

Population status and trends in the abundance of the fur seals at Macquarie Island



Subantarctic fur seal pups: A Wiebkin

Report to the Department of the Environment, Water, Heritage and the Arts

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1 EXECUTIVE SUMMARY

Macquarie Island is the only breeding population of the threatened subantarctic fur seal in Australian territory. Following the elimination of the endemic population by 19th century sealers, the Macquarie Island population has had a complex recolonisation history, and now consists of three species that hybridise. Establishment and growth of breeding populations on Macquarie Island has been slow due to its distance from major population centres, differences in the colonisation times of males and females of each species, and extensive hybridisation among all three species.

The Department of the Environment, Water, Heritage and the Arts (DEWHA) *Recovery Plan for Subantarctic fur seals and southern elephant seals* (the Recovery Plan) aims to, “determine the rate of population change and population size by undertaking scientifically robust, regular and repeatable population surveys”. Status and trends in abundance and extent and trends in hybridisation of subantarctic fur seals can only be monitored using population censuses and molecular genotyping. This was last achieved in 2003. This project reports on population censuses and DNA sampling of fur seals at Macquarie Is in the 2007/08 season.

During the 2007/08 fur seal breeding season at Macquarie Island, 217 fur seal pups were born. Based on phenotypes of the 203 pups captured and sampled, the cohort comprised 43 (21%) subantarctic fur seals, 148 (73%) Antarctic fur seals and 12 (6%) hybrids. However, based on previous analyses of eight pup cohorts where both phenotype and genotype data are available, these estimates are unlikely to be correct.

The Recovery Plan is scheduled to be reviewed in 2009. Changes in the status and trends in abundance of the subantarctic fur seal population at Macquarie Island can only be quantitatively assessed through genetic analysis of cohort samples. We recommend that DEWHA funds the analysis of additional cohorts in order to meet the recommendations of the Recovery Plan. We also recommend integrating genotypic and demographic data to provide a quantitative assessment of the significance of three key threatening processes: hybridisation, predation of pups by hooker sea lions and climate change, all of which may be affecting the recovery of the subantarctic fur seal at Macquarie Island. Finally, strong support should be given to assist the maintenance of the annual fur seal monitoring program at Macquarie Island, as this is the only program that provides a comprehensive analysis of the status, trends and threatening processes of the threatened subantarctic fur seal and hence the only means of providing outcomes to satisfy the requirements of the Recovery Plan.

2 INTRODUCTION

Populations of fur seals on most subantarctic islands were severely over-harvested last century. Fur seals (*Arctocephalus* spp.) were abundant at Macquarie Island (54° 30' S, 158° 56' E) when sealers discovered it in July 1810. Intense and indiscriminate harvesting followed, which resulted in the extermination of the population by 1820 (Shaughnessy and Fletcher 1987). Over the following 100 years, royal and king penguins (*Eudyptes schlegeli* and *Aptenodytes patagonicus*) and elephant seals (*Mirounga leonina*) were harvested for their oil, and fur seals were occasionally seen and killed (Mawson 1943). Based on shipping logs, at least 199,444 fur seal skins are estimated to have been taken (Shaughnessy and Fletcher 1987, Ling 1999), but there are no known specimens or taxonomic descriptions of fur seals from Macquarie Island during this period; thus, the identity of the original species remains uncertain.

Sealers are reported to have called the original fur seal at Macquarie Island the 'Upland Seal', or 'seal of the high ground' (Lesson 1828). Shaughnessy and Fletcher (1987) argued that because sealers began harvesting in July (austral winter) of 1810 and obtained a large number of skins (5,000) between May and October of the following year, the original species was unlikely to have been the Antarctic fur seal, which is absent from its breeding grounds between May and November. Both subantarctic and New Zealand fur seals are present on breeding grounds throughout the winter months as the pups of these species do not wean until September or October (Mattlin 1981, Kerley 1983, Bester 1987, Goldsworthy 2006). The unique 'Upland seal' was also reported by Lesson (1828) to exclusively inhabit Macquarie Island and the Antipodes Islands (49° 41' S, 178° 45' E). Taylor (1992) hypothesised that 'Upland Seals' were not a different species, but rather juvenile New Zealand fur seals, and that Macquarie and the Antipodes Islands may never have supported large breeding populations. Shaughnessy and Fletcher (1987) suggest that the 'Upland Seals' of Macquarie Island were most likely to have been the subantarctic fur seal or a distinct, now extinct species, although other species may have used the island.

When an Australian National Antarctic Research Expedition (ANARE) station was established on Macquarie Island in 1948, a small number of New Zealand fur seals was recorded in summer on the northern tip of the island (Gwynn 1953). In March 1955, a fur seal pup was discovered in Goat Bay on North Head Peninsula (Fig. 2), the first evidence of breeding since the sealing era (Csordas 1958). Small numbers of pups (0-6) were recorded annually until 1979-1980 (Csordas and Ingham 1965, Shaughnessy and Fletcher 1987), and

since then, the number of pups born has increased steadily (Shaughnessy and Fletcher 1987, Shaughnessy et al. 1988, Shaughnessy and Goldsworthy 1993).

Macquarie Island is unique among fur seal populations in that it contains three species, Antarctic (*Arctocephalus gazella*), subantarctic (*A. tropicalis*) and New Zealand fur seals (*A. forsteri*). Early reports assumed that the pups born since 1955 were New Zealand fur seals (Csordas and Ingham 1965). However, in 1981-1982 it was established that the breeding group consisted of Antarctic and subantarctic fur seals, while the New Zealand fur seal appeared to be non-breeding (Shaughnessy and Fletcher 1987). The recovery has been relatively slow and although annual increases in pup production were very high between 1974-1991 (21%/yr), since then the annual increase in pup production has slowed to about 6%/yr. The slow rate of recovery is likely due the isolation of Macquarie Island from other subantarctic islands, and the complex process of colonisation of each species and their hybridisation.

The fur seal population at Macquarie Island represents one the most significant mammalian hybrid zones, and is the only significant location of hybridisation among all pinniped species. A major analysis of the extent, trends, processes and implications of hybridisation has recently been completed (Lancaster et al. 2006, 2007a,b). This included the genotyping of over 1,000 fur seal pups over 12 years (1992-2003) from eight entire cohorts, and about 300 adults. The results of this work have identified that the annual representation through pup production from Antarctic (59-61%) and subantarctic fur seals (11-22%) has increased in the population and the level of hybridisation has decreased from around 30% to 17% over this period (Lancaster et al. 2006). Hybridisation involves all three fur seal species, hybrids appear to be fertile, but hybrid males have lower reproductive success than pure species males (Lancaster et al. 2006, Lancaster et al. 2007a, b). The reproductive success of hybrid females relative to pure species has not been determined.

