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Three—

History and Present Status of Southern Elephant Seal Populations

Richard M. Laws

ABSTRACT. The total world population of southern elephant seals in 1990 was estimated at 664,000. Of the three (or four) main stocks, South Georgia and Peninsula Valdes account for 60% of the total; Isles Kerguelen, 28%; and Macquarie Island, 12%. The species was hunted for its oil in the eighteenth and nineteenth centuries and subsequently recovered under protection. The only large-scale industry this century was a government-licensed one at South Georgia, from 1909 to 1964, which was restricted to adult males. The history and rational basis for this industry is described here, including some effects of sealing, population decline from 1931 to 1951, and subsequent recovery to sustained yield level under a research-based management plan. Pup production was estimated, population models were drawn up, and the size of the South Georgia population in 1951 was calculated. A comprehensive survey in the 1985 breeding season indicated the same annual pup production as for 1951 and a population of 357,000 in 1990. Population models indicate that some 75% of the adult male population is at sea during the breeding season, which has implications for aquatic mating of virgin females and nonpregnant mature females.

A literature review of other stocks examines various estimates of pup production by site and years between 1949 and 1990 and converts these by a raising factor to estimates of total population sizes by years. During this period, different stocks of southern elephant seals have increased (Península Valdes, Argentina, by 144% since 1975); have probably remained stable after rapid recovery from exploitation (South Georgia, 15% due to postexploitation recovery of the male stock); or have decreased dramatically at annual rates varying between 2.1% and 8% at different places and periods. Total percentage decreases since 1949 are estimated at 50% for Heard Island, 84% for Marion Island, 57% for Macquarie Island, 96% for Campbell Island, and 93% for Signy Island.

This chapter sets the scene for the more detailed discussions presented by those studying key colonies. Those discussions deal with the factors responsible for changes in population number and advance hypotheses to account for the precipitous decline of certain populations.

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[Full Size]

Fig. 3.1

Breeding distribution of southern elephant seals in 1990. Closed circles: known

breeding colonies (area proportional to the estimated population sizes except for

colonies of less than 5,000). Open circles: probable small breeding

populations. Fuller data are presented in table 3.1.

In terms of numbers, the southern elephant seal, M. leonina , is one of the more abundant seal species in the world. There are three main stocks, defined (Laws 1960) as the South Georgia stock, the Kerguelen stock, and the Macquarie Island stock (fig. 3.1). The first is the largest numerically and includes elephant seal breeding colonies in the Scotia arc (South Georgia, South Orkney Islands, South Shetland Islands, South Sandwich Islands) and Gough and Bouvet islands, together with South America and

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the Falkland Islands. Although more recent information indicates movements between South American and Falkland Islands elephant seal colonies (Laws, unpubl.), up to now no movements have been reported between them and the remaining colonies; so there may be four stocks. The second stock includes Kerguelen and Heard islands, Marion and Prince Edward islands, and Iles Crozets. Single births have been recorded at Amsterdam and St. Paul islands and South Africa (Laws 1960). Finally, the Macquarie Island Stock includes Macquarie Island, Campbell Island, Auckland Islands, and Antipodes Islands, and one birth has been reported from Tasmania (Laws 1960). A very small number of births have also been reported from the Antarctic continent (Murray 1981). The centers of the three main stocks are roughly 90° and 107° longitude apart, except in the Pacific Ocean sector (163°), which is devoid of suitable islands in the right latitudes and supports no breeding colonies. Genetic studies by N. J. Gales, M. Adams, and H. R. Burton (1989) reported on elephant seal blood samples from Heard and Macquarie islands that were examined for protein variation. They concluded that the two populations "may have diverged genetically, and a very limited gene flow exists between the islands, a finding consistent with limited information from mark-recapture studies" (57). It is likely that a similar division exists between them and the South Georgia stock.

