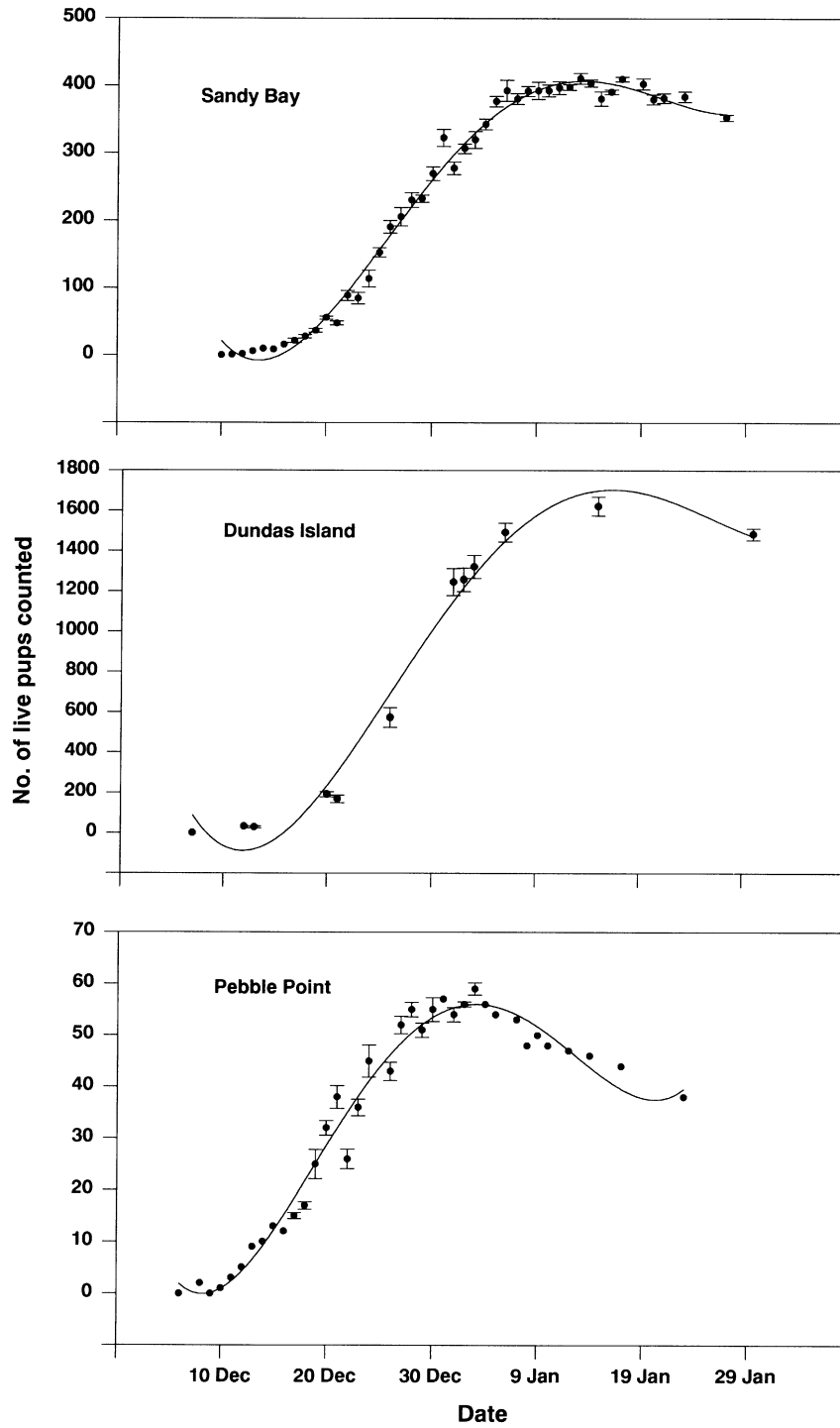


Fig. 2. Number of live pups counted (mean \pm SE) at Sandy Bay, Dundas Island and Pebble Point during the 1994/95 breeding season with fitted fourth-order polynomials.