Macquarie Island is the only breeding site of the subantarctic fur seal in Australian waters, and this species may have formed the breeding population prior to sealing. Because of its restricted range within Australian waters and its very small population size (about 100 seals), the 'The Action Plan for Australian Seals', (Shaughnessy 1999) recommended its nomination to the Australian *Endangered Species Act*. The species is now listed nationally as a threatened species under the *EPBC Act*, and a recovery plan has been drafted, which requires ongoing monitoring of pup production and assessment of potential risks to the population. The last accurate assessment of a pup cohort at Macquarie Island was in the 2003-04 season, when 37 subantarctic fur seal pups were born. Samples have been collected from the 2005-06 and 2006-07 pup cohorts.

2 AIMS AND OBJECTIVES

This project targeted the aims of the *Recovery Plan for Subantarctic fur seals and southern elephant seals*. The project aimed to monitor pup abundance, and collect skin samples from the 2007/08 cohort of fur seal pups at Macquarie Island to enable subsequent DNA analyses. This will facilitate the final aim, to summarise the status and trends in abundance of the subantarctic fur seal, and the extent of hybridisation with Antarctic and/or New Zealand fur seals. Because there is extensive hybridisation among the three fur seal species that breed at Macquarie Is we also summarise the population trends of the three species.

3 METHODS

Study site

The main concentrations of breeding fur seals at Macquarie Island are located in three bays (Secluded Beach, Aerial Cove and Goat Bay), on North Head Peninsula (Fig. 1). Single pups have occasionally been recorded in Garden Cove on North Head Peninsula and a small number of pups (1-2) have been found south of North Head Peninsula at Hurd Point, Windsor Bay, Brothers Point, Lusitania Bay and Handspike Point (Fig. 1). Groups of non-breeding fur seals occur along the east coast of the island and on the northwest, southeast and southwest points. Few fur seals have been reported on the west coast south of Handspike Point (Fig. 1), despite regular surveys by researchers working on sea birds and elephant seals.

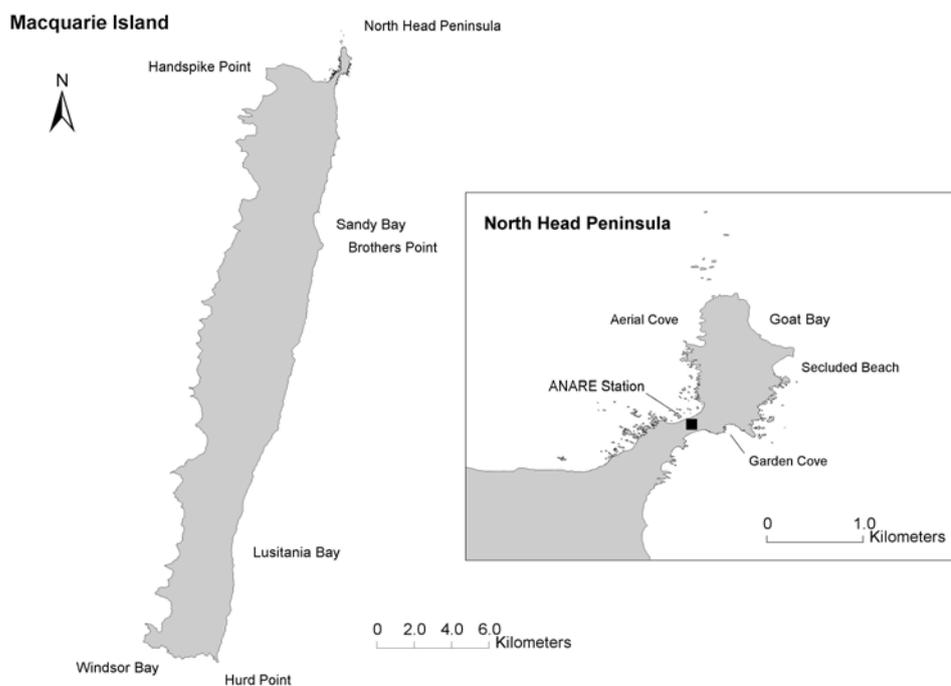


Fig. 1. Map of Macquarie Island showing the locations where fur seal pups have been recorded, with an inset map of North Head Peninsula.

Estimation of fur seal pup abundance

This project was conducted on Macquarie Island between November 2007 and April 2008. Pups are born at Macquarie Island over a two-month period, from mid November to early January, with most pups born in December (Shaughnessy et al. 1988). Breeding seasons are named here by the year in which they commenced. During this period, daily surveys in the

breeding colonies on North Head Peninsula were undertaken to monitor changes in pup abundance, record new births and mark and sample pups.

Pups remain with their mothers for 7-10 days following birth, after which the mother leaves to forage at sea. Mothers then alternate between foraging trips at sea (usually lasting 3-4 days) and shore bouts of 1-2 days to nurse their pups. While mothers are at sea pups progressively move further away from breeding territories, making them accessible to researchers without disturbing other breeding animals.

Annual pup production for each species is determined through a tagging program whereby all pups within a season are tagged (both flipper tags and implanted RFID transponders) in order to establish a marked/known-aged population for the purposes of calculating age-specific survival and fecundity. Pups are identified by numbers bleached onto their dark natal fur during the first few weeks after birth, and are not tagged until they are sufficiently robust, usually a month after birth. During the tagging procedure, pups are sexed, weighed and a transponder is inserted under the skin (for permanent identification in case of tag loss). A small piece of skin (usually the last 1mm of the tip of the hind flipper) is sampled for DNA analysis. Samples are collected from the entire cohorts of pups annually, which provide the necessary information to underpin species and hybrid identification.

The total number of pups born was calculated based on the number of pups marked (bleached or tagged) plus those known to have been born that went missing before marking. Species were identified based on external characteristics and vocalisations following Shaughnessy et al. (1988) and Goldsworthy et al. (1997). Individuals that showed intermediate characteristics or characteristics of more than one species were classed as 'putative hybrids' (F1 hybrids or backcrosses). Hybrid pups are often difficult to distinguish from pure species based on phenotypic characteristics (Wynen 2001).

4 RESULTS

Abundance of fur seal pups in the 2007/08 season

In the 2007/08 season, 217 fur seal pups were recorded (Fig 2). This figure is compiled from the number of pups marked, pups seen with tagged females (but were not marked i.e. went missing), recovery of dead pups (not marked) and from counting the number of pups present in the territories on a daily basis. Pups that were marked were scored based on phenotype, with 148 pups classed as *A. gazella*, 43 *A. tropicalis* and 12 hybrids (Fig 3a).

Collection of skin samples from fur seal pups in 2007/08

Of the 217 fur seal pups that were recorded, 203 of these were captured between one and three weeks after they were born, when their mothers were at sea foraging. The pups were biopsied, to collect a DNA sample, and given a bleach number so they would not be sampled twice.

Trends in total fur seal pup production

Between 1954-2007 (54 seasons), the annual pup production for the species aggregate increased from 1 to 217 pups. However, the trend in pup production varied markedly during this period (Fig. 2). Between 1954-1974 (21 seasons), pup production showed little change, with the number of pups recorded ranging from 0 to 4 (mean = 1.3 ± 1.3 SD). The greatest period of increase (22.0% per year) occurred between 1974-1991, when pup production increased exponentially ($r = 0.199$, 18 seasons) (Fig. 2). In 1991, the annual rate of increase in pup production declined and has since remained about 6.0% per year (1991-2007, $r = 0.058$, 16 seasons). Annual increases in pup production have been positive since 1983, except between 2001-2002 when there was a drop in pup production of 9.7% (from 164 to 148).

