DYNAMICS OF AN ISOLATED POPULATION OF WEDDELL SEALS (*LEPTONYCHOTES WEDDELLII*) AT WHITE ISLAND, ANTARCTICA

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A small population of Weddell seals (*Leptonychotes weddellii*) was studied at White Island, Antarctica, where it is apparently isolated from other populations of Weddell seals by 18 km of floating glacier ice. The seals at White Island have increased from only nine in 1968–1969 to 26 seals older than pups in 1993–1994, with a concurrent decline in body condition. No evidence of immigration or emigration was found. Higher survival of adult seals, lower fecundity, and higher mortality of pups occurred at White Island relative to seals in an open population only 30 km away in Erebus Bay. High neonatal and preparturient mortality at White Island, including pups with congenital deformities, suggest that genetic viability of this population is questionable. If it remains isolated, the population of Weddell seals at White Island is a model for small populations of endangered seals and possibly for conditions leading to speciation in polar phocids.

Key words: *Leptonychotes weddellii,* Weddell seals, small populations, population dynamics, survival, reproduction, McMurdo Sound, Antarctica

The ecology of small populations has relevance from both conservation and evolutionary perspectives; populations usually become small before becoming extinct, and genetic changes that can lead to speciation occur more readily in small populations (Bush et al., 1977; Templeton, 1981; Wright, 1978). Currently, several species of pinnipeds are threatened with extinction, or have gone through historic population bottlenecks (Hoelzel et al., 1993; Kretzmann et al., 1997; Nowak, 1991). The study of small isolated populations of an unthreatened species may provide insights into processes that only occur at very small population size without the compelling necessity of intervention that exists for an endangered species.

Isolated from the open sea by ca. 18 km of permanent glacial ice, White Island, Antarctica (78°5′S, 167°30′E, Fig. 1), is home to a small population of Weddell seals (*Leptonychotes weddellii*). The population was discovered in 1958 (Heine, 1960; Stirling, 1972). Subsequent assessment by Stirling (1972) revealed an adult population of about nine unusually large seals. The life history, population dynamics, and behavior of Weddell seals have been well documented in nearby Erebus Bay (Kaufman et al., 1975; Siniff et al., 1977; Stirling, 1969; Testa, 1987*a*, 1987*b*; Testa and Siniff, 1987; Testa et al., 1990) and elsewhere around Antarctica (Bertrum, 1940; Croxall and Hiby, 1983; Lindsey, 1937; Lugg, 1966).

Because its population of seals is unusual and possibly unique, the northwestern side of White Island was recommended in 1985 as one of several Sites of Special Scientific Interest (SSSI) by parties to the Antarctic Treaty under their Agreed Measures for the Conservation of Antarctic Fauna and Flora. There are questions about the degree of genetic isolation of this population, its possible evolutionary divergence and adaptation to severe conditions, and its long-term viability (Stirling, 1972). We used tagging

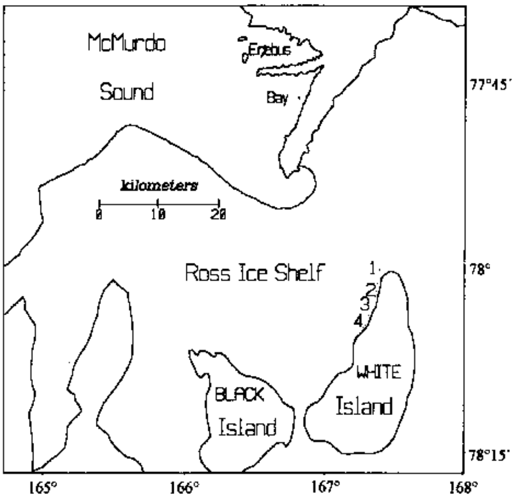

FIG. 1.—White Island, the surrounding Ross Ice Shelf, and Erebus Bay on the coast of Ross Island, Antarctica. Females with pups were always seen in location 2, whereas males, subadults and some non-breeding females were seen in locations 1, 3, and 4.

and handling of seals to detect changes in population size and body condition undergone by the population of seals at White Island since Stirling's (1972) initial assessment. We also compared body condition and life history characteristics of this population to those of the open population at nearby Erebus Bay. Such comparisons should clarify the significance and potential scientific value of the isolated seal population at White Island.