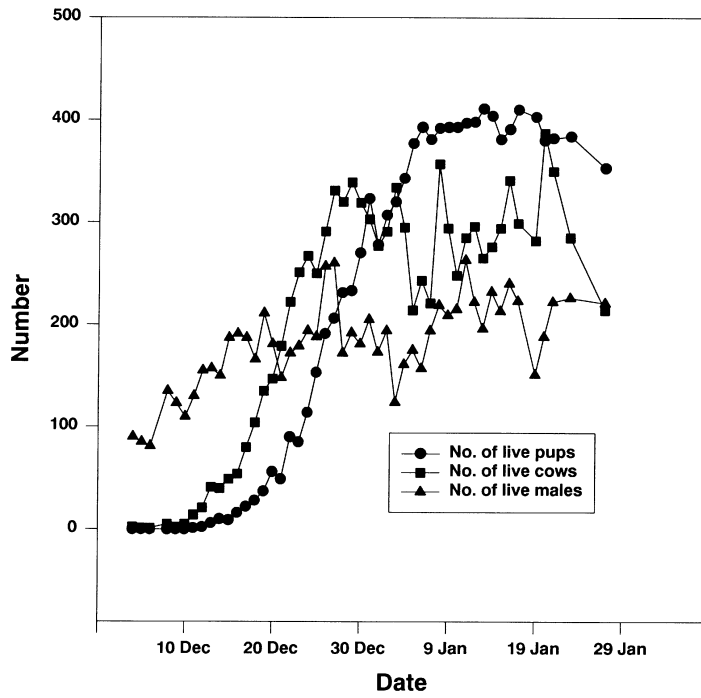


Fig. 3. Number of live pups, cows and non-juvenile males counted on Sandy Bay during the 1994/95 breeding season.

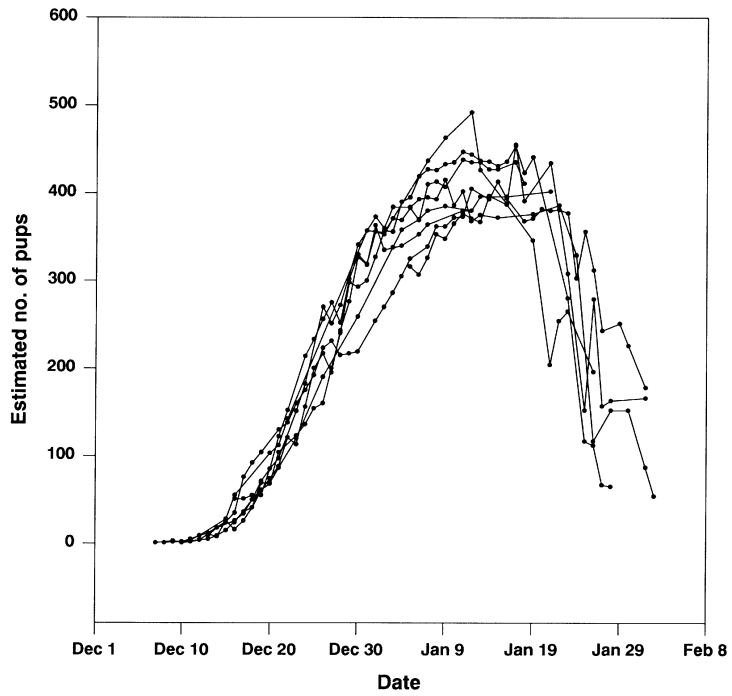


Fig. 4. Number of live pups counted for selected years at Sandy Bay from 1972 to 1993.

experiment estimated the live pup population to be 421 ± 3.9 (estimate \pm SE) (Table 1). On the same day as the mark–recapture estimate a direct count yielded an estimate of 404 ± 1.7 pups. The mark–recapture estimate is used as the most realistic estimate of pup production as it theoretically accounts for hidden animals not seen during direct counts. An estimated 46 sea lion pups had died prior to the mark–recapture experiment. Consequently, the estimated pup production on Sandy Bay for the 1994/95 season was 467 pups. The estimated pup mortality for the first month of the pupping season was 9.8%. The mark–recapture estimate of live pup numbers for the 1995/96 season was 417 ± 2.8 . In all, 38 pups had died, yielding a pup-production estimate of 455 pups with an estimated pup mortality of 8.4%.