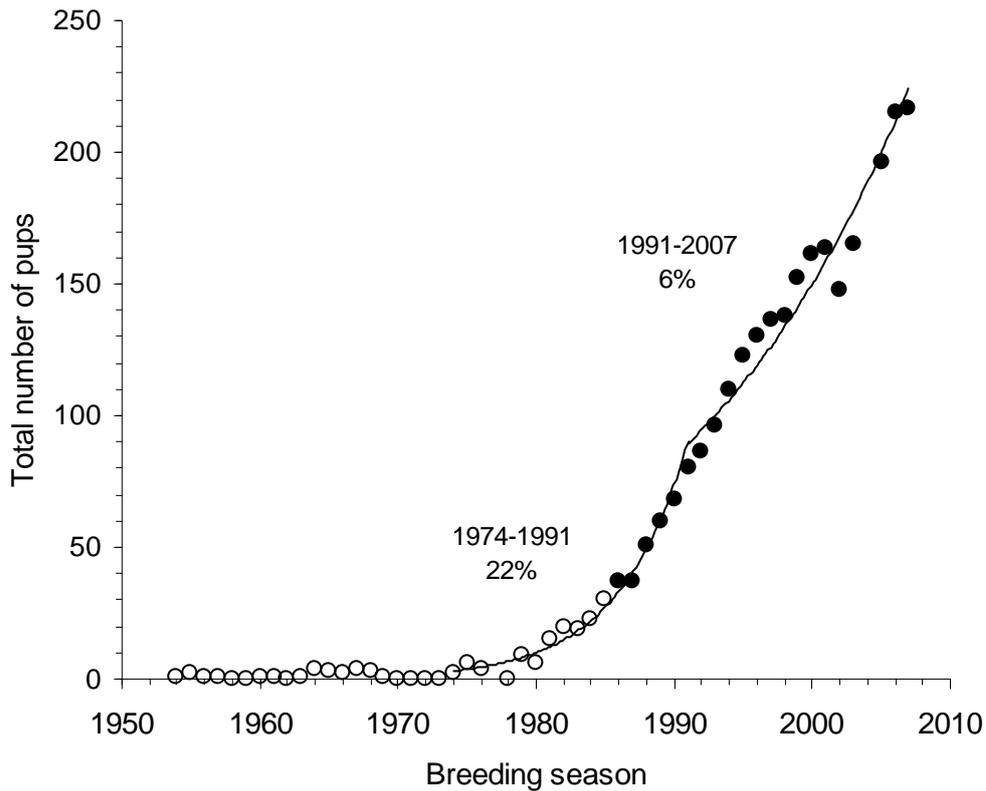


Fig. 2. Changes in the number of fur seal pups (species combined) at Macquarie Island between 1954-2007. Open circles indicate estimates based on limited seasonal pup counts. Closed circles indicate estimates based on daily censuses during the pupping season. Mean annual percentage rates of increases for different time periods are shown.

Trends in species-specific pup production

Between 1986-2007 over 85% of pups were classed by species each season (mean $94.6 \pm 4.1\%$). Based on phenotypic assessment of 18 pup cohorts between 1986-2007, the numbers of Antarctic and subantarctic fur seal pups born each season increased by about 10.7% and 9.5% per year, respectively, while the number of hybrid pups remained low (Fig. 3a). Over this period, the percentage of pups of Antarctic fur seal phenotype increased ($F = 7.090$, $df = 17$, $P = 0.018$), but the percentage of subantarctic fur seals did not change significantly ($F = 2.810$, $df = 17$, $P = 0.114$) and the percentage of hybrids decreased ($F = 6.883$, $df = 17$, $P = 0.019$, $r^2 = 0.32$). In the 2007 breeding season, 203 pups were assigned a phenotypic class, and of these 73% were Antarctic, 21% subantarctic and 6% hybrid fur seals.

Genotypic assessment of species identity was determined from 94% ($n = 1,007$) of pups from eight cohorts between 1992 and 2003. Antarctic fur seal pups made up 59% ($n = 599$, range 53.3-63.1%), 17% (173) were subantarctic (range 11.5-22.2%) and 24% (235) were hybrid (range 16.0-31.1%) (Fig. 3b, Lancaster et al. 2006). Over this period the number of Antarctic and subantarctic fur seal pups increased significantly by 7.1% ($F = 85.996$, $df = 7$, $P < 0.001$, $R^2 = 0.94$) and 13.6% per year ($F = 138.388$, $df = 7$, $P < 0.001$, $r^2 = 0.96$), respectively, whereas the number of hybrids remained unchanged ($F = 0.040$, $df = 7$, $P = 0.848$, $r^2 = 0.01$) (Fig. 3b). As a consequence, the overall proportion of hybrids declined significantly over this period ($F = 12.906$, $df = 7$, $P = 0.0115$, $r^2 = 0.68$), while the proportion of Antarctic fur seal pups remained unchanged ($F = 1.819$, $df = 7$, $P = 0.009$, $r^2 = 0.86$), and the proportion of subantarctic fur seals pups increased ($F = 37.045$, $df = 7$, $P < 0.001$, $r^2 = 0.96$). In the most recent cohort genotyped (2003, $n=162$), 61.7% of pups were Antarctic fur seals, 22.2% subantarctic fur seals, and 16.1% hybrid (Fig. 3b, Lancaster et al. 2006).