MATERIALS AND METHODS

White Island (Fig. 1) was visited during five austral summers from 1990–1991 through 1994–1995, but seasonal timing of those visits varied. In 1990–1991, the island was visited in early February when seals were molting and probability of haulout for both sexes was relatively high. In 1991–1992 and 1994–1995, the island was visited only in late November–early December (three times and once, respectively), after pups were born and while males were likely to be spending most of their time in water defending territories (Siniff et al., 1977). In 1992–1993 and 1993–1994, five visits in each year spanned both breeding and molting seasons (late November to early February). In addition, counts of seals were made from an overflying helicopter on 6 February and 23 November 1991.

All seals were handled in accordance with the conditions set forth in permits issued to J. W. Testa and M. A. Castellini under the U.S. Marine Mammal Protection Act and the U.S. Antarctic Conservation Act. Adults were captured using the bagging technique of Stirling (1966). All adults and pups were tagged with cattle ear tags in both rear flippers. Blood was taken from each individual and archived for later genetic analysis. Unusual scars or injuries also were recorded. Whenever possible, length and axillary girth were measured at initial capture of seals ≥1 year. Length was measured in a straight line from the tip of the tail to the tip of the nose while the animal was restrained. The ratio of girth : length was calculated as an index to each animal's fatness, or condition (Stirling, 1971, 1972). Three pups judged by stage of molt to be near weaning in November–December 1992 were placed in a mesh bag and weighed from a digital hanging scale (resolution <1 kg). Comparable length, girth, and weight data were collected from Weddell seals in Erebus Bay (30 km north) in the same period and seasons of study (Testa and Siniff, 1987). Measurements were compared between sites with *t*-statistics (Zar, 1974). Because only 3 pups were weighed at White Island, the hypothesis that their weights differed from those at Erebus bay was tested by direct calculation of probability under the null hypothesis that weights from White Island came from the distribution of weights observed at Erebus Bay (Larson and Marx, 1981).

Thirteen censuses of seals were conducted on the ice surface from 1991–1992 to 1993–1994 by searching SW to NE along the tidal crack. All untagged seals were tagged during censuses, and mother-pup associations were noted. Thorough searches were made for dead pups in all areas that showed evidence of haulout (urine, feces, snow-drifted depressions). Multiple visits in 1991–1992, 1992–1993 and 1993–1994 made discovery of all dead pups on the surface in those years highly probable.

Minimum population estimates were based on the number of seals of either sex that were seen and tagged. Mark-recapture procedures (Lebreton et al., 1992; Pollock et al., 1990) were used to make unbiased estimates of population size

TABLE 1.—*Numbers of seals older than pups that were tagged at White Island each season and estimated by tagging alone (minimum number alive, MNA) and by mark-recapture (M-R) methods (Pollock et al., 1990). Because all pups were tagged annually beginning in 1991–1992, untagged seals older than pups when first encountered were assumed to have been present in previous years for the MNA estimate. Pups seen after their birth year were included in the MNA estimate as yearlings. Seals missing for 2 years (1 male and 3 females) were assumed to have died after the last year seen. Standard errors are shown where calculable for M-R estimates (program Jolly—Pollock et al., 1990). Males were unlikely to be seen in 1991–1992 and 1994–1995 due to the timing of those censuses from November to mid-December.*

