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Advances in New Zealand mammalogy 1990–2000: Pinnipeds

R. G. Harcourt*

Both morphological and molecular studies now suggest that the affinities of the pinnipeds lie within the suborder Caniformia, within the order Carnivora (Rice 1998).

FAMILY OTARIIDAE

The New Zealand fur seal *(Arctocephalus forsteri)* is the only fur seal which can be called a permanent resident of the New Zealand mainland. It also breeds on Macquarie Is.: about 1200 *A. forsteri* may be seen there in late February early March, alongside two related species, the subantarctic fur seal *(A. tropicalis)* and the Antarctic fur seal *(A. gazella* (Goldsworthy et al. 1999). A few *A. tropicalis* are occasionally seen on the New Zealand mainland (Taylor 1990; C. Bradshaw pers.comm.; pers.obs).

19. NEW ZEALAND FUR SEAL

Arctocephalus forsteri (Lesson, 1828)

Field sign

C. Littnan (pers. comm.) photographed a single regurgitate containing over 20 entire arrow squid at the Nuggets, Otago, in July 1996. Otoliths (fish ear bones) tend to be smaller in scats than in regurgitates (Fea et al 1999; Holborrow 2000).

Measurements

The mean mass of 14 territorial adult males on Kangaroo Island, Australia, was 135–137 kg; the mean for all 19 males measured during the breeding season was 126.3 ± 22.9 kg, maximum 160 kg (Troy et al. 1999). Males shot during the early part of the breeding season at the Open Bay Islands ranged from 49.5 to 154.1 kg (Mattlin 1978a, 1981). Males caught in Otago outside the breeding season weighed between 119 and 137 kg (R. G. Harcourt unpubl. data). By contrast, females weighed on average 39 kg, maximum 69 kg (Schulman 1996; Wickens & York 1997). Birth mass varies considerably by location, and among years at each site. Male pups are consistently heavier than females. Mean birth mass for male pups at different locations ranged from 3.9 kg in the early 1970s at the Open Bay Islands, to 5.6 kg at Kangaroo Island in 1988 (Goldsworthy 1992; Schulman 1996; Lea & Hindell 1997). Estimated birth mass for female pups ranged from 3.3 kg at the Open Bay Islands in 1974 to 4.8 kg on Kangaroo Island in 1988.

Growth rates also vary substantially between populations and among years. For instance,

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growth to 50 days ranged from 46 gd^{-1} for females and 45 gd^{-1} for males at the Open Bay Islands in 1974; 56 gd^{-1} (f), and 60 gd^{-1} (m) at the same location in 1975; 56.7 to 66.7 gd^{-1} at Cape Foulwind in 1992; 65 gd^{-1} (f), 72 gd^{-1} (m) in Otago in 1994; to 88 gd^{-1} (f), and an extraordinary 116 gd^{-1} for males, at Maatsuyker Island, Tasmania (Chilvers et al. 1995; Schulman 1996; Lea & Hindell 1997).

Distribution

The Australian and New Zealand populations were once considered geographically isolated and genetically distinct, but Lento et al. (1997) have suggested that there is also significant genetic variation within the New Zealand population. They postulate that a western breeding population, or subspecies, ranged from western and southern Australia to the east and west coasts of the South Island, and a southern one inhabited New Zealand's subantarctic islands including the Snares, Campbell, Chatham, Antipodes and Bounty Islands. The paucity of western and southern Australian haplotypes in the New Zealand region also suggests that the Australian population was once distinct. After both populations were decimated by sealing, the southern population recolonized parts of the vacated areas on the South Island, Tasmania and Australia, creating a zone of secondary hybrid contact with the remnant western population. This hypothesis awaits testing. For the effects of pre-historic Maori hunting on distribution, see Smith (1989).

The Australian population of the New Zealand fur seal (c. 34 600 in 1991, now at least 40 000: Gales et al. 2000) is widely distributed among islands off the southern coast from 117° to 136°E (Shaughnessy et al. 1994). Arnould et al. (in press) report that New Zealand fur seals have started recolonising several breeding sites in eastern Bass Strait, and some offshore islands up the east coast of Australia.

Dix (1993a) reported that breeding has recommenced on the North Island after a long absence; pups have been sighted from 1991 onwards at a small colony at Cape Palliser near Wellington, and there have been unconfirmed reports of pupping on the Sugar Loaf Island near New Plymouth. Around the South Island, numerous new breeding colonies have formed in the last two decades. For example, by 1998 there were 68 known colonies on Otago Peninsula, of which 27 were breeding rookeries (Harcourt & Lalas 1995; Lalas & Harcourt 1995; Taylor et al. 1995; Ryan et al. 1997; Lalas & Murphy 1998; Bradshaw et al. 1999, 2000).

Habitat

Two recent studies have attempted to identify what terrestrial features might predict the locations of new breeding rookeries. Ryan et al. (1997) reported that, on Banks Peninsula, rookeries usually had large angular boulders, steeply sloping beaches and numerous escape zones, crevices and ledges, while non-breeding haul-outs were less steep with smaller rounder boulders and a lower exposure to the sun. They suggested that these features might allow managers to predict where new breeding colonies are likely to be established, but Bradshaw et al. (1999) found no obvious differences between breeding and non-breeding habitat around 2500 km of coastline of the South Island. Rather, they thought that other features, such as site fidelity, gregariousness, proximity to food and the degree of human disturbance, were important in predicting the fur seals' choice of sites.

The seals' choice of marine habitat is known only for lactating females from the Open Bay Islands (Mattlin et al. 1998) and from Otago (Harcourt et al. 1995; Harcourt & Davis 1997). Females are in general midwater feeders, and forage relatively close to the breeding site in summer when their pups are small, venturing only as far as the edge of the continental shelf and just over the slope (Harcourt et al. 1995). Later in the year they venture over the continental shelf edge and beyond, up to 220 km from the breeding colony in water over 1000 m deep (Harcourt & Davis 1997). Females dive deeper and for longer in autumn and winter (Harcourt & Davis 1997; Mattlin et al. 1998).

Food

The most comprehensive studies of fur seal diet in New Zealand waters have all been done during the last decade. Dix (1993b) reported that hoki (*Macruronus novaezelandiae*), jack mackerel (*Trachurus declivis*) and various lanternfish are the main prey species in Cook Strait. By contrast, a study of fur seal diet on Otago Peninsula found that arrow squid (*Nototodarus sloanii*) was the dominant prey item in summer and autumn in both 1994 and 1995. Winter diet varied between years, with a combination of barracouta (*Thyrsites atun*), mackerel (*Trachurus* sp) and New Zealand octopus (*Octopus maorum*) dominating in winter and spring of 1994, and ahuru (*Auchenocerus punctatus*), a shallow inshore species, in winter 1995 (Dickson 1996; Fea et al. 1999). Still farther south, arrow squid were dominant in the summer fur seal diet off Long Reef (Fiordland), Codfish Island and Bench Island (Foveaux Strait); hoki were important prey at Long Reef, and mackerel at all sites in winter (Holborow 2000). A list of all known prey species of the New Zealand fur seal, with locations and seasons, is given in Table 1.

