Variability in a crabeater seal population and the marine ecosystem near the Antarctic Peninsula
by Peter Laurens Boveng

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University

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A population of crabeater seals, Lobodon carcinophagus, inhabiting the sea ice and waters surrounding the Antarctic Peninsula was studied to clarify the nature of variability in the population age structure. Understanding this variability is important for efforts to identify effects of climate change and marine resource exploitation in the Southern Ocean. Previous studies of this variability — fluctuations in strengths of annual cohorts — have termed it periodic and investigated its relationship to variability in other species of Antarctic seals. In the present study, the more fundamental question is first addressed, of whether the variability is a genuine demographic phenomenon or an artifact of sampling or analysis. Then the evidence is examined for support of an interpretation of periodicity. Because age-estimation errors are known to reduce variability in estimates of cohort strength, and because crabeater seal ages are subject to estimation errors, the effects of those errors are evaluated. Features of the crabeater seal natural history were used to generate hypotheses about expected correlations between the cohort strengths and sea ice extent, surface air temperature, the Southern Oscillation, and an index of leopard seal (Hydrurga leptonyx) populations.

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It was concluded that because the crabeater seal cohort fluctuations seem to represent a genuine demographic phenomenon and because these catch-at-age data are unique among the ice breeding Antarctic seals (top marine predators) further study is warranted, perhaps focusing on shorter time scales and refinements to the data on potential environmental and ecological cause of cohort variability.

VARIABILITY IN A CRABEATER SEAL POPULATION AND THE MARINE ECOSYSTEM NEAR THE ANTARCTIC PENINSULA

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Montana State University
1993

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APPROVAL

of a thesis submitted by

Peter Laurens Boveng

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

7/26/93
Date

Chairperson, Graduate Committee

Approved for the Major Department

7/24/93
Date

Head, Major Department

Approved for the College of Graduate Studies

8/1/93
Date

R L Brown
Graduate Dean

STATEMENT OF PERMISSION TO USE

Signature Peter L Boveng

Date 23 JULY 1993

Dedicated to my ever-inspiring grandmother,
M. Helene Boveng.

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A population of crabeater seals, *Lobodon carcinophagus*, inhabiting the sea ice and waters surrounding the Antarctic Peninsula was studied to clarify the nature of variability in the population age structure. Understanding this variability is important for efforts to identify effects of climate change and marine resource exploitation in the Southern Ocean. Previous studies of this variability — fluctuations in strengths of annual cohorts — have termed it periodic and investigated its relationship to variability in other species of Antarctic seals. In the present study, the more fundamental question is first addressed, of whether the variability is a genuine demographic phenomenon or an artifact of sampling or analysis. Then the evidence is examined for support of an interpretation of periodicity. Because age-estimation errors are known to reduce variability in estimates of cohort strength, and because crabeater seal ages are subject to estimation errors, the effects of those errors are evaluated. Features of the crabeater seal natural history were used to generate hypotheses about expected correlations between the cohort strengths and sea ice extent, surface air temperature, the Southern Oscillation, and an index of leopard seal (*Hydrurga leptonyx*) populations.

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CHAPTER 1

INTRODUCTION TO CRABEATER SEALS AND THEIR HABITAT

This dissertation is about annual variability in a population of crabeater seals (*Lobodon carcinophagus*) inhabiting the waters surrounding the Antarctic Peninsula. Biological and environmental data are examined to determine how the seal population, other components of the ecosystem, and the physical environment varied during the past four decades. In this chapter, I present the rationale for undertaking this research, an introduction to the biology of crabeater seals, a description of the study area, and a brief overview of the remaining chapters followed by a summary of the principal hypotheses that guided the research.

Rationale for the Research

During the past two decades of research in Southern Ocean ecology, variability has increasingly been recognized as a characteristic feature of the Antarctic marine ecosystem. It is now widely acknowledged that understanding this variability, encompassing broad ranges of temporal and spatial scale, is crucial to such endeavors as detecting impacts of climate change and managing Southern Ocean resources. Indeed, a recent symposium volume (Kerry and Hempel 1990) was organized around the theme of "short- and long-term changes in Antarctic ecosystem and community structure caused by natural and human factors" and two-thirds of its papers pertained to the marine ecosystem. Another symposium volume (Sahrhage 1988) was dedicated entirely to the theme of variability in Antarctic ocean resources.

One of the resources upon which much attention is presently focused (e.g., Nicol and de la Mare 1993) is the enormous stock of Antarctic krill (*Euphausia superba*), a shrimp-like crustacean that supports many of the marine mammal and seabird species of the Southern Ocean. Following the 20th-century depletion of the populations of large krill-consuming whales, krill have become the subject of debate and speculation over whether recent changes in seal and seabird populations have resulted from the removal of whales or from unrelated environmental and ecological factors (e.g., Fraser *et al.* 1992; Croxall 1992). The most actively studied species in those efforts are Antarctic fur seals (*Arctocephalus gazella*), several species of penguins (*Pygoscelis* sp.), and some albatrosses (*Diomedea* sp.). Crabeater seals, on the other hand, have scarcely been studied from the standpoint of their population responses to ecological variability (but see Bengtson and Laws 1985; Testa 1990; Testa *et al.* 1991). A unique and specialized trophic position, a strong association with sea ice, a role as a major prey of leopard seals (*Hydrurga leptonyx*), and a large population size make crabeater seals a potentially fruitful and informative species in this regard. It was with these concepts in mind that I undertook this dissertation research, with the aim of contributing to the understanding of what regulates crabeater seal populations.

Crabeater Seal Biology

The crabeater seal (*Lobodon carcinophagus*) is one of the most numerous large mammals in the world, probably numbering at least 7 million (Erickson and Hanson 1990). The species has a circumpolar distribution in the Southern ocean and is almost always found in Antarctic pack ice and near the ice edge (Øritsland 1970; Siniff *et al.* 1970; Erickson *et al.* 1971; Gilbert and Erickson 1977; Erickson and Hanson 1990; Joiris 1991; Ribic *et al.* 1991). During the austral summer, when sea ice recedes toward the Antarctic continent, crabeater seals move south, following the retreating ice edge, and are found in highest densities in "residual pack ice regions" (Gilbert and Erickson 1977). The most prominent of these regions are the Weddell Sea to the east, and the Amundsen-Bellingshausen Sea to the west of the Antarctic Peninsula; these regions are further described in the section entitled Description of the Study Area.

The common name "crabeater" and the latin specific name *carcinophagus* are misnomers, for these seals feed almost entirely on krill (*E. superba* and *E. crystallorophias*) (Bengtson 1982; Green and Williams 1986; Lowry *et al.* 1988; Bengtson and Stewart 1992). It has been estimated that crabeater seals may consume as much as 63 million metric tons of krill per year (Laws 1977a); for comparison, the total human harvest of all marine species is approximately 97 million metric tons annually (FAO 1992).

Compared to most non-Antarctic pinniped species, relatively little is known of crabeater seal breeding and reproductive habits because they breed and bear young during October (Siniff *et al.* 1979; Shaughnessy and Kerry 1989) in the Antarctic pack ice zone, making observation difficult logistically. The sexes of crabeater seals exhibit relatively little dimorphism (though females may be slightly larger than males) and they do not form large conspicuous breeding groups typical of most pinnipeds; instead they form widely dispersed "family groups" (Siniff *et al.* 1979; Shaughnessy and Kerry 1989) consisting of a female, her pup, and an attendant male that breeds with the female after she weans the pup.

Crabeater seals have elaborately lobed teeth, presumably an adaptation to their specialized diet. The teeth exhibit a fine-structure that makes it possible to estimate the age of a seal by counting annuli in cementum or dentine (Laws 1958, 1962, 1984; Bengtson and Siniff 1981). Detailed species accounts for crabeater seals have been presented by Kooyman (1981) and Laws (1984).

Description of the Study Area

Location and Size

The Antarctic Peninsula is a geographically prominent feature of the Antarctic continent (Figure 1). It forms the boundary of the atlantic and pacific sectors of the Southern Ocean and is surrounded to the east by the Weddell Sea and to the west by the Amundsen-Bellingshausen Seas and the Bransfield Strait. All of the crabeater seal data used in this study were collected in the seasonal pack ice zone near the coast of the Antarctic Peninsula, near the South Shetland Islands, or near the South Orkney Islands. The total study area encompassed approximately 800,000 km^2.

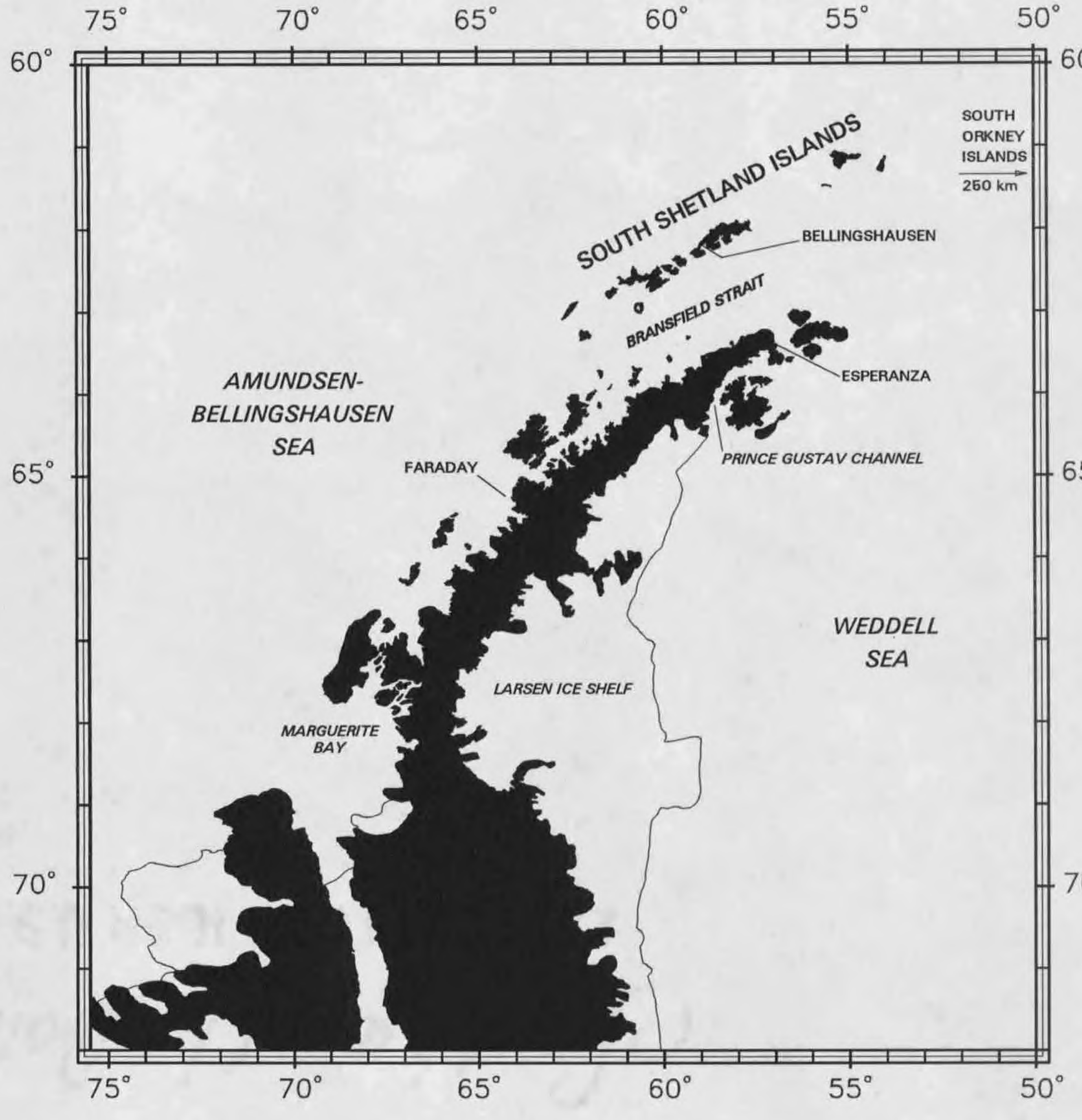

Figure 1. The Antarctic Peninsula region. Crabeater seal specimens were collected near the coast of the Peninsula between Marguerite Bay and Prince Gustav Channel, near the South Shetland Islands and near the South Orkney Islands. The straight-line distance between Marguerite Bay and Prince Gustav Channel is approximately 690 km.

Climate

The majority of the collection area described above lies between the mean January surface air isotherms of 0 °C and +2 °C and between the mean July surface air isotherms of -18 °C and -8 °C (Phillpot 1985). The entire region is subject to a semiannual oscillation in barometric pressure, with minima corresponding to the times of maximum (September/October) and minimum (February/March) sea-ice extent (Gordon 1988; Jacka and Budd 1991). A more detailed consideration of air temperature, barometric pressure, and sea ice is presented in Chapter 3.

Oceanographic Conditions

Like all the waters surrounding Antarctica, the coastal waters of the Antarctic Peninsula region are very cold; summer (January-May) near-surface temperatures are typically between -1 °C and +1 °C (Sievers and Nowlin 1988). The hydrographic structure of the region is profoundly influenced by the interaction of the Antarctic Circumpolar Current (ACC) and the bottom topography. The constriction of the Drake Passage (between South America and the Antarctic Peninsula) and the relatively shallow water to the east, plus the arrangement of the continental land masses and nearby islands combine to form consistent fronts and water masses (Sievers and Nowlin 1988). Some of these hydrographic features, such as the Weddell-Scotia Confluence are associated with locally high productivity (e.g., El-Sayed 1988) and/or recurring concentrations of krill (e.g., Nast *et al.* 1988). In addition to the influences of topography and currents, the effects of sea ice -- both in stabilizing vertical water structure near the melting ice edge and in providing substrate, nutrients and refuge for algae on the undersurface (e.g.

Smetacek and Passow 1990; Smetacek *et al.* 1990) -- may be responsible for the bulk of the primary production that supports the populations of krill used most extensively by crabeater seals. These ideas are explored more completely, especially with regard to variability of resources, in the final chapter.

Overview of Remaining Chapters

Chapter 2 is a study of interannual variability in the age structure of a crabeater seal population. A series of estimates of cohort, or year-class, strength from 1940 to 1990, with variation that has been described as periodic (Laws 1984; Bengtson and Laws 1985; Testa *et al.* 1991), is derived from updated catch-at-age data and tested to determine whether the fluctuations are genuine demographic events or artifacts of sampling or of analysis. The effects of uncertainty in age estimation are quantified. A revised series of cohort strengths is presented, which partially corrects for imprecision in the age estimates. In addition to a critical evaluation of the nature of variability in population dynamics of the seals, new estimates are presented for the crabeater seal life table, based on more data and more recent statistical techniques than previous estimates.

In Chapter 3, environmental and climatological data from the past several decades are examined and compared to elucidate the major physical features that may have influenced the ecology of the Antarctic Peninsula region. Relationships among surface air temperature, an index of the Southern Oscillation, and sea ice are described and quantified. These relationships are used to generate an hypothesis to account for interannual variability in the population of crabeater seals around the Antarctic

Peninsula.

In Chapter 4, conclusions are presented about the extent to which the observed patterns in crabeater seal age structure can be explained by the environmental data and by other ecological factors. Specifically, the ability to explain variability in cohort strength using environmental data from Chapter 3 is tested. Alternative ecological (biotic) mechanisms for the fluctuations are evaluated. The potential utility of using crabeater seal catch-at-age data as a tool for monitoring changes in the marine ecosystem is evaluated. Finally, hypotheses are proposed concerning predator-prey relationships between crabeater and leopard seals; proposals for future experiments that could be used to test those hypotheses are also presented.

Hypotheses

To summarize the preceding overview, the principal hypotheses guiding this research were:

(1) Variability in the age structure of crabeater seals sampled near the Antarctic Peninsula represents true demographic variability rather than simple variation due to chance, the sampling procedure, or the analysis;

(2) Environmental factors, such as sea ice extent and surface air temperature in the Antarctic Peninsula region, exhibit fluctuations of several years duration that are identifiable throughout the region; and

(3) Interannual variability in the age structure of crabeater seals can be explained by variability in the environment.

CHAPTER 2

COHORT VARIABILITY IN CRABEATER SEALS

Introduction

Given a set of data concerning the age structure of a population, questions naturally arise about what can be inferred of the history of the population: Can vital rates be estimated from the data, and if so, what are those rates? Is there evidence that recruitment or survival varied during the lifespans of the animals represented in the data? In this chapter, questions of a similar nature are explored using age-structure data from a population of crabeater seals inhabiting the waters around the Antarctic Peninsula. First, the methods are described for collection of samples and determination of ages. Then the data are used to estimate age-specific survival rates and relative strengths of the cohorts born between 1945 and 1988. Various tests are employed to determine whether the cohort strengths differ significantly from one another and whether the observed time series behavior could have arisen by chance. Finally, the effects are evaluated of errors in age determination on the estimates of cohort strength. It is found that variability in estimated year-class strength is greater than would be expected from considerations of the sampling process alone, and it has stronger autocorrelation than would be expected if year-class strength was independent among years. These results lead to hypotheses about the causes of the variability which are explored in Chapters 3 and 4.

Specimen Collections

Specimens were obtained from crabeater seals collected between 1964 and 1990 in the vicinity of the Antarctic Peninsula, South Shetland Islands, and South Orkney Islands (see Chapter 1 for description of the study area) (Øritsland 1970; Laws 1977b, 1984; Bengtson and Laws 1985; Lowry *et al.* 1988; Bengtson, unpublished). Samples were available from a total of 2,852 seals collected as food for sledge dogs and for research (1967-1977), for research only (1981-1990), and as part of an experimental commercial harvest (1964). Collection techniques varied somewhat from year to year (discussed below), but in most cases the sampling consisted of taking all seals encountered by researchers working either near a research station or from a vessel. Although there were many types of field data and tissue samples collected from each seal, the primary data for this study derive from teeth; at least one tooth was collected from each seal for age determination.

The age of each seal was generally estimated by counting layers in the cementum of a longitudinal thin (0.1-0.15mm) section cut from a post-canine tooth (usually the third lower post-canine). Ages of samples from 1964 were estimated from transverse sections of canine teeth. Sample preparation and age estimation techniques are considered in detail later in this chapter (under Effects of Age-Estimation Errors); the intervening analyses and discussion are conducted as if the age of each seal was known with certainty.

Table 1. Numbers of crabeater seal specimens collected near the Antarctic Peninsula, 1964-1990. Specimens were tallied only if date of collection and estimated age were both available (1967 collection notwithstanding).

		Number Collected			
Year	Months	Male	Female	Unknown	Total
1964[1]	Aug-Oct	125	161	6	292
1967[2]	unknown	0	0	111	111
1969[2]	Feb-Mar	51	60	0	111
1970[2]	Feb	0	65	0	65
1971[2]	Feb-Mar	3	46	0	49
1972[2]	Feb	64	89	0	153
1973[2]	Feb-Mar	131	127	0	258
1974[2]	Feb-Mar	162	196	1	359
1975[2]	Feb	42	44	0	86
1976[2]	Feb	42	51	0	93
1977[2]	Mar	19	41	0	60
1977[3]	Nov	8	95	0	103
1981[3]	Dec	52	50	0	102
1982[3]	Jan-Mar	227	210	0	437
1985[4]	Aug-Sep	24	26	0	50
1986[5]	Feb-Mar	21	23	0	44
1986[5]	Nov	54	59	0	113
1988[5]	Jun-Jul	22	25	0	47
1989[5]	Jan	55	80	0	135
1989[5]	Feb-Mar	45	43	0	88
1990[5]	Feb	53	43	0	96
Total		1,200	1,534	118	2,852

[1] Øritsland (1970)
[2] Laws (1977b, 1984)
[3] Bengtson and Laws (1985)
[4] Lowry *et al*. (1988)
[5] J.L. Bengtson, National Marine Mammal Laboratory, Seattle, WA, unpublished data

In addition to collection of tissue samples, the sex, length, and girth were recorded for most seals taken, as well as the date, time, and location of collection.

Table 1 shows the distribution of samples by sex, month and year. Note that in three of the collections (1970, 1971 and November 1977), females were deliberately sampled preferentially; implications of this selectivity are discussed in the analyses below. Note also that in 1967 the sex of each seal was not recorded; the individuals from that collection are used here only in analyses with the sexes pooled. Finally, note that although some samples were obtained during each month of the year except April and May, most samples were collected during the austral summer months of February and March. Collection dates are unknown for the 111 individuals collected in 1967, but it was assumed that they were collected in February and/or March because all other specimens from the British Antarctic Survey collections (1969 through March 1977) were obtained during those months. Specimens obtained between 1964 and 1985 have been described elsewhere (Øritsland 1970; Bengtson and Siniff 1981; Laws 1984; Bengtson and Laws 1985; Lowry *et al.* 1988). Descriptions of collections obtained between 1986 and 1990 have not previously been published.

For the analyses of age structure that follow, it is advantageous to express the age of each seal as it would have been on some standard date. Because crabeater seal pups are nearly all born in a relatively short period in September and October (Siniff *et al.* 1979), I chose to standardize ages to a date just after completion of pupping, say 1 November. Thus, an individual collected in March of 1982 and estimated to be 3 years of age, for example, was considered to have reached the age of 3 on 1 November 1981, and therefore to belong to the cohort born in 1978. This scheme is supported by the observation that tooth readers usually would not count the currently formed layer of cementum as an annual increment in teeth collected prior to about July or August when the layer becomes recognizable and thick enough to suggest a year's growth. This scheme ignores the fact that the age structure (proportion at each age) of the population may change throughout the year due to mortality rates that vary with age. I assume, however, that the effect of this distortion on the analyses that follow is slight compared with the effects of random sampling variation.

Because teeth collected from crabeater seals in June or later months usually exhibit an outer cementum layer that gets counted as a whole year during age determination, any collections obtained after June and before pupping is complete (late October) will be missing all or part of the first age class (individuals less than one year old). At that time in the annual life history cycle, the first age class comprises the near-term fetuses carried by the mature females that are pregnant. I therefore included near-term fetuses as the first age class of the collections obtained in August-October of 1964 and June-July of 1988. In this manner, 35 male, 29 female and 6 sex-unknown fetuses were included in the first age class of the 1964 collection; 9 male and 13 female fetuses were included in the first age class of the 1988 collection.