	Females				Males			
Year	New seals	MNA	M-R	(*SE*)	New seals	MNA	M-R	(*SE*)
1990–1991	10				5			
1991–1992	3	16	14	(1.9)	1	11	11	(9.0)
1992–1993	3	18	17	(0.9)	3	10	8	
1993–1994	0	16	16		2	10	10	(2.0)
1994–1995	0				0			

and estimate survivorship. Estimates were made separately for males and females due to their different haulout behavior and hence, sightability. Because annual survival rates were of interest, mark-recapture observations were pooled within years for the first three years (i.e., an animal was counted as seen regardless of the number of times it was seen), except for males in 1993–1994. No males were seen in the single visit made in early December 1994. Dividing observations of males in 1993–1994 into two time periods (prior to and after 31 December) met the assumptions of mark-recapture estimators while allowing an additional year's survival estimate. The program Surge (Lebreton et al., 1992) was used to obtain survival estimates. In addition to a simple enumeration of minimum number alive, program Jolly (Pollock et al., 1990) was used to estimate population size for seals older than pups.

RESULTS

Captures and distribution.—Forty-eight seals were tagged or collected as natural fatalities at White Island in the 5 years of study. Eleven male and 19 female Weddell seals older than pups were individually identified (Table 1). Of the 19 females, three were first tagged as pups, and three were identified as subadults or yearlings at the time they were tagged and would not have reached maturity during our study (Testa, 1987*b*). Three males and three females had evidence of being tagged prior to 1979 in an earlier effort by researchers from New Zealand (I. Stirling, pers. comm.), so they must have been ≥12 years old. Ten of the males and 16 of the females were seen in 1993–1994 when most censuses were conducted after the breeding season and the likelihood of finding all seals was high, suggesting that one male and three females had died. Only one visit was made (early December) in the 1994–1995 season; 10 adult females and no males were resighted.

Seals were distributed much as described by Stirling (1972). In November and December, non-parturient adult females and subadults were found in the southern or northern ends of the crack system on the NW side of White Island, whereas females with pups occupied its center (Fig. 1). Open water was found in the larger cracks that formed in summer at the northern end and the center of the crack system, but juveniles still tended to occupy edges of the distribution of seals at the island.

Population size.—With few individuals in a population, mark-recapture estimates can behave erratically, and it is difficult to conduct valid goodness-of-fit tests for heterogeneity in sighting probabilities (Pollock et al., 1990). Nevertheless, estimates of

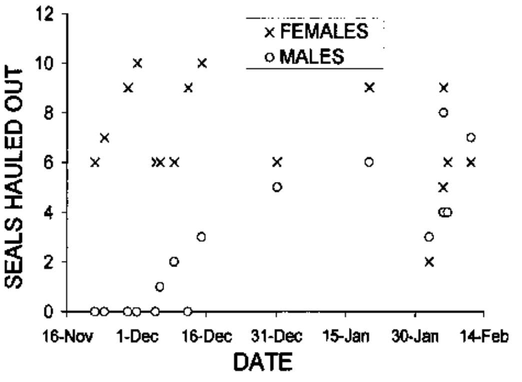

FIG. 2.—Seasonal progression of numbers of adult Weddell seals hauled out at White Island from 1990–1991 to 1994–1995. Parturition and breeding took place in November and December; molting occurred in January and February.

population size for both sexes were similar to numbers of individual seals determined by enumeration, although standard errors for the mark-recapture estimates were incalculable in some cases (Table 1). Differences in probabilities of sighting exist between females with pups and those without pups in November–December, and possibly among males (Bartsh et al., 1992; Testa and Siniff, 1987). Pooling sightings from several occasions within years provided high probabilities of sighting for females but had somewhat less effect on sightability of males, which was lower in any one visit than for females (Fig. 2). Heterogeneity in probabilities of sighting causes underestimation of population size due to individuals that habitually avoid the ice surface and escape detection. However, such biases would have equal or greater effect on the enumeration estimates (Pollock et al., 1990). The appearance of only two new males in 1993–1994 and no new adult females after the third field season (Table 1) suggests that all females had been tagged and only a small number of males, if any, escaped detection during the study.

Aerial survey on 6 February 1991 detected 18 seals hauled out along the crack at White Island. The aerial survey on 30 November 1991 detected nine seals (six adults and three pups). Both counts are similar to counts made during censuses on the surface at the same time of year (Fig. 2), except that censuses on the surface in late 1991 detected three dead pups that were not visible from the air.