Pebble Point, Enderby Island

The maximum mean count of live pups at Pebble Point during the 1994/95 breeding season was 59 ± 0.6 pups on 3 January 1995. At this time an estimated 12 pups had died, yielding a pup-production estimate of 71 pups. Pup mortality during the three-and-a-half-week pupping season was estimated to be 16.9%. The maximum mean count of live pups at Pebble Point during the 1995/96 breeding season was on the 10 January 1996 when 49 pups were counted; 20 dead pups had been removed from the colony. Consequently, the estimated pup production for 1995/96 was 69 pups with pup mortality estimated to be 29%.

Dundas Island

The highest mean estimate of live pups acquired from direct counting during the 1994/95 pupping season on Dundas Island was 1623 ± 27 pups on 15 January. The estimate of live pups from the mark–recapture experiment conducted on 21 January was 1603 ± 20.1 pups. No direct counting was undertaken on the day of the mark–recapture estimate. The estimated pup mortality on 21 January was 234 pups, yielding an estimate of pup production of 1837 pups and a mortality rate of 12.7%. During the 1995/96 pupping season no direct counts were made. The mark–recapture experiment on 21 January provided an estimated live pup population of 1810 ± 21.9 pups. In total, 207 pup carcasses were counted on Dundas Island on 21 January, which yields an estimated pup production for the 1995/96 season of 2017 pups and a mortality rate of 10.3%.

Figure of Eight Island

In all, 123 live pups were counted on Figure of Eight Island on 11 January 1995. Dead pups were not counted during this survey. We used the mean mortality of Sandy Bay (9.8%), Dundas Island (12.7%) and Pebble Point (16.9%) for 1994/95 to estimate mortality at Figure of Eight Island at 20 (13.1%). Consequently, the pup-production estimate for 1994/95 was 142 pups. During the 1995/96 season two counts were conducted on 5 and 24 January. The higher count of live pups was made on the second count when 113 live pups and 31 dead pups were counted, yielding a pup-production estimate of 144 pups and a mortality of 21.5%.

Campbell Island

Sea lion pups were not counted or tagged during the 1994/95 or 1995/96 pupping seasons. Some counts and tagging of sea lion pups has been undertaken in previous years. As sea lions are widely dispersed around Campbell Island and much of the terrain they utilise is vegetation that is very hard to walk through, there has been no complete survey of all sea lions on Campbell Island conducted at one point of the breeding season. Rather, counts have been conducted at different times of the season at different locations and it is not possible to use these data to estimate total pup production. We have used data from tagging to estimate a minimum level of pup production. The amount of effort invested in pup-tagging programmes varied between years. During the 1991/92 breeding season 98 pups were tagged and 24 dead, untagged pups were counted (M. Frazer, personal communication). Thus, for that season a minimum estimate of pup

production is 122 pups. Although in 1991/92 there was a higher tagging effort than in most years, untagged pups were still seen after the tagging had stopped (M. Frazer, personal communication). The pup-production estimate for 1991/92 is used here as the estimate for pup production in the two years of this study.

The power of future estimates of pup production to detect change

Annual estimates of pup production, as opposed to less frequent estimates, would have the effect of most rapidly increasing the power to detect a trend, irrespective of the size of trend (D). Fig. 5 shows the change in power as the number of annual estimates increases for three scenarios; D equals 1%, 2% and 4% respectively.