Following the protocol described above for assigning ages to the seals, the 21 collections shown in Table 1 were treated as representing samples of the crabeater seal population age structure on 1 November in 17 of the 26 years spanned from the first collection to the last. For example, the collections obtained in August–September of 1985 and in February–March of 1986 (Table 1) were combined and treated as a sample of the age structure in November of 1985. The entire series of collections then,

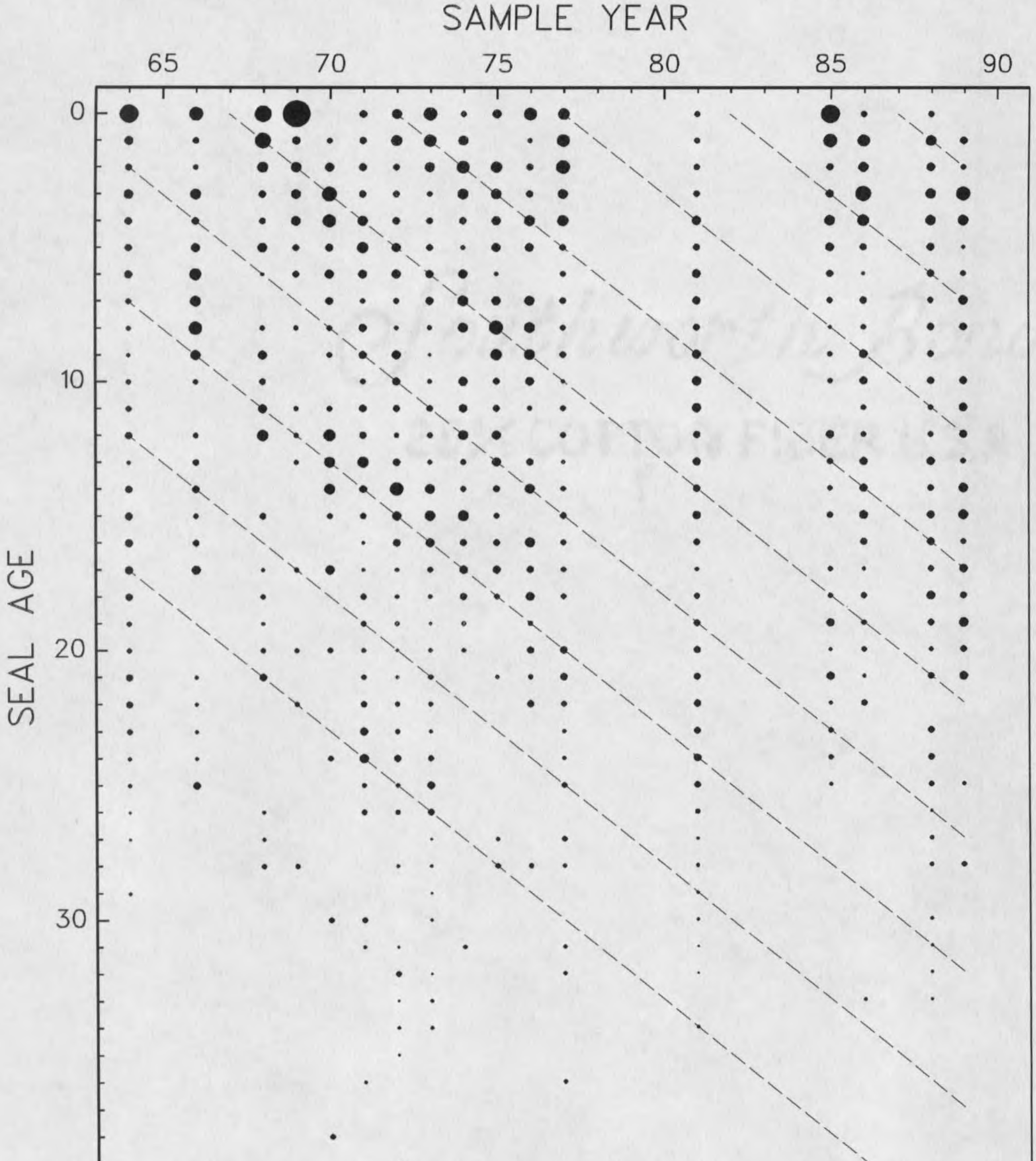

Figure 2. Age distribution of crabeater seals collected between 1964 and 1990. Ages and sample years were assigned as if all samples were made on 1 November of each year. The area of the circle at each coordinate is proportional to the number of seals of a particular age, collected in a particular year, normalized by the total collected in that year. Dashed lines have been added to assist the eye in following cohorts through time.

is represented in Figure 2, wherein the area of each circle is a multiple of the proportion of an annual sample observed to be a particular age in that year.

Age-Specific Survival

Age composition data can be used to estimate survival or mortality parameters, subject to certain assumptions. The resulting estimates may be useful for population modeling, comparisons of life histories between species or populations, or further estimation of parameters such as cohort strengths. If the age data originate from a survey that follows the absolute size of one or more cohorts through time, survivorship (denoted l_x and defined as the probability of surviving from birth to age x) can be estimated directly, producing estimates relevant to those cohorts. When, as in this study, the age data consist of "ensemble" samples from many cohorts sampled at several different times (the "standing" age distribution), where only relative frequency is known, the relative initial strengths of the cohorts must be accounted for or assumed to follow some (perhaps constant) pattern in order to draw inference.

Because initial estimates of survivorship are required for the analysis of cohort strengths, I pooled the ensemble samples and assumed, for this portion of the analysis, that the variability in initial sizes of the cohorts in these samples was limited to random variability around some long-term mean, and not subject to a systematic trend. This approach offers the benefit of large sample sizes for the survivorship estimates.

Choice of Models

An extensive literature on survival of long-lived mammals indicates that mortality rates are not constant with age for most species (e.g., Bourlière 1959; Caughley 1966; Spinage 1972; Siler 1979; Barlow 1982; de la Mare 1985; Gage 1988; Barlow and Boveng 1991). The five-parameter competing-risks model introduced by Siler (1979, 1983) has been shown to fit a wide variety of mammalian survivorship schedules (Siler 1979; Barlow 1982; Gage and Dyke 1988; Barlow and Boveng 1991). The Siler model assumes that age-specific risk of mortality is the sum of an exponentially decreasing hazard that is dominant during immaturity, an age-independent hazard, and an exponentially increasing hazard that reflects senescence in older age classes. The age-specific mortality rate, then, is

$$\mu_t = a_1 e^{-b_1 t} + a_2 + a_3 e^{b_3 t}\,, \tag{1}$$

where the terms associated with the exponentially decreasing risk are subscripted 1, the constant term is subscripted 2, and the terms associated with the exponentially increasing risk are subscripted 3. The resulting form for survivorship, which is more conveniently written as its natural logarithm, is:

$$\log l_x = -\int_0^x \mu_t \, dt = -\frac{a_1}{b_1}\left(1 - e^{-b_1 x}\right) - a_2 x + \frac{a_3}{b_3}\left(1 - e^{b_3 x}\right)\,. \tag{2}$$

Survivorship schedules of crabeater seals were modeled by fitting the observed age distributions to the Siler model using maximum likelihood estimation. The likelihood function was based on an assumption of multinomial sampling of the age distribution. The distributions of ages of male and female crabeater seals are shown separately in Figure 3, with curves showing the expected distributions derived from estimates of the Siler survivorship parameters. Although it might appear from Figure 3 that females have higher survivorship than males, this is partially an artifact of sampling; in 1970, 1971, and November of 1977, female seals were sampled preferentially, inflating the sample size for females.

A statistical test is required for determining the significance of a difference between the true survivorship schedules of males and females. One test for differences between two distributions is the Kolmogorov-Smirnov (K/S) test (e.g., Press *et al.* 1992). The K/S test is a non-parametric test relying on the sampling properties of the maximum difference between the cumulative distribution functions of two distributions. Applying the K/S test to the age distributions of male and female crabeater seals suggests that the difference between the distributions is not significant (K/S = 0.044, P=0.143). Figure 4 shows the fitted survivorship curves for males and females plotted on the same axes; the curves are similar in shape, though it appears that males may have higher mortality early in life.

As a further test on the differences between male and female survivorship, the respective age distributions were resampled in a bootstrap fashion (Efron 1982) 500 times, estimating parameters of the Siler model from each bootstrap replication. These "bootstrapped" Siler curves were used to compute survivorship to each age, up to 39 years. The central 95% of the resulting distributions of age-specific survivorship is

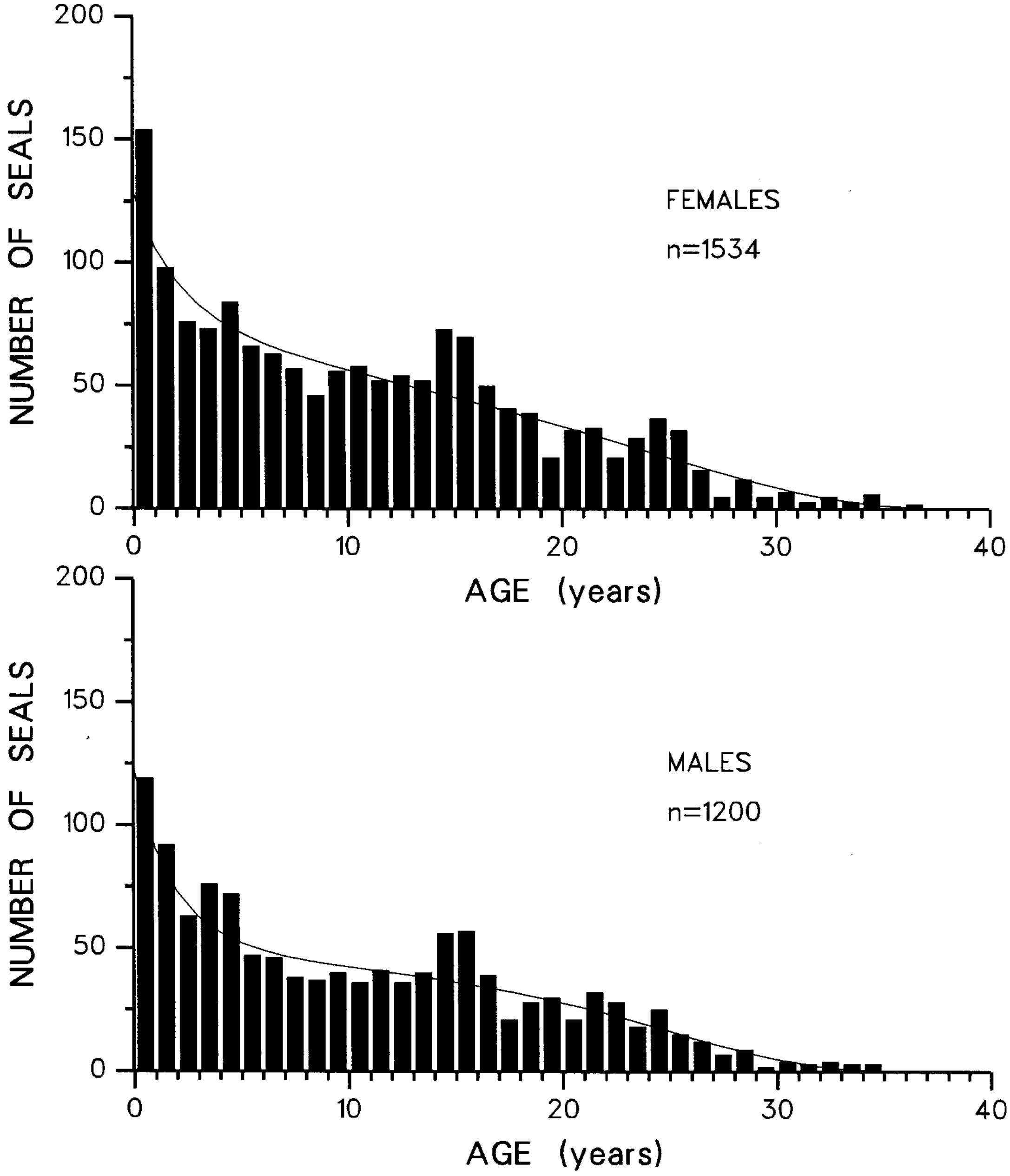

Figure 3. Age structures of male and female crabeater seals, all collections pooled. Model age structures, obtained by maximum likelihood estimation of Siler survivorship functions, are shown as curves.

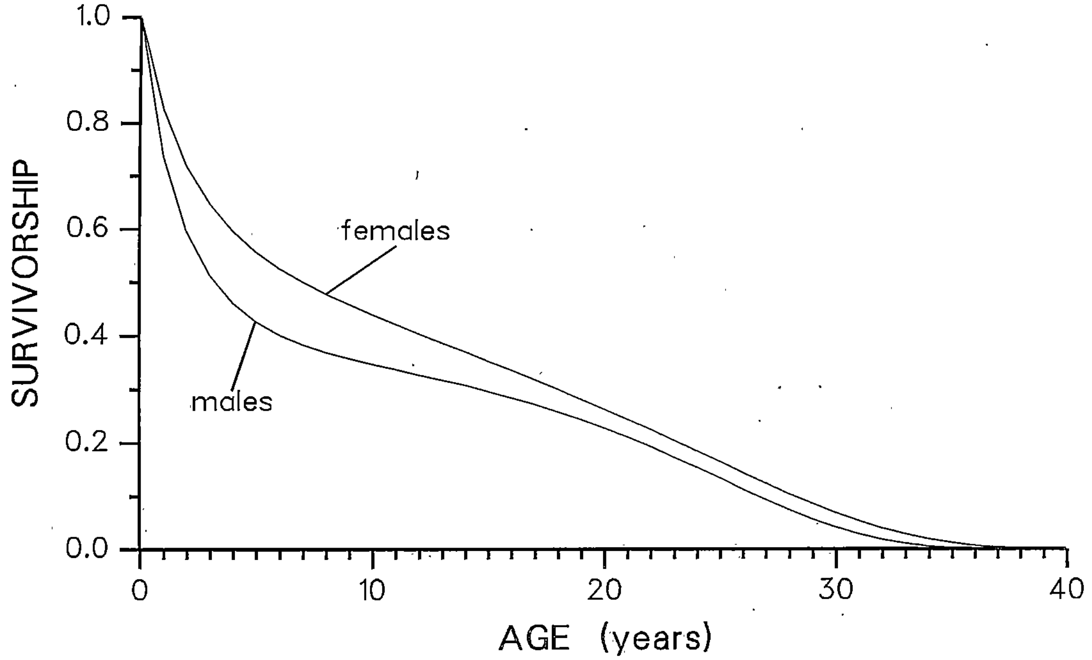

Figure 4. Survivorship curves, estimated for male and female crabeater seals by maximum likelihood using the five-parameter Siler model.

shown for males and females in Figures 5 and 6, respectively. It can be seen that the central 95% of the survivorships for males defines a band slightly larger than the difference between the sex-specific curves shown in Figure 4. Moreover, the variability is substantially greater in the estimates of female survivorship; the mean survivorship curve for males would fall entirely within the 95% band from the bootstrap replications for females.

On the basis of the tests described above, the age distributions of male and female crabeaters were pooled, including 118 additional individuals for which the sexes were unknown, to produce an overall age distribution for 2,852 seals. This pooled distribution and the fitted survivorship curve are shown in Figure 7, and the Siler parameters for the fitted curve are given in Table 2. Central 95% bands from 500 bootstrap replicates are shown in Figure 8. The pooled survivorship curve is used later in maximum likelihood estimation of cohort strengths.

Table 2. Maximum likelihood estimates of Siler survivorship parameters for crabeater seals. The lower and upper bounds of the central 95 percent of estimates from 500 bootstrap samples and the inter-parameter correlations are also shown.

	Parameters				
	a_1	a_2	a_3	b_1	b_3
Estimate	0.495	$5.53\text{x}10^{-5}$	0.00935	0.604	0.111
2.5 %ile	0.112	$5.95\text{x}10^{-6}$	$2.15\text{x}10^{-4}$	0.230	0.100
97.5 %ile	1.26	0.045	0.0117	1.805	0.234

	Correlations				
	a_1	a_2	a_3	b_1	b_3
a_1	1.000				
a_2	0.000	1.000			
a_3	0.016	-0.815	1.000		
b_1	0.999	0.000	0.016	1.000	
b_3	-0.024	0.862	-0.915	-0.024	1.000

Although five parameters are required to produce a curve that can accommodate the features of the Siler model (rapidly declining hazard to immatures, constant hazard and increasing hazard of senescence), the model is over-specified in the sense that there are substantial correlations among several combinations of the parameters (Siler 1983). It is therefore inadvisable to interpret individual parameter values. Rather, pairs of

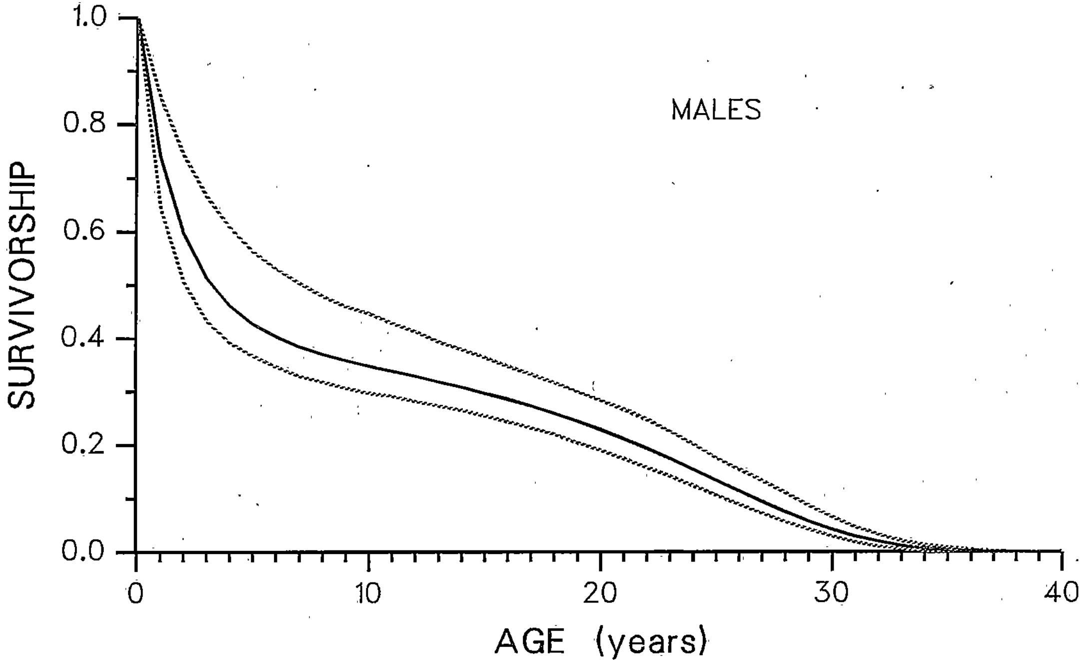

Figure 5. Estimated survivorship schedule for male crabeater seals, showing central 95% of bootstrap replicates.

values or perhaps even the entire survivorship schedule should be the focus of interpretations. For example, there is a large number of combinations of values of parameters a_1 (initial immature hazard), b_1 (rate constant for decay of immature hazard), and a_2 (constant hazard rate) that would adequately describe a given mammalian survivorship schedule from birth to breeding age; a slight reduction in b_1 can be offset by an increase in a_2, for example. These "intercorrelations" (Siler 1983) among the parameters were computed (Table 2) from the results of bootstrap estimation of parameter variances. The high correlation between a_1 and b_1 is not surprising, given the model; for a particular data set, a large value for the initial hazard due to immaturity (a_1) must be offset by a rapid decline in the immature component of mortality (large value of b_1). A similar condition exists for the parameters a_3 and b_3, the parameters describing the senescent component of mortality.

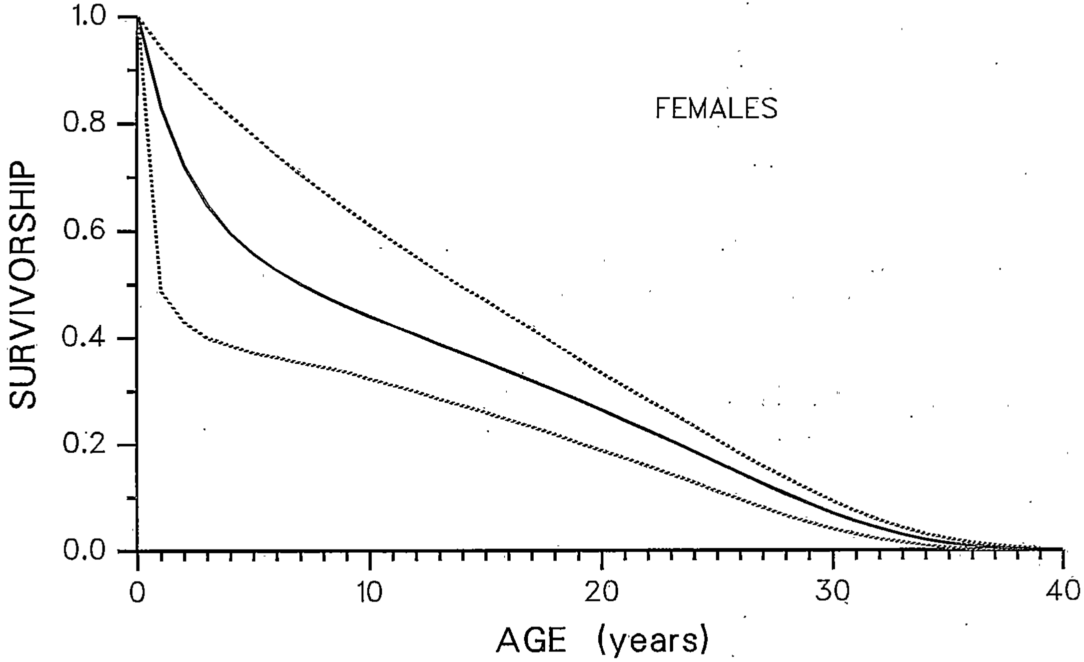

Figure 6. Estimated survivorship schedule for female crabeater seals, showing central 95% of bootstrap replicates.

In addition to the problem of high correlations among parameters, interpretation of the Siler estimates obtained in this manner are further complicated by two assumptions required for estimation of survivorship from age structure data: (1) that sampling is random with respect to age, and (2) that recruitment is constant (i.e., the cohorts represented in the sample were all of the same initial size). The first assumption may not be strictly true for the crabeater seals in this sample; young seals, especially young of the year, may not haul out on the ice in the same proportions as older age classes (Siniff *et al.* 1979) and may therefore be less susceptible to sampling. The second assumption is almost certainly not true for this sample and indeed, the majority of the remainder of this chapter is devoted to determining the nature of variability in past recruitment of the study population. Therefore, I defer presentation of a crabeater seal life table until after the effects of recruitment variability and age-selective sampling can be assessed.

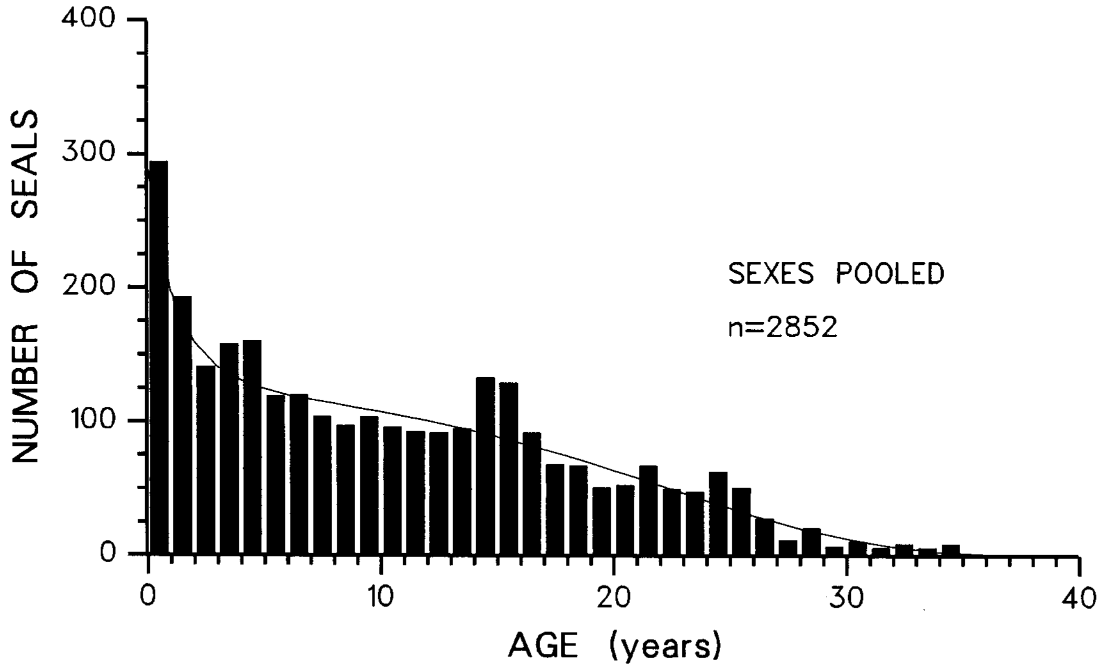

Figure 7. Age distribution of the pooled (male, female, and unknown sex) sample of crabeater seals. A model age structure, obtained by maximum likelihood estimation of Siler survivorship parameters is shown as a curve.