No seals were sighted at White Island that had been tagged at the nearest coastal population of Weddell seals (Erebus Bay), where close to one-half of the adult seals and virtually all pups were tagged. Also, no seals from White Island have ever been seen in Erebus Bay, where intensive censuses were conducted (Testa and Siniff, 1987). This is consistent with Stirling's (1972) contention that the population at White Island is isolated from the coastal population of Weddell seals.

Adult survival.—Because effort and seasonal timing of censuses varied among years, we tested the improvement in fit of the general Jolly-Seber model over the simpler model of constant survival using the likelihood ratio test (Lebreton et al., 1992). The general model did not significantly improve a constant survival model for either males (deviance = 3.22, $d.f. = 3$, $P = 0.36$) or females (deviance = 5.46, $d.f. = 3$, $P = 0.14$). Annual survival was 0.925 ± 0.039 (*SE*) for females and 0.947 ± 0.045 (*SE*) for males.

Natality and survival of juveniles.—We assumed that females observed at any time with a pup or that exceeded 220 cm in length (Hill, 1987) were adult in 1990–1991, and that two adult females that disappeared after 1992–1993 died in that year. There were 12 adult females in 1991–1992 and 1992–1993, and 10 in 1993–1994 and 1994–1995. Of the 12 females that appeared to be adult at the start of the study and survived at least 1 season, only seven were observed with pups or lactating at some time during the study. Twenty-one pups were born in the 4 years, but only 17 parturient females could be identified in those same years. The pups born represented a 48% average annual pupping rate for 44 adult female seal-years observed. Six

TABLE 2.—*Length (cm), girth (cm) and girth : length ratio as an index to condition* (SE) *of adult Weddell seals from White Island* (n = *21) and Erebus Bay* (n = *311), Antarctica.* P-*values are shown for* t-*tests with 330* d.f.

Measurement	White Island	Erebus Bay	*t*	*P*
Length	231.9 (5.3)	217.3 (1.1)	3.24	0.00
Girth	184.8 (3.5)	175.8 (1.0)	2.25	0.03
Girth : length	0.80 (0.01)	0.81 (0.03)	0.84	0.40

pups (29%) died before weaning, a significantly higher mortality rate than observed at Erebus Bay in a typical year (e.g., in 1993, 24 of 450 pups were found dead, $\chi^2 = 13.36$, *d.f.* = 1, $P < 0.001$). At least three of the dead pups at White Island were stillbirths, and two of these had congenital deformities. One pup died at 4 weeks of age of pneumonia (J. E. Blake, DVM, University of Alaska Fairbanks, pers. comm.). Three of the 16 born prior to 1994–1995 (19%) survived at least 1 year.

Physical condition.—After testing for differences by gender in length, girth and girth : length ($t < 1.43$, *d.f.* = 330, $P > 0.15$), sexes were pooled. Both length and girth of adult seals were significantly larger at White Island than at Erebus Bay (Table 2). However, seals at White Island and Erebus Bay had nearly the same ratio of girth : length, or the "fatness index" used by Stirling (1972). Seals measured at White Island in the 1960s (index = 0.976 ± 0.045 *SE*) were significantly fatter by this index ($t = 6.88$, *d.f.* = 24, $P < 0.001$) than those we measured (index = 0.799 ± 0.040 *SE*).

Timing of births at White Island was not conclusively determined, but pups at White Island appeared ca. 3 weeks younger (by stage of molt) than those in Erebus Bay when the former was visited in late November-early December. Three pups weighed at White Island in mid- to late December appeared close to weaning and weighed 144 kg, 172 kg and ≥145 kg (an aggressive mother and resistance by the third pup made a more accurate weight impossible). By comparison, only three of 110 pups weighed near weaning in Erebus Bay in 1993 exceeded 143 kg and the maximum was 159 kg ($P < 0.001$).