Other dietary records include little blue penguins (Notman 1985; Dix 1993b) and an unidentified diving petrel, *Pelecanoides* spp. (Holborrow 2000). Benthic and demersal prey increase in importance in autumn and winter, as inferred from dietary records of seals inhabiting Otago Peninsula and offshore islands of southern New Zealand and foraging on the continental shelf (Fea et al. 1999; Holborow 2000).

Adult females have been observed drinking directly from fresh water streams running off cliffs above colonies (R. G. Harcourt, pers. obs), and males may sip at freshwater pools during their fasting period (Mattlin 1978a). This habit may introduce problems for studies of energetics using isotope dilution techniques, as unquantifiable biases may be introduced.

Social organization and behaviour

Males gaining possession of prime territories, characterised by plentiful cooling substrates (Carey 1991), early in the season have to face challenges from neighbours or from late arrivals throughout the breeding season and fight frequently. Males attempting to hold territories were aged between 7 and 15 years (Troy et al. 1999).

Outside the breeding season, Johnstone & Davis (1987) report that male fur seals spent less time lying about (59.6%) and more time interacting and engaging in comfort behaviours such as scratching and grooming.

Once females have given birth they remain close to the birth site for up to 10 days. Oestrous females usually mate only once, most often about eight days post-partum, for 5–45 minutes, mean 13.3 min (Goldsworthy & Shaughnessy 1994). Carey (1991) demonstrated experimentally that females preferentially select areas with cooling substrates, whether shade or pools. They became more aggressive near the time of birth, and like other otariids, vigorously repelled approaching conspecifics of any sex or age class during the period immediately after birth (Harcourt 1992).

Pups are highly precocial and start suckling within 60 minutes of birth. Suckling bouts are relatively short at first (e.g. 7 min) but will increase in duration throughout lactation, eventually exceeding 33 min. By June pups may spend 30% of their time suckling on their mother's first day back from a foraging trip (Chilvers et al. 1995, Lea & Hindell 1997).

Table 1 Cephalopods and fish represented in New Zealand fur seal diet.

		Location and Season						
Common name	Genus or species	Kaikoura#	Otago	Cook Strait	Cape Foulwind#	Fjordland	Foveaux Strait	Snares
Arrow Squid	*Nototodarus sloanii*		S, A,Spr			S,W,Spr	S,A,W,Spr	S,A
Warty Squid	*Moroteuthis*		W					
Antarctic flying squid	*Todarodes filipovae*						S	
Squid (not identified)	Ommastrephidae						S	
Squid (not identified)	Architeuthidae							A
Squid (not identified)	Gonatidae					A*		
New Zealand Octopus	*Octopus maorum*		A,W			##	S,A,W	W
Lamprey	*Geotria australis*		W					
Hagfish	*Eptatretus cirrhatus*					Spr		
Spiny Dogfish	*Squalus acanthias*		W					Spr
School shark	*Squalus acanthias*							Spr
Sprat	*Sprattus*		W	S**			W,Spr	
Silverside	*Argentina elongata*		W*		A			
Lightfish	*Diplophos*		W*					
Lanternfish	*Electrona*		S*,A,W, Spr*			A*,S		A*
Lanternfish	*Gymnoscopelus*		*			S	W	Spr,A*
Lanternfish	*Lampanyctodes hectoris*	#	S,A,W,Spr	W		A,W*Spr*.S*	Spr,S,A	A*,S,Spr*
Lanternfish	*Symbolophorus*	A,W	S,A,W,Spr	W, Spr	W	W*,Spr*	W*,Spr*,S	A*,Spr*
Ahuru	*Auchenoceros punctatus*		W		A,W*			
Red Cod	*Pseudophycis bachus*		S,A,W,Spr	Spr				Spr,S
Hoki	*Macruronus novaezelandiae*	A,W	A	S,A,W,Spr	S	S,A,W,Spr	S,A,W	A,W,Spr
Rattail	*Coelorinchus*		W*			S*,A*,W,Spr*		S
Mackerel	*Trachurus*		A,W,Spr	W,Spr		W	S,A,W,Spr	W
Tarakihi	*Nemadactylus macropterus*		W					
Opalfish	*Hemerocoetes*		W*					
Graham's Gudgeon	*Grahamichthys radiata*		A*,S*,Spr*					
Barracouta	*Thyrsites atun*		A,Spr				S,A,W,Spr	
Frostfish	*Lepidopus caudatus*		Spr					
Warehou	*Seriolella*		A,W,Spr			A,Spr	A*	
Lemon Sole	*Pelotretis flavilatus*		W*					
Sole	*Peltorhamphus*		W*				Spr*	
Flounder	*Rhombosolea*		W					
	G. piabilis		W*					

Table 1 Contd

Common name	Genus or species	Location and Season						
		Kaikoura#	Otago	Cook Strait	Cape Foulwind#	Fjordland	Foveaux Strait	Snares
Blue Cod	*Parapercis colias*		W					
Triple Fin	Tripterygiidae		W*				Spr*	
	P. parallelum		W*					
Waryfish	*Scopelosaurus*					S*A*		
Dory	*Cyttus* sp					Spr		
Yelloweyed mullet				S**		Spr		
Dwarf cod	*Austrophycis marginata*						S*,Spr*	
Oliver's rattail	*Coelorinchus oliverianus*						S	
Redbait	*Emmelichthys nitidus*						A*,S,W	Spr,S,A
Yellow weever	*Parapercis gilliesi*						W	
Silver warehou	*Seriolella punctata*						Spr	A*
Southern blue whiting	*Micromesistius australis*						W**	Spr
Javelin fish	*Lepidorhynchus denticulatus*					Spr*	W,S	Spr
Deepsea smelt	*Bathylagus* sp			S,A,Spr		W	W**	W,S,A
Deepsea smelt	*Nansenia* sp							A*,S
Common roughy	*Paratrachichthys trailli*					S		Spr*,S*
Seaperch	*Helicolenus*							Spr
Pilchard	*Sardinops neopilchardus*	A		S**				
Anchovy	*Engraulis australis*				A*,W#			
Source			1,2,3	4	5	6, 7	6,7	6

*trace elements only, <1% estimated biomass
**sampled in one season only
#Carey sampled scats only, and only Autumn and Winter of one year. Complete list not available, only numerically important species.
##Street reported that one seal shot at Bench Island had 11.2 lb of fresh octopus in its stomach but season is not given
1. Fea et al. 1999. 2. Dickson 1996. 3. Tate 1981. 4. Dix 1993b. 5. Carey 1992. 6. Holborow 2000. 7. Street 1964.

Reproduction and development

Median pupping date varies between sites, from 9–16 December at the Open Bay Islands, December 21 on Kangaroo Island and December 24 in Otago. On Kangaroo Island, 90% of pups were born over a 34 day period, and in Otago, a 55 day period (Goldsworthy & Shaughnessy 1994; Lalas & Harcourt 1995).

Females remained near the birth site with their pups for the perinatal attendance period (PAP) of between 6 and 18 days (Harcourt et al. 1995), although during apparently long PAPs, females will go on very short foraging trips of 3–4 hours at a time. They then alternate feeding and suckling, gradually lengthening the time at sea throughout lactation, and conversely reducing the time ashore (eventually to only 1½ days, Schulman 1996). By winter, females in Otago will spend an average of 11 days at sea on a single foraging trip, and 91% of their active time is spent away from the rookery (Harcourt et al. unpubl. data). Pups are weaned around September.