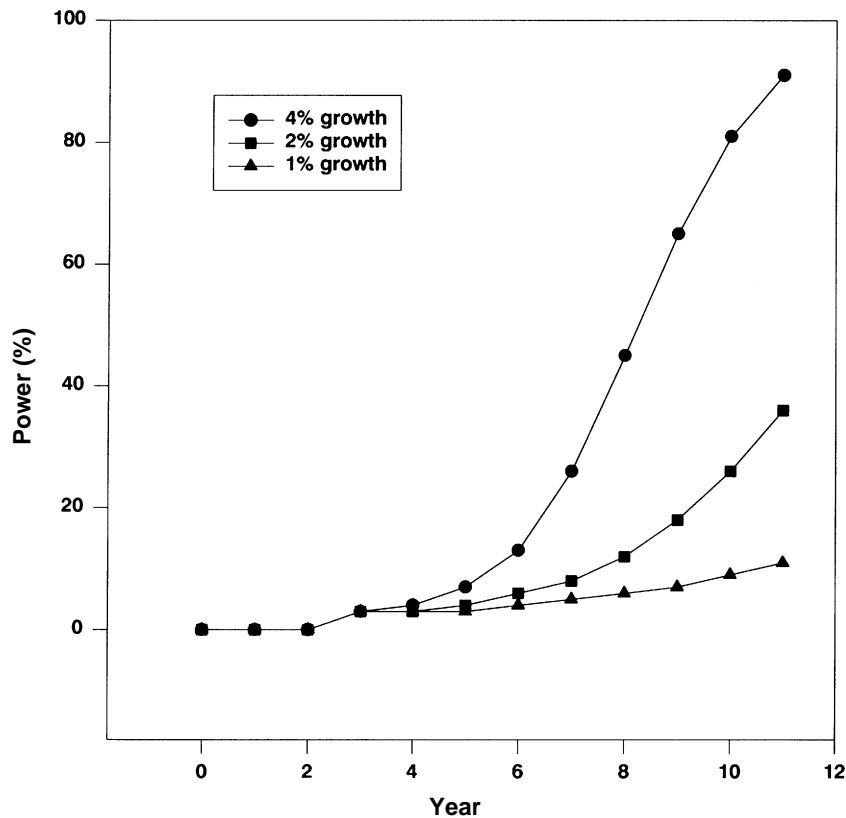


Fig. 5. The power to detect an actual 1%, 2% or 4% change in pup production when conducting annual mark-recapture estimates (CV of 2%) for up to 11 years, assuming the s.d. of log-production about a linear trend to be 0.09, and a 10% probability of incorrectly detecting a trend.

Absolute abundance of New Zealand sea lions

For absolute abundance estimates of *P. hookeri* the pup-production estimates from Table 1 were used. Where mark-recapture estimates of pup production had been conducted, the mean estimate was added to the estimate of mortality at that time for total pup production. Where multiple counts were conducted the mean estimate was used and added to the mortality estimate. If only a single count was conducted, or a point estimate from a previous year used (Campbell

Island), this was added to the mortality estimate. Consequently, the total pup production estimates (\pm SE) for 1994/95 and 1995/96 were 2640 ± 21 and 2807 ± 22 respectively. Pup production for the Auckland Islands (excluding Campbell Island) was 2518 ± 21 and 2685 ± 22 for the two seasons.

The absolute abundance estimates of *P. hookeri* derived from the simulations (given to the nearest 100) are 11 700 and 12 500 for the 1994/95 and 1995/96 seasons respectively. The lower and upper 2.5 percentiles from the simulations were used to calculate 95% confidence intervals (CI) for the two seasons; these are 10 500–13 100 and 11 100–14 000 respectively.

The abundance estimates for the population(s) of *P. hookeri* at the Auckland Islands (excluding Campbell Island) are 11 200 (CI: 10 000–12 500) and 11 900 (CI: 10 600–13 400) respectively.

The probability of a pup reaching adulthood was 49% (95% CI: 39–61%). The estimate of adult female survival rate from the model was 82% (95% CI: 76–86%). The factor by which the pup production can be multiplied to predict absolute abundance is 4.4 (95% CI: 4.0–5.0).

A check on the sensitivity of the results for each input parameter indicated that *R* was most influential (rank correlation with the estimate of *N* is -0.84 for both years). This is not surprising, given that *R* is a denominator in the estimate of *N*. The other rank correlations were less than 0.4 in magnitude, so only *R* was used for sensitivity analysis. The effect of changing *R* to a uniform distribution (with the same minimum and maximum as before) was to lower the mean *N* by 0.4% for both years and widen the lower and upper limits by 2.1% and 2.8% respectively.