Five (17%) of the seals >1 year at White Island showed evidence of eye trauma, an uncommon injury in Erebus Bay (J. W. Testa, in litt.). Three of those were instances of a clouded eye, one seal had a cut eyelid, and another's eye was inflamed and nearly closed. Breathing holes at White Island are heavily congested with crystalline platelet ice (Kooyman, 1981) that could cause these injuries. Cuts too small and precise to be caused by seal bites, were observed on the rear flippers of some seals and also could have been caused by platelet ice. Males occasionally showed bite marks on the flippers or around the penal orifice, but were much less scarred from fighting than males at Erebus Bay where such wounds are common (Bartsh et al., 1992; Stirling, 1969, 1971).

DISCUSSION

Stirling (1972) reported that the population of Weddell seals at White Island appeared stable at about nine adults in the 1960s, based on the similarity of two aerial surveys in 1960–1961 and 1967–1968 (Table 3). Our results, however, show that the population has grown to 26 seals in 27 years ($\lambda = 1.04$), with a similar increase in pups born per year (Table 3). Timing and frequency of I. Stirling's visits and absence of untagged seals in the last 2 years of that study were similar to our own efforts and results. That growth occurred between 1969 and 1979 also was confirmed by M. A. Castellini (pers. comm.), who found ≥14 adult seals at White Island in 1979–1981 (Table

TABLE 3.—*Comparison of numbers of Weddell seals reported at White Island from 1958 to 1995.*

Source	Year	Aerial survey	Adults counted	Pups counted
Deverall (1961)	1958–1959	11		
Stirling (1972)	1964–1969	11	9	2–3
Castellini (1992, pers. comm.)	1979–1981		≥14	3–5
This study	1991–1995	18	26	4–6

3). There was no account of this population in naturalist's reports of British expeditions in the area in 1901, 1910, or 1916 (Richards, 1962; Wilson, 1907, 1972), although it is not clear from those accounts if White Island was visited.

Stirling (1972) estimated a minimum survival rate of 0.87 for adults and 0.27 for pups at White Island. These are comparable to the rates of survival reported here (0.95 and 0.925 for adult males and females and 0.19 for pups surviving 1 year). Survival of adults at nearby Erebus Bay is lower (0.85 for females and 0.76 for males—Testa and Siniff, 1987), and reproductive rates are higher (0.55–0.75—Testa, 1987*b*) than at White Island. Although both Stirling (1972) and M. A. Castellini (pers. comm.) found a high proportion of pups dying at White Island, sample sizes were insufficient to characterize pup mortality with precision. In our study, preweaning mortality of pups at White Island (0.29) was unusually high compared with pups at Erebus Bay, where it was near 0.05 and has never exceeded 0.1 when determined by direct counts of dead pups (Schreer et al., 1997; Stirling, 1971; Thomas and DeMaster, 1983). The presence of pups with congenital deformities during our study suggests that inbreeding could be a factor in low production and survival of pups at White Island.

At present, body size of adult seals and weights of pups at weaning are significantly larger at White Island than at Erebus Bay. Because adults increase in length with age (Hill, 1987), high survival of adults and the resulting skew in age distribution at White Island may contribute to the difference in body size between these populations. Also, because the animals are long-lived, adults alive during this study may have been born when growth rates were more similar to those reported by Stirling (1972). Although the adult seals at White Island are larger in total body size, body condition (as indexed by girth:length) declined since the 1960s, in conjunction with increased density of seals. Prey of Weddell seals at White Island are primarily midwater fish and cephalopods (Castellini et al., 1992), which must be advected under the Ross Ice Shelf to seals confined to the White Island crack system. Increased competition for available food would be expected in this confined habitat with increased numbers of seals. However, rapid pre-weaning growth of pups and similarity in body condition of adult seals from White Island and Erebus Bay suggest that food is not yet limiting for adults.

Stirling (1972) suggested that access to breathing holes in winter at White Island was limiting colony size. Thickness of the ice at White Island is much greater than at Erebus Bay where annually formed ice of ca. 2 m in thickness predominates (Castellini et al., 1992). Open water, apart from a few cracks in mid-summer, rarely is seen at White Island, and access holes are small even in February (Kooyman, 1981). Holes often were filled with platelet or brash ice (M. A. Castellini, pers. comm.; J. W. Testa, in litt.). Pups were observed lying on top of crystalline-platelet ice that fills such holes, whereas adult seals would burrow through it to reach the water. Limited access to breathing and exit holes may reduce survival of pups.