Species misidentification

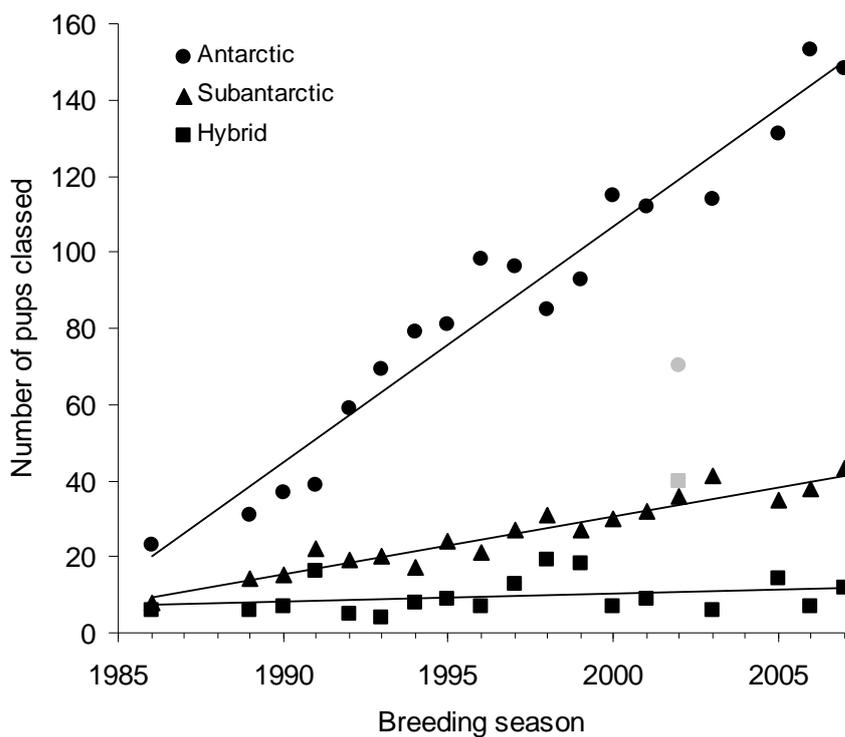
Comparison of phenotypic and genotypic assessment of 990 pups born between 1992-2003 (8 years) indicated that, Antarctic and subantarctic fur seals were correctly assigned to their respective species in 81% and 78% of cases, respectively, and hybrids in 72% of cases (as subsequently confirmed by genetic analysis). Of the 229 hybrids identified from genetic analysis, only 25% (58) of these were assigned as hybrids based on their phenotype (i.e., 75% were misidentified as belonging to a pure species). This resulted in an overestimation of the true number of Antarctic and subantarctic fur seals and an underestimation of the number of hybrid pups in the population. The direction of error was similar between years except for one year (1999), when phenotypic assessment underestimated the number of subantarctic pups sampled (27 versus 30). On average, phenotypic assessment overestimated Antarctic and subantarctic fur seal pups classed each year by $16.7 \pm 5.1\%$ and $19.1 \pm 18.4\%$ respectively, and underestimated hybrids by an average of $241 \pm 131\%$ per year. In other words, the number of pups identified genetically as Antarctic fur seals was 0.83 ± 0.05 times that identified by phenotypic assessment (range 0.76-0.91), subantarctic fur seals were 0.81 ± 0.18 times that identified by phenotype (range 0.5-1.11), and the number of hybrid pups was 3.42 ± 1.13 times that identified based on phenotype alone (range 1.26-5.25).

The slope of the regression of the number of pups classed each year based on phenotypic assessment did not differ significantly from that based on genotype for each species or hybrids (all $P > 0.10$, Fig. 3b), but in all cases differed in elevation (all $P < 0.05$, Fig 3b). Although phenotypic and genotypic assessments resulted in similar trends in pup production for each species and hybrids for the period examined, the absolute number of Antarctic and subantarctic fur seal pups born each season was overestimated, and the number of hybrid pups born underestimated using phenotypic assessment (Fig. 3b).

Table 1. Comparison of the phenotype and genotype assessment of 990 pups of each fur seal species and hybrids sampled and assessed between 1992 and 2003 (8 cohorts) at Macquarie Island. The values in bold indicate the number (and percentage) of pups that were correctly assigned by phenotypic assessment. The percentage of cases where the genotype of pups agreed with the phenotype assignment is also presented

Phenotype	Genotype			Total	Phenotype assignment % correct
	Antarctic	Subantarctic	Hybrid		
Antarctic	569	4	131	704	81%
Subantarctic	6	159	40	205	78%
Hybrid	14	9	58	81	72%
Total	589	172	229	990	
Genotype agrees with phenotype assignment	97%	92%	25%		79%

(a)



(b)

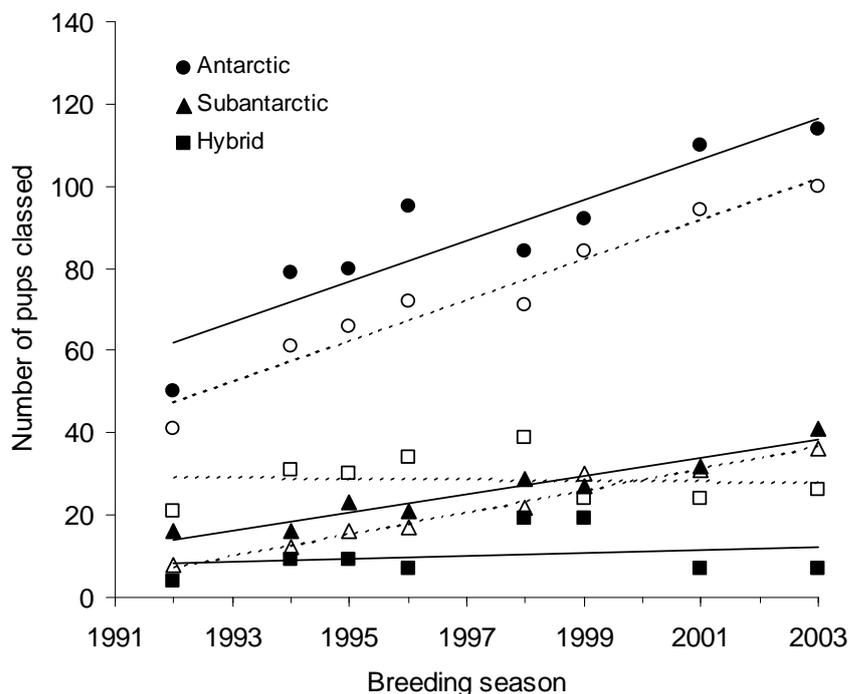


Fig. 3 (a) Trends in the number of pups classed as Antarctic, subantarctic and putative hybrid fur seals at Macquarie Island (1986-2007), based on phenotypic assessment. Outlying values in 2002 are indicated in grey. (b) Comparison of the trends and number of pups of each species and hybrids for which both phenotypic (solid symbols) and genotypic (open symbols) data were available, for 8 cohorts between 1992-2003 (from Lancaster et al. 2006).

5 DISCUSSION

DNA sampling of the 2007/08 fur seal pup cohort

The DNA samples collected from the 2007/08 cohort of fur seal pups at Macquarie Is will enable DNA-based assessment of the population status and trends in abundance of subantarctic, Antarctic and hybrid fur seals. Funding is now required to support collection of DNA samples in the 2008/09 season (to be provided by Australian Antarctic Division in 2008/09), and analysis of DNA samples collected over the previous 5-years (support required from DEWHA). These data will be required to accurately report on the population status and trends in abundance of the *threatened* subantarctic fur seal.

Population trends of the fur seal species at Macquarie Island

The general pattern of population recovery or colonisation of Antarctic and subantarctic fur seals at Macquarie Island is similar to that reported for other fur seal populations in the Southern Ocean. Roux (1987) identified four main stages in the recovery of fur seal populations: survival, establishment, recolonisation and maturity. The current rate of increase for Antarctic fur seals at Macquarie Island (about 11%/year) suggests that this population is about to enter the colonisation phase, where population growth rates exceed 15%/year, and where densities reach high values on original breeding sites resulting in local immigration to nearby beaches (Roux 1987).

The current rate of increase of around 8%/year for subantarctic fur seals suggests that this population is still in the establishment phase, characterised by low densities, few breeding animals and population growth rates <10% (Roux 1987). In contrast, the New Zealand fur seal, although the most numerous fur seal species on Macquarie Island during summer, has yet to establish a breeding population, due to the absence of reproductively mature females.