Population dynamics

Numbers

The size of the total fur seal population within the New Zealand region is unknown, although a figure of 100 000 (with no calculable confidence limits) has been suggested (Taylor 1992, Taylor et al. 1995, Wickens & York 1997; Goldsworthy et al. 1999). This estimate was based on estimated numbers and rates of growth at different colonies. However, pup production is the only reliable method of determining the size of a fur seal population and to date, it has not been measured throughout the New Zealand distribution. In fact, neither the general rate of increase nor total abundance is known with any precision, although a concerted effort over the last decade has produced estimates of rate of increase and abundance for particular regions. At the Open Bay Islands the population has been stable, with pup production fluctuating around 1400 a year, since 1970 (Best 1994). In Nelson/northern Marlborough and at Stephens Island, annual rates of increase since 1972 of 23% and 20% have produced a total estimated population of 2410 and 1353 seals respectively in 1994 (Taylor et al. 1995). At Otago Peninsula, where there were no breeding rookeries in the 1970s, the population has been growing at between 25% and 30% per year since 1982, to a total of more than 8500 seals in 1996 (Lalas & Harcourt 1995; Bradshaw et al. 2000). Similar growth rates (19%) have been found in the Catlins, where there are now about 2000 seals (Lalas & Murphy 1998). Taylor (1982) reported an annual rate of increase for the Bounty Islands of close to 5% since the early 1900s, with an estimated population of more than 20 000 animals on the early 1980s. This increase dates from the beginning of protection (see below) and is not at present constrained by habitat requirements. On the other hand, Taylor (1992) estimated that the population at the Antipodes Islands is lower (about 2000 in 1985) and not showing any signs of increase. On the Snares Islands, Carey (1998) suggested, from sporadic counts, that after a period of rapid increase in the 1950s and 1960s, the population may now be stable at approximately 1500.

Sex ratio

C. J. A. Bradshaw (pers. comm) found, in one very large sample, a male-biased sex ratio, but it was significant only in non-ENSO years. He suggested that this plasticity in sex ratios may be a strategy by which females can respond to environmental variability. By contrast, the sex ratio of adults on rookeries is, at first glance, distinctly female biased. However, cross-sectional counts can mislead. Across an entire breeding season, and counting all known males present at the rookery during the season (defined as individuals that secure tenure for more than one day), the male:female ratio can be considerably lower. Harcourt (unpubl. data) reported that at Fuchsia Gully in Otago, a medium sized breeding colony, the operational sex ratio was of the order of 1:1.06 in the years 1993/94 and 1995/96 when all known males were included. Maximum known ages remain at 15 years for males and 14+ years for females (Troy et al. 1999).

Mortality

At three rookeries in Otago in 1998, Bradshaw (1999) estimated pup survivorship to 150 days of between 0.82 ± 0.03 and 0.97 ± 0.03, considerably higher than was estimated by Mattlin (1978b) at the Open Bay Islands (about 0.80 from birth to 50 days and 0.60 from birth to 300 days). There were several differences between these studies that invalidate direct comparisons. First, the Open Bay Islands are a stable population, whilst in Otago the population is growing exponentially. Second, there might have been environmental differences between the years measured. Third, Mattlin (1978b) based his estimates on a decline in single population estimates with no variance calculated, whereas Bradshaw (1999) did not count mortality during the breeding season. As recognised by the authors, the first method includes unknown biases, and the second method may overestimate survivorship.

Predators, parasites and disease

Hooker's sea lions are known to eat fur seal pups (Bradshaw et al. 1998; Robinson et al. 1999). New Zealand fur seals are often killed as bycatch in the hoki fishery off the west coast of the South Island, in the trawl squid fishery west of the Snares Islands, and in the southern blue whiting fishery around the Bounty Islands (Baird & Bradford 2000). The Royal Forest and Bird Protection Society has estimated that more than 10 000 seals may have drowned in nets between 1989 and 1998. The fishing industry has introduced a voluntary code of practice to attempt to minimise bycatch.

Significance to the New Zealand environment

New Zealand fur seals are listed under Appendix 11 of CITES. Tourism is increasingly targeting fur seals, and there are a number of swim-with-seals programs especially in Kaikoura. All tourist operations which feature seals as part or all of their program are required to hold a Department of Conservation Marine Mammal permit.

20. NEW ZEALAND SEA LION

Phocarctos hookeri (Gray, 1844)

Measurements

Adult males average 240–350 cm in standard length and 320–450 kg; females, 180–200 cm and 85–160 kg (Gales in press).

Distribution

The principal rookeries are found in the Auckland Is. group, on Enderby Is., Sandy Bay and Pebble Point; and at Dundas and Figure-of Eight Is. (Childerhouse & Gales 1998; Gales & Fletcher 1999). There is also a small breeding population on Campbell Island (Cawthorn 1993; Gales & Fletcher 1999). A smaller rookery was reported previously at the Snares (Crawley & Cameron 1972) but no pups in natal pelage have been seen there in the last four years (Gales & Fletcher 1999). Pups are sometimes born at haul-out sites on Otago Peninsula, at Butterfield Beach on Stewart Island, and occasionally on Codfish Island (Childerhouse &

Gales 1998). Male New Zealand sea lions visit Macquarie Island regularly (Robinson et al. 1999; McMahon et al. 1999a), and presumably all the other subantarctic islands occasionally. Aggregations, predominantly of subadult males, haul out at several sites on the Otago Peninsula all year round, and include animals tagged as pups in the Auckland Is (Lalas & McConkey 1994).

The prehistoric distribution has been described in detail by Childerhouse & Gales (1998). Sea lion remains dating from pre-European times have been reported from 47 sites around New Zealand, from North Cape to Stewart Island, and east to the Chatham Islands, mostly in Maori or Moriori middens. However, despite the wide distribution, only two sites on the New Zealand mainland and the Chathams (Delaware Bay and Paturau in Nelson) have yielded remains of pups, which Worthy (1994) suggests would indicate pre-historic breeding sites.

Habitat

The terrestrial habitat of the New Zealand sea lion is diverse. In the Auckland Islands, females and young occupy areas of grassy sward (primarily *Poa* tussock), herb fields, (megaherbs such as *Stilbocarpa* sp and *Hebe elliptica* bushes) and *Metrosideros* forest behind the beach (Gales 1995). On Otago Peninsula (pers. obs) sea lions of both sexes and all ages may move well inland and shelter in forest.

The marine foraging habitat of lactating females from the Auckland Islands is mainly benthic, either over the continental shelf or on the shelf edges (Gales & Mattlin 1997). Off the Otago Peninsula, males also appear to forage inshore on the shelf floor, concentrating in shallow waters typically less than 20 m deep in winter and spring, venturing a little further offshore in summer and autumn though probably still restricted to the continental shelf (Lalas 1997).