The sealers of the eighteenth and nineteenth centuries came first to hunt the more valuable fur seals for their pelts but did not ignore the larger species, which was hunted for its oil. The right whalers in southern waters also took elephant seals. As fur seals declined, the sealers concentrated more on elephant seals (Bonner 1982; Headland 1989). In his chronological list of Antarctic expeditions, R. Headland (1989) analyzed 930 voyages to the Antarctic between 1786 and 1928, the majority by U.S. (46.4%) and British (19.1%) ships, and showed the frequency of sealing voyages by year. There were progressively lower peaks, separated by periods of partial recovery, about 1820, 1842, 1855, 1875, and 1906. The early voyages primarily took fur seals, which were hunted almost to extinction; the objective of the later voyages was primarily the elephant seal. It is not known how many elephant seals were taken during this period, but it was probably in excess of one million of both sexes, assuming that the original populations totaled at least 600,000 to 750,000, as in this century (Laws 1960; McCann 1985). The sealing industry had virtually ended by 1909, and protection was subsequently conferred on most stocks, which recovered from the overhunting.

The only large-scale elephant sealing during this century was the government-licensed industry at South Georgia between 1909 and 1964 (see Laws 1953a , 1960; Bonner 1958; and Headland 1984), although small numbers were taken in other places, particularly Kerguelen, where 12,000 bulls were taken between 1958 and 1964 (van Aarde 1980). Over the course of sixty-five years, some 260,000 elephant seals, predominantly adult males, were taken at South Georgia (Headland 1984). The industry came to an

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end in 1964 as a result of the collapse of the whaling industry at South Georgia; the sealing industry was on a firm sustainable yield basis. As will be shown, the size of the South Georgia elephant seal population in 1951, when government-controlled sealing was at its height, was similar to the size of the population in 1985, some twenty years after sealing had ended. However, the populations in the Kerguelen and Macquarie islands stocks declined steadily over forty years from 1950, even in the absence of sealing. It seems that the elephant seal population in Argentina has been increasing in recent years.

Below I describe the recent history of twentieth-century sealing at South Georgia, because of its relevance to estimating abundance and trends, and what is known about population sizes this century in the three (or four) main stocks, which are considered separately. Estimates, updated to 1990, are given for the total world population of the species.

South Georgia Stock

The Sealing Industry, 1910–1964

The biological basis underpinning rational exploitation of this species is its highly polygynous land-breeding behavior. The sexes are nearly equal in numbers at birth, and a single adult male can serve a large number of cows. In fact, the overwhelming majority of matings are carried out by a very small minority of breeding bulls; according to M. N. Bester and I. S. Wilkinson (this volume), "dominant bulls controlling the harems achieved over 98% of all matings." A large surplus of males can therefore be taken from the beaches without affecting recruitment to the population. Polygyny has resulted in the socially mature male being on average about eight times the weight of the average breeding female (Laws 1984). As the sealing industry sought oil from the blubber, it was most convenient to take the bulls in the earlier part of the breeding season in the spring, when the oil yield is greatest. Because the larger males haul out first on the beaches, the sealers automatically selected the largest animals. Oil yields from autumn sealing are lower, and this practice was discontinued in the 1950s.

To prevent recurrence of the former indiscriminate slaughter, the Falklands Islands government introduced the Seal Fishery Ordinance in 1899 (improved by further ordinances in 1904, 1909, and 1921), with the intention of placing the industry on a rational basis. The coastline of South Georgia was divided into four sealing divisions (and four reserves where no seals were taken). The divisions were generally worked in rotation, each year one of them being closed to sealing. Licenses to take a stipulated number of adult male elephant seals were issued annually to the sealing company. The first license was issued in 1909 to the oldest established whaling company at South Georgia, which held a monopoly until the 1961–1962

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season. There was no sealing in 1962–1963, and licenses were issued to a Japanese company for the last two seasons, 1963–1964 and 1964–1965. With the cessation of autumn sealing in the 1950s, sealing began early in September and ended about mid-November. The sealing methods are described in detail by me (Laws 1953a ) and by Bonner (1958). Although attempts were made to utilize carcasses, this was found to be uneconomical and the sole product of the industry continued to be blubber oil.