Macquarie Island is one of the last fur seal colonies in the Southern Ocean to be recolonised following past sealing activities. Other recently recolonised populations include Heard Island (Shaughnessy and Goldsworthy 1990), Île Saint Paul and Îles Crozet (Jouventin et al. 1982, Guinet et al. 1994). At Macquarie Island, the first pup was recorded in 1954/55, but between 1954-1974 (21 yrs) very few pups (<4) were born each year. The extensive delay between the cessation of sealing and establishment of breeding colonies (130+ years) is likely to be due to the absence of a remnant population and the isolation of Macquarie Island from other major fur seal colonies, which were undergoing establishment and recolonisation during the same period. The nearest breeding population of subantarctic fur seals is at Île Amsterdam some 6,200 km to the northwest. In 1956, the population there entered the establishment

phase with a growth rate of 7.9% from 1956-1970 (Roux 1987). The nearest populations of Antarctic fur seals are at Heard Island and Îles Kerguelen, 5,200 and 5,800 km to the west, respectively. Breeding at Heard Island was first recorded in 1963 and between 1986-2000 pup production increased by about 12% (Page et al. 2003). By the late 1980s the population at Îles Kerguelen was also thought to be in the recolonisation stage (Roux 1987). In contrast, the nearest breeding populations of New Zealand fur seals are comparatively close by, at Auckland and Campbell Islands, 660 and 720 km to the northeast, respectively. Little information is available on the size and status of populations in New Zealand during this period, but total numbers were estimated to be around 1,000-2,000 at Auckland and Campbell Islands (Mattlin 1987). Bounty Island (1,600 km northeast of Macquarie Island) accounts for the largest breeding population south of New Zealand (3,280 pups in 1980) and is estimated to have increased at an average rate of 5% per year between 1903-1980 (Lalas and Bradshaw 2001).

One peculiar aspect of the colonisation of breeding fur seals at Macquarie Island is that female Antarctic fur seals dispersed to the island and commenced breeding many years (up to 35) before the first males of this species were observed holding breeding territories. This is in marked contrast to usual pattern of dispersal and colonisation described for many otariids, where males typically disperse to distant sites (Shaughnessy and Goldsworthy 1990, Carlini et al. 2006), while females display greater site fidelity (Boyd et al. 1998, Raum-Suryan et al. 2002).

Continued immigration of subantarctic fur seals is supported by sightings at Macquarie Island of juvenile animals tagged as pups at other locations ($n = 7$ from Île Amsterdam, Beuplet et al. 2005). In addition, several untagged adult female Antarctic and subantarctic fur seals are sighted at Macquarie Island each breeding season. These females are unlikely to have originated from Macquarie Island because all pup cohorts and a large number of adult females have been tagged since 1986 (Goldsworthy et al., unpublished data). Tag resights suggest that subantarctic fur seal immigrants may originate from Île Amsterdam. A study of the geographical distribution of genetic lineages of fur seals throughout the Southern Ocean also suggests that Macquarie Island was recolonised by subantarctic fur seals from Île Amsterdam, Marion Island or both, while Antarctic fur seals were most likely from Îles Kerguelen (Wynen et al. 2000).

The slower rate of population growth in recent years at Macquarie Island may reflect the slowing of growth and stabilisation in recent years of other fur seal populations. At Île Amsterdam and Île Saint Paul, subantarctic fur seal populations appear to have stabilised, with an overall population growth rate estimated to be 0.5% in 1993 (Guinet et al. 1994). At

Marion Island, the subantarctic population was thought to be approaching maturity, but has since increased, although at a much slower rate than experienced in the 1980s (Hofmeyr et al. 2006). Antarctic fur seal populations were still increasing (17% per year) at Marion Island between 1994-2003 (Hofmeyr et al. 2006), but appear to have stabilised at locations (Bouvetøya, South Sandwich and South Shetland Islands) closer to the global population centre at South Georgia (Boyd 1993, Goebel et al. 2003, Hofmeyr et al. 2005). However, as noted by Guinet et al. (1994), care is required in interpreting population trends as many are based on limited counts.

Alternately, if growth rates of other populations have declined due to emigration, as suggested for South Georgia (Boyd 1993), the slowing of growth at Macquarie Island may indicate a change in localised food resources affecting immigration. Available breeding habitat may also be limited due to the occupation of suitable habitat by New Zealand fur seals and large penguin colonies. The high level of hybridisation between species may also have influenced population growth during this period, particularly if hybrids have reduced reproductive success, survival or site fidelity (Lancaster et al. 2007a).

Trends in the extent of hybridisation between subantarctic, Antarctic and New Zealand fur seals

Macquarie Island is the only subantarctic island where Antarctic, subantarctic and New Zealand fur seals are sympatric and where hybridisation among all three species has been recorded. Antarctic and subantarctic fur seals have also been reported to hybridise at Prince Edward Islands and Îles Crozet where they breed sympatrically (Condy 1978, Kerley 1983, Kerley and Robinson 1987, Bester et al. 2003, Hofmeyr et al. 2006, Kingston and Gwilliam 2007). However, the estimated level of hybridisation at Macquarie Island (16-30%, based on genotype, Lancaster et al. 2006) is much higher than reported elsewhere (1-2%, Kingston and Gwilliam 2007).

Recent studies using molecular techniques to investigate hybridisation and backcrossing among the three species at Macquarie Island suggest that the field method of identifying pups by phenotypic characteristics significantly underestimates the number of hybrid pups in the population (Goldsworthy et al. 1999, Wynen 2001, Lancaster et al. 2006). Comparison of phenotypic and genotypic assessment of 990 pups born between 1992-2003 (8 cohorts) indicated that the number of hybrid pups identified using genotypic methods was on average 3.42 times that reported based on phenotypic characteristics. As a result, the number of Antarctic and subantarctic pups born each year based on phenotypic assessment was overestimated by an average of $16.7 \pm 5.1\%$ and $19.1 \pm 18.4\%$, respectively. Considerable variation between years in the accuracy of phenotypic assignment probably reflects inter-

observer differences and experience in species and hybrid identification, which has been made more difficult due to hybridisation among all three species. Backcrossing would also confound phenotypic identification of species and hybrids, as pups are likely to look less recognisably hybrid beyond the F_1 generation, and over 50% of pups born in the population are post- F_1 hybrids or backcrosses (Lancaster et al. 2006). Overall, 76.6% of genotypic hybrids that were incorrectly assigned were classed as Antarctic fur seals and 23.4% were incorrectly assigned as subantarctic fur seals. Antarctic-New Zealand fur seal hybrid pups appear to be particularly difficult to identify based on phenotype, possibly because there are no pure New Zealand pups born on the island for field operators to compare characteristics.

Despite the apparent overestimation of pure Antarctic and subantarctic fur seal pups born each year based on phenotypic assessment, analysis of pup numbers based on genotype of most (94%) pups born between 1992-2003 (8 cohorts) showed similar trends (Fig. 3b). Nevertheless, it should not be assumed that future phenotypic assessment will be as accurate as those from 1992-2003 due to an increase in the number of backcrosses in the population and variation in field operator experience. Therefore, to determine rates of change of each species accurately it is essential that genotypic assessments are made.