Food

Diet

There are no published quantitative estimates of diet of the New Zealand sea lion from the centre of its distribution in the Auckland Islands. Anecdotal reports suggest that the diet is broad, perhaps with a concentration on arrow squid during the breeding season. There are however two comprehensive studies of diet at the outer limits of its range. Lalas (1997) examined diet, of principally male sea lions, based on fortnightly collections over a 12 month period at Papanui beach in Otago. Teleost fish dominated the diet, although elasmobranchs (skate, *Raja* sp. and spiny dogfish *Squalus acanthias*) and cephalopods (principally octopus *Octopus maorum*) were also important. Seasonal changes included: barracouta, *Thyrsites atun*, dominant throughout the year, jack mackerel, *Trachurus* sp., important in summer-autumn, and flounder, *Rhombosolea* sp., greenbone, *Odax pullus*, and paddlecrab, *Ovalipes catharus*, important in winter-spring. These changes in diet are likely to reflect differences in foraging behaviour, as flounder, an inshore benthic species, is fished commercially throughout the year, yet the sea lions fed on them only in winter and spring. Bradshaw et al. (1998) reported remains of New Zealand fur seal pups in sea lion regurgitate in Otago.

McMahon et al. (1999a) report on the diet of individually recognisable sea lions based at Macquarie Island. There they feed predominantly on fish, and their major prey species do not overlap with those eaten by sympatric fur seals or penguins, except the sub-Antarctic tooth fish (*Zanclorhynchus spinifer*) which is also eaten by Gentoo penguins (*Pygoscelis papua*). Other abundant teleost fish were Patagonian tooth fish (*Dissostichus eleginodes*) and the angler fish (*Chaunax* spp.). No seasonal changes were apparent. The Macquarie Island sea lions also fed on fur seal pups and Gentoo penguins (Robinson et al. 1999; McMahon et al.

1999a). Male sea lions at Dundas Island occasionally abduct pups of their own species, and cannibalism has been observed (Wilkinson et al. 2000). Wilkinson estimated the energy benefit to a male of eating one pup is about 75 MJ, or more than one day's requirement.

Feeding behaviour

Lactating female New Zealand sea lions dive deeper and longer than any of the other otariids (Gales & Mattlin 1997). Mean dive duration was 3.4–3.9 min, mean maximum of 8.3 ± 1.7 min, and the longest recorded dive lasted 11.5 min. Mean dive depth was around 121–123 m, mean maximum of 353 ± 164 m, and an absolute maximum depth of 550 m (Gales & Mattlin 1997; Costa & Gales in press). Females dive continuously while foraging, and have the largest blood volume (and hence largest oxygen storing capacity) of any otariid (Costa et al. 1998). Their at-sea metabolic rates are 5.8 times the predicted basal rate for terrestrial mammals of equal size, within the range of other otariids for which measurements have been made. New Zealand sea lions spend 2–4 times more time at sea diving, with a diving effort 4–7 times greater, than does the Antarctic fur seal, the only other species for which comparable data are available. These data suggest that New Zealand sea lions may regularly operate near their physiological maximum (Costa & Gales in press).

Social organization and behaviour

Within harems, females are tolerant of young pups but, like many pinnipeds (Maestripieri 1992), less tolerant of neighbouring females shortly after giving birth. Fostering of pups is not uncommon, with 6% of females simultaneously nursing more than one pup (Gales in press). Gales (in press) has hypothesised that this may be associated with kin selection in small populations, but this has yet to be tested. Like other pinnipeds, females and pups identify one another by both sound and smell, although the high proportion of adoptions suggest that the pup recognition mechanism is relaxed compared to fur seals (Best 1974; Marlow 1975).

Females depart to sea for their first foraging trip shortly after mating, and then make regular foraging trips of an average 1.7 days (range 1.1–3.4 days), returning to suckle their pups for 1.2 days (range 0.8–2.3 days) between trips (Gales & Mattlin 1997). Lactation is presumed to last about 10 months (Gales 1995).

Reproduction and development

In 1994/95, the duration of pupping was 33 days at Sandy Bay, 35 days at Dundas Island and 24 days at Pebble Point (Gales & Fletcher 1999). Peak pupping was 10 days earlier at Pebble Point than at Sandy Bay and Dundas.

Little is known about the reproductive physiology of the New Zealand sea lion, but they do have embryonic diapause, as in the New Zealand fur seal and all other otariids (Boyd 1992).

Population dynamics

Numbers

The abundance of the New Zealand sea lion has been the subject of intensive investigation in response to concerns related to the Auckland Island squid fishery. Gales & Fletcher (1999) used a model based on estimated pup production, calculated either from intensive mark/recapture and/or from regular counts at all five main breeding sites. Total pup production for the 1994/95 and 1995/96 breeding seasons was 2640 and 2807 respectively, including an estimated pup mortality during the breeding season of 10%. Their estimates of absolute abundance were 11 700 (95% CI 10 500–13 100) for 1994/95, and 12 500 (95% CI 11 100–14 000) from 1995/96 (Gales & Fletcher 1999). Counts done sporadically between 1972 and 1993 suggest that the population at Sandy Bay has been relatively stable over that period. Power analysis suggests that, to detect broader trends for the whole population, frequent long-term estimates of pup production are required (Gales & Fletcher 1999). Survivorship and longevity have not been comprehensively measured but are currently under investigation.

Productivity

Based on sightings of females tagged as pups, Cawthorn (1993) suggested that females become sexually mature at three years of age and produce their first pups at four years. They can potentially pup annually thereafter, but actual pregnancy and pupping rates are unknown. Normal pup mortality (except in 1998, see below) is at least 10% during the breeding season. Since Cawthorn et al. (1985) reported that 12% of pups at Enderby Island died when trapped in rabbit burrows or seal wallows, rabbits have been eradicated from Enderby.

Predators, parasites and disease

Sharks are presumed to be the most significant natural predator of sea lions, and many individuals show evidence of previous attacks (Gales in press). Visiting leopard seals have been reported to take small sea lions (Falla 1965). Infanticide and cannibalism by males has also been observed (Wilkinson et al. 2000).

In January 1998 there was a mass mortality of young sea lions, during which time 53% of pups died within a few weeks of birth, as well as over 20% of juveniles, adult males and breeding females (Gales in press). This event has been attributed to a gram negative pleomorphic bacterium, most likely a member of the *Campylobacter* genus (Duignan et al. 1999). Estimates of pup production in January 1999 and 2000 were about 5% lower than those in 1998, but whether this is outside natural variation for this population is unknown (I. Wilkinson pers. comm.).

The impact of the trawl bycatch has been of grave concern. The Ministry of Fisheries estimates that from 17 to 141 sea lions per year were killed in the Auckland Island squid fishery in 1988–1998. Modelling suggests that, without amelioration measures, the upper range of this bycatch is unsustainable (Woodley & Lavigne 1993; Gales 1995). Management measures so far implemented include:

1 a marine mammal sanctuary prohibiting commercial fishing within 12 nautical-miles of the Auckland Is;
2 government observers stationed on trawlers to record the incidence of marine mammal bycatch (7–32% of tows observed in the years 1988–1997; bycatch on observer boats 0.6%–3.8%);
3 a delay in the opening of the fishery until February 1 (past the breeding season);
4 a voluntary code of practice aiming at reduction in bycatch, which includes a provision that any vessel which catches three or more sea lions will be removed from the fishery and its procedures reviewed (this stipulation has not always been followed);
5 MALFIRM, a Maximum Allowable Level Of Fishing Related Mortality, calculated at the beginning of each season (usually between 60–80 sea lions). When MALFIRM is reached the government closes the fishery for the season. MALFIRM was exceeded every year between 1995 and 1998, and the fishery was closed early for the last three years, i.e., 1996, 1997 and 1998.