Around Erebus Bay, subadults commonly segregate from adult seals and live closer to the edge of the shore-fast ice (Stirling, 1969; J. W. Testa, in litt.). Such segregation exposes immature seals to greater risk of predation by killer whales (*Orcinus orca*) and leopard seals (*Hydrurga leptonyx*) but also reduces their competition with the more efficiently diving adults (Burns and Testa, 1997). At White Island, adults and subadults can only segregate along the single tidal crack. Interactions and competition between the age classes at White Island are, therefore, likely to be more intense, whereas danger from large predators is non-existent.

Stirling (1972) reviewed several accounts of apparently isolated populations of Weddell seals around the Ross Sea. Such isolated subpopulations of this widely distributed pinniped may represent an important evolutionary phenomenon. The present distribution of phocid seals is concentrated at high latitudes and Antarctic phocids are among the most highly specialized (De Muizon and Hendey, 1980). Yet, the paleobiogeography of phocid seals is constrained by the availability of fossils, which are known predominantly from temperate regions (De Muizon, 1982). The radiation of the Antarctic lobodontine tribe into four extant species probably occurred at high latitude (Arnason and Widegren, 1986; Hendey, 1972) well after the isolation of Antarctica by the Antarctic circumpolar current (DeMuizon and Hendey, 1980; Fordyce, 1989). There have been virtually no geographic barriers to seals surrounding Antarctica since the Oligocene (25×10^6 years ago) except for possible oceanographic barriers such as ice. It is possible that the dynamic nature of glacial and sea ice and opportunities for isolation of small populations, like that at White Island, were important in the radiation of polar pinnipeds.

Size of the seal population at White Island is similar to that suggested for northern elephant seals (*Mirounga angustirostrus*) at the most severe level of a population bottleneck that occurred around 1884 (Hoelzel et al., 1993). Hoelzel et al.'s (1993) models were based on levels of genetic variation remaining at present and likely scenarios of population depletion and recovery. At present, total genetic variation among adult Weddell seals at White Island is comparable to that at Erebus Bay (E. A. Perry et al., in litt.). Long-term monitoring of the Weddell seals at White Island may provide a test of models predicting the rate of loss of genetic diversity at low population size. Similarly, viability of this population will be tested by its long-term persistence.

At present, it appears that the White Island population is geographically isolated, with close ca. 26 seals older than pups. The population has almost tripled in size since the mid 1960s while adult body condition has declined. The population exhibits higher adult survival, a lower reproductive rate, later parturition dates, and higher mortality of pups than the open population at nearby Erebus Bay. Presence of congenitally deformed pups, and low production and high mortality of pups suggest that inbreeding occurs. Further study of the seals at White Island may provide insights about the long-term viability and loss of genetic diversity in small populations, and into the radiation of ice-inhabiting seals. White Island's protected status, which is based on the scientific value of its seal population, will be ensured under a new Protocol on Environmental Protection under the Antarctic Treaty (1991) and associated management plans.

Acknowledgments

This work was supported by grants DPP-8816567 to J. W. Testa and OPP-9119885 to J. W. Testa and M. A. Castellini from the National Science Foundation. We are grateful to the United States Antarctic Program for all aspects of logistic support in Antarctica, and to A. R. Ajmi, J. M. Burns, M. A. Castellini, B. Fadely, J. Fadely, T. Gellatt, K. K. Hastings, S. K. Lewis, D. Munson, L. Rea, J. F. Schreer, P. D. Shaughnessy, D. B. Siniff, and K. Turco for their assistance in the field. J. Berger, I. Stirling and two anonymous reviewers commented on drafts of the manuscript.

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Submitted 20 October 1997. Accepted 17 April 1998.

Associate Editor was Edward J. Heske.