Discussion

Pup-production estimates

Determining the abundance of a mammalian population is a complex task that is constrained by our usually poor understanding of population structure, our inability to define boundaries accurately between sub-populations and the constraints of the assumptions on which most census techniques are dependent. In this sense the New Zealand sea lion represents one of the more straightforward species for which an abundance estimate can be calculated. Firstly, in common with most other polygynous pinnipeds, pupping occurs annually within a limited, predictable time-frame. Estimates of pup production are the best index of relative population status and provide the best measure from which overall population size can be estimated (Berkson and DeMaster 1985). This is because pups represent the only age class that is readily recognisable and is restricted to land; other age and sex classes are more widespread and it is not possible to estimate accurately the proportion of animals that are on land at the time of the census. Furthermore, pups are relatively easy to handle and represent good experimental animals for mark–recapture estimates of abundance. Secondly, the distribution of *P. hookeri* is highly localised, with over 95% of pupping occurring at the Auckland Islands and about 95% of this pup production occurring at three of the four breeding sites. Campbell Island is the only *P. hookeri* breeding site away from the Auckland Islands.

We report estimates of pup production derived from two methodologies – direct repeated counts with multiple observers and a mark–recapture estimate. The former method was used to determine the pupping curve from which an appropriate timing for the mark–recapture experiment could be determined. The direct-count method provided estimates of visible live pups with narrow confidence intervals but was not able to correct for pups hidden by terrain or other animals. This bias is likely to be inconsistent, and thus impossible to correct for, as it will vary with sea lion behaviour, which is influenced by pup age, weather and stage of the breeding season. The mark–recapture method provided similarly low standard errors but was not biased by obscured animals. The timing of this experiment was central to the high precision as it ensured that the requirements for a simple mark–recapture study were met, these being: all pups were accessible for marking; pups were highly mobile and mixed well after being marked; mortality of pups was negligible and assumed to be zero for the 24 hours of the experiment; pupping had ceased, the pups were not yet swimming and cows had not started to move their

pups away from the island (no emigration). Furthermore, the ease of conducting multiple recaptures, and including most of the pup population in the recapture, significantly improved the precision of the estimate (Rice and Harder 1977). Estimates of live pup numbers obtained from both direct counting and mark–recapture are available for Sandy Bay, Enderby Island in January 1995. The difference between the estimates can be interpreted as either the direct count methodology under-estimating pup numbers by 4.0%, or the mark–recapture estimate over-estimated pup numbers by 4.2%. We suggest the former interpretation to be the more likely.

The two pup-production estimates for 1994/95 and 1995/96 we report suggest an increase of about 6% between the two years. In fact, pup-production estimates were relatively consistent at all but Dundas Island where production increased by almost 10%. Such an increase is unlikely, and is probably indicative of the stochastic nature of such processes. Estimates of pup production from forthcoming seasons will provide clearer measures of the degree of stochasticity of the rate of change.

Despite the high level of precision of the mark–recapture pup-production estimates, the power to detect a change in production over time was low (Fig. 5). If pup production at Dundas Island is relatively stable (as appears to be the case for Sandy Bay), then the true change in population size will be low (probably less than 4%) and it will take well over a decade to quantify such a trend with any confidence. Clearly, the power to detect change can be increased by making a decision to increase the accepted probability of wrongly detecting a change. Similarly, future pup-production estimates are likely to change our estimate of the standard deviation around a log-linear trend; if this is found to be less than 0.09, the power to detect change will increase. For eight seasons of direct counts at Sandy Bay, the standard deviation (of estimated peak pup numbers) about a log-linear trend is 0.07, suggesting that the equivalent figure for mark–recapture estimates (at time of maximum pup numbers) will be about the same or smaller. Notwithstanding this, the clear message from the power analysis is that long-term, frequent estimates of pup production are necessary if managers wish to predict trends with any confidence.