Significance to the New Zealand environment

New Zealand sea lions are now listed as Vulnerable with the IUCN red data book. The

Department of Conservation draft management plan aims to remove the New Zealand sea lion from its current, threatened, status by 2019.

FAMILY PHOCIDAE

Two subfamilies of phocids, the Phocinae and Monachinae, are recognized by most authorities on the basis of recent cladistic analyses (Rice 1998). The Monachinae has eight extant species (the Caribbean monk seal *Monachus tropicalis* is recently extinct, last reliable report dating back to 1952), comprising the monk seals (two extant species), the elephant seals (two species) and the Antarctic seals (4 species). All five New Zealand phocids belong to the Monachinae (Rice 1998).

21. SOUTHERN ELEPHANT SEAL

Mirounga leonina (Linnaeus, 1758)

Description

Elephant seals are unique amongst seals in having a catastrophic moult, during which large ragged patches of hair and epidermis are sloughed off. The moult incurs high energetic costs associated with the replacement epidermal growth required, and presumably also a thermal cost associated with the perfusion of epidermal tissues with blood. By hauling out during the moult the elephant seal also incurs fasting costs. Boyd et al. (1993) calculated that the cost of the moult to female elephant seals is a substantial component of their annual energy budget: it is equivalent to at least half of what they invest in rearing a pup to weaning, and accounts for their total energy gain during the period they forage at sea post weaning before returning for the moult.

Elephant seals swim at a mean speed of about 2.1ms^{-1}, and they will travel 70–80 km d^{-1} en route to foraging grounds (McConnell & Fedak 1996; Hindell & Lea 1998). They are the deepest-diving of all pinnipeds, and dive more or less continuously when at sea (90% of their time below the surface). Hindell et al. (1991) measured mean dive duration at 22 min; mean surface interval only 2–3 min; the longest dive recorded, 120 min, was only part of a series of long dives by a female. Mean dive depth for a larger sample was 400 m; dives to deeper than 1 km are regularly observed and several individuals have been recorded diving to 1500 m!

Measurements

On Macquarie Is., adult males reached up to 5.36 m standard length and 3700 kg; females were much smaller, but variance in size was three-fold (mean 506 kg ± 111, range 346–803 kg) (Fedak et al. 1996). Newborn pups weighed over 40 kg (41.8 ± 6.9 kg) at Macquarie Is. and about the same (42.5 ± 1.5 kg, range 19 to 63 kg) at South Georgia (Arnbom et al. 1993; Hindell & Slip 1997). At weaning, 18–23 days later, pups weighed between 113 kg ± 16.6 kg at Macquarie Island and 120 kg ± 27.5 kg, range 38 to 147 kg, at South Georgia (Arnbom et al. 1993; Hindell & Slip 1997).

Distribution

There is a significant and growing population at Peninsula Valdés on mainland South America (Campagna et al. 1993). The three main breeding stocks are centred in the three southern oceans, with smaller populations within these three provinces. In the South Atlantic elephant seals breed on the Falkland Islands, South Georgia; at Peninsula Valdés, Argentina; South Signy, South Shetland and South Orkney Islands; at Gough Island and Bouvet. In the

Indian Ocean they breed at Marion, Crozet, Kerguelen and Heard Islands, and in the South Pacific they breed at Macquarie, Campbell and the Antipodes Islands (Slade 1997).

Genetic studies suggest that there is little interchange between the three main stocks, and the Peninsula Valdés population is demographically distinct from the South Georgia stock, which itself is more closely related to the Heard Island population (Slade 1997). During their long forays to sea, the different stocks may occasionally overlap at foraging grounds. Elephant seals have been reported many thousands of km from their natal sites; one young female hauled out to moult 5200 km from her birth site, Macquarie Island, and was seen later to have returned there (Hindell & McMahon 2000).

The New Zealand population is concentrated on the Antipodes Is. (Taylor & Taylor 1989) and on Campbell Island. Between Oamaru and Nugget Point, pups were recorded frequently between 1965 and the early 1990s (C. Lalas pers.comm.).

Food

The diet of elephant seals at sea is poorly known because they spend considerable periods (months) diving hundreds of kilometres from land (Hindell et al. 1991; McConnell & Fedak 1996). Therefore, reconstructions of the diet from samples retrieved from haulouts may not represent their diet as a whole. The stomachs of 51 seals lavaged at South Georgia contained 14 species of squid from 11 families, and two species of octopod from one family, but no fish (Rodhouse et al. 1992). Green & Burton (1993) found that the diet at Heard Island and Macquarie consisted predominantly of cephalopods and fish. At Heard Is., fish appeared in 77.3% of stomachs, plus five species of squid, mainly two species of *Moroteuthis*; at Macquarie, both Antarctic and non-Antarctic species were taken, including fish (33.8%), and a high proportion of *Histioteuthis eltaninae*.

Social organization and behaviour

Recent detailed studies of elephant seal behaviour have been made by Arnbom and colleagues at South Georgia (Arnbom et al. 1993, 1994; Fedak et al. 1996); Hindell, Burton and colleagues on Macquarie and Heard Is. (Hindell & Burton 1988; Hindell et al. 1994; Slip et al. 1994), Bester and team on Marion Island (Bester & Pansegrouw 1992; Wilkinson & Bester 1990; Wilkinson 1991), Campagna and team at Peninsula Valdés, Argentina (Campagna et al. 1992, 1993; Baldi et al. 1996) and Galimberti and Boitani in the Falkland Islands (Galimberti & Boitani 1999).

Reproduction

Genetic analyses of paternity have demonstrated that, although alpha males achieve the highest reproductive success, they do not successfully exclude other males. At Peninsula Valdés, 21of 50 pups sampled were sired by a male other than the current local alpha male (Hoelzel et al. 1999). Of these, three were sired by previous alpha males, one by an alpha at another harem, one that had been an alpha at another harem previously, six by non-alpha males. The other 10 could not be matched to any males sampled at the beach. Only 30.8% of observed copulations resulted in reproductive success for that male, confirmed from later paternity tests (Hoelzel et al. 1999). More than half the females observed at Peninsula Valdés copulated with more than one male (Campagna et al. 1993).

The exact timing of reproduction varies among rookeries, later at higher latitudes. Across their distribution, the day the maximum number of females is hauled out varies from 2 October at Punta Delgada (42° 30′S) through 18 October at Heard Island (53°00′S) to 25 October at South Georgia (54° 19′S) and King George Island (62° 16′S)(Campagna et al. 1993; Galimberti & Boitani 1999). The duration of the parturition period is reasonably consistent across their distribution at close to 60 days, and the number of females ashore approximates a Gaussian model (Hindell & Burton 1987; Galimberti & Boitani 1999). Small females tend to arrive earlier than large females, and the departure date is slightly more irregular than arrival. Larger females may suckle their pups for longer, presumably having larger fat reserves (Campagna et al. 1992).

Weaned pups stayed ashore for 40–50 days, fasting on stored blubber reserves, thereby losing about 30% of their mass (Arnbom et al. 1993). During the post weaning fast they gradually increased the proportion of time spent learning to swim, including expeditions of up to 10 km from the natal site (Falabella & Campagna 1999). By the end of December all weaners had left the beaches, and they did not reappear until May through mid-July (mean trip duration 182 ± 51 days, Slip 1997; Bell et al. 1997). Their body mass increased by about 75% during this first foraging trip, at a rate of about 300 g per day (0.34 ± 0.12 kgd^{-1}; Bell et al. 1997).