Although the phenotypic method for identifying pure species was reasonably accurate for the years analysed, the assignment of hybrids as pure species significantly overestimated the actual number of pups of each species. While this error may not bias trends in pup production over time, the high level of interannual variability in the accuracy of identifying subantarctic fur seals reduces the power of phenotypic assessment methods to provide an accurate measure of short-term changes in their population status and provide an accurate estimate of their population size. This is particularly important for the monitoring of subantarctic fur seals, which have been classified as vulnerable in Australian waters under the *Environmental Protection and Biodiversity Conservation Act 1999 (EPBC Act)*. Because the population of subantarctic fur seals is small (< 40 pups), small changes in the extent or direction of the misidentification error, due to variation in field observer experience or changes in hybrid types, may have a significant effect on the degree of over- or underestimation of absolute number of pups born each year.

While populations of each species remain low and levels of hybridisation are high, genotypic identification methods remain the most scientifically robust and repeatable means of monitoring pup production. Determining species identity of pups based on phenotypic characteristics can only provide an approximate measure of species status; at best correctly assigning about 92-97% of individuals to the correct species. It is an inappropriate method for identifying hybrids because it overestimates actual numbers of pure Antarctic and

subantarctic fur seals in the population. Further, phenotype is also unable to distinguish hybrid type (i.e., various crosses and backcross combinations, Lancaster et al. 2006), which is important for examining the direction of hybridisation. Given that hybrids form a substantial component of the fur seal aggregate at Macquarie Island, genetic analysis of hybridisation needs to be included in ongoing monitoring of the status and population growth of each species.

Summary

The colonisation of Macquarie Island by fur seals has been slow and complex due to several confounding factors, including its isolation from the major breeding population centres, differences in the timing of the colonisation by males and females of each species, and extensive hybridisation. Differences in the population growth of each species reflect differences in the timing and pattern of colonisation, but are also likely to be influenced by differences in life history and responses to changes in environmental conditions. While the populations of both Antarctic and subantarctic fur seals continue to grow, further examination of the influence of hybridisation, predation by Hooker's sea lions and environmental factors on population dynamics and long-term population growth is required.

6 RECOMMENDATIONS

The *Recovery Plan for Subantarctic fur seals and southern elephant seals* (Recovery Plan) is scheduled to be reviewed in 2009. It is noted that the actions to achieve the Recovery Plan objectives (270(2)c) are to:

- determine the rate of population change and population size by undertaking scientifically robust, regular and repeatable population surveys; and
- identify any emerging actual impacts that will have an immediate affect on the species and thus on its recovery, and to facilitate the development of appropriate responses.

In order to address the key Actions of the Recovery Plan with respect to subantarctic fur seals, we recommend the following:

1. The Department of the Environment, Water, Heritage and the Arts (DEWHA) fund the genotype analyses of additional cohorts in order to facilitate meeting the recommendations of the Recovery Plan. This work is currently unfunded through the Australian Antarctic Divisions Australian Antarctic Science (AAS) grants scheme.
2. We also recommend integrating genotype and demographic data to provide quantitative assessment of the significance of three key threatening processes, hybridisation, predation of pups by hooker sea lions and climate change, all of which may be affecting the recovery of the subantarctic fur seal at Macquarie Island.
3. There should be continuing support to maintain the annual fur seal monitoring program at Macquarie Island that has been supported by the Australian Antarctic Division for over 22 years (since 1986) (Goldsworthy et al. AAS PN 859 'The conservation of fur seals in the Antarctic marine ecosystem'). This is the only program that is capable of providing analyses of the status, trends and threatening processes of the threatened subantarctic fur seal. As such it provides the only means to deliver against the requirements of the Recovery Plan, and therefore support for its maintenance should be provided by DEWHA.

Additional support for 1 and 2 are given below:

Genotyping of cohorts to assess status and trends in abundance

Genetic analysis of the population currently provides the only means to accurately monitor changes in the status and trends in abundance of each species and levels of hybridisation in the Macquarie Island fur seal population. It underpins demographic studies by providing genotype and hybrid status information so that accurate measures of species-specific and hybridisation rates can be determined and monitored.

As indicated above, determining the species identity of pups using their phenotype can only provide a qualitative measure of species status, at best correctly assigning about 80% of individuals to the correct species. It is an inappropriate method for determining hybrids, because it can only detect about 25% of hybrid pups (ie. worse than chance), and cannot resolve hybrid composition (ie. various crosses and backcross combinations, Wynen 2001; Lancaster unpublished data). It is not possible to assess the status and trends in abundance of each fur seal species at Macquarie Is, because 75% of hybrid pups are described as either Antarctic or subantarctic fur seals based on their phenotype.

Hybridisation is a critical component to the fur seal population at Macquarie Island and genetic analysis of hybridisation needs to be an inclusive part of monitoring the recovery of each species' population. The most accurate means by which quantitative measures of species' pup production and the level of hybridisation can be determined is from genetic analysis.

The importance of hybridisation in the Macquarie Island fur seal population should not be underestimated, given its small size and the ability of hybrid adults to have a profound effect on species composition (Lancaster et al. in review). Until hybridisation declines an insignificant level, genotyping methods provide the only means of obtaining estimates on species and hybrid status.

Actions of the subantarctic fur seal recovery plan focus around monitoring populations to "...determine the rate of population change and population size by undertaking scientifically robust, regular and repeatable population surveys." As detailed, quantitative robust assessment of the status of the subantarctic fur seal population can only be achieved through genetic screening of pup cohorts.

Assessment of impact of hybridisation on the recovery of the subantarctic fur seal.

The level of hybridisation at Macquarie Island is unprecedented in pinnipeds and high in mammals, but between 1992 and 2003 the level of hybridisation declined (Lancaster et al. 2006). Hybridisation involves all three fur seal species that occur on Macquarie Island. Most hybrids (60%) are Antarctic x subantarctic; but a third (33%) are Antarctic x New Zealand fur seal crosses, and 7% Antarctic x subantarctic x New Zealand fur seal crosses

Several factors have been identified as important in moderating hybridisation in the population:

- i) availability of conspecific males, which due to the asynchronous colonisation of Macquarie Island by males and females of each species, has led to marked asymmetries in sex-ratio, especially in Antarctic fur seals;
- ii) Female mate-choice (where females avoid mating with heterospecific and hybrid males), has been identified as an important moderator of hybridisation (Goldsworthy et al. 1999; Lancaster et al. 2007). Exactly which traits females use to distinguish conspecific mates from heterospecifics still remains unclear, but male phenotype, including pelage, vocalisation and odour may all be important (Goldsworthy et al. 1999; Page et al. 2001; 2002).
- iii) Habitat selection - Genetic and observational data show that Antarctic fur seals breed on the open, pebbled beaches of Secluded Beach and Aerial Cove, while subantarctic fur seals appear to prefer the bouldered coves of Goat Bay and southern Secluded Beach (Lancaster et al. unpublished data; Lancaster 2007). This variation in habitat preference has reduced heterospecific encounters and hybridisation. In contrast, hybrid adult females have reduced habitat preference and alternate breeding between pebbled and bouldered beaches, thereby mating with both parental species and producing more diverse hybrid offspring (Lancaster et al. unpublished data). Southern Secluded Beach, where the two habitat types converge, has been identified as an important “hotspot” for ongoing hybridisation between Antarctic and subantarctic fur seals. It contains the highest concentration of Antarctic - subantarctic hybrid pups born each season, possibly because it is the only area where both species breed in substantial numbers (Lancaster et al. unpublished data).