For many years, the annual quota under license was fixed at 6,000. But in 1948, it was raised to 7,500; in 1949 and 1950, to 9,000; and in 1951, was set at 8,000. Until 1952, the quota was divided equally among the three divisions worked each year, although seal abundances in the four divisions have probably always been unequal. The sealing regulations were altered in 1952 as a result of recommendations made by me (Laws 1960).

Effects of Sealing

Previously, I have presented a variety of evidence that indicated that from the late 1930s onward there were adverse changes in the population, despite the conservation measures in force (Laws 1960). Most significant, it was shown that the average catch of seals per catcher's day's work (CDW) in October had progressively declined by 28% from 1931 to 1951. Over these two decades, there had also been a decline in the oil yield per seal and a lengthening of the season, trends that had begun well before the higher catches in 1948–1951. Consideration of the sex ratios on the breeding beaches, harem sizes (on exploited beaches and in a reserve), and the low average age of males on the breeding beaches supported the indications that the demonstrated decline in the catch per unit effort represented a real decrease in the size of the adult male component of the population.

In Laws 1960, I reported counts of seals on beaches in Divisions I–III and one count in Division IV. These counts were corrected for date and for pup mortality, based on my research, and I concluded that approximately 20,000 pups were born in Division I and 15,000 in Division II. Supplementary information was obtained from the sealers which indicated that seals were much more abundant in Divisions III and IV, and I assumed that 32,500 pups were born in each of these divisions, making an estimated total of approximately 100,000 pups that survived to weaning. Assessing pup mortality from birth to weaning at 2% gave a figure of about 102,000 pups at birth.

I constructed population models to assess the size of the total population in each division, based on my demographic research, on the size of the commercial catches in previous years, and on the age composition of the commercial kill of males in 1951, based on growth layers in the teeth (Laws 1952, 1953b ). Some assumptions were made, and predictions about certain future statistics were advanced, the confirmation of which later appeared to support the assumptions. The results of these calculations were estimates of

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the size of the population in each division and of the annual accessions to each age class (see Laws 1960 for details). Other information on breeding behavior suggested that the stock of breeding bulls in each division should be kept equal to one-twelfth of the stock of adult cows, and on this basis surplus accessions of bulls for all divisions combined were calculated at 5,842, close to the average annual catch. But the catches in Divisions I and II for this period were, respectively, about 24% and 65% higher than the estimated surpluses for those divisions, whereas the catches in Divisions III and IV were well below.

Therefore, a new system was introduced in 1952 to control sealing. Most important, divisional quotas were set for the five years 1952–1956, proportional to the estimated size of the available surplus in each division. A safeguard was introduced to monitor the age composition of the catch, by requiring canine teeth to be collected from a 5% sample of the catch which would subsequently be examined to determine age structure of the catch. A minimum length regulation was introduced.

Favorable results were immediately apparent, with a rise in the catch per CDW of 26% over the first 4-year period. In general, sealing operations were conducted earlier (midseason date two weeks earlier) and the average oil yield increased substantially. About 300 teeth were collected annually between 1952 and 1964 for age determination, and W. N. Bonner made control collections from a total of over 400 seals caught. The mean age of the catch sample in 1951 was 6.64 ± 0.34 (SE) years; in 1952, it was 7.20 ± 0.14; and it increased to level off at about 7.71 ± 0.19, 7.70 ± 0.18, and 7.69 ± 0.15 years in 1961, 1963, and 1964, respectively (Laws 1979). This leveling off confirmed that the catch size was sustainable; it corresponds to the estimated average age on attaining social maturity, and the management strategy was to monitor the age distribution of the catch and to adjust annual quotas, as necessary, so as to keep the average age of the catch at 7½ to 8 years. The success of this policy gave confidence in the general accuracy of the estimates of population abundance and life table parameters (see below).