Population dynamics

Numbers

The elephant seal population in the Atlantic is stable or growing, while the populations in the Indian and Pacific Oceans have been declining, although the decline appears to have halted in some areas.

On South Georgia the population is >460 000 (54% of the world's population); annual pup production is about 100 000; and there has been no change in abundance for at least 45 years (Laws 1994; Boyd et al. 1996). At Peninsula Valdés, the latest population estimate is 45 800 animals excluding pups; annual pup production is >9 000, and the population is growing at approximately 2.8% per year (Campagna et al. 1992; Lewis & Campagna 1999). On Macquarie Island the population is down to about 90 000, from a high of 156 000 in 1959, and is continuing to decline at 1.2% per year (Hindell 1991; C. McMahon pers. comm.). At Iles Kerguelen, the population declined from about 70 000 in the 1950s to 35 000 in the mid–1980s, was stable for a period and is now about 40 000 and rising at about 1% a year (Guinet et al 1992). On Heard Island, the population has also declined, and pup production is down to just over 13 000 in 1985 from more than 32 000 in 1946 (Burton 1986).

Few elephant seals breed in the New Zealand region; pup production on Campbell Island has declined by 97%, from 191 pups in 1947 down to 5 in 1986 (Taylor & Taylor 1989), whereas 113 pups were born on Antipodes Island in 1978. The Antipodes group may now support the main New Zealand breeding population (Taylor & Taylor 1989).

Age and mortality

Males can live to 23 years, but have significantly lower age-specific survival than females; 97.4% have died by the age of 10 (Hindell 1991). At Marion Island males do not generally live beyond 13 years, and 93% of females do not reach 14 years (Hindell 1991; Pistorius et al. 1999). However, females branded as pups on Macquarie Island have been seen alive and still successfully breeding at 23 years of age (Hindell & Little 1988). Females first bred at between 4 and 7 years of age (mean at Macquarie Island 5.2 ± 1.8 years) and the estimated annual fecundity rate at South Georgia was 0.391 (Hindell 1991). At Peninsula Valdés, 96% of females that came ashore gave birth, and in the Falkland Islands, 100% (Campagna et al. 1993; Galimberti & Boitani 1999). The successful pupping by the 23 year old females seen by Hindell & Little (1988) suggest that there may be no reproductive senescence.

Typically, across different populations the sex ratio is unbiased. Although sexually mature from about 5 years of age, males are not socially mature enough to engage in the conflict in the breeding areas until much older. They start attending breeding harems at the age of 10 years, and some (16%) males do manage to breed at that age, but few males under 12 successfully hold status in harems (Jones 1981). At Macquarie Island, where the population is currently declining at a rate of 1.2% a year, survivorship was 78% from 1–3 years of age and 85% from four years on (McMahon et al. 1999b; C. McMahon pers. comm.). Pre-weaning mortality was around 5% (Hindell & Burton 1987; McMahon et al. 1999b). By contrast, on Marion Island, where the population declined at 2.5% a year from 1986 to 1991, and 4.3% from 1991–1997, survivorship from 1–3 years was only 69% for males and 74% for females; from 4–9 years, male survivorship was 66% and female 75% (Pistorius et al. 1999). Adult mortality appears to be an important component of the decline at Marion Island.

Predators, parasites and disease

Killer whales regularly kill young elephant seals at Macquarie Island, Crozet Island and in Argentina (Lopez & Lopez 1985; Guinet 1991). M. W Cawthorn (unpubl. data) has seen wounds caused by sharks, leopard seals and killer whales, and observed New Zealand sea lions killing and eating yearling elephant seals at Campbell and Auckland Islands.

Significance to the New Zealand environment

The trade in southern elephant seal blubber oil finished in 1830, although a well-managed sealing industry continued at South Georgia until 1964. That population continues to decline, perhaps, according to Hindell and colleagues, because the population has overshot the carrying capacity since cessation of exploitation. If so, the continued decline may soon level out, as has happened in the Iles Kerguelen (Hindell & Burton 1987; Hindell 1991; Guinet et al. 1992).

There is always keen local interest when elephant seals come ashore near populated areas. An old male, 'Humphrey', frequented the Coromandel Peninsula and the Bay of Plenty each summer for the five years to 1989/90 (illustrated in Anon. 1990), and more recently 'Homer' chose to haul-out, first in Christchurch for several years and then in Gisborne in 2000. Although popular with locals and visitors, the impact of an amorous, two tonne male elephant seal on cars and other structures is significant.

Populations at Macquarie Island and South Georgia receive visits from tour ships, strictly controlled under the Antarctic treaty. Englehard et al. (1999) have begun to measure the impact of research and other forms of human disturbance on female elephant seals and their pups. Females in areas often visited by people do appear disturbed, as they move about the beach more frequently, but the implications of this are still to be determined.

Elephant seals are protected fully, both in New Zealand waters (Marine Mammals Protection Act 1978) and south of 60^0S (Antarctica (Environmental Protection) Act 1994) which implements the Convention for the Conservation of Antarctic Seals (1972). They are assessed as Vulnerable under the IUCN (1994) red data book classification.

22. WEDDELL SEAL

Leptonychotes weddellii (Lesson, 1826)

Measurements

Female Weddell seals in McMurdo Sound range from 187.0 to 265.0 cm, nose to tail length (Hastings & Testa 1998). Female mass is highly variable through the year; 14 post-partum mothers weighed between 342 and 524 kg (mean = 447 ± 52 kg, Tedman & Green 1987). Females live mostly on stored blubber reserves during lactation, though some individuals do feed occasionally (Testa et al. 1989; Hindell et al 1999). Because lactation lasts up to 7 weeks, the loss in female mass is enormous, averaging 4.55 ± 1.24 kgd^{-1}, totaling up to 249 kg, or 59% of their body weight, by the time the pups are weaned (Tedman & Green 1987).

Males range from 201 to 293 cm in length, but also vary considerably in mass between years, and males too lose significant mass over the course of the breeding season (Bartsch et al 1992; Harcourt et al. 1998, unpubl. data). At the beginning of the breeding season in 1986, 16 males varied from 283 to 414 kg (mean = 365 kg); by the end of the season they ranged from 185 to 332 kg (mean = 273, n=14), a loss of 2–3 kgd^{-1} (Bartsch et al 1992). At a neighbouring colony in 1997–1999, males weighed from 314.5 to 465 kg (mean = 393 ± 44.8 kg, n=28) at the beginning of the breeding season, 293.5 to 428.5 kg at the end (mean = 348 ± 30.0 kg, n = 24)(Harcourt et al. 2000a, unpubl. data). The mean weight of pups at birth is 24 kg (n = 14, Tedman & Green 1987).

On White Island both sexes are larger than elsewhere; females have been weighed at up to 686 kg, males up to 554 kg (Castellini et al. 1992).

Distribution

Weddell seals are most abundant in the fast-ice which abuts the Antarctic coastline, and breed in areas where perennial tide cracks form in the ice (Castellini et al. 1992). They also inhabit pack ice at lower densities (e.g., 0.029 seals per nm^2, Bester et al. 1995). Small breeding populations may also found on some of the subantarctic islands, including a small relict population of about 100 based on Larsen Harbour, South Georgia (Laws 1994).