Absolute abundance estimates

The estimate of absolute abundance of *P. hookeri* we report is based on estimated probability distributions of life-history parameters, many of which are unknown for this species. Where there are no data these estimates are based on what is reported for other otariids. Age at first reproduction has been estimated for *P. hookeri* at four years old, based on resightings of breeding cows that had been tagged as pups (Cawthorn 1993; N. Gales, unpublished data). As we have no estimates of juvenile survival for *P. hookeri* we used estimates from *Eumetopius jubatus* that were calculated during a period of population stability (Anne York, personal communication). These estimates resulted in about 49% of female pups surviving to the age at first reproduction. In comparison, Calkins and Pitcher (1982) estimated that 47% of *E. jubatus* female pups survive to their third birthday, and York (1994) estimated this figure to be 48%. Estimates for this parameter in *Callorhinus ursinus* have varied from 45 to 63%, reflecting changes in population demographics as well as methods of estimation (Keyes 1965; Lander 1981; York 1987). Our estimate of the range for the female reproductive rate was chosen to reflect those reported for other otariids. These are 60–75% for *E. jubatus* (Pitcher and Calkins 1981; Calkins and Pitcher 1982), 77% for the Australian sea lion, *Neophoca cinerea* (Higgins 1993), $74 \pm 2\%$ for *C. ursinus* (Payne 1977), and 85% for *Arctocephalus gazella* (Boyd *et al.* 1990). The inferred annual survival rate for adult female *P. hookeri* of 82% from our model is lower than that reported for *C. ursinus* (89%: Chapman 1964) or *A. gazella* (92%: Boyd *et al.* 1990), but is included within the range reported for *E. jubatus* (80–93%: York 1994). This relatively high mortality rate may well reflect the processes driving a stable population, as opposed to an expanding one, or alternatively may reflect an inappropriate selection by us of ranges for juvenile survival or female reproductive rates.

The abundance estimate yields a pup-production multiplier (i.e. abundance estimate divided by estimated pup production) of 4.4, which is in close accord with others reported for otariids: 4.23

for *A. forsteri* (Crawley and Brown 1971); 4.9 for *A. forsteri* (Taylor 1982); 4.1 for *A. gazella* (Payne 1979); 4.5 for *Eumetopius jubatus* (Calkins and Pitcher 1982); 3.8–4.8 for *N. cinerea* (Gales *et al.* 1994); and 3.5–4.5 for increasing populations of most polygynous pinnipeds (Harwood and Prime 1978).

P. hookeri is one of the least abundant of the Otariidae. Only the Guadelupe fur seal (*Arctocephalus townsendi*) has a substantially smaller population of about 6000 (Reijnders *et al.* 1993). The Juan Fernandez fur seal (*Arctocephalus philippii*) and the Australian sea lion (*Neophoca cinerea*) both have estimated populations of a similar size to that of *P. hookeri* (Reijnders *et al.* 1993; Gales *et al.* 1994); all other otariids are substantially more abundant. The range of *P. hookeri* is also limited in comparison to those of other pinnipeds, increasing the potential vulnerability of this species. The International Union for the Conservation of Nature and Natural Resources (IUCN) currently lists this species in the threatened category as ‘vulnerable’ (IUCN 1996) on the basis of its highly restricted distribution (fewer than 5 locations).

Population trends and impacts

Counts of sea lion pups conducted prior to this study at Dundas Island and Figure of Eight Island were too infrequent, too variable in effort and detail, and too variable in terms of date to provide indications of trends. Surveys at Sandy Bay, Enderby Island were conducted on a more frequent basis and show that for the past three decades, all but one of the maximum pup counts conducted were of 358–475 pups; this is in close accord with the pup-production estimates we report in this study. The single count of 180 pups made during the 1977/78 breeding season was made late in the season (26 January) when many pups would have dispersed from the beach into the surrounding rata forest. The only counts conducted prior to 1972 were by Falla during the 1942–44 Cape Expedition, who reported 350 cows pupping annually on Sandy Bay (Falla 1965). It is tempting to infer from these data that the Sandy Bay sea lion population has been relatively stable for the past 50 years. However, as the counts were not standardised by date or method it is not possible to identify trends in pup production. The more recent counts conducted at Sandy Bay since 1972 (Best 1974; M. Cawthorn, unpublished data) conducted systematically through 8 breeding seasons, suggest that pup production has been stable there since that time.

The sea lion rookery at Pebble Point appears to have increased during the past few years. Prior to this study, frequent counts of pups conducted during most breeding seasons in the late 1970s and the 1980s recorded maximum pup production of 25 (M. Cawthorn and S. Mitchell, personal communication). The finding that about 70 pups were born at this site during both breeding seasons on which we report represents a real increase. Interestingly, this rookery has a shorter breeding season than Sandy Bay or Dundas Island (25 days *cf.* about 35 days), the peak of the pupping curve is at least ten days earlier and mortality is higher. It is possible that these variations are associated with this rookery being populated by mostly older females who tend to pup earlier in the breeding season, along with less experienced bulls. Equally, it may be that the site itself is less suitable for a rookery than the other sites. We have no data to support or refute either hypothesis.