Population Size in 1951

In formulating my recommendations, I had constructed provisional life tables for the two sexes. These life tables adjusted for 102,000 births annually indicated an average midyear population of about 310,000 elephant seals at South Georgia in 1951, that is, about 3.1 times the number of births (see Laws 1960 for details). I reviewed available information on other breeding colonies of the overall South Georgia stock and concluded that its total size was a little more than 315,100.

McCann (1985) revised the life tables, assuming higher female fecundity (88% vs. 82.5%). He found no change in the number of pups born in Cumberland Bay, no evidence for an increase or decrease in the cow

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population, and no significant change in the age at first pupping since 1964. He concluded that "a suitable factor by which to convert pup counts to total population of all animals older than pups of the year at the end of the breeding season is 3.5" (14). McCann (1980) also found no difference in body size in 1976–1977 compared to 1948–1951. He reported a three- to fourfold increase since exploitation ended in numbers of bulls ashore, an increase in the mean age of harem bulls, and increased average harem size; he also found that bulls hauled out earlier in the season and stayed ashore longer. There was little change in the number of breeding cows or their age structure. (Comparisons were with results in my papers, based on fieldwork in 1948–1951, listed in Laws 1960.) McCann (1985) concluded that the South Georgia population in 1980 was 350,000 (actually, it should have been 357,000 if calculated from births × 3.5).

McCann's estimate was derived from the 1951 estimate of pups born and his life tables for an unexploited population. In 1951, however, at the height of the sealing period, even assuming a similar pup production, the total population should have been somewhat lower, because the numbers of adult males were reduced in the exploited population. Comparison of Laws (1960) and McCann (1985) shows that the female life tables are really quite similar (perhaps not surprising as McCann adopted some important parameters from me, especially first- and second-year survival); the male life tables differ only in the higher first- and second-year mortality assumed by me and in the reduced survival of older males in the exploited population.

I have therefore recalculated the exploited male life table, by raising the first-year survival to the female level, as McCann did; this gives almost identical survival rates for the two models up to 6 years. Above 6 years the selective removal of older males reduced the adult male population, so that in the exploited 1951 population model there was virtually no survival beyond age 12, compared with age 20 in McCann's (1985) life table. I have calculated the number of adult males estimated by the two models, assuming 54,000 male pups at birth in both exploitation and postexploitation models; McCann reported a sex ratio of 53% males at birth. For the 1951 model there were 17,280 males aged 7 to 12 years (none were older), and for 1985 there were an estimated 36,000 aged 7 to 20 years (the upper limit). The difference is nearly 19,000, suggesting that the 1951 total South Georgia population size was actually about 338,000 (357,000 – 19,000). Sealing ended in 1964, so the recovery in adult male numbers should have been virtually complete by 1970 as full cohorts successively acceded to the adult male population.

Population Size in 1985

The elephant seal population of South Georgia was surveyed comprehensively during the 1985 breeding season (McCann and Rothery 1988). There were 87,711 females and 10,260 adult males counted on shore, and the

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female counts were corrected using a model of haul-out distribution over time to adjust for the date of count. The annual pup production was estimated to be about 102,000, the same as the estimate in Laws (1960). I actually counted 26,260 live pups in Divisions I and II and gave an estimate for pup production, corrected for date of count, of 31,075; I rounded up this estimate to 35,000, to allow for the beaches I did not visit. This can be compared with T. S. McCann and P. Rothery's (1988) corrected total of 34,665 in these two divisions, which is very close. McCann and Rothery obtained corrected pup counts of 42,892 and 24,676 for Divisions III and IV, respectively, and suggested that as the numbers in Divisions I and II were approximately the same in 1985 as in 1951, the same should be true of the totals in Divisions III and IV. Thus, there is a good basis for assuming that the number of pups was indeed about 102,000 in both periods, and applying the factor 3.5 gives a population other than pups of 357,000 in 1985. (A possible but small source of error lies in the adoption of my 1960 estimate of pup mortality (2%); e.g., Condy [1978] estimated preweaning mortality at 6%.)