Testa (1994) used satellite telemetry to track the over-winter movements in the Ross Sea of 18 parous female Weddell seals aged 6 years and over. Seals that normally bred in the eastern part of McMurdo Sound spent most of the winter in the middle and northern parts of the sound before the annual shore-fast ice had formed in those areas, or in the pack ice 0–50 km north of the sound and Ross Island. Some traveled considerable distances to the middle and northwestern parts of the Ross Sea; one female swam over 1500 km in total (Testa 1994). Burns et al. (1999) tracked 23 weaned pups, most of which left their natal area in McMurdo Sound by the end of February, and traveled north along the Antarctic continent coastline. Some pups returned, but others were last located more than 400 km from McMurdo. From the routes plotted, pups apparently preferred to remain closer to the coastline than did adults.

Habitat

Fast ice varies in thickness from a few cm to 3 m or more, and may extend up to 400 km from the coast depending upon season (Castellini et al. 1992). The seals haulout on the ice surface adjacent to perennial cracks in the ice which form as a result of tidal movements and wind, and also at tidal cracks that form along the shore-line. They maintain access to the surface by reaming the ice with their teeth, and keep breathing holes open in the deeper cracks throughout the year. There is a single isolated population at White Island, cut off from the main McMurdo population by an 18 km wide unbroken ice shelf 10–100 m thick. The 30-odd seals in this population produce 3–5 pups per year, which have high neonatal and preparturient mortality and various congenital deformities, indicating a degree of inbreeding (Castellini et al 1992; Testa & Scotten 1999).

McMurdo Sound is relatively deep, and is the location of the most intensive studies. The seals use all parts of it (Castellini et al. 1992). They are deep divers, and in McMurdo Sound usually dive between 100 and 350 m, maximum 751 m (Castellini et al 1992; Schreer & Testa 1996; Davis et al 1999; Harcourt et al. 2000b). Evidence from dive recorders and from analysis of diet suggests that much of their foraging is pelagic, although benthic prey are also taken (Plotz et al. 1991; Burns et al. 1998). In shallower areas such as Terra Nova Bay (<300 m) in the Western Ross sea, 45% of dives were less than 100 m (Castellini et al. 1992).

Food

Weddell seals feed principally on fish and cephalopods, plus crustacea, especially prawns, but not krill (Green & Burton 1987; Castellini et al 1992; Burns et al. 1998). The predominant prey species, both by frequency of occurrence and by weight, in McMurdo Sound, at Davis Station, and in the Weddell Sea, is a notothenid, the Antarctic silverfish (*Pleurogramma antarticum*) (Green & Burton 1987; Plotz et al. 1991; Castellini et al. 1992; Burns et al. 1998). Other important fish prey species include the pelagic notothenids *Pagothenia borchgrevinki* and benthic *Trematomus* spp. (Castellini et al. 1992; Burns et al. 1998). Weddell seals are renowned for hunting the large (up to 77 kg) Antarctic cod (*Dissostichus mawsoni*), however, after examining enrichment of natural occurring isotopes in seal blood, Burns et al. (1998) suggested that cod may not contribute significantly to their overall diet. Davis et al. (1999) attached video cameras to the heads and backs of Weddell seals in McMurdo sound and observed them hunting Antarctic cod at depth, and flushing *P. borchvgrevinki* from within the platelet ice immediately below the fast ice surface by expelling air bubbles. They did not observe a successful capture of cod. Larger yearling Weddell seals in McMurdo Sound make long, shallow dives, and appear to forage on benthic species such as *Trematomus* spp., whilst smaller yearlings forage pelagically on prey species similar to those taken by adults (Burns et al. 1998). One Weddell seal was observed repeatedly killing and eating adult Gentoo penguins (*Pygoscelis papua*) in 1996/1997 (Cobley & Bell 1998) and Todd (1988) earlier reported a single attack on a Chinstrap penguin (*Pygoscelis antarctica*).

Social organization and behaviour

Weddell seals exhibit moderate polygyny, with sex ratios at colonies varying between 2.8:1 and 8.9:1 over the course of a breeding season (Hill 1987). The underwater territories of adult males in breeding areas change in size over the course of the breeding season, and residents can be displaced after repeated challenges (Bartsh et al. 1992; Harcourt et al. 1998). Males share breathing holes, but the volume of individual male territories may vary fivefold (Harcourt et al. 2000a).

Weddell seals are the most vocal of all seals; 21 to 44 vocalisation types have been classified, varying with location, and there is significant seasonal and geographic variation in calls and songs (Terhune et al. 1993; Morrice et al. 1994; Pahl et al. 1996). Males call almost continuously during the breeding season, and only males emit the trills (in McMurdo Sound) or songs (in Vestfold Hills Fiords) which are probably used for territorial defense (Morrice et al. 1994).

Reproduction and development

Spermatogenesis is initiated in August, and viable sperm are produced from October through December; in January males become azoospermic (Smith 1966). Males first show spermatogenesis at three years, but are not mature and do not attend breeding colonies until 5–7 years (Bartsh et al. 1992). Successful (territorial) males are generally over seven years old, and may hold territories up to at least 13 years of age, although the average age of first breeding is still unknown (Testa 1997).

Females can pup from as early as two years of age, but in McMurdo Sound the average age of first reproduction is six (range 2–11 years; Hastings & Testa 1998). Further north in

Antarctica the age of first reproduction is later; the average age at first sighting with a pup is seven years at Signy Island and eight years at the Vestfold Hills. Reproductive rate is approximately 0.68, but varies annually in a predictable 4–5 year cycle, between 0.55 and 0.75 (Testa et al. 1990), and females continue to reproduce throughout their life (to 18 years+) with no evidence of reproductive senescence (Testa 1987). Pups born to older and more experienced females survive better (Hastings & Testa 1998).

Pups begin to dive within two weeks of birth. The number of dives per day, and their mean depth and duration, increase rapidly over the first three months of life (Burns & Testa 1997). The first dives by pups rarely exceed 20 m and 2 min, but by weaning at 6–7 weeks they are already capturing *P. antarcticum* and can dive to mean depths of 50 to 70 m for 3–4 min; by 12 weeks these figures are closer to 100 m and 5–6 min (Burns & Testa 1997). Dive depth and duration is closely linked to age over the first three months, but beyond that age dive ability is not related to age, except that older pups dive more frequently (Burns & Testa 1997). Pups 13 weeks old dive to a mean depth of 116 ± 13 m and 5.6 ± 0.5 min, significantly shallower than yearlings (200 ± 35 m, 8.7 ± 0.6 min) and adult seals (144 ± 83 m, 10.4 ± 2.9 min, Castellini et al. 1992; Burns & Testa 1997).

Population dynamics

Age and mortality

Pre-weaning mortality is low in Weddell seals (mean 0.13, range 0.06–0.22) but varies significantly with maternal age, since females >10 years old are more likely to wean their pup successfully (Schreer et al. 1996; Hastings & Testa 1998). Survival from 0–1 years is 0.429, from 1–2 years 0.635 and from 2– 6 years 0.806 and comparable to adults (Hastings et al. 1999). Juvenile survival overall (0–6 years inclusive) is higher in females (0.142, versus 0.093 in males), and in the offspring of older, more experienced mothers (Hastings & Testa 1998; Hastings et al. 1999). The minimum adult male (5 years +) survival rate of Weddell seals in McMurdo Sound is 0.762, with the maximum age recorded, 22 years (Testa & Siniff 1987). The survival rate of adult females is about 0.85 but declines to 0.74 from ten years and older. The oldest females known were aged 25 years (Testa & Siniff 1987).