P. hookeri has been subject to various human-induced impacts. The direct take of sea lions for pelts and food around the Auckland Islands during the last century cannot be quantified, but was responsible for a marked decrease in population size. Prior to this, the subsistence kill of sea lions for food by Maori and Moriori around New Zealand and the Chatham Islands led to the marked range reduction, with the current population primarily restricted to the Auckland Islands (Childerhouse and Gales 1988; Smith 1989). Since the mid-1800s harvesting has not occurred, but some pup mortality has occurred from entrapment in rabbit holes. Rabbits were introduced to Enderby Island in 1865 and eradicated in 1993. Prior to eradication, mortality due to entrapment in burrows was estimated to average 12 pups per annum (M. Cawthorn, personal communication). This mortality represented approximately 2–3% of current pup production at this site.

The most significant, current, anthropogenic source of mortality of *P. hookeri* is from fishing bycatch. In managing this interaction it is necessary to define which ‘population’ is the source of

the sea lions killed. Taylor (1995) identified the potential problems of managing removals from populations without adequate understanding of population structure and dispersal rates. Whilst we are able to report here on relative levels of pup production at different sites for *P. hookeri* we know little of movement between these breeding sites. We have observed pups marked on Dundas Island swimming to Enderby Island when only a maximum of 6–8 weeks of age, and resightings have demonstrated that female pups born and marked on Dundas Island have been found to breed at Sandy Bay. Similarly, sea lion pups tagged at Sandy Bay have been sighted hauled out on Campbell Island (Gales 1995). Furthermore, little variation has been found at the cytochrome B site for *P. hookeri* and no rookery-specific markers could be identified (G. Lento, personal communication). As the commercial trawl fishery for squid occurs exclusively on the southern Snares Shelf and the Auckland Islands Shelf, which population(s) of *P. hookeri* should be included in calculations of a bycatch limit? The major risk identified by Taylor (1995) in ignoring population structure is depletion of the harvested population if only an aggregate population is being monitored and this differs from the harvested population. In the case of *P. hookeri* it would seem prudent to establish bycatch limits based on pup production from the Auckland Island colonies only (i.e. exclude Campbell Island) and to ensure that these three colonies are monitored closely for evidence of change. Concomitant with this is the need to accurately estimate bycatch rates, particularly of female sea lions, such that our ability to forecast potential impacts on the population (monitored through pup production) can be maximised.

Future surveys and demographic parameters

Determining trends in *P. hookeri* populations is a key to the immediate management strategies for limiting the impact of bycatch. We have demonstrated that the power to detect trends reduces dramatically if pup-production estimates are made on a less than annual basis. Consequently, we recommend that annual estimates of maximum pup production be undertaken for at least the next 5–10 years for the Sandy Bay, Pebble Point and Dundas Island populations. These populations can be surveyed by a single team of people based on Enderby Island. Mark–recapture techniques should continue to be used for Sandy Bay and Dundas Island, whilst direct counts are suitable for the smaller colony at Pebble Point. Access to Figure of Eight Island is more difficult and the timing of surveys is limited by weather. Surveys at this site should continue to be undertaken when possible by the survey team based on Enderby Island. Direct counts of pups are suitable for this site.

Estimates of pup production at Campbell Island are difficult because the sea lions are distributed widely around the island, the vegetation is difficult to walk through, and the animals are well hidden. An attempt to conduct a complete count and a mark–recapture estimate of pup production on this island should be undertaken in the near future. The results of that effort should be used to plan a future strategy for determining trends in pup production at Campbell Island. Regular monitoring of sea lion numbers, particularly pup production, should continue at all other sites where sea lions have been recorded. The numbers of animals at most sites are very low, and surveys can be conducted as a part of other work programmes.

Clearly the utility of our population model is compromised by the lack of data on some key parameters. Reproductive rate and survival are the critical parameters that, if measured, would greatly strengthen the model. Survival rates of juveniles should be estimated by monitoring the recruitment of permanently marked pups (flipper tags and passive integrated transponder tags) into the reproductive population. Survival rates of adult females should be estimated from models based on a determination of the non-juvenile female age structure (from examination of growth layers in teeth). All females captured for tooth extraction should be permanently marked and monitored through successive breeding seasons to determine the reproductive rate.

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