Thus, the total pup production at South Georgia was very similar in two estimates 34 years apart. This suggests that the South Georgia population may have been almost stable since 1951, apart from an increase in adult males after sealing ended in 1964. However, McCann and Rothery (1988) show that substantial annual fluctuations occurred in the number of cows ashore on certain beaches, and their data suggest a possible decline in the 1960s. It seems likely therefore that over the last 40 years, the South Georgia population size has fluctuated around 350,000.

The 1985 count and model presented above indicate that of some 36,000 adult males (aged 7 to 20 years) estimated to be in the South Georgia population, only some 10,000 were counted on land at any one time during the breeding season, and about 26,000 were therefore in the sea, since they have not been seen elsewhere on land. This is relevant to hypotheses about the mating of the virgin females; they are very rarely seen on the breeding beaches in the breeding season, yet the 1985 model (McCann 1985) indicates that some 21,000 virgin females (equivalent to about a sixth of all mature females) mate for the first time at age 3. I observed aquatic matings and believed that newly mature females mate for the first time not on land but in the sea, probably during the usual breeding season of the adult cows (Laws 1956). (With 88% fecundity, the model also indicates that 12% of all adult females—an estimated 14,000—would be nonpregnant in the pupping season and probably also would mate aquatically). Behavior during the aquatic phase of the life cycle may have implications for the causes of the decline in other southern elephant seal populations (SCAR 1991; Bester and Wilkinson, this volume; Hindell, Slip, and Burton, this volume; Fedak et al., this volume).

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Other Populations in the South Georgia Stock

Patagonia and the Falkland Islands

I estimated less than 1,000 pups born in the Falkland Islands, representing a population of less than 3,500 (Laws 1960); there is no recent information. For Patagonia, at Península Valdes, I. S. Carrara (1952) estimated a population of approximately 1,000 in 1951; J. A. Scolaro (1976) estimated 3,933 pups born in 1975, implying a population of 13,800 (3.5 × births); D. F. Vergani, M. N. Lewis, and Z. B. Stranganelli (1987) estimated 6,737 pups born there in 1982 (pop. 23,579), increasing at 5.1% annually between 1975 and 1982. C. Campagna and M. Lewis (1992) give the results of eight surveys from 1969 to 1990, corrected for date and area surveyed, concluding that 7,455 pups were born in 1982 (pop. 25,092) and 9,636 pups were born in 1990 (pop. 33,726), having increased at 3.2% annually since 1982.

South Orkney Islands

I estimated the size of the breeding population I studied at Signy Island to be 300 in 1948–1950 (Laws 1960). Subsequently, this has decreased to less than 20 (unpublished British Antarctic Survey records).

King George Island

Vergani (pers. comm.) reported 708 pups born in 1980, declining to 560 by 1990, which represents total populations of approximately 2,500 and 2,000.

Nelson Island

Vergani, Lewis, and Stranganelli (1987) reported 106 pups born in 1985, representing a population of approximately 370.

Avian Island

One birth has been reported from Avian Island (68° S.) (unpublished British Antarctic Survey record).

Gough Island

Bester (1980; pers. comm.) reported 32 pups born in 1977 and 28 in 1990, suggesting a stable population of about 105.

South Sandwich Islands and Bouvet Island

The species probably breeds in small numbers on these islands, but there is no information.

These populations represent a total of about 39,720 in 1990, about 10% of the total South Georgia stock in 1990, which is estimated at about 397,000 compared with McCann's (1985) estimate of some 369,000 based on counts spread over earlier years (table 3.1). The difference is due to a real increase in the Península Valdes population and the upward revision of the earlier South Georgia estimate to allow for the recovery of the adult male stock as disc**ussed above.**