Significance to the New Zealand environment

Killing of Weddell seals for dog meat and to support expeditions and Antarctic bases ceased in 1986, and dogs are no longer allowed in Antarctica under the Antarctica (Environmental Protection) Act 1994. Antarctic tourism is increasing; 12 000 visitors were reported in the 1999/2000 season. In the Ross Sea region, tourism is currently restricted to ship-board visits, so tourists can enter the region only in January and February, after the breeding season of the Weddell seal. The potential impact of tourism warrants investigation, in advance of the inevitable expansion of tourism to areas where the seals breed, and limited studies have recently been started (Turner & Harcourt 2000). An Environmental Code of Conduct requires all visitors to Antarctica with Antarctica New Zealand to:

1. Keep a minimum distance of 5 m from any animal unless it comes to you;
2. Take special care when photographing to ensure this distance is maintained;
3. Do not walk through bird and seal colonies;
4. Keep noise to a minimum in the vicinity of wildlife;
5. Do not take vehicles within 200 m of wildlife.

23. LEOPARD SEAL

Hydrurga leptonyx (Blainville, 1820)

Distribution

In winter, young leopard seals are regularly seen hauled out on the South Island of New Zealand, in Tasmania and as far north as Sydney, Australia. The highest concentrations are found along the edge of the pack-ice, and their distribution varies by age class; the larger, presumably older, animals are more widely separated (Rogers & Bryden 1997).

Food

Leopard seals have a diverse diet, ranging from krill, cephalopods and fish, through penguins, fur seals, crabeater seals and juvenile elephant seals (Green & Williams 1986; Rogers & Bryden 1995; Walker et al. 1998). They will ambush Adélie penguins (*Pygoscelis adeliae*) amongst the ice-floes and waters adjacent to their rookeries; stalk penguins under thin ice, breaking through with their heads to seize them; and wait for them at the ice edge, either as they return to the rookery or ice edge, or when groups depart to sea. Different hunting tactics seem to be favoured by particular individuals (Rogers & Bryden 1995). Muller-Schwarze (1984) suggested that leopard seals could remove 2.4% of the Adélie colony at Cape Crozier in a season; Penny & Lowry (1967) suggested 5% at the same rookery, and Rogers & Bryden (1995) report a similar rate at Prydz Bay (2.7% of a population of 215 000 penguins). As leopard seals are usually widely dispersed, they are mainly solitary hunters, but there are reports of pairs of seals hunting together and even of food sharing (Hiruki et al. 1999).

At Elephant Island in the South Shetland Islands, leopard seals apparently have prevented population growth at least one colony of Antarctic fur seals (*Arctocephalus gazella*) and possibly also elsewhere in the region (Boveng et al. 1998).

Social organisation and behaviour

Mating of leopard seals has never been seen in the wild, although it has been described in captivity (Rogers et al 1996). In the shifting environment of the pack ice, adults are widely dispersed and males are unable to monopolise females in the manner of Weddell or elephant seals, so the degree of polygyny is thought to be low (Bester et al. 1995; Rogers & Bryden 1997). Underwater vocalizations are important in both spacing and mating behaviour. Calls are of low to medium frequency (300–3500 Hz) and long in duration, of 12 distinct types with associated behaviour (Rogers et al. 1996). Half these call types were associated with agonistic interactions, were local type calls, and were heard through most of the year. The other half were broadcast calls produced by lone seals, either the female when sexually receptive, or by a mature male only during the breeding season. Rogers et al. (1996) hypothesised that these broadcast calls serve an important part of the mating behaviour of these solitary pack-ice breeding seals. The lowest frequency call is particularly powerful and resonant, and can be heard at the surface and felt through the ice.

24. CRABEATER SEAL

Lobodon carcinophagus (Homron & Jacquinot, 1842)

Food

Crabeater seals are capable of diving for at least 15 min and to depths greater than 480 m, but 90% of their dives were in the 10 to 40 m range where krill were most abundant (Bengtson &

Stewart 1992; Nordoy & Blix 1998). They made up to 225 dives a day, and most (80%) were of short duration (< 3 minutes). Bengtson & Stewart (1992) suggested that the few deeper dives (300–450 m) were made to enable the seals to move away from the noise of the pack ice continually bumping and grinding in the swell, so as to listen, either for other seals or for krill swarms. Crabeater seals show a clear preference for hauling out during daylight and foraging during darkness, and for diving deeper near sunrise and sunset. This type of dive pattern is common amongst marine predators that forage on vertically migrating prey such as krill.

Population dynamics

The continental population of crabeater seals in the mid-1980s (15 million animals) had reportedly declined by up to 60% since the late 1960s. One suggested explanation is the recovery of populations of baleen whales, which compete with crabeaters for the same food (krill). Commercial harvesting of krill may also be a factor (Erickson & Hanson 1990). However, Green et al. (1995) have questioned whether this supposed decline in pack ice seal numbers is real, because of the limited and uneven census data. In 1999/2000 the multinational Antarctic Pack Ice Seal Program (APIS) conducted simultaneous surveys for pack ice seals around the Antarctic continent. Only when these results have been processed, will more precise estimates finally be available.

25. ROSS SEAL

Ommatophoca rossi Gray, 1844

Distribution

Ross seals were thought to prefer the heavy pack ice, which was supposed to explain why they were rarely seen. However, two recent studies have succeeded in tagging Ross seals to study both movements and dive behaviour (Bengtson & Stewart 1997; Blix & Nordoy 1998). Satellite tracking shows that at least some individuals spent considerable periods away from pack ice. One seal followed for 230 days spent most of the time between February and September foraging in the open sea, not hauling out for up to 39 days. Although this study only followed a single animal, it is possible that Ross seals inhabit the dense pack only during the breeding season.

Food

Blix & Nordoy (1998) reported an average of 113 dives a day by a satellite-tagged Ross seal, evenly distributed throughout the 24 hours, to all depths between 12 and 400 m. Bengtson & Stewart (1997) reported a mean dive depth and duration of 100 m and 6.4 min, deepest near twilight and shallowest at night. The water depth in this area was about 225 m, suggesting the animal was not diving to the bottom. Dives made by Ross seals were usually deeper than those made by crabeaters foraging in the same areas. The deeper dives of Ross seals were presumably related to their diet, which is predominantly fish (particularly *P. antarcticum*), and cephalopods (*Psychoteuthis glacialis* and *Allouroteuthis antarcticus*), in contrast to the krill-specialist crabeaters (Skinner & Klages 1994; Bengtson & Stewart 1997).

Population dynamics

The most recent estimate for the population of Ross seals is 131 000 (Erickson & Hansen 1990). Ross seals made up only 3.4% of pack ice seals in surveys in 1991–1992 (Bester et al. 1995).

Significance to the New Zealand environment

The Ross seal is listed as a Specially Protected Species under the Antarctica (Environmental Protection) Act 1994 Appendix A.

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