Hybrids are reproductively viable, but hybrid males have lower reproductive success (Lancaster et al. 2006, Lancaster et al. 2007). The reproductive success of hybrid females relative to pure species has yet to be determined. The fitness cost of hybridisation is important to understand, because it is impacting on the recovery of the subantarctic fur seal population at Macquarie Island.

Assessment of impact of predation by Hooker sea lions on the recovery of the subantarctic fur seal.

Pup mortality is typically assessed in pups to about three months of age at Macquarie Island. Data are available for most years between 1994/95 and 2006/07. Pup mortality rates have varied considerably between years, ranging from 14% to 64%, and averaging 27% (sd = 13%, n = 11 years, Goldsworthy et al. unpublished data). Very high mortality reported in 1996 was attributed to predation by a single Hooker sea lion (HSL) (Robinson et al. 1999). Probable cause of death has been determined for 196 pups. The most common cause of death to pups less than 4 months old is HSL predation, which accounts for 50% of all deaths. Stillbirths (24%), starvation (16%), and trauma (usually due to sub-adult and adult males, 8%) account for the remainder. It is likely that many, and possibly most of the unknown mortalities (bodies missing and recovered) are due to HSL predation (Robinson et al. 1999). All these categories amount to 79% of mortalities.

The pre-weaning mortality rates for low-density Antarctic fur seal colonies at other locations typically range from 3-6% (Doidge et al 1984, Shaughnessy and Goldsworthy 1990). The overall rate of mortality to three months of age of 27% is high for a low-density colony, and most of this is due to HSL predation. Hooker sea lion predation poses the most significant pre-weaning mortality threat to fur seal pups. Changes in the rates of predation between years are likely to significantly influence juvenile survival and recruitment rates, and therefore intrinsic rates of growth in the Macquarie Island subantarctic fur seal population.

Assessment of the potential impacts of climate change on the recovery of the subantarctic fur seal.

Research conducted through the Macquarie Island fur seal program has uncovered some unique relationships between regional oceanographic variability, fur seal reproductive rates, pup growth and diet, which provide some of the clearest high-trophic predator responses to environmental variability in the Southern Ocean. These include:

i) Fecundity - Fecundity rates (percentage of live females that pup) in fur seals at Macquarie Island, range between 60% and 85% each year. We have identified a very strong negative relationship between fecundity and the preceding average autumn sea-surface temperatures (SSTs) in the 1° x 1° region immediately north of the island encompassing the fur seal foraging grounds (Goldsworthy et al. unpublished data). Fur seals mate between November-December and have a four-month delayed implantation period before active gestation begins (around March/April). Nutritional stress during the autumn months may cause the variability observed in fecundity rates, and suggests that in years of lower than average SST around the island, local production and food availability is enhanced and results in high pupping rates

in the following breeding season. Higher than average SSTs around the island may be indicative of reduced production, resulting in nutritional stress of females and correspondingly poor pupping rates in the following breeding season.

ii) Pup growth - Equally strong relationships have been found between SST and pup growth rates, but within the season for pup growth measured. Pup growth measured to 90 days of age, shows a strong negative relationship with summer SSTs north of Macquarie Island, with the best relationship found for January (linear regression, $P < 0.0001$, $R^2 = 0.802$) (Goldsworthy et al. unpublished data).

Together, these relationships with SST explain 80% of the variance in reproductive rates and pup growth, which demonstrates how small increases in SST affect both the number and quality of offspring produced from season to season (Goldsworthy et al. unpublished data).

iii) Fur seal diet - The diet of fur seals at Macquarie Island consists almost entirely of myctophid fish, notably *Electrona* spp. Preliminary analyses indicate that in the presence of cool SSTs north of the island, *Electrona* is abundant in the diet, and following these seasons fecundity rates are highest.

The results provide some of the most compelling Southern Ocean data on the potential implications of climate change to high trophic-level predators such as fur seals. We can now directly predict how warming of the ocean will affect the reproductive output (both number and quality of offspring) at annual and lifetime scales. Although these relationships have been determined mainly for Antarctic fur seals, the patterns appear universal among species at Macquarie Island, given the diet and foraging locations are the same for both species (Robinson et al. 2002).

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8 REFERENCES

- Beauplet G, Barbraud C, Chambellant M, Guinet C (2005) Inter-annual variation in the post-weaning survival of subantarctic fur seals: influence of pup sex, growth rate and oceanographic conditions. *J Anim Ecol* 74: 1160-1172.
- Bester MN (1987) Subantarctic fur seal, *Arctocephalus tropicalis*, at Gough Island (Tristan Da Cunha Group). In: Croxall JP, Gentry, RL, (eds.) Status, Biology, and Ecology of Fur Seals. NOAA Tech Rep NMFS 51: 57-60
- Bester MN, Ryan PC, Dyer BM (2003) Population numbers of fur seals at Prince Edward Island, Southern Ocean. *Afr J Mar Sci* 25: 549-554
- Boyd IL (1993) Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarct Sci* 5: 17-24
- Boyd IL, McCafferty DJ, Reid K, Taylor R, Walker TR (1998) Dispersal of male and female Antarctic fur seals (*Arctocephalus gazella*). *Can J Fish Aquat Sci* 55: 845-852
- Carlini AR, Daneri GA, Casaux R, Marquez MEI (2006) Haul-out pattern of itinerant male Antarctic fur seals (*Arctocephalus gazella*) at Laurie Island, South Orkney Islands. *Polar Res* 25: 139-144
- Condy PR (1978) Distribution, abundance and annual cycle of fur seals (*Arctocephalus* spp.) on the Prince Edward Islands. *S Afr J Wildl Res* 8: 159-168
- Csordas SE (1958) Breeding of the fur seal, *Arctocephalus forsteri* Lesson, at Macquarie Island. *Aust J Sci* 21: 87
- Csordas SE, Ingham SE (1965) The New Zealand fur seal, *Arctocephalus forsteri* (Lesson), at Macquarie Island, 1949-64. *CSIRO Wildl Res* 10: 83-99
- Goebel ME, Vallejos VI, Trivelpiece RWZ, Holt RS, Acevedo, J (2003) Antarctic fur seal pup production in the South Shetland Island. In: Lipsky J. (ed.) AMLR 2001/2002 Field Season Report. NOAA Tech Memo NMFS-SWFSC-350
- Goldsworthy SD (2006) Maternal strategies of the New Zealand fur seal: evidence for interannual variability in provisioning and pup growth strategies. *Aust J Zool* 54: 31-44
- Goldsworthy SD, Pemberton D, Warneke RM (1997) Field identification of Australian and New Zealand fur seals, *Arctocephalus* spp., based on external characters. In: Hindell M, Kemper C (eds.) Marine Mammal Research in the Southern Hemisphere Volume 1: Status, Ecology and Medicine. Surrey Beatty and Sons, Chipping Norton, pp 63-71
- Goldsworthy SD, Boness DJ, Fleischer RC (1999) Mate choice among sympatric fur seals: female preference for conphenotypic males. *Behav Ecol Sociobiol*, 45, 253-267