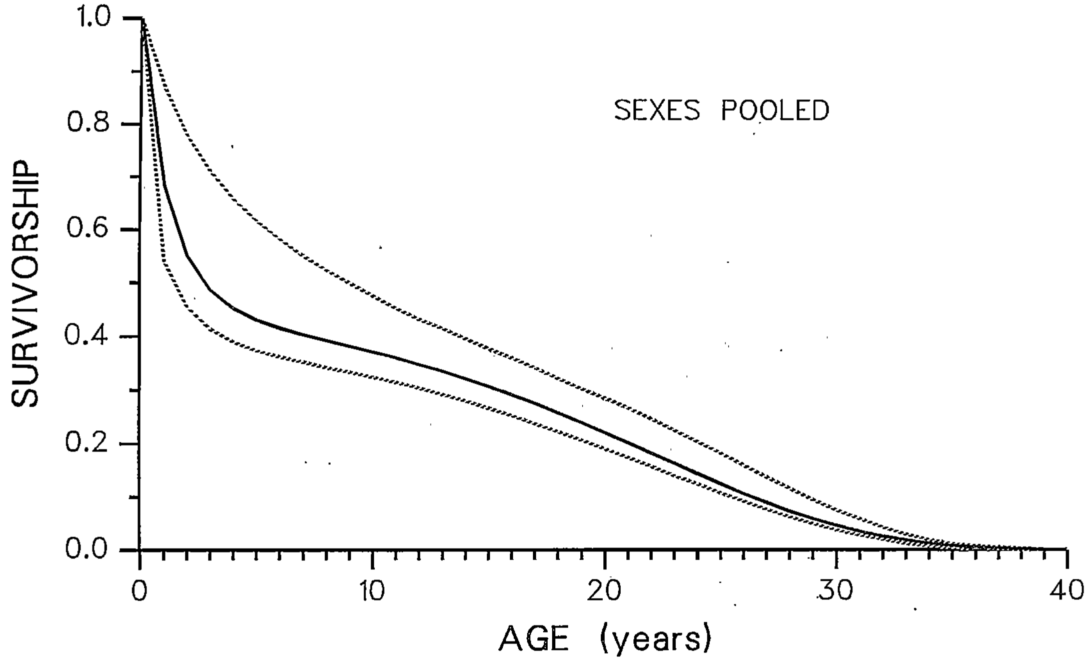

Figure 8. Estimated survivorship function of crabeater seals (males, females and seals of unknown sex pooled). The central 95% from the distribution of bootstrap replicates is shown between the dotted lines.

Cohort Strength

Background

Previous analyses of portions of the crabeater seal age-structure data have concluded that cohort strength has varied in a periodic fashion since the mid-1940s (Laws 1984; Bengtson and Laws 1985; Testa *et al.* 1991). The question of whether other biological and physical processes in the Antarctic marine ecosystem vary periodically has been the focus of several recent studies (Pozdeeva *et al.* 1990; Testa *et al.* 1991; unpublished manuscripts cited in Croxall 1992). It therefore seems appropriate to investigate more fully the nature of variability represented in crabeater seal cohorts; in particular the reliability of the cohort strength estimates should be assessed in order to make more informed judgements about the interannual variability. Contingent on the results, further investigation of the relationship between crabeater seal population dynamics and environmental factors may be warranted.

The population of crabeater seals inhabiting the Antarctic Peninsula region between about 1945 and 1990 had an age composition that probably varied through time due to random events and changes in rates of mortality and reproduction. The net results of those changes in vital rates would be corresponding changes in the proportional representation of the cohorts that compose the population. Note that variability in either survival or reproduction, or both, can be responsible for variable representation of cohorts. A cohort could be strongly represented in a sample due to relatively large initial size (reproduction) or relatively high survival. Effects of survival and reproduction are thus confounded. Moreover, in order simply to estimate (non-trivially) the parameters of cohort strength from catch-at-age data, it is necessary to reduce the number of parameters to some number smaller than the number of cells in the catch-at-age matrix. Here, I allow survival rates to vary with age but not with time (i.e., I assume that age-specific survival is constant from year to year). Alternative formulations are possible, in which both cohort size and early survival rates are allowed to vary, but are not considered here.

Having chosen to hold survival constant, the quantities of interest become the initial sizes of crabeater seal cohorts. The data available in the present case were sampled from a study population of unknown size; therefore cohort sizes can only be estimated relative to one another (i.e., unique to a scalar multiple).

Methods

I estimated the relative sizes of crabeater seal cohorts born between 1945 and 1988 near the Antarctic Peninsula by a maximum likelihood method.

Derivation of the Likelihood Function. Let Y_i denote a sample of seals collected in year i, y_{ij} be the number of seals of age j collected in year i, and n_i be the total number of seals collected in year i:

$$Y_i = (y_{i0}, y_{i1}, y_{i2}, \ldots, y_{ik}) \tag{3}$$

$$n_i = \sum_{j=0}^{k} y_{ij} \tag{4}$$

If each n_i was fixed by the sampling effort expended in year i and seals were collected at random with respect to age, each Y_i would be a sample from a multinomial distribution with parameters n_i and $\{p_{i0}, p_{i1}, p_{i2}, \ldots, p_{ik}\}$ where p_{ij} is the probability that an individual collected in year i is of age j. In reality however, the n_i's are not truly fixed, but are themselves random variables. Thus, estimates produced from this model will be conditional on the observed n_i's. Then the likelihood of obtaining a particular outcome, Y_i, given the observed n_i's, is given by:

$$L(Y_i) = \frac{n_i!}{y_{i0}!\,y_{i1}!\,y_{i2}!\ldots y_{ik}!}\,p_{i0}^{\,y_{i0}}\,p_{i1}^{\,y_{i1}}\,p_{i2}^{\,y_{i2}}\ldots p_{ik}^{\,y_{ik}}\ . \tag{5}$$

By extension, the likelihood function for a series of m independent collections is:

$$L(Y.) = \prod_{i=1}^{m} L(Y_i)\ . \tag{6}$$

Taking the logarithm and substituting (5) in the right-hand side yields:

$$\log L(Y.) = \sum_{i=1}^{m}\log L(Y_i) = \sum_{i=1}^{m}\left[\log n_i! - \sum_{j=0}^{k}\log y_{ij}! + \sum_{j=0}^{k} y_{ij}\log p_{ij}\right]\ . \tag{7}$$

Now, p_{ij} is the proportion of individuals of age j in the population in year i. Noting that the number of individuals of age j in year i can be expressed as the product of l_j the survivorship to age j and $N_{i\text{-}j,0}$ the number of individuals that were of age 0 in year i-j, the p_{ij}'s can be rewritten as:

$$p_{ij} = \frac{N_{ij}}{\sum_{j=0}^{k} N_{ij}} = \frac{l_j N_{i-j,0}}{\sum_{j=0}^{k} l_j N_{i-j,0}}\ . \tag{8}$$

Making a final substitution for the p_{ij}'s in (7), the logarithm of the likelihood function for the entire collection is:

$$\log L(Y.) = \sum_{i=1}^{m}\left[\log n_i! - \sum_{j=0}^{k}\log y_{ij}! + \sum_{j=0}^{k} y_{ij}\left[\log l_j + \log N_{i-j,0} - \log\sum_{j=0}^{k} l_j N_{i-j,0}\right]\right] \quad (9)$$

Note that (9) is a function of survivorship and year-class size in the sampled population; because there is no term in the equation relating population size to sample size (an efficiency or "catchability" term), maximizing the function in terms of $N_{i-j,0}$ and l_j produces a series of "relative" cohort strengths, unique only to within a scalar multiple, assuming age-constant catchability. The fitted values of $N_{i-j,0}$ then represent the relative year-class sizes under the original assumptions. Note also that because the first two terms of the outer sum in (9) depend only on the data and not on the parameters, maximizing the sum of the third term is equivalent to maximizing the likelihood.

The number of potential parameters in (9) has implicitly been reduced by assuming that l_j, the probability of surviving from birth to age j, is constant from year to year. However, because crabeaters are long-lived (up to 39 years in this sample), it is desirable to further reduce the number of parameters by modeling the survivorship function. I represented age-specific survival by a Siler model as did Testa *et al.* (1991). Substitution of (2), evaluated at $x=j$, into (9) reduces the number of survivorship parameters in the likelihood function from $k+1$ (40 in this case) to five.

Estimation of Cohort Strengths. Maximum likelihood estimates of the cohort strengths and survivorship parameters were found using the downhill simplex method of Nelder and Mead (1965), as implemented by Press *et al.* (1992). This method requires an initial guess for the value of each parameter to be estimated, as well as an initial specification of the multidimensional volume within which to begin the "downhill" search for the solution. In all cases in this study, the cohort strengths were initially set equal to 1.0 (logarithm equal to 0).

The choice for the initial values of the survivorship parameters is less simple than for the cohort strengths. The Siler function is highly non-linear in its parameters and is mathematically defined over a range of parameter values, some of which are not biologically plausible. Because Testa *et al.* (1991) used a fitting procedure that required specification of a linear model, they were forced to conduct a grid search over the space of two of the Siler parameters. They limited their search to biologically realistic values of the parameters b_1 and b_3, but still obtained an unrealistic survivorship model for crabeater seals (their survivorship schedule dropped to about one percent by age 22, which seems too young in respect of the age distribution shown in Figure 7).

I chose to limit the parameter space for the Siler model by first obtaining maximum likelihood estimates from the entire crabeater collection, pooled across years. This produced the survivorship curve shown in Figure 7. The parameters for this survivorship function (Table 2) were used to initialize the simplex.

As was mentioned in the section titled Age-specific Survival, the first age class may be underrepresented in the catch-at-age data. Also, Testa *et al.* (1991) found little relationship between estimated cohort strengths and the numbers of age-0 seals in the samples. I therefore excluded the first age class when estimating cohort strengths. I also chose to exclude data from all cohorts older than age class 20 in 1964 (1945 cohort; recall Figure 2) for two reasons: (1) to limit the time required to find the maximum likelihood solution (increases as the square of the number of parameters), and (2) because the environmental and ecological time series that are compared in Chapter 4 with the cohort strengths were not available from years earlier than about 1949 (allowing leads and lags of five years to be compared).

Summary statistics (mean, variance, etc.) for the cohort strength estimates were computed by standard statistical methods. The time-series characteristics of the cohort series were determined by the Box-Jenkins ARIMA (autoregressive integrated moving average) model identification procedures (Box and Jenkins 1970). ARIMA model coefficients were estimated using the Gaussian maximum likelihood routine (arima.mle) in the S–Plus statistical software (Statistical Sciences, Inc. 1993). Alternative model formulations were compared using the Akaike Information Criterion (AIC) (Akaike 1974).

Results

The series of estimated cohort strengths is shown in Figure 9. I hereafter refer to this as the "modeled" series. It is nearly identical to one obtained by Testa *et al.* (1991), except for the inclusion of more recent estimates (1986-1988) in the present study.

The mean of the modeled cohort strengths for the years 1945-1988 is 1.098 and the variance is 0.184; both are dependent on the (arbitrary) scale of the estimates and are determined partly by the choice of initial values used in the maximum likelihood estimation procedure. Therefore, the coefficient of variation (0.39) is a more informative measure of variability than the variance. The median cohort strength estimate is 1.012, only slightly less than the mean. The greatest cohort strength (2.14) differs from the least (0.436) by a factor of about 5.

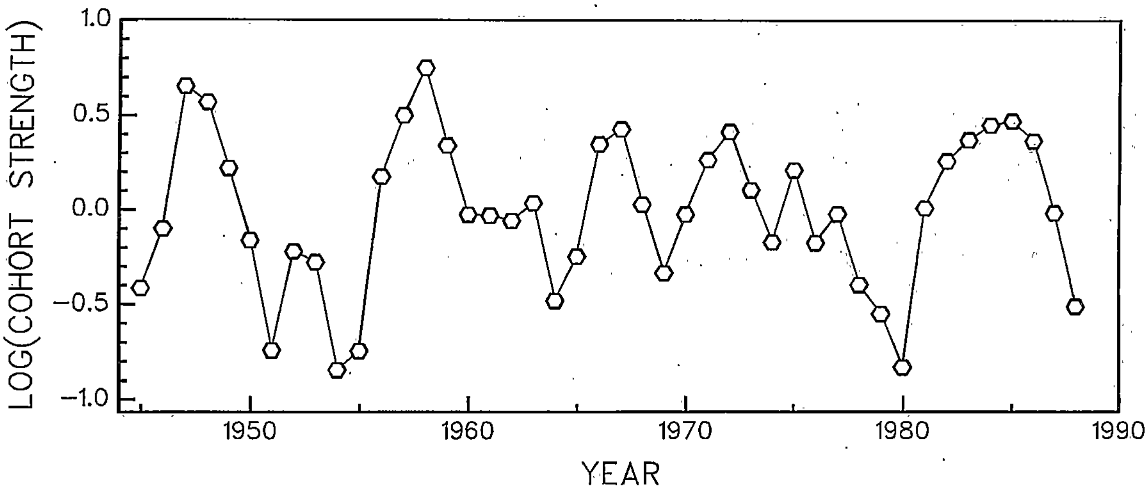

Figure 9. Natural logarithms of estimated historical cohort strengths obtained by maximum likelihood using the crabeater seal age data (the "modeled" cohort series).

The frequency distribution of cohort strengths (Figure 10) appears slightly skewed. Recruitment data often have been observed to be distributed lognormally, at least for marine fish populations (Peterman 1981). Log-transformation of the cohort strengths did result in greater symmetry, but did not greatly modify the perceived shape of the distribution because log x is approximately equal to x-1 over this range of values.

The autocorrelation function (ACF) for the first 15 lags of the modeled cohort series is shown in Figure 11. The correlations of 0.57 at a lag of one year and -0.49 at a lag of seven years are significant at α=0.05, considering all lags 1-15 simultaneously (the method used to adjust the P-values for simultaneous inference is discussed in detail in Chapter 3, where it is used more extensively). The non-zero values of the ACF suggest a moving average process (Box and Jenkins 1970) of order

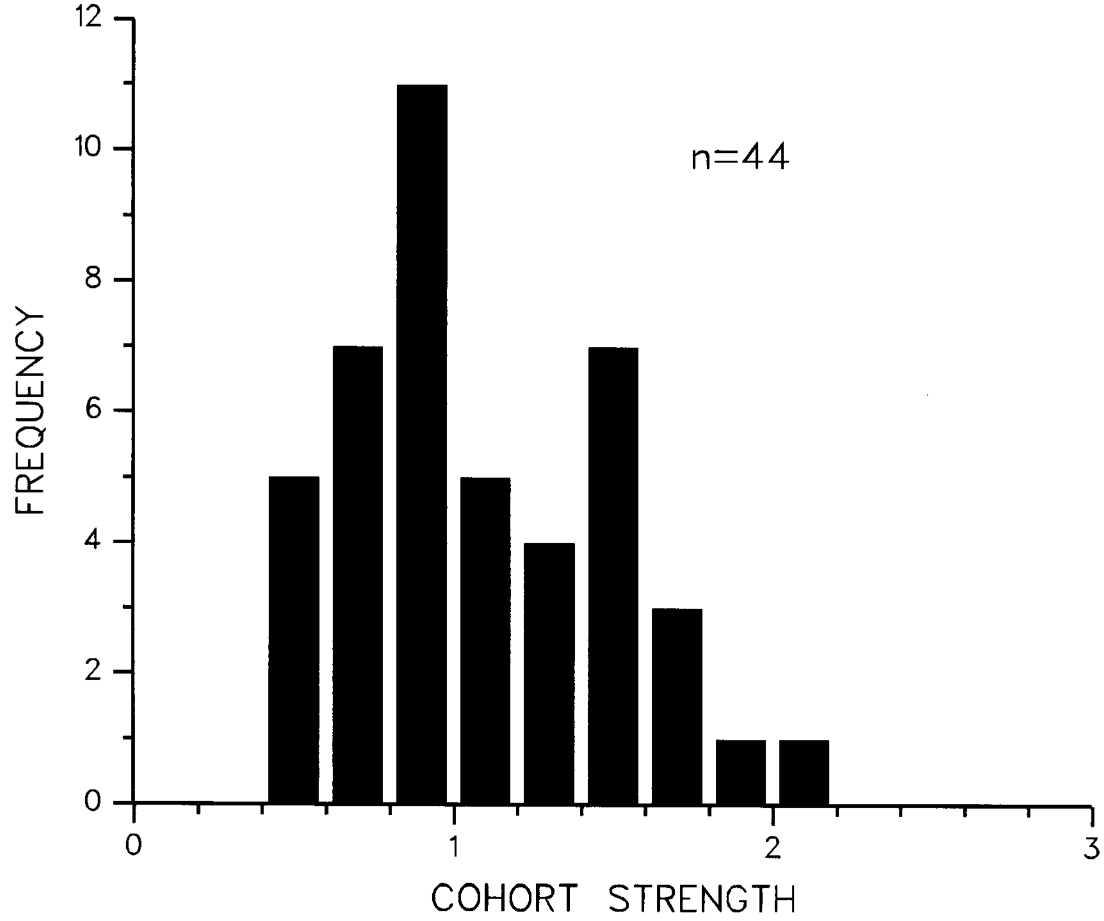

Figure 10. Frequency distribution of cohort strength estimates from Figure 9.

1 and perhaps as high as order 7 (although the non-significant correlations at orders 2-6 complicate the interpretation). The partial autocorrelation function (Figure 11) has significant coefficients at lags of one and two years, suggesting an autoregressive model of order 2 (Box and Jenkins 1970). In fact, however, a pure autoregressive model of order 7 provides the best fit (i.e., minimum AIC) among ARIMA(p,d,q) models where the autoregressive order $p \leq 16$, the difference order $d=0$, and the moving average order $q=0,1$, or 7. The AR(7) (autoregressive order 7) coefficient estimates and standard

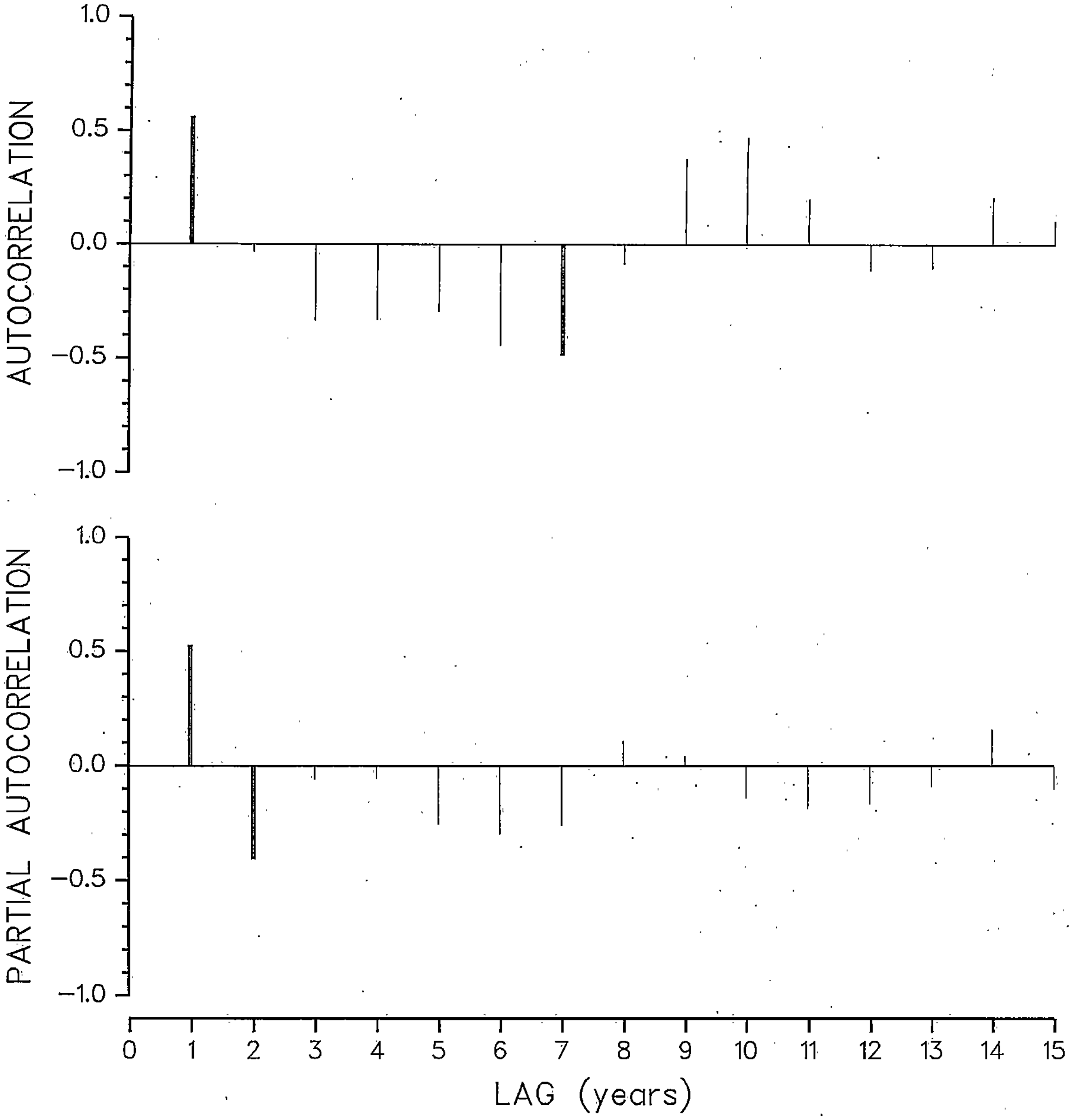

Figure 11. Autocorrelation and partial autocorrelation functions for the modeled series of cohort strengths (Figure 9). Bold bars indicate correlations significant at an experiment-wise (lags 1-15) level of $\alpha=0.05$.

errors are shown in Table 3. The one-step-ahead predictions from the AR(7) model are compared with the modeled series of cohort strengths in Figure 12. The results of these time series analyses are discussed further after presentation of methods and results from investigations into the degree of uncertainty associated with the modeled series of cohort strengths.

Table 3. Coefficients and standard errors for an autoregressive model of order 7, estimated from the modeled series of crabeater seal cohort strengths by maximum likelihood assuming a Gaussian model for the noise term.

Order	Coefficient	Standard Error
1	0.522	0.159
2	-0.294	0.177
3	-0.205	0.180
4	0.065	0.183
5	-0.200	0.180
6	-0.200	0.177
7	-0.273	0.159

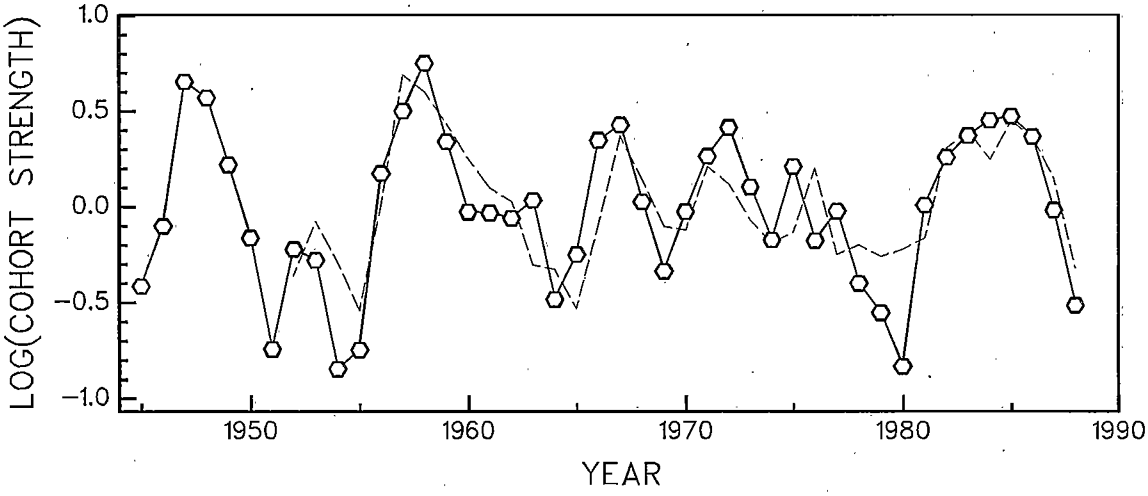

Figure 12. One-step-ahead predictions (dashed line) from an autoregressive model of order 7, superimposed on the modeled series of cohort strengths.

Uncertainty in Cohort-Strength Estimates

Having estimated a series of cohort strengths, it seems logical to ask, "what is the likelihood that such a series could have arisen by chance alone, under some specified null hypothesis about the true cohort strengths?" Several forms of the null hypothesis may be interesting. For example, one might wish to know whether a series of estimates with variance as large or larger than the estimated variance could result from true cohort strengths that were constant from year to year. Or, could a true cohort series with variance equal to the estimated series, but with no autocorrelation, result in a series like the one observed? Alternatively, the observed pattern could be turned into a null hypothesis to investigate whether multinomial sampling from a population like that implied by the estimates would reliably reveal the true pattern. Each of these tests, and its associated assumptions, is discussed below.

Methods and Results

Tests to evaluate the uncertainty in cohort strength estimates were conducted by bootstrap and Monte Carlo techniques. The bootstrap techniques utilized samples drawn from the empirical distribution of the catch-at-age data. The Monte Carlo techniques utilized sampling from distributions defined by parameters estimated from the data.

Bootstrap samples — themselves multinomial — were drawn repeatedly from the catch-at-age distribution, keeping each collection size fixed at the observed value. Each bootstrap sample was analyzed by the same maximum likelihood procedure that generated the modeled series of cohort strengths. In Figure 13, the modeled cohort strengths are shown with the bounds of the central 95% of the cohort strengths obtained from 500 bootstrap samples. It is clear from Figure 13 that any curve drawn within the central 95% values from the bootstrap samples would preserve the general interannual pattern found in the modeled series of cohort strengths.

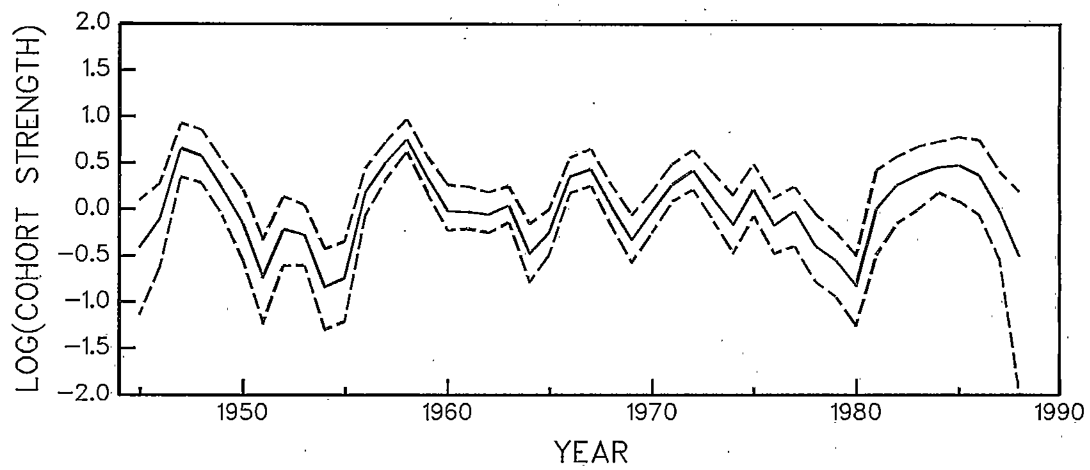

Figure 13. Estimates of historical cohort strength; dashed lines indicate the central 95% of outcomes from 500 bootstrap samples drawn with replacement from the age data. Sample sizes were fixed at the observed collection sizes.

The bootstrap estimation procedure described above treats the sample size in each collection year as fixed. This assumption may not be valid; the nature of the research expeditions or commercial harvests that acquired the samples was such that weather, logistics, and distribution of seals could combine to impart a random element to collection size. Moreover, even the years in which collections occurred may not have been truly fixed, depending to some extent on availability of vessels and funding. To investigate the effect of these random elements on the estimated variances of the cohort strengths, a Monte Carlo scheme was used. In this scheme, only the number of collections (17) was fixed. The 17 collection years were chosen randomly from the interval 1964-1989. The collection size for each year was chosen randomly from a normal distribution with mean and variance equal to the observed mean and variance of the collection sizes. The sample age distribution within each collection was drawn in a multinomial fashion from the hypothetical ("modeled") age structure implied by the modeled cohort strengths and associated survivorship model. A new survivorship curve was estimated for each Monte Carlo replicate by a maximum likelihood fit to the age structure obtained by pooling the collection years. The resulting survivorship curve was used to initialize the maximum likelihood procedure for cohort strength estimation from that Monte Carlo replicate. The results from 500 replicates are shown in Figure 14. The band formed by the central 95% of Monte Carlo estimates is wider than that in Figure 13, but the pattern of variability is still clearly identifiable with the modeled series of cohort strengths.

The bootstrap tests described above address the question, "if the true age structure of the crabeater population was like the one defined by the modeled series of cohort strengths (Figure 9) and the survivorship in Figure 7, would the true pattern be detected using a sampling scheme like the one that was employed for this study?" This is related to the concept of statistical power, i.e., what is the probability that an event of a specified magnitude would be detected (called significant) using a test of a particular size (α level). The other concept of statistical performance of interest in this situation is that of Type I error; how likely is it that the observed pattern could have arisen by chance from a true population in which the pattern does not occur. Further bootstrap tests were employed to investigate this issue; one test used constant cohort strengths and a second used cohort strengths independently and identically distributed (i.i.d.), with variance equal to the variance of the estimated time series.

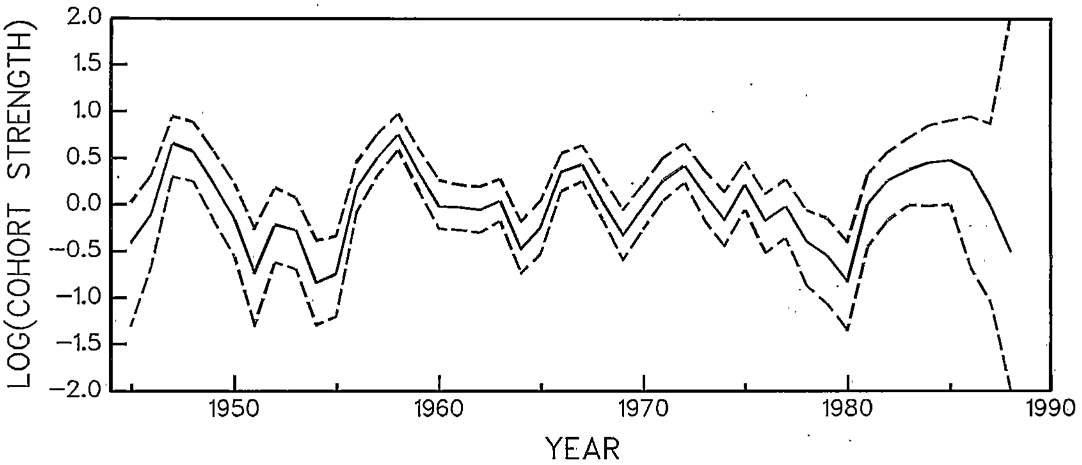

Figure 14. Estimates of historical cohort strength; dashed lines define central 95% of Monte Carlo outcomes drawn with replacement from the modeled age structure. For each Monte Carlo sample, collections were simulated for 17 years at random in the interval 1964-1989. Sample sizes for each collection were chosen randomly with replacement from the observed sample sizes.

The central 95% band for Monte Carlo cohort strengths from the scenario with true cohort strengths constant is shown in Figure 15. If that band is assumed to represent a joint 95% confidence interval for the cohort strengths, about 2 to 3 (0.05 times 44) cohort strengths would be expected to fall outside the interval by chance alone, under a null hypothesis of constant true cohort strengths. In fact, 18 values in the modeled series of cohort strengths fell outside the band. The probability — from the binomial distribution — of 18 or more values outside the band is approximately 10^{-12}.

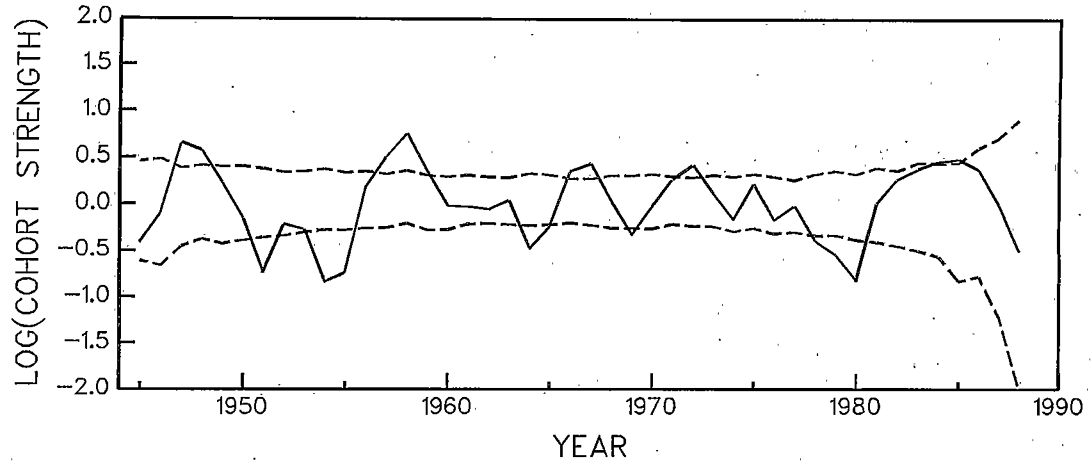

Figure 15. Estimates of historical cohort strength; dashed lines indicate the central 95% of 500 Monte Carlo outcomes sampled from a stable age structure (constant cohort strength) defined by the Siler model shown in Table 2. Sample sizes and collection years were chosen in the same manner as for Figure 14.

Even if the central 95% of the bootstrap cohort strengths overestimated the true confidence interval by as much as 5%, the probability of 18 or more values outside the band would be only 10^{-8}. Thus, the observed variability is much greater than would be expected under constant cohort strengths. Because the true cohort strength and the survivorship were constant in this simulation, the variability indicated by the confidence bands is due entirely to the sampling process and serves to illustrate the amount of the variation in cohort strength estimates that could be due solely to the sampling scheme. It seems, from these results, unlikely that the catch-at-age data came from a population with constant cohort strength.

It may be difficult to envision a real population characterized by truly constant recruitment. Therefore, a more reasonable choice might be to simulate a population with a variance in recruitment equal to the observed variance of the modeled cohort strengths, but without the autocorrelation of the observed cohort strengths. Then the test should be to determine how frequently a result is obtained which is similar to or more extreme than the observed pattern.

The second test, employing independent, identically distributed (i.i.d.) true cohort strengths, produced the distribution of estimates shown in Figure 16 (as in Figure 13, the dotted lines represent the central 95% bounds of the outcomes). Not unexpectedly, the confidence band just encompasses the extremes of the modeled series; variability of the input process is approximately preserved by the sampling and estimation procedure. The more interesting aspect though, addressed by this simulation, is how likely is an outcome with time-series properties (e.g., autocorrelation) like those of the modeled series.

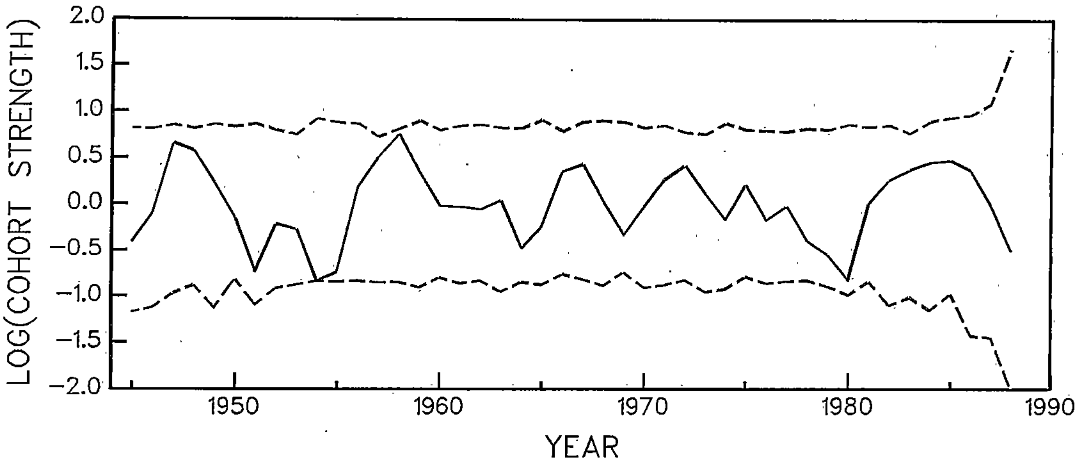

Figure 16. Estimates of historical cohort strength; dashed lines indicate the central 95% of 500 Monte Carlo outcomes sampled from model age structures defined by cohort strengths drawn randomly from a lognormal distribution with the same mean and variance as the modeled series. Sample sizes and collection years were chosen in the same manner as for Figure 14.

The autocorrelation in the true cohort strengths at lag 1 was stored during each Monte Carlo replicate for comparison with the autocorrelation at lag 1 of the cohort strengths estimated from the Monte Carlo sample data. This allowed a test of whether the autocorrelation of the modeled series could have arisen strictly from the sampling and estimation procedure. The true and estimated autocorrelations (lag 1) are shown in quantile-quantile (Q-Q) form (Chambers *et al.* 1983) in Figure 17. The nearly perfect correlation between the quantiles indicates that the model sampling and estimation procedures are not modifying the distribution of lag-1 autocorrelations. The observed lag-1 autocorrelation of the modeled series reported above is 0.57; this value is greater than any of the 500 lag-1 autocorrelations obtained by Monte Carlo simulation from a series of true cohort strengths with no lag-1 autocorrelation.

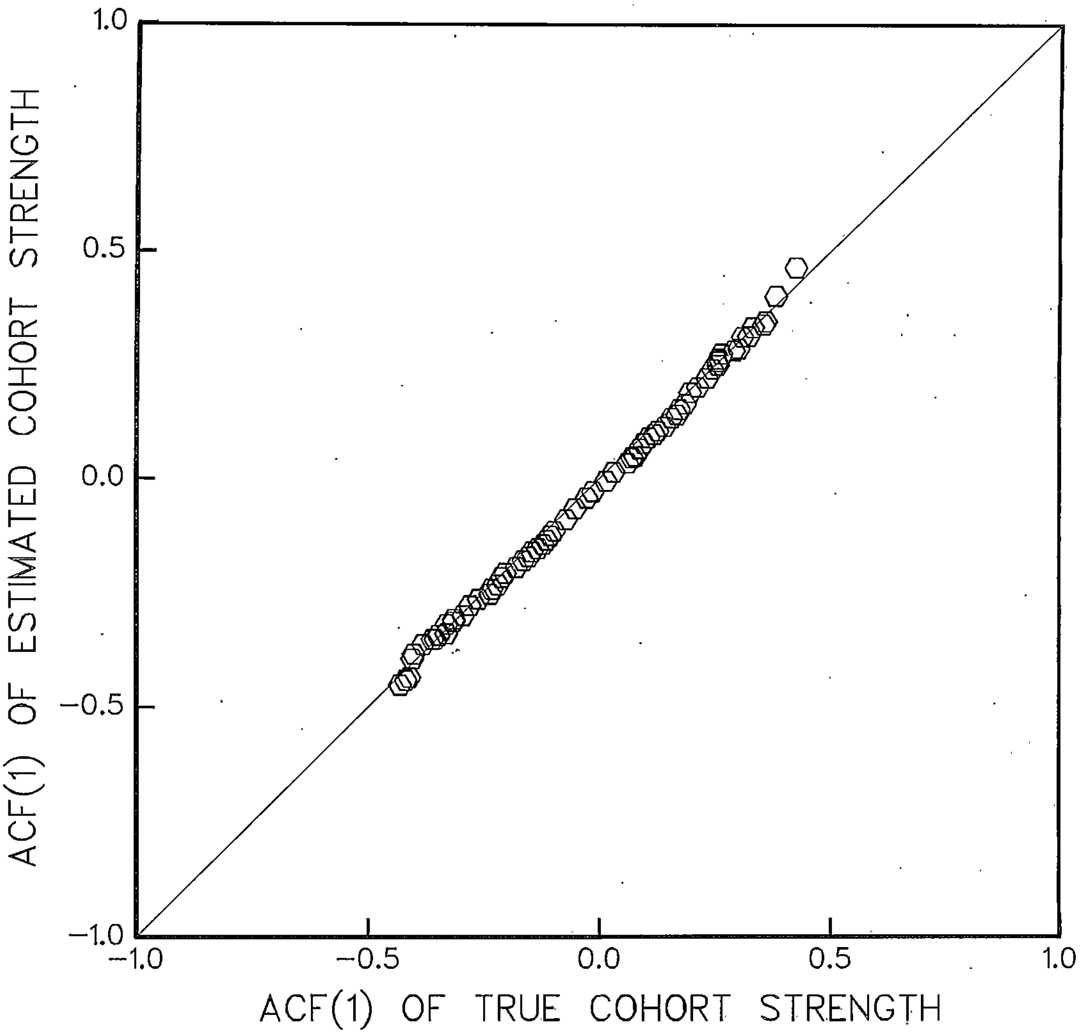

Figure 17. Q-Q plot of true versus estimated lag-1 autocorrelations in simulated series of crabeater seal cohort strengths. The true autocorrelations were measured in hypothetical series composed of i.i.d. cohort strengths. The estimated autocorrelations were measured in series obtained by multinomial sampling from the population defined by the true series and maximum likelihood estimation.

Discussion

The bootstrap and Monte Carlo tests described above suggest that the variation in the modeled cohort strengths reflects genuine demographic variation. The empirical distribution (Efron 1982) of the catch-at-age data implies rather narrow confidence bands around the modeled cohort strengths (Figure 13). Allowing for random sample sizes increased the confidence bands only slightly. Thus, the estimates seem quite well determined by the sample age structure. The Monte Carlo simulations suggest that although substantial variation could be due to random sampling events, there is a coherence among adjacent year classes (autocorrelation) that is unlikely to be due to chance or to the estimation procedure. Therefore, it seems highly unlikely that the features previously interpreted by others as variation in cohort strength could have arisen by chance from a stable population or as artifacts of analysis, provided the assumptions are true. It remains to be shown, however, whether the cohort variation is somehow patterned or periodic.

Much effort has been devoted to the study of cycles in vertebrate populations, most notably several species of mammals and birds in the North American tundra and boreal forest (reviewed in Akçakaya 1989; Sinclair *et al.* 1993). Those studies have been based upon relatively long time series exhibiting many cycles of about 10 years duration, so there can be little doubt that the fluctuations are nearly periodic. There has, however, been considerable debate about the period of the cycles and the causes.

Variability in crabeater seal cohorts has also been said to be cyclic (Laws 1984; Bengtson and Laws 1985; Testa *et al.* 1991), with a period of approximately four to five years. It must be noted, however, that the crabeater seal series is relatively short and that an apparent cycle of four or five years duration could be expected to arise by chance from non-cyclic variation much more readily than say, a ten year cycle. The

AR(7) model I fit to the cohort series has some periodic characteristics; its power spectrum has strong peaks at periods of 11 and 4.9 years. Other autoregressive models that fit the data almost as well (e.g., AR(2) and AR(3)) have only a single, rounded peak at about 7.3 years. Thus, any periodic characteristic of the cohort series is not well determined. Moreover, in an informal test I simulated time series from those autoregressive models, of the same length as the modeled cohort series, and roughly half of the simulations had no appearance (to me) of periodicity. Thus, despite the indications from the Monte Carlo tests that there is genuine variability in crabeater seal cohorts an interpretation of periodicity is unsupported.

The assumptions upon which the preceding estimation of cohort strengths depends are: (1) sampling was random with respect to the true population age distribution of seals; (2) the ages of seals in the sample are known; and (3) survivorship is constant over time and can be adequately described by an age-specific five-parameter Siler model. Assumption (1) relates not only to cohort strength estimation but also to age-specific survival. In the section below titled A Life Table for Crabeater Seals, I return to the problem posed earlier (in the section titled Age Specific Survival) of accounting for cohort variability and age-biased sampling when estimating survival rates. Then I discuss the effects of relaxing assumption (2) in the section titled Effects of Errors in Age Estimation. Assumption (3) relates to the question of whether variability in cohort strength is caused by variation in survival, reproduction or a combination of the two. Alternative formulations of the likelihood function (equation 9), in which both cohort size and survival are allowed to vary, are possible but not considered in this study.

A Life Table for Crabeater Seals

In the section above, titled Age-Specific Survival, I deferred computation of a life table until the effects of cohort variability and possible age-biased sampling (particularly undersampling of young-of-the year) could be accounted for. The survivorship model estimated simultaneously with cohort strengths implicitly accounted for variability in initial sizes of cohorts (recruitment). Below I consider possible age-biased sampling and compute an alternate survivorship curve.

Aside from a comment by Øritsland (1970) regarding the 1964 collection, there is little documentation of known or potential biases with respect to ages of the crabeater seals collected. The data used here from the 1964 collection are a subsample of the entire collection from that year and may be biased toward breeding age individuals (Øritsland 1970). Because the mean age at sexual maturity for this crabeater seal population in 1964 has been estimated to be approximately 2.5 years (Bengtson and Laws 1985), this bias, if present, would probably be limited mostly to the first few age classes. Moreover, if this were the only age-bias in the data used here, it would have little effect on estimation of parameters from the combined samples from 1964-1989. As a further test on whether the first age class might have been substantially underrepresented in the catch-at-age data, I used data on pregnancy rates (Laws 1984) and — assuming a stable, stationary population and primary sex ratio of 1:1 — computed the number of offspring expected from a population with the age structure implied by the Siler model estimated earlier.

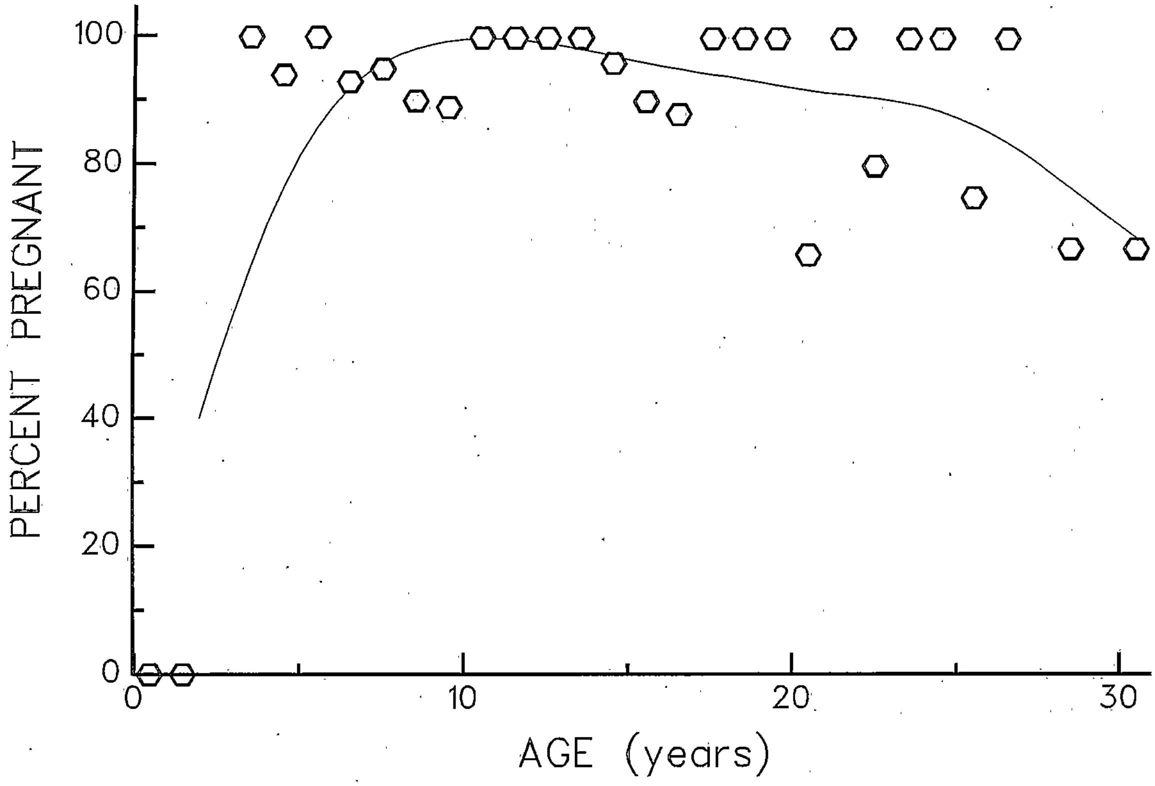

Figure 18. Age-specific pregnancy rates of crabeater seals (Laws 1984) smoothed by cubic spline regression (curve).

The age-specific pregnancy rates (Laws 1984) were smoothed by a cubic spline (Figure 18) and arbitrarily set to zero below age two and to decline linearly from the smoothed value at age thirty to zero at age forty. Then the survivorship curve obtained simultaneously with the modeled series of cohort strengths was used to convert the pregnancy rates to fecundities and compute the number of offspring expected from the model age structure. The results (Table 4) imply that approximately 80% of newborn crabeater seals die within their first year and that the "catchability" of first-year seals is only about one-third that of older age classes.

The life table in Table 4 may seem unusual in that first-year survival is typically higher for long-lived mammals with relatively low fecundity. This result is, however, consistent with evidence from natural history observations that first-year mortality of crabeater seals of the Antarctic Peninsula may be very high. Siniff and Bengtson (1977) and Siniff *et al.* (1979) demonstrated that scars borne by nearly all (80% to more than 90% in some samples) adult crabeater seals are the results of attempted predation by leopard seals during the crabeaters' first year of life. The implication is that virtually all young-of-the-year crabeater seals in this population are subject to attempted predation by leopard seals and the proportion that succumb could be quite high. The adult survival rates and pregnancy rates are also quite high and perhaps have evolved to compensate for the first year mortality.

Table 4. Life table for crabeater seals based on the survivorship model estimated simultaneously with the modeled series of cohort strengths and age specific pregnancy rates, assuming a stable, stationary population and a sex ratio at birth of 1:1. Where a range of ages is shown, survivorship corresponds to the upper bound of the range.

Age (x)	Survivorship (l_x)	Annual Survival (p_x)
0	1.000	0.21
1	0.208	0.81
2	0.168	0.88
3	0.148	0.93
4	0.138	0.95
5	0.131	0.96
6-11	0.110	0.97
12-13	0.102	0.96
14-15	0.094	0.95
16-17	0.084	0.94
18	0.079	0.93
19	0.073	0.92
20-25	0.038	0.9
26-30	0.014	0.8
31-34	0.004	0.7
35-37	0.001	0.6
38-39	<0.001	0.5

Effects of Errors in Age Estimation

The analyses presented thus far have treated the ages of seals in the sample as known. In fact, estimates of age from cementum lines in seal teeth are subject to error. The sources of error include variation among seals in the clarity of cementum annuli, variation among teeth and types of teeth within individuals, variation in the quality of the cut section used for age estimation, and variation among and within readers who count the cementum annuli. The remainder of this chapter is devoted to the implications of this uncertainty for the results presented above.

Age estimation error can be manifested as bias and/or imprecision. Bias is generally more difficult to detect than imprecision, usually requiring known-age specimens for estimation. There are no known-age crabeater seal teeth available for assessment of bias in age estimation, but several lines of evidence suggest that bias is not a significant problem. First, most seals have a clearly identifiable neonatal line in the dentine, marking the time of parturition; subsequent deposition of the first few cementum layers matches the deposition of distinct dentine layers (Laws 1958, 1962), indicating that one cementum growth layer corresponds to one year's growth. Second, animals known to be pups at the time of collection exhibit an incomplete outer cementum layer, indicating that the deposition count starts with zero at birth. Finally, known-age specimens from other phocid species such as harbor seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) have been aged accurately — to within one year of the true age — by counting cementum layers, even for fairly old (e.g., 19-26 years) specimens (Laws 1962). I have therefore assumed throughout this study that the crabeater seal age estimates are unbiased.

Like bias, imprecision would perhaps also best be estimated from known-age specimens, but techniques are available for assessing the degree of imprecision from multiple independent readings of specimens of unknown age, assuming the readings are unbiased. Statistical methods for accomplishing this have recently been developed in association with age-structured fishery modeling efforts, and the same techniques can be applied to the crabeater seal data.

Several authors have investigated the effect of age estimation errors on estimates of recruitment or cohort strength (e.g., Rivard 1989; Bradford 1991) and on estimates of mortality (Barlow 1984). It is well known from these studies that imprecision in age estimation leads to underestimated variance of recruitment (cohort strength). Due to age estimation errors, some fraction of the individuals in a strong cohort will be assigned to adjacent cohorts. The spreading of individuals from weak to strong cohorts is less pronounced because fewer individuals are available to be misclassified. Therefore, the apparent variability in relative cohort sizes is less than the true variability. This "smoothing" effect can also lead to inflated autocorrelation in estimates of recruitment and reduced correlation with potentially important environmental factors. Because these effects are all of concern with respect to the crabeater seal data, I used a statistical model of the age-error process in an attempt to obtain improved estimates of the population age distribution. The new age distribution was analyzed by the cohort techniques described above.

Methods and Data

Age estimation. Age estimates used in this study were produced under a variety of circumstances. All estimates were based on microscopic examination and enumeration of cementum lines in an optically transluscent thin section of a tooth, but the number of readers (and readings), the tooth type, and preparation of the sections varied among the several collections. The tooth type was the least variable of these factors; all ages were estimated from longitudinal sections of a third or fourth lower post-canine except those from specimens collected in 1964, which were estimated from cross-sections of lower canines. I assume here that tooth type has no significant effect on the analyses.

Each tooth section from the 1977-1989 samples was read at least three times; sections from earlier samples were typically read once or twice. For some collections, the readings were accomplished by independent readers, for others by a single reader, and for still others, several readers each made multiple readings. In all cases, readers did not have access to results from other readers. When a single reader made multiple readings, results of previous readings were not available to the reader during subsequent readings. Because of the complexity imposed by the numerous combinations of readers and readings/tooth employed in this study, I assume that variation among tooth readers is the same as variation among readings and that all readings from a particular seal are independent of one another.

Final age estimates, based on one or more independent readings, were assigned by *ad hoc* rules that varied among the samples. These rules are described below, to the extent that they could be recalled by the investigators (T. Øritsland, pers. comm.; R.M. M. Laws, pers. comm.; J.L. Bengtson, pers. comm.). These final ages were considered by the respective investigators to be "best" estimates, including considerations of such factors as the experience of the tooth readers but without explicit use of the statistical sampling properties of the age determination procedure. I have therefore termed the final age estimates "subjective" ages, though they are not entirely subjective (having been based on counts of cementum annuli).

Subjective ages derived from multiple readings were assigned to seals in the 1977-1989 samples by the following rules: If, after 3 readings at least two were in agreement and the third differed by no more than one year, the agreed age was assigned. If the high and low readings among the three differed by two years, the middle age reading was assigned. If neither of the above criteria were met, additional readings (up to a maximum of 6) were obtained (without access to previous results) until at least two agreed or three readings spanned no more than two years of age.

Details of the determination of final ages for seals in the 1966-1976 samples are not presently available, but they were likely based on two readers examining each tooth until they agreed on the age (J.L. Bengtson, pers. comm.). Teeth from seals in the 1964 sample were read once each (T. Øritsland, pers. comm.) and the single reading represents the final age estimate.

The rules for assigning ages have implications for the variability of age determination. For example, teeth read more than three times are generally more variable than those with only three readings (except for collections in which more than

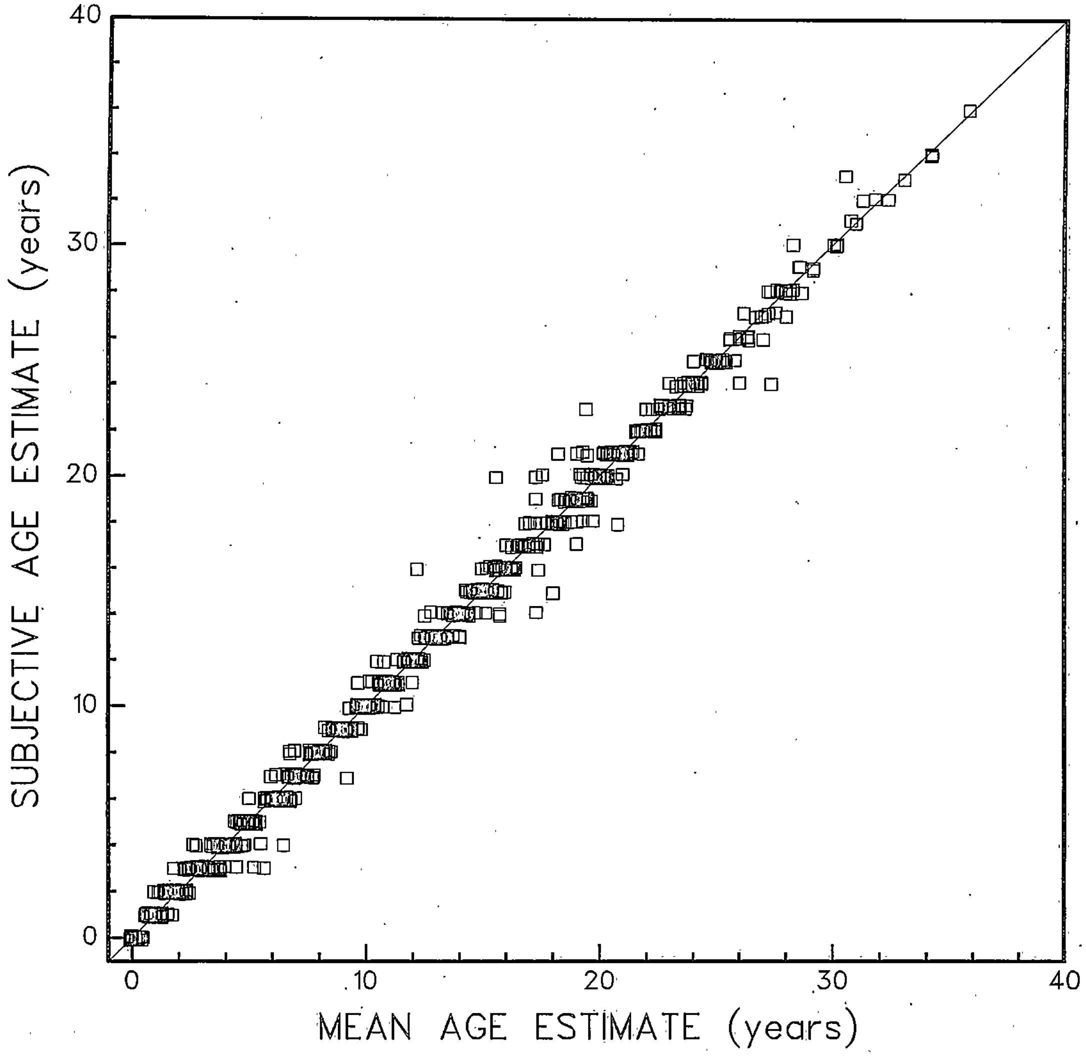

Figure 19. Subjective age estimate for each of 1,216 crabeater seals from the 1977-1989 samples plotted against the average of individual tooth readings from each seal. The rules for producing the subjective estimates from the individual readings are given in the text.

three readings were obtained before applying the subjective age rules). For the most part, however, the subjective estimates correspond well with the mean of the individual readings (Figure 19).

Individual readings of tooth sections were available only for the 1977-1989 samples (e.g., Figure 2). Combined, these represent 1,216 specimens with an average of 4.2 readings per specimen. These readings are used below to model the age-error process, allowing estimation of catch-at-age distributions that may be more accurate than the distributions of observed ages.

Modeling the age-error process. Let the true (but unknown) distribution of catch-at-age be represented by the column vector C. Then form a matrix Q, by the elements q_{ij}, each of which is the probability that an animal with true age j will be observed as having age i. Then

$$C^* = CQ \tag{10}$$

represents the expected distribution of ages observed with error. Note that a particular catch-at-age data set represents one stochastic realization of the error process denoted by the matrix Q; unless sample size is very large, the observed catch-at-age is unlikely to equal C^*. For that reason, and because the matrix Q is nearly singular for many plausible age estimation error processes, applying Q^{-1} to the observed catch-at-age may not yield the true age distribution.

The observed catch-at-age data (with errors) can be modeled as a mixture of component distributions, where each component is some fraction of the total population (e.g., Böhning *et al.* 1992; Laird 1978; Dempster *et al.* 1977). If p_x is the true fraction of the total population in age class (component) x, then $\{ p_x: x=1,m\}$ is the true age distribution, which is the quantity of interest. Denoting the probability density for the xth component as $q(y \mid \theta_x)$, an observation Y has probability density

$$f(y) = \sum_{x=1}^{m} p_x \, q(y \mid \theta_x) \qquad (11)$$

Estimates of the true age distribution can be obtained via the EM algorithm (Dempster *et al.* 1977) or by direct maximization of the likelihood written in terms of the observed data (Richards *et al.* 1992); the latter method, which I use here, produces simultaneous estimates of a reduced-parameter form of $\boldsymbol{Q}$.

When multiple independent readings of each animal's age are available, the probability density for ages estimated with errors can be modeled (Richards *et al.* 1992) subject to two assumptions: (1) all errors are due to imprecision (age estimates are unbiased), and (2) for observed age Y and true age X, $\mathrm{P}(Y=x \mid X=x) > \mathrm{P}(Y=y \mid X=x)$ for all $y \neq x$. The latter assumption is equivalent to specifying that within a column of the matrix $\boldsymbol{Q}$ described earlier, the maximum classification probability occurs on the diagonal. Because the error process will tend to be similar for adjacent age classes, a matrix such as $\boldsymbol{Q}$ can be approximated by a family of parametric distributions with parameters of location and dispersion that depend upon age. For example, Richards *et al.* (1992) used a family of discrete approximations to normal distributions wherein the mode was equal to true age and variance scaled (possibly non-linearly) from a minimum for the youngest age class to a maximum for the oldest. This representation then, requires only three parameters to define $\boldsymbol{Q}$. With slight modification of the notation of

Richards *et al.* (1992), let $Q(\Phi)$ represent the parametric classification matrix and let $\Phi = (\sigma_1, \sigma_m, \alpha)$. Then construct each element $q(y|x,\Phi)$ of $Q(\Phi)$ by the sequence

$$\sigma_x = \begin{cases} \sigma_1 + (\sigma_m - \sigma_1)\dfrac{1-e^{-\alpha(x-1)}}{1-e^{-\alpha(m-1)}} \; ; & \alpha \neq 0 \\ \sigma_1 + (\sigma_m - \sigma_1)\dfrac{x-1}{m-1} \; ; & \alpha = 0 \end{cases}$$

$$r_{yx} = \frac{1}{\sqrt{2\pi\sigma_x}} e^{-\frac{1}{2}\left[\frac{y-x}{\sigma_x}\right]^2} \tag{12}$$

$$q(y|x,\Phi) = \frac{r_{yx}}{\sum_{y=1}^{m} r_{yx}} \; .$$

In this formulation, σ_1 and σ_m are analogous (but not exactly equivalent) to the standard deviations of the observed age y when the true age x equals 1 and m, respectively, and α determines the linearity of the change from σ_1 to σ_m (linear when $\alpha=0$).

The likelihood for a catch-at-age sample of size n, where each member of the sample has been subjected to k independent age readings is

$$L(Y|P,Q) = \prod_{i=1}^{n} \sum_{x=1}^{m} p_x \prod_{j=1}^{k} q(y_i|x,\Phi) \; . \tag{13}$$

Maximizing this likelihood as a function of p_x and Φ produces simultaneous estimates of the true sample age distribution and the parameters defining Q, respectively.

The likelihood shown in (13) was used to estimate the age-error parameters and true age distributions for each of the samples from 1977 to 1989 (e.g., Figure 2). For the samples from 1964 to 1976, only the final age estimate (i.e., not the individual age readings) was available for each individual. It was known, however, that the 1964 age estimates generally resulted from one reading and the 1966-1976 estimates were mostly obtained from two readings. Therefore, I formed a composite estimate of Φ by maximizing (13) over the pooled samples from 1977 to 1989. Then I assumed that each age estimate from the 1964 sample represented one random draw from this composite age-error distribution and the age estimates from the 1966 to 1976 samples represented means of two random draws from the composite distribution. This allowed estimation of the true age distribution for all samples in the collection, producing a new catch-at-age distribution that was then subjected to cohort analysis.

Results and Discussion

The estimates of the true age distributions are shown in Figure 20 along with the observed age distributions for the samples from 1977 to 1989. It can be seen that the effect of accounting for age estimation error is generally to increase the heights of the peaks and decrease the heights of the troughs in the observed age distributions, especially toward the middle age classes. Note also that some samples (e.g., 1985) are less affected by the process of adjustment for age estimation errors than others (e.g., 1989).

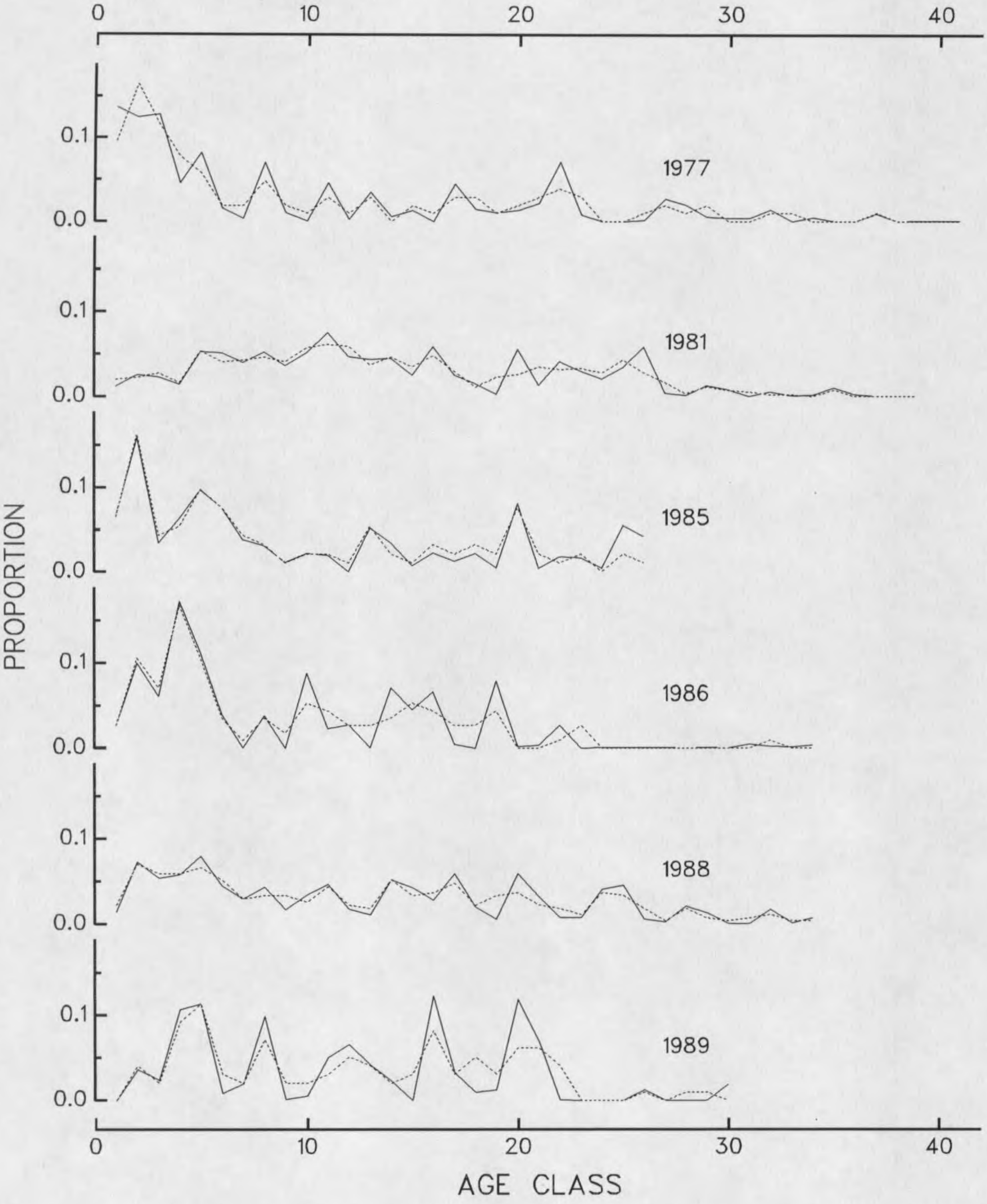

Figure 20. Maximum likelihood estimates of true age distributions (solid lines). The observed age distributions are shown as dotted lines.

The age estimation error parameters for each sample from 1977 to 1989 and the pooled sample are shown in Table 5. The variation due to age estimation error is typically less than would be expected under a Poisson process (i.e., $\sigma^2_m < m$ in most cases). The standard deviation seems to increase approximately linearly with true age (α is near 0) in most cases, as well.

Table 5. Parameter estimates defining the age classification error matrix *Q* for the crabeater seal sample age structures from 1977-1989, and for those samples pooled.

Sample	No. Seals (n)	Max. Age (m)	σ_1	σ_m	α
1977	103	41	0.640	4.15	-0.028
1981	539	39	0.690	3.15	-0.031
1985	92	26	0.490	9.66	-0.033
1986	113	34	0.308	7.83	-0.064
1988	270	34	0.232	1.69	0.128
1989	99	30	0.025	2.10	0.089
pooled	1,216	41	0.478	2.78	0.016

The series of cohort strengths estimated from the samples adjusted for age estimation error is shown in Figure 21. The adjustment procedure changed only slightly the pattern and variability of cohorts 1960-1988 (note that the *y*-axis scales of Figures 9 and 21 are different), but earlier cohorts were made to appear much more variable. The increased variability in cohort estimates was an expected result, although the concentration of the effect into the first few cohorts in the series was not. It is possible that the increased variability of the earlier cohorts resulted from incorrect assumptions about the age-error process affecting the 1964-1976 samples. Recall that the original age readings were not available for those samples and it was assumed that the error process was the same as for the 1977-1989 samples and further that the 1964 teeth were read once and the 1966-1976 teeth were read twice. Because the main difference between the age-error corrected series and the original modeled series of cohort strengths may be simply an effect of the assumptions, I chose to use the original modeled series when comparing cohort variability with environmental variability in Chapter 4.

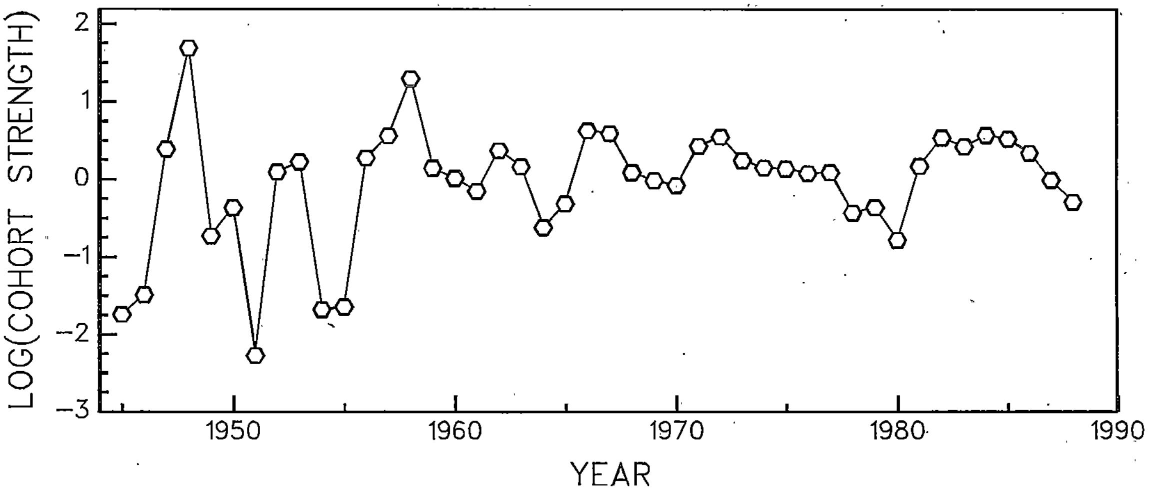

Figure 21. Estimates of crabeater seal cohort strengths, adjusted for error in age estimation.

CHAPTER 3

VARIABILITY IN THE ENVIRONMENT

Introduction

That the Antarctic marine environment is a highly variable place has perhaps never been in question. The seasonal changes apparent in weather and ocean features (especially the annual advance and retreat of sea ice) are extreme. Moreover, there is growing evidence for enviromental changes occurring on time scales of several years to decades. A complete description, however, of the magnitude and timing of this variability has yet to emerge. The polar regions, and particularly Antarctica, have been identified as likely to be most affected by global climate change or the earliest to exhibit evidence of global change (Manabe and Stouffer 1980; Sansom 1989; Gloerson and Campbell 1991; Walsh 1991). Unfortunately, data coverage for detecting changes in Antarctica is more sparse than for most other regions of the world. In particular, time series with potential for establishing background variability are generally short; most meteorological records, for example, have been kept only since the International Geophysical Year (1957/58). Data resources for studies of variability in sea ice — one of the most dramatic features of variability in the marine ecosystem and perhaps the most important for crabeater seals — are limited to recent data from satellites in the 1970s and 1980s. There are, however, a few records from the Antarctic Peninsula region, of surface air temperature and barometric pressure extending back to the turn of the century (Jones and Limbert 1987). There is also a long-term record of barometric pressures from the south Pacific region, associated with the phenomenon known as the Southern Oscillation, that may help to provide clues about sources of variability in the Antarctic. In this chapter I explore the variation over the past few decades in these environmental parameters. More specifically, I demonstrate graphically that variations in these parameters are coherent over the Antarctic Peninsula region and therefore have potential to influence marine populations of that region.

First, I describe the origins of data on surface air temperature, barometric pressure, and sea ice. Next, I describe methods used in common for analyses of all three data sets. I then present summary analyses separately for each environmental parameter and relationships between them. Evidence is discussed, from previous continent-wide studies, for statistical relationships among these environmental parameters. Finally, I conduct a new analysis of the relationships, tailored specifically to the Antarctic Peninsula region. In the following chapter, the relationships between the crabeater seal data and the environmental parameters are explored.

Data Sets

Surface Air Temperature

Air temperatures have been recorded at most Antarctic research stations at least since the International Geophysical Year (1957/58), with one record dating back to 1903. These temperatures, recorded hourly, have been compiled, edited, and reported as monthly means (Jones and Limbert 1987). I used the time series of surface air temperatures from stations in the Antarctic Peninsula and Weddell Sea region to create a composite index of monthly mean temperature for the region from which the crabeater seal specimens (see Chapter 2) were collected.

Five research stations (Islas Orcadas, 60°44'S 44°44'W; Signy, 60°45'S 46°30'W; Esperanza, 63°24'S 56°59'W; Bellingshausen, 62°12'S 58°56'W; and Faraday, 65°15'S 64°16'W) in the vicinity of the Antarctic Peninsula (Figure 1) have time series of surface air temperature that are long enough and complete enough to be of use in comparison with other environmental time series and with crabeater seal data. The data (Jones and Limbert 1987) consist of 417 monthly mean temperatures from each station, beginning with March, 1952 and concluding with December, 1986.

There were 16 observations missing from Bellingshausen; these were estimated by linear regression from Signy temperatures. There were 17 observations missing from Esperanza; these were estimated by linear regression with Islas Orcadas. Because of the high correlation between the records from Signy and Islas Orcadas and the close geographic proximity of the two stations, only the data from Signy were used in further analyses. Figure 22 shows the time series from the four remaining stations, standardized and then smoothed with a center-weighted 12-month moving-average filter. With the annual cycle thus largely removed, strong coherence among the stations can be seen in the lower frequency variations of the time series. Most of these variations are seen in the independently measured records from all four stations and therefore must certainly represent periods when the regional temperature deviated from the long-term average annual means. The correlations among the stations are shown in Table 6.

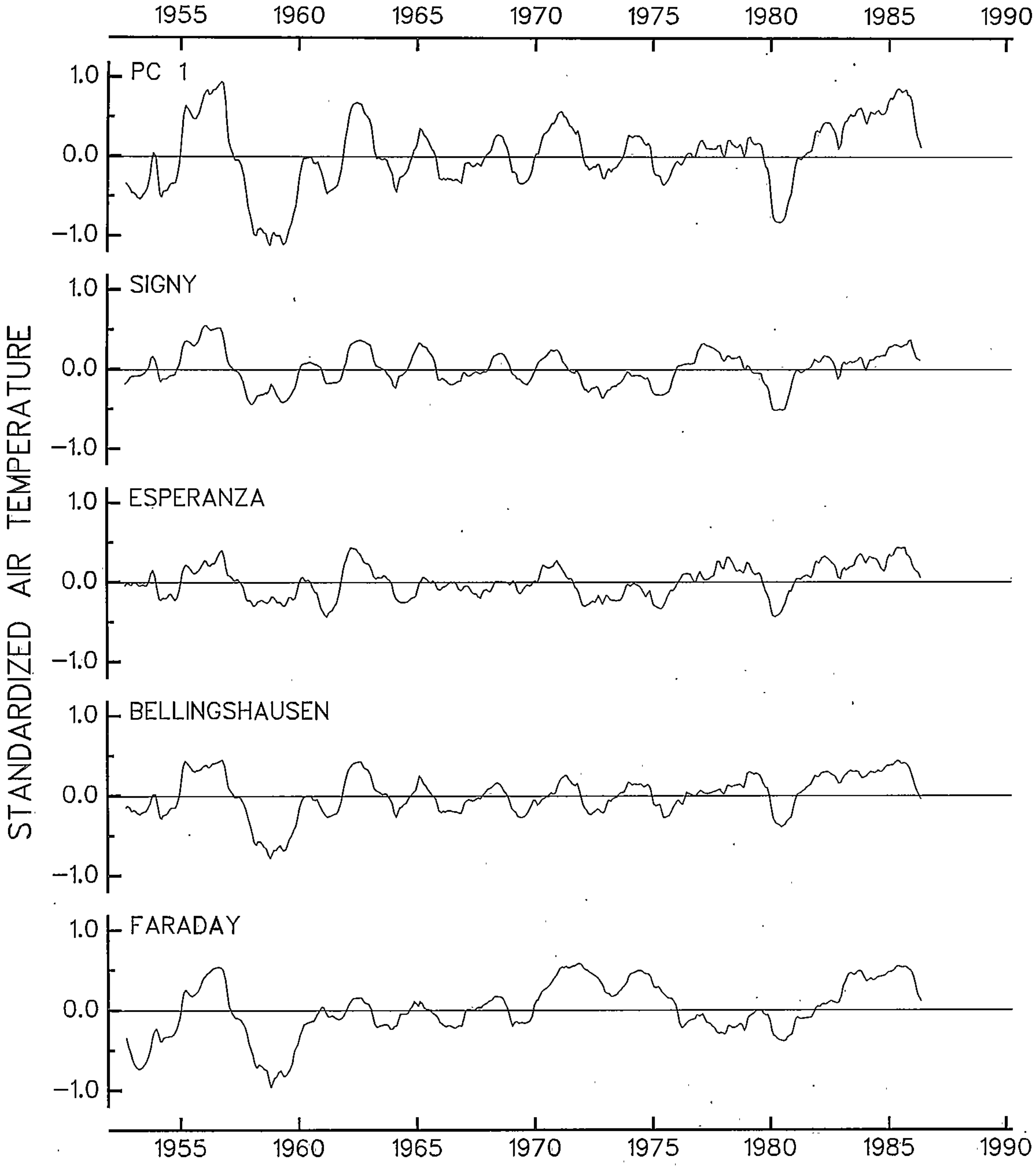

Figure 22. Twelve-month center-weighted moving averages of standardized monthly mean surface air temperatures from four stations on or near the the Antarctic Peninsula. The first principal component (PC 1) is also shown.

Table 6. Correlation matrix and principal components analysis of monthly mean surface air temperatures from four Antarctic research stations, 1953-1986.

	Correlations			
	Signy	Esperanza	Bellingshausen	Faraday
Signy	1.000			
Esperanza	0.867	1.000		
Bellingshausen	0.919	0.878	1.000	
Faraday	0.849	0.765	0.908	1.000

	Principal Components			
	I	II	III	IV
Signy	0.506	-0.104	0.816	-0.259
Esperanza	0.488	-0.702	-0.465	-0.229
Bellingshausen	0.516	0.105	-0.037	0.850
Faraday	0.490	0.696	-0.341	-0.398
Eigenvalue	3.595	0.238	0.110	0.057
Proportion of Variance	0.899	0.059	0.027	0.014

On the supposition that a linear combination of data from several stations would be less influenced than a single station by "noise" from small-scale (spatial and temporal) variation among stations, I conducted a principal components analysis of the matrix of correlations among stations. This analysis yielded a component (PC 1) composed of nearly equal weights from all four stations and which accounted for 90% of the total variance (Table 6). This principal component was used in all further analyses to represent the surface air temperature regime of the Antarctic Peninsula region (Figure 22, top panel).

Barometric Pressure

Two measures of barometric pressure lend themselves to this study. The first is the set of monthly mean sea-level pressures measured at the same stations that produced the surface air temperature data (Jones and Limbert 1987). The barometric pressures exhibited correlations among stations similar to those of the temperatures, and were subjected to principal components analysis in a like manner. The first principal component (PC 1) consisted of nearly equal weightings for all stations and accounted for 92% of the standardized variance (Table 7). The standardized pressures from the four stations and the first principal component are shown as center-weighted 12-month moving averages in Figure 23.

The second set of barometric pressures is the series of monthly mean sea-level pressures measured at Darwin, Australia (e.g., Deser and Wallace 1987). Although geographically far-removed from the Antarctic Peninsula, these data are of interest because of their relation to the Southern Oscillation. Several studies have suggested relationships between the Southern Oscillation and ecological phenomena in Antarctica (Priddle *et al.* 1988; Croxall *et al.* 1988; Fukuoka *et al.* 1990; Testa *et al.* 1991; Chastel *et al.* [in press]). These studies are inconclusive with regard to the strength of such relationships and the lag between the Southern Oscillation and any associated effects in Antarctica. Therefore, I have included the Darwin pressure data with the aim of providing additional information from new analyses of their relationship with environmental data from the Antarctic Peninsula.

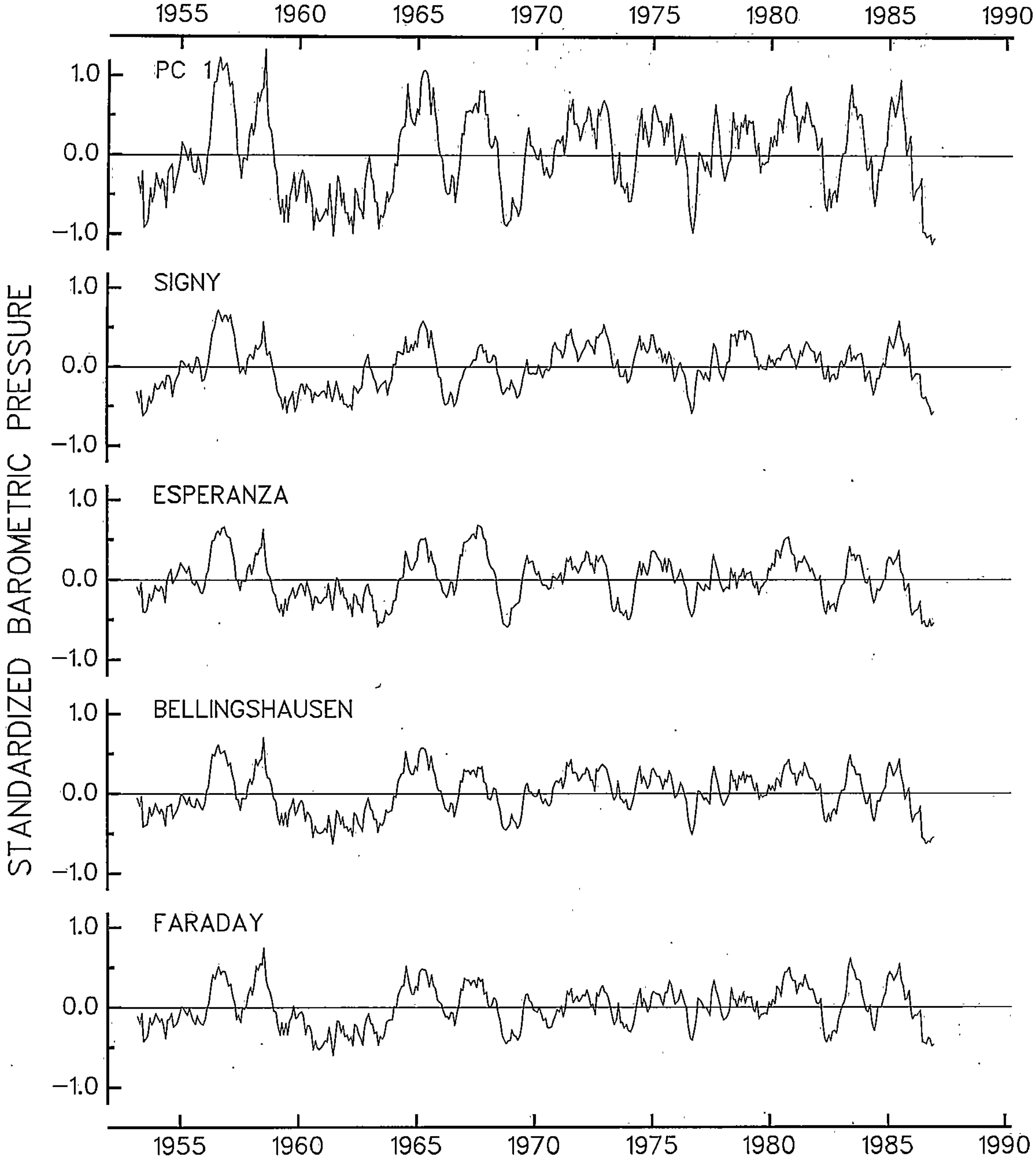

Figure 23. Twelve-month center-weighted moving averages of standardized barometric pressures from four stations on or near the Antarctic Peninsula. The first principal component (PC 1) is also shown.

Table 7. Correlation matrix and principal components analysis of monthly mean sea-level barometric pressures from four Antarctic research stations, 1953-1986.

	Correlations			
	Signy	Esperanza	Bellingshausen	Faraday
Signy	1.000			
Esperanza	0.822	1.000		
Bellingshausen	0.873	0.939	1.000	
Faraday	0.793	0.930	0.975	1.000

	Principal Components			
	I	II	III	IV
Signy	0.474	-0.858	0.024	-0.197
Esperanza	0.504	0.256	-0.825	-0.003
Bellingshausen	0.516	0.117	0.349	0.773
Faraday	0.505	0.430	0.444	-0.603
Eigenvalue	3.669	0.238	0.079	0.014
Proportion of Variance	0.917	0.059	0.020	0.003

Sea Ice

The U. S. Navy/National Oceanic and Atmospheric Administration (NOAA) Joint Ice Center (JIC) has produced weekly charts of Antarctic sea ice since January 1973 (e.g., Godin 1979; Gross 1986). The charts are compiled from various types of satellite imagery, mostly from passive microwave radiometry (Weatherly *et al.* 1991). Jacka (1990) and Jacka and Budd (1991) digitized the northern limit of the ice edge shown on the JIC charts, at intervals of 10° longitude and averaged the weekly values to form a

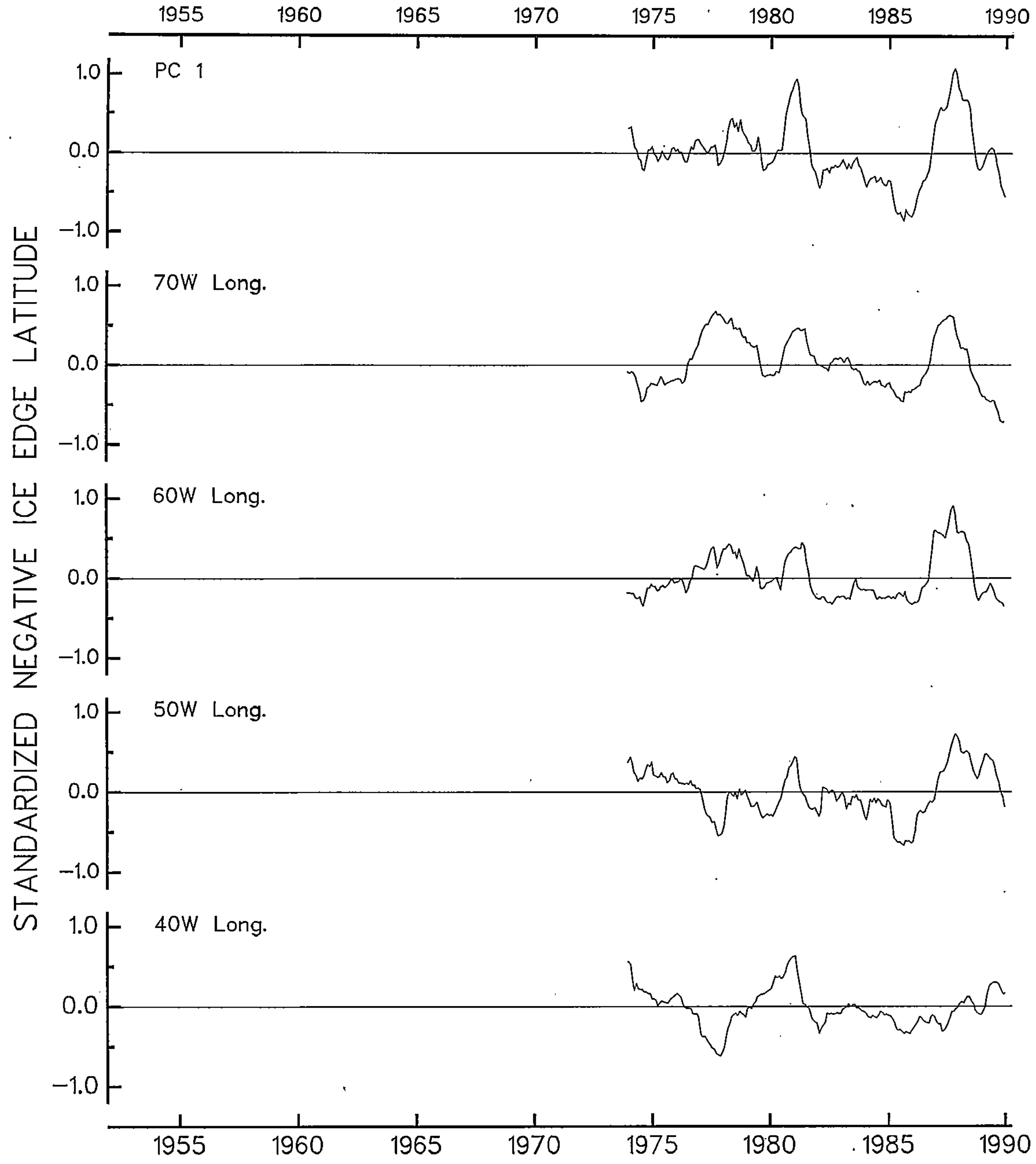

Figure 24. Twelve-month center-weighted moving averages of standardized monthly mean ice edge latitudes measured at four longitudes surrounding the Antarctic Peninsula. The first principal component (PC 1) is also shown. The raw data (degrees south latitude) were transformed to negatives so that upward on the graph signifies more ice.

monthly time series for each longitude interval. Here, I use their data for longitudes 40°W-70°W (Figure 24). These four time series were standardized and subjected to principal components analysis in the same manner as were the temperature and barometric pressure data (Table 8). The first principal component accounted for 76% of the variance. This principal component was multiplied by -1 (so that positive anomalies signify greater ice extent) and used as the index of sea ice conditions for further analyses.

Table 8. Correlation matrix and principal components analysis of monthly mean latitude of the northern edge of the sea ice, measured at four longitudes surrounding the Antarctic Peninsula, 1973-1990.

	Correlations			
	70°W	60°W	50°W	40°W
70°W	1.000			
60°W	0.830	1.000		
50°W	0.663	0.693	1.000	
40°W	0.635	0.591	0.702	1.000
	Principal Components			
	I	II	III	IV
70°W	0.513	-0.440	-0.314	-0.667
60°W	0.511	-0.501	0.062	0.695
50°W	0.499	0.329	0.776	-0.198
40°W	0.475	0.668	-0.543	0.180
Eigenvalue	3.060	0.484	0.296	0.159
Proportion of Variance	0.765	0.121	0.074	0.040

Statistical Methods

To begin to assess the nature of patterns in the three time series described above, the autocorrelation functions were examined. An example, using the surface air temperature series, is shown in Figure 25. The strongly seasonal nature of the time series is evident from the large positive and negative correlations that recur at lags of 12-month multiples. This feature, shared by all the environmental time series (except perhaps barometric pressure from the Antarctic Peninsula region), indicates that most of the variation arises from the seasonal climatic cycle. This relatively high-frequency variation is not of interest for a decade-scale comparison with annual estimates of crabeater seal cohort strengths. Furthermore, any analysis of cross-correlations between pairs of such seasonal variables would be dominated by the seasonal pattern. Rather, the interest is in whether there are patterns in the environmental data spanning several (say, 2 to 5) years that coincide with patterns in the crabeater seal data. These lower-frequency variations may be masked in the raw data by the seasonal pattern. Therefore, I "decomposed" each environmental series into three additive components: seasonal, trend and remainder.

If the seasonal component is taken as a relatively constant annual cycle of higher temperature in summer and lower in winter, attention can be focussed on the trend and remainder components. The resulting trend should indicate periods when the temperature in the Antarctic Peninsula region was higher or lower than the long-term average; this can be compared to biological or other physical time series to assist in explaining their variability. The remainder should be no more than "white noise", random fluctuations with no significant serial correlation or other patterns.

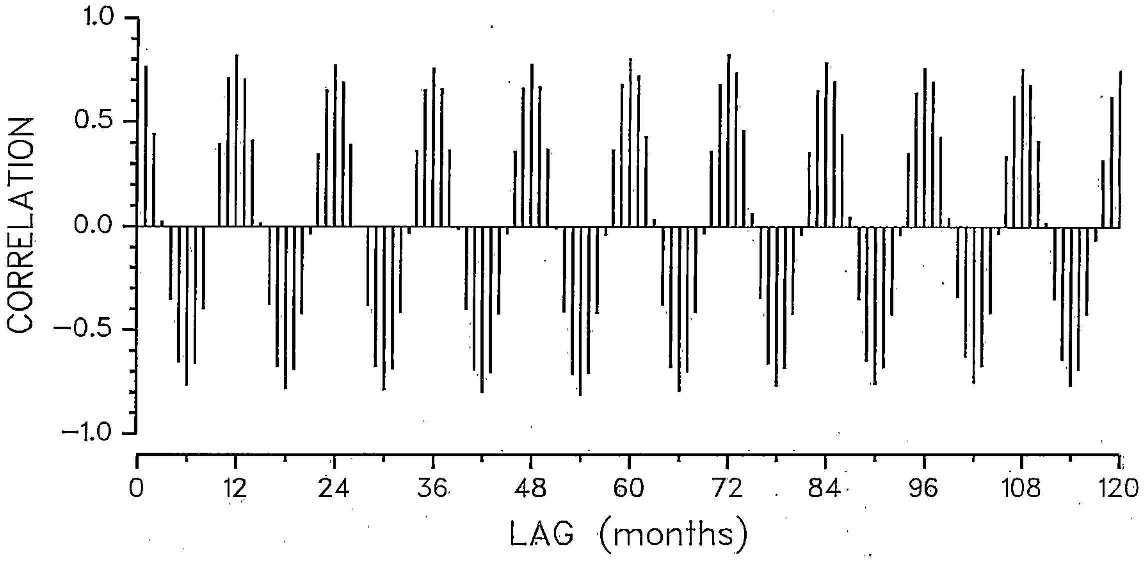

Figure 25. Autocorrelation function for the index of surface air temperature from the Antarctic Peninsula region, 1953-1986.

The decompositions were accomplished by the method called STL (Seasonal-Trend decomposition based on Loess) (Cleveland *et al.* 1990). This procedure forms the seasonal component by smoothing each monthly subseries (i.e., January values from all years, February values from all years, etc.) separately and connecting the smoothed values into a monthly series. This seasonal component is then subtracted from the raw data, leaving trend combined with noise. The latter series is smoothed to get the trend component, leaving a remainder component that should be indistinguishable from "white noise" if the decomposition is to be meaningful. The procedure is adjusted to a particular time series by choosing the lengths of smoothing windows for the two smoothing steps. I discuss the choice for smoothing-window length in the results section below.

The trend components were analyzed for cross-correlations between the environmental parameters at lags and leads of up to 60 months. Cross-correlations were tested for significance using the approximate (large sample) variance estimator:

$$var[\rho_{xy}^{T}(m)] \doteq T^{-1} \ , \tag{14}$$

where x_t and y_t are observed at time points $t = 0, 1, \ldots, T\text{-}1$ and $\rho_{xy}{}^{T}(m)$ is the cross-correlation of y_t with x_{t+m} (Shumway 1988, p. 27). Because the cross-correlations at large lags are based on smaller sample sizes than those at small lags — especially when using the short time series for ice — I modified the variance estimator slightly by accounting for the effect of the lag on the sample size:

$$var[\rho_{xy}^{T}(m)] \doteq (T-m)^{-1} \ . \tag{15}$$

This variance was used to compute a *P*-value for each cross-correlation coefficient, from the two-tailed critical values of the standard normal distribution. These *P*-values were then adjusted for simultaneous testing (all lags and leads tested) to allow comparison with an experiment-wise Type I error probability of $\alpha = 0.05$. To adjust the *P*-values, I used the procedure by Hommel (1988) as described by Wright (1992).

Results

Seasonal Decompositions

Surface Air Temperature. In Figure 26, the air temperature series is shown in its original form (first principal component from four stations) and decomposed into seasonal, trend and remainder series. The trend line suggests that the 1950s were characterized by periods of 2 to 3 years of unusually high or low temperatures. From 1960 to about 1980, there were small to moderate fluctuations. The 1980s began substantially colder than usual, but then warmed for a relatively prolonged period of about 5 years. Comparison of the trend with the non-decomposed series (PC 1) indicates that the trend results primarily from variations in the winter minimum temperatures; the summer maximum temperatures are much less variable. Note that the seasonal component has been made to be quite consistent over the duration of the series by choosing a long seasonal smoothing window (31 months). This ensures that the variations in winter minimum temperatures result in trend variation rather than variation in the seasonal cycle.

<u>Barometric Pressure - Antarctic Peninsula</u>. The results of STL decomposition of the Antarctic Peninsula station barometric pressures are shown in Figure 27. An obvious result is that the seasonal component is complex, having two maxima and two minima per year. This has been described as a "semiannual wave" that occurs south of approximately 50°S (van Loon and Shea 1988). Because the troughs coincide with both minimum and maximum extent of sea ice, there may be little information in barometric pressure data about sea ice variations that may have occurred before sea ice imagery began to be acquired. For that reason, and because all STL decompostions of these barometric pressure data resulted in remainder components that were highly correlated with the raw data, I did not use Antarctic Peninsula pressure data in further analyses.

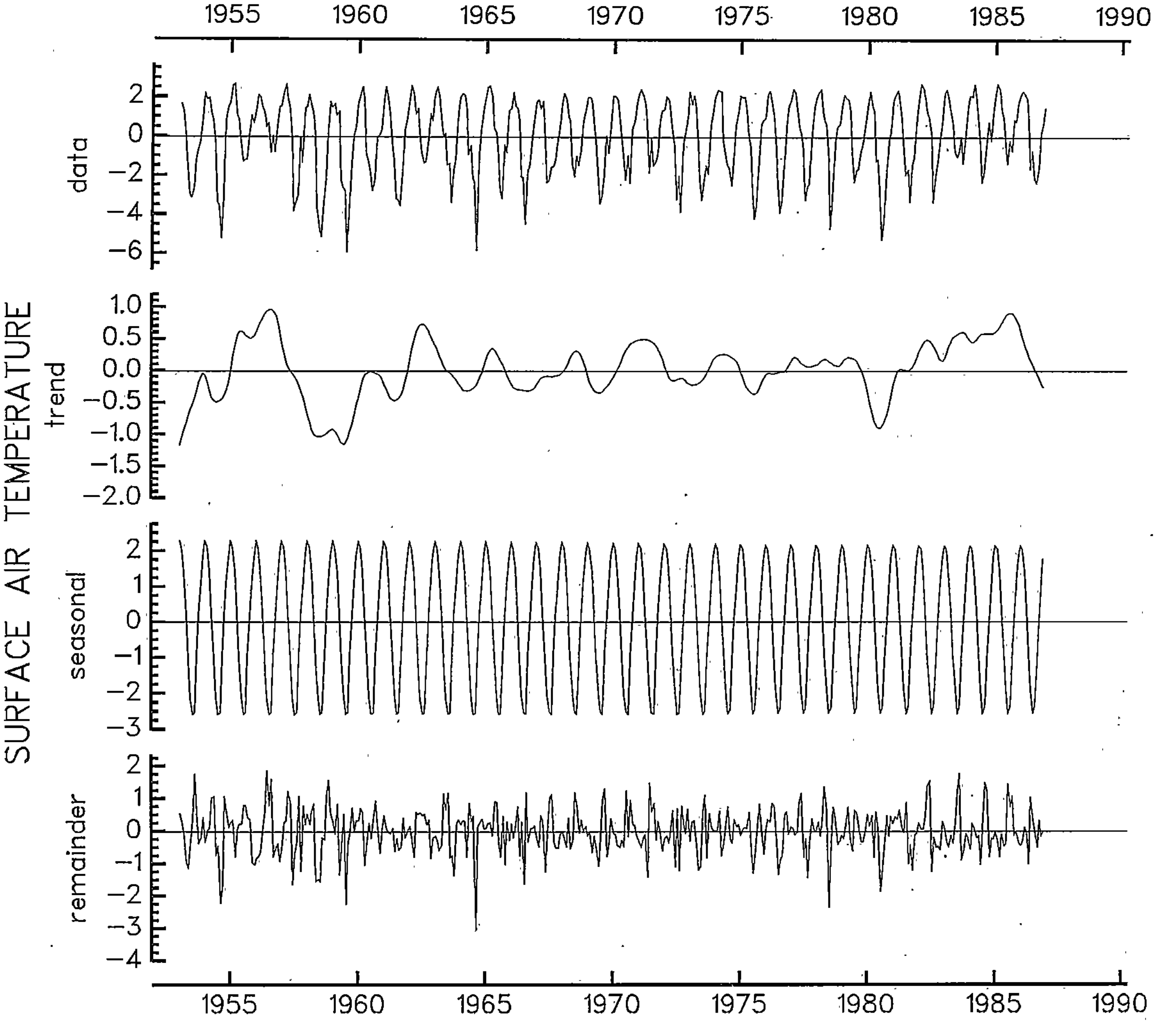

Figure 26. Decomposition of the surface air temperature data (PC 1) into seasonal, trend and remainder components by the STL method.

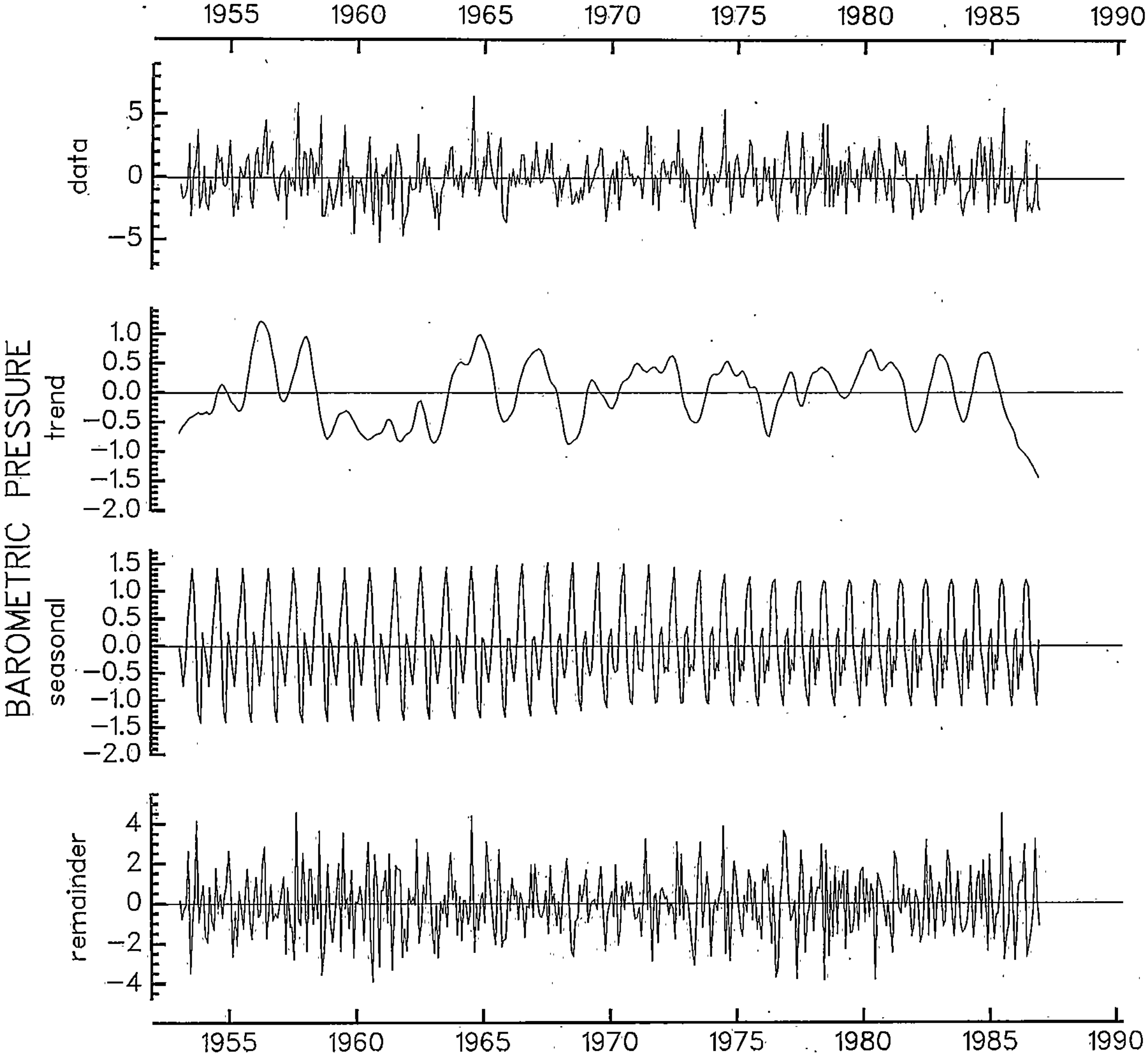

Figure 27. Decomposition of the Antarctic Peninsula barometric pressure data (PC 1) into seasonal, trend and remainder components by the STL method.

Barometric Pressure – Darwin. The seasonal component of the Darwin barometric pressure series (Figure 28) is simpler than that from the Antarctic Peninsula, with one cycle per year. The general range of frequencies in the trend variation appears similar to that of the air-temperature series.

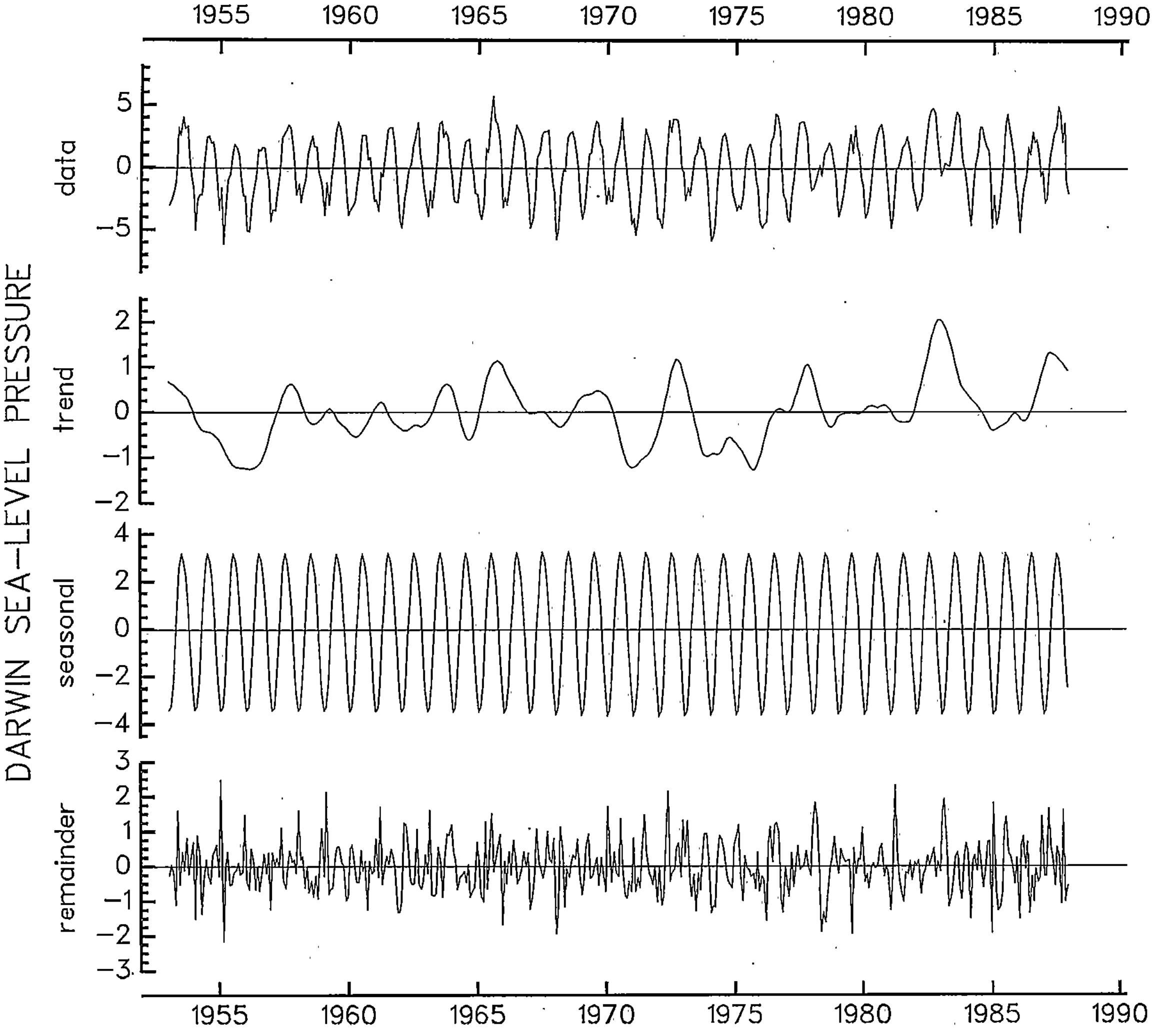

Figure 28. Decomposition of the Darwin sea-level pressure data into seasonal, trend and remainder components by the STL method.

Sea Ice. The decomposition of sea ice data is shown in Figure 29 on the same time scale as were the temperature and pressure data to facilitate comparison. Note that the ice edge latitudes were multiplied by minus one so that greater sea ice extent is toward the top of the figure. The trend of the relatively short time series for ice will be more influenced than the other series by the values near the ends, which have greater uncertainty than the central values as a result of the smoothing procedure (Cleveland *et al.* 1990).

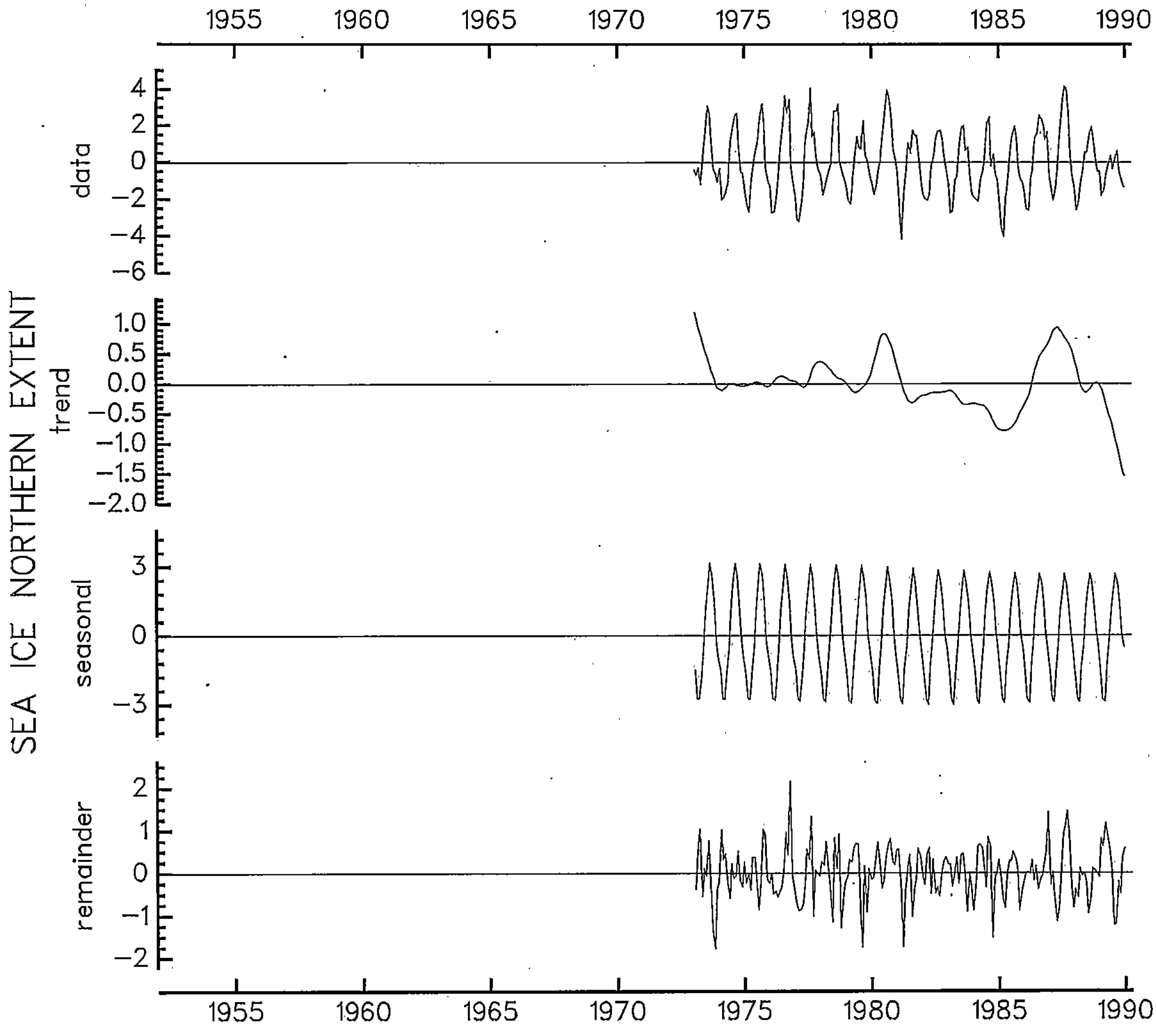

Figure 29. Decomposition of sea ice data into seasonal, trend and remainder components by the STL method.

Cross-Correlations

Air Temperature and Darwin Barometric Pressure. Figure 30 shows the cross-correlations between Antarctic Peninsula air temperature trend and Darwin sea level pressure trend. The correlations are generally low, and are mostly significant for pressure leading temperature and not significant for pressure lagging temperature. The peak correlations occur for pressure leading temperature by 24 months (ρ=0.32), 57 months (ρ=0.33), and 4 months (ρ=−0.23) and temperature leading pressure by 14 months (ρ=0.24).

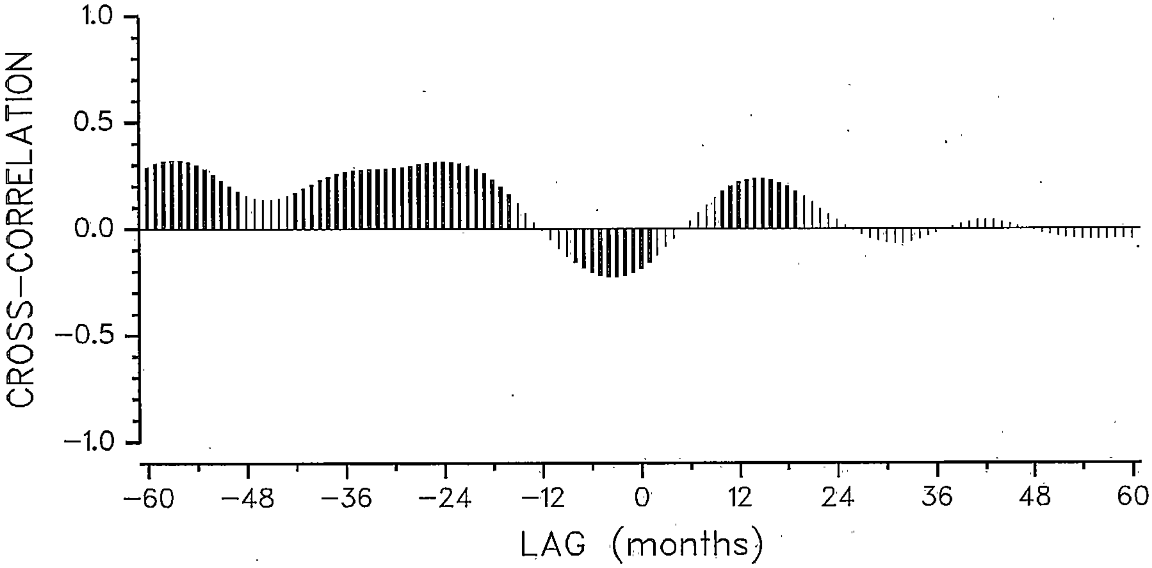

Figure 30. Cross-correlations between STL trends for Antarctic Peninsula surface air temperature and Darwin barometric pressure. Temperature leads pressure for positive lags. Correlations significant at an experiment-wise (all lags tested) level of α=0.05 are indicated with bold bars.

Air Temperature and Ice Extent. The trend components of Antarctic Peninsula air temperature and sea ice extent are strongly and negatively correlated ($\rho = -0.82$) at zero lag (Figure 31). Over the entire range of lags and leads, the cross-correlations are roughly symmetric. This result is related to questions about a the so-called "temperature-ice-albedo feedback" mechanism (e.g., Weatherly *et al.* 1991) which is considered in the discussion below.

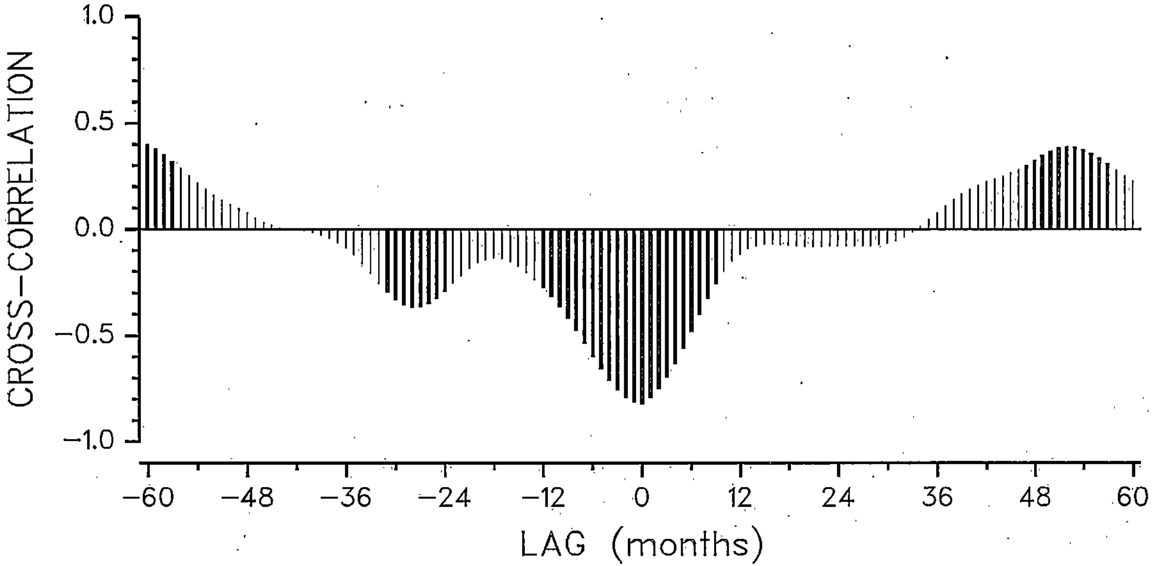

Figure 31. Cross-correlations between STL trends for Antarctic Peninsula surface air temperature and ice extent. Temperature leads ice for positive lags. Correlations significant at an experiment-wise (all lags tested) level of $\alpha=0.05$ are indicated with bold bars.

Barometric Pressure and Ice Extent. All of the significant cross-correlations between Darwin pressure and Antarctic Peninsula ice extent occur for pressure leading or concurrent with ice extent (Figure 32). The peaks occur at lags of 0 months ($\rho=0.25$), 24 months ($\rho=-0.52$) and 50 months ($\rho=0.33$).

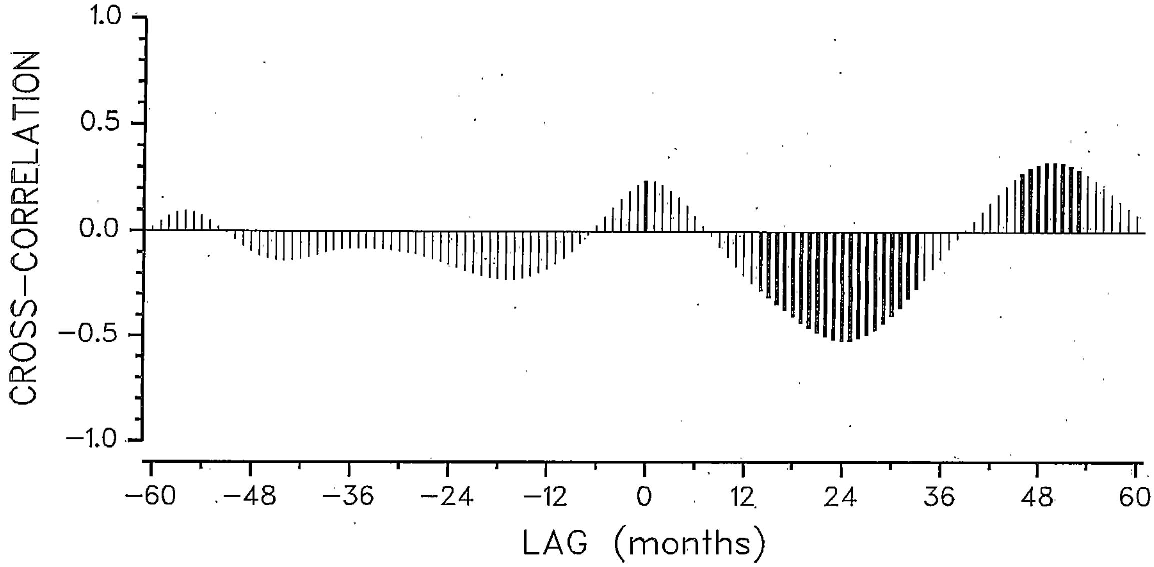

Figure 32. Cross-correlations between STL trends for Darwin sea-level pressure and ice extent. Sea-level pressure leads ice for postive lags. Correlations significant at an experiment-wise (all lags tested) level of $\alpha=0.05$ are indicated with bold bars.

Discussion

There are several alternatives to the technique used here (STL) for resolving the low-frequency trends in environmental time series. Examples include methods as simple as taking the 12-month center-weighted moving average or more complex model-based procedures (e.g., Hillmer & Tiao, 1982; Shumway 1988). Because the principal aim is to resolve the gross features and patterns of several years' duration from monthly data for comparison with the relatively crude annual time series of crabeater seal cohort strengths, the particular smoothing technique will have little effect on the outcome. For example, I obtained nearly identical results for cross-correlations between temperature and sea ice whether the 12-month moving averages or the STL trends were used. I chose the STL method because it produces additive components that are easily subjected to further tests. For example, the remainder component could be tested for departures from "white noise" characteristics. Other tests could be applied to the seasonal component, as well.

Ice–Temperature Relationship

Early attempts to describe the relationship between sea ice and climate in Antarctica (reviewed by Heap 1964) were motivated by the need to predict sea ice conditions for navigation. These studies were subject to the limitation that ice conditions could only be observed from ships or from stations occupied year-round. More recent studies of sea ice and climate relationships have focussed on detection of climatic change (Raper *et al.* 1984; Jacka and Budd 1991; Weatherly *et al.* 1991), usually on a continent-wide basis. Despite advancements in capabilities of remote sensing from satellites, the sea ice record remains the limiting factor in these analyses due to the shortness of the time series, which began in 1973. Although these studies have been unable to demonstrate clear and consistent relationships between variations in surface air temperature and in sea ice, two lines of evidence suggest that such an endeavor might prove fruitful when limited in scope to the Antarctic Peninsula region.

First, Sansom (1989) found strong coherence between four widely separated Antarctic stations, in the de-seasonalized trends of surface air temperatures from the late 1950s to the late 1980s. This suggests that there are discernable trends in temperature and there should be reason to suspect that the coherence would be even stronger when limited to a small subset of the area considered by Sansom (1989).

Second, Weatherly *et al.* (1991) suggested that the strongest correlations between sea ice and air temperature at research stations might occur when the stations are in close proximity to the ice, as occurs in the Antarctic Peninsula region. They found strong ice–temperature correlations in that region, using seasonally averaged data (i.e., January, February and March combined; April, May and June combined; etc.) and considering the Weddell Sea ice separately from that of the Amundsen-Bellingshausen Sea.

Because the crabeater seal population of interest in my study was sampled from both sides of the Antarctic Peninsula, I used an index of ice extent that combined the western Weddell Sea with the eastern Amundsen-Bellinghausen Sea and found that the strong correlation between sea ice and air temperature still held. The cross-correlations I found between surface air temperature and sea ice latitudinal extent were roughly symmetric with respect to leads and lags, providing no information about causal relationships between the two variables or about the direction of the "temperature-ice-albedo feedback" (Weatherly *et al.* 1991). The concept of this feedback includes the effect of air temperature on formation of ice at the water surface as well as the effect of reflectance (albedo) from sea ice on air temperature. Although it is widely acknowledged that both phenomena occur, it remains unclear which is most responsible during the various phases of seasonal expansion and contraction of sea ice extent. Despite this lack of understanding of the mechanisms, the strong correlation between Antarctic Peninsula surface air temperature and sea ice may prove useful to this and other studies seeking to relate ecological phenomena to variability in sea ice because the long series of air temperatures may serve as a proxy for the relatively short series available for sea ice.

Southern Oscillation Effects on the Antarctic Peninsula

The tendency for sea ice and surface air temperature of the Antarctic Peninsula to correlate with prior sea-level pressures at Darwin, Australia adds support to other studies — reviewed by Smith (1991) — that have suggested the existence of such a link. To the best of my knowledge, however, none of those studies have indicated that there may be a two-year lag associated with the phenomenon. Smith (1991) found that the sign of Antarctic temperature and pressure anomalies change during the periods from one year before to one year after prominent minima in the Southern Oscillation Index (maxima in Darwin pressure series). His conclusion, however, was that patterns in the atmospheric flow over the major drainage basins of the Antarctic continent may be responsible for maintaining persistent meteorological features in the New Zealand region which may in turn affect the El Niño Southern Oscillation (Trenberth 1980). Thus, if the correlations I observed for Darwin pressure leading Antarctic Peninsula temperature and sea ice by two years reflect genuine forcing of the Peninsula region by events in the south Pacific, the relationship between Antarctica and the Southern Oscillation may be bi-directional: Atmospheric circulation in the Ross Sea region influencing the Southern Oscillation could eventually (perhaps two to three years hence) affect the Antarctic Peninsula environment and its biota. This could be related to a circumpolar precession of sea-ice anomalies on a cycle of about 7-8 years that has recently been reported (Pozdeeva *et al.* 1990; unpublished manuscripts cited in Croxall (1992)). Detection and documentation of such relationships have just begun. Rapid progress in this area should be possible with increased use of satellite remote sensing and increased coverage of meteorological monitoring stations in and around Antarctica (Stearns and Weidner 1991).

CHAPTER 4

ENVIRONMENTAL AND ECOLOGICAL FACTORS IN CRABEATER SEAL POPULATION DYNAMICS

The aim of this chapter is to explain as completely as the present data allow, the factors responsible for cohort variability during the past four to five decades in crabeater seals of the Antarctic Peninsula. Previous studies are reviewed to establish which factors are candidates for population regulation. These factors include environmental (physical) and ecological phenomena. The results of Chapters 2 and 3 are used to estimate the amount of cohort variability that might be explained by variations in sea ice, surface air temperature, or barometric pressure. Previously published data on variability in leopard seal populations are tested for potential to explain crabeater seal cohort variability. Other factors, such as disease and reduced competition for food following the harvest of large whales are discussed but not tested quantitatively. Finally, an experiment is proposed to further distinguish among certain environmental and ecological causes of the crabeater seal population variability.

Factors Potentially Affecting Cohort Strength

Environmental Factors

Sea Ice. Temporal variation in sea ice extent could cause variation in crabeater seal populations because several lines of evidence suggest that the seals are dependent upon sea ice to breed, bear young, avoid predation, rest between foraging bouts, and capture food.

During the pupping, lactation and breeding period (September-October), crabeater seals appear to depend on sea ice floes, as there are no accounts of these activities observed on other substrates. After giving birth, each lactating female fasts and remains on an ice floe with her pup, nursing it for a period of about four weeks (Siniff *et al.* 1979; Shaughnessy and Kerry 1989). Copulation with an attendant male after the pup is weaned is presumed to take place on ice floes, though it is unknown whether successful mating can also occur in the water.

During the austral spring and summer months of November-March, weaned crabeater seal young-of-the-year may require sea ice for refuge from leopard seal predation (Siniff and Bengtson 1977; Siniff *et al.* 1979). Although most adult crabeater seals bear scars from encounters with leopard seals, the encounters nearly all take place during the first year of life, probably shortly after weaning (Siniff and Bengtson 1977; Siniff *et al.* 1979). Although a sample of 45 crabeater seal pups (prior to weaning) had no leopard seal wounds (Siniff and Bengtson 1977), circumstantial evidence suggests that leopard seals may occasionally take crabeater pups on ice floes (Siniff *et al.* 1979). Nevertheless, most of the evidence indicates that young crabeater seals are frequently preyed upon in the water and presumably the predation rate would be higher at times when the safety offered by large platforms of sea ice is relatively unavailable.

All age classes of crabeater seals may need sea ice to haul out upon between feeding bouts (Erickson *et al.* 1989; Bengtson and Stewart 1992). For example, Bengtson and Stewart (1992) found that in a sample of six seals equipped with time-depth recorders, each individual hauled out on at least 80% of the days observed. The haulouts occurred during daylight hours, between nightly feeding bouts. The reasons that seals haul out are not known, but could be related to thermoregulation, prey availability or resting.

Finally, crabeater seals may be dependent upon sea ice in at least two aspects of foraging. First, the seals may require, during certain periods of the year, ice cover for locating and capturing krill that graze the algae growing on the ice undersurface (Stretch 1988). Second, and perhaps less direct but potentially as important, krill production and overwinter survival may be linked to sea ice abundance and distribution (Marschall 1988) such that entire year-classes of krill may fail when sea ice conditions are unfavorable.

Because most of these potential dependencies of crabeater seals upon sea ice involve the ice conditions in the first year of the seals' lives, I hypothesized that cohort strength would be positively correlated with sea ice extent in concurrent years (zero lag).

Other Environmental Factors. Other environmental parameters that might be linked to crabeater seal populations and that have been recorded for long enough to support quantitative comparisons include surface air temperature and barometric pressure. Surface air temperature could be related to the seal populations through links to sea ice (e.g., the "temperature-ice-albedo feedback" (Weatherly *et al.* 1991)). If so, it may be easier to detect a relationship between sea ice and cohort strength using surface air temperature data because of the longer temperature record and high correlation between sea ice and surface air temperature (Chapter 3). I therefore hypothesized that the zero-lag correlation between surface air temperature and cohort strength would be negative (positive correlation between sea ice and cohort strength).

Variability in barometric pressure could influence seal populations through seasonal changes in wind patterns that disrupt typical hydrographic structure and thereby affect krill distribution. Priddle *et al.* (1988) suggested that this link might explain fluctuations in krill predator performance at South Georgia (e.g., Bengtson 1988). There are considerably fewer data available for assessing whether a similar link occurs between atmospheric variation and crabeater seals of the Antarctic Peninsula.

Ecological Factors

I include in this category both intrinsic biotic factors such as disease and external biotic factors such as predation and competition.

Disease. Two studies suggest that crabeater seal populations may occasionally be subject to epizootic infections severe enough to cause population or cohort variability. First, there was a mass dying of crabeater seals in the western Weddell Sea in 1955 (Laws and Taylor 1957). Approximately 85% of the crabeater seals wintering in Prince Gustav Channel died, probably from viral infections. Many aborted fetuses, but no births or live pups were observed in that area. Second, antibodies to canine distemper virus were found in blood collected from crabeater seals in 1989 along both sides of the Antarctic Peninsula (Bengtson *et al.* 1991). Canine and phocine distemper viruses have been responsible for widespread mortality in Baikal seals (*Phoca sibirica*) and European harbor seals (*Phoca vitulina*). If similar infections occur in crabeater seals, they could be the cause of at least some of the observed cohort variability. Note that the weakest cohorts in the modeled series of cohort strengths (Figure 9) are those born in 1954 and 1955. Allowing for effects of age estimation error, that result is consistent with an interpretation of reproductive failure of the 1955 cohort, perhaps from an infectious disease (Laws and Taylor 1957).

Predation. As discussed above, leopard seal predation may play a major role in regulation of crabeater seal populations (Siniff and Bengtson 1977; Siniff *et al.* 1979). Little is known of variability in leopard seal populations near the Antarctic Peninsula but annual sightings of leopard seals at Macquarie Island, south of Australia, have undergone substantial fluctuations during the past four decades (Rounsevell and Eberhard 1980; Rounsevell 1988; Testa *et al.* 1991). Although these data concern primarily immature leopard seals, they may be indicative of fluctuations in abundance and/or distribution of other age classes as well. If so, and if similar fluctuations occur near the Antarctic Peninsula, the documented high frequency of predation by leopard seals on young crabeater seals would imply the potential for leopard seal population variability to cause the variability described for crabeater seals in Chapter 2. There is insufficient information available on which to base an *a priori* hypothesis concerning the correlation between cohort strengths of crabeater seals of the Antarctic Peninsula and sightings of leopard seals at Macquarie Island.

Competition. There has been much interest in the effects of a "krill surplus" that may have resulted from the removal of most of the large krill-consuming whales from the Southern Ocean (e.g., Laws 1977b). Bengtson and Laws (1985) noted that their measure of cohort strength increased in the years immediately following peaks in whaling activities during the 1950s and 1960s. However, other periods of high cohort strengths in their data and in the longer time series estimated by Testa *et al.* (1991) and in this study (Figure 9) are associated with periods of little or no whaling. Thus, it seems unlikely that substantial variation in cohort strengths could be explained by variation in competition pressure caused by variation in whaling activities. Several recent studies have concluded that the "krill surplus" concept is too simplified to explain the recent patterns in abundance of Antarctic marine mammals and seabirds (Fraser *et al.* 1992; Croxall 1992). In any case, there are virtually no data available to document that krill became more available to seals and birds following reduction of whale stocks and few data to document abundance or condition of the species that may have been affected.

Methods

Cross-correlations between the modeled series of crabeater seal cohort strengths (from Chapter 2) and sea ice extent, surface air temperature, Darwin sea-level pressure (from Chapter 3) and leopard seals sighted at Macquarie Island (Rounsevell and Eberhard 1980; Rounsevell 1988) were computed at leads and lags of up to five years. The trend components from STL decompositions (Chapter 3; Cleveland *et al.* 1990) were used to represent the three environmental parameters. Because the modeled series of cohort strengths is an annual series and the environmental series are monthly, the latter were converted to annual values by averaging over the period from November through October (the annual cycle for crabeater seals, beginning just after completion of pupping). The log-transformed numbers of annual sightings were used for the leopard seal time series.

P-values were computed for all cross-correlations by the complementary error function of the standardized Fisher z-transformed values of the coefficients (Press *et al.* 1992). For the *a priori* hypotheses set forth above, the statistical significance of the correlations were judged by whether the P-value was less than α=0.05. For relationships not associated with an *a priori* hypothesis, statistical significance of each correlation was judged by adjusting the P-value for comparison with an experiment-wise (all lags considered simultaneously) α-level of 0.05 (Wright 1992).

Results

Sea Ice

The cross-correlations between crabeater seal cohort strength and sea ice extent are shown in Figure 33. The *a priori* hypothesis set forth above, that cohort strength would be positively correlated with sea ice extent in concurrent years, must be rejected, for the zero-lag correlation is only -0.111 (P=0.683). In fact, the highest correlation is negative (ρ=-0.612) with sea ice leading by one year, but is not significantly different from zero when all leads and lags up to five years are considered. The lack of significance for such a high correlation is due to the shortness of the sea ice time series.

Because there is a high negative correlation between sea ice and surface air temperature (ρ=-0.82), the longer record of temperatures may serve as a proxy for sea ice extent.