- Guinet C, Jouventin P, Georges J-Y (1994) Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St. Paul and Amsterdam) islands and their possible relationship to El Niño Southern Oscillation. *Antarct Sci* 6: 473-478
- Gwynn AM (1953) Notes on the fur seals at Macquarie Island and Heard Island. Australian National Antarctic Research Expedition Interim Reports 4: 1-16
- Hofmeyr GJG, Krafft BA, Kirkman SP, Bester MN, Lydersen C, Kovacs KM (2005) Population changes of Antarctic fur seals at Nyrøysa, Bouvetøya. *Polar Biol* 28: 725-731
- Hofmeyr GJG, Bester MN, Makhado AB, Pistorius PA (2006) Population changes in Subantarctic and Antarctic fur seals at Marion Island. *S Afr J Wildl Res* 36: 55-68
- Jouventin P, Stahl JC, Weimerskirch H (1982) La recolonisation des Îles Crozet par les otaries (*Arctocephalus tropicalis* et *A. gazella*). *Mammalia* 46: 505-514
- Kerley GIH (1983) Relative population sizes and trends, and hybridisation of fur seals *Arctocephalus tropicalis* and *A. gazella* at the Prince Edward Islands, Southern Ocean. *S Afr J Zool* 18: 388-392
- Kerley GIH, Robinson TJ (1987) Skull morphometrics of male Antarctic and subantarctic fur seals, *Arctocephalus gazella* and *A. tropicalis*, and their interspecific hybrids. In: Croxall JP, Gentry RL (eds.) *Status, Biology, and Ecology of Fur Seals*. NOAA Tech Rep NMFS 51: 121-132
- Kingston JJ, Gwillian J (2007) Hybridization between two sympatrically breeding species of fur seal at Îles Crozet revealed by genetic analysis. *Con Genet* 8: 1133-1145
- Lalas C, Bradshaw CJA (2001) Folklore and chimerical numbers: review of a millennium of interaction between fur seals and humans in the New Zealand region. *New Zeal J Mar Fresh Res* 35: 477-497
- Lancaster ML (2007) A longitudinal investigation of hybridisation in three species of fur seal (*Arctocephalus* spp.) at subantarctic Macquarie Island. PhD Thesis, La Trobe University, Victoria, Australia
- Lancaster ML, Gemmell NJ, Negro S, Goldsworthy S, Sunnucks P (2006) Ménage à trois on Macquarie Island: hybridization among three species of fur seal (*Arctocephalus* spp.) following population extinction. *Mol Ecol* 15: 3681-3692
- Lancaster ML, Bradshaw CJA, Goldsworthy SD, Sunnucks, P (2007a) Lower reproductive success in hybrid fur seal males indicates fitness costs to hybridization. *Mol Ecol* 16: 3187-3197
- Lancaster ML, Goldsworthy SD, Sunnucks, P (2007b) Multiple mating strategies explain unexpected genetic mixing of New Zealand fur seals with two congeners in a recently recolonized population. *Mol Ecol* 16: 5267-5276
- Lesson R-P (1828) Phoque. In: Bory de Saint-Vincent, JBG (ed.) *Dictionnaire Classique d'Histoire naturelle* Vol. 13, Rey et Gravier, Paris, pp 400-426

- Ling JK (1999) Exploitation of fur seals and sea lions from Australian, New Zealand and adjacent subantarctic islands during the eighteenth, nineteenth and twentieth centuries. *Aust Zool* 31: 323–350
- Mattlin RH (1981) Pup growth of the New Zealand fur seal *Arctocephalus forsteri* on the Open Bay Islands, New Zealand. *J Zool Lond* 193: 305-314
- Mattlin RH (1987) New Zealand fur seal, *Arctocephalus forsteri*, within the New Zealand Region. In: Croxall JP, Gentry, RL, (eds.) Status, Biology, and Ecology of Fur Seals. NOAA Tech Rep NMFS 51: 49-51
- Mawson D (1943) Macquarie Island, its geography and geology. *Aust Antarct Exped Sci Rep, Ser A, Vol 4*, 194 pp.
- Page B, Welling A, Chambellant M, Goldsworthy SD, Dorr T, van Veen R (2003) Population status and breeding season chronology of Heard Island fur seals. *Polar Biol* 26: 219-224
- Raum-Suryan KL, Pitcher KW, Calkins DG, Sease JL, Loughlin TR (2002) Dispersal, rookery fidelity, and metapopulation structure of Steller sea lions (*Eumetopias jubatus*) in an increasing and a decreasing population in Alaska. *Mar Mammal Sci* 18: 746–764
- Robinson S, Goldsworthy SD, van den Hoff J and Hindell MA (2002) The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *A. tropicalis* at Macquarie Island during the austral summer. *Marine and Freshwater Research*. 53: 1071-1082
- Roux J-P (1987) Recolonization processes in the subantarctic fur seal, *Arctocephalus tropicalis*, on Amsterdam Island. In: Croxall JP, Gentry, RL, (eds.) Status, Biology, and Ecology of Fur Seals. NOAA Tech Rep NMFS 51: 189-194
- Shaughnessy PD, Fletcher L (1987) Fur seals, *Arctocephalus* spp., at Macquarie Island. In: Croxall JP, Gentry, RL, (eds.) Status, Biology, and Ecology of Fur Seals. NOAA Tech Rep NMFS 51: 177-188
- Shaughnessy PD, Goldsworthy SD (1990) Population size and breeding season of the Antarctic fur seal *Arctocephalus gazella* at Heard Island - 1987/88. *Mar Mammal Sci* 6: 292-304
- Shaughnessy P, Goldsworthy S (1993) Feeding ecology of southern fur seals (*Arctocephalus* spp.) and their management at Heard and Macquarie Islands. *Proc NIPR Symp Polar Biol* 6: 173-175
- Shaughnessy PD, Shaughnessy GL, Fletcher L (1988) Recovery of the fur seal population at Macquarie Island. *Pap Proc R Soc Tas* 122: 177-187
- Taylor RH (1992) New Zealand fur seals at the Antipodes Islands. *J R Soc New Zeal* 22: 107-122

-
- Wynen, L (2001) Phylogenetic Relationships, Population Genetics and Hybridisation of Two Species of Southern Fur Seal (*Arctocephalus* spp.). PhD Thesis, University of Tasmania, Hobart, Australia
- Wynen LP, Goldsworthy SD, Guinet C, Bester MN, Boyd IL, Gjertz I, Hofmeyr GJG, White RWG, Slade R (2000) Post-sealing genetic variation and population structure of two species of fur seal (*Arctocephalus gazella* and *A. tropicalis*). *Mol Ecol* 9: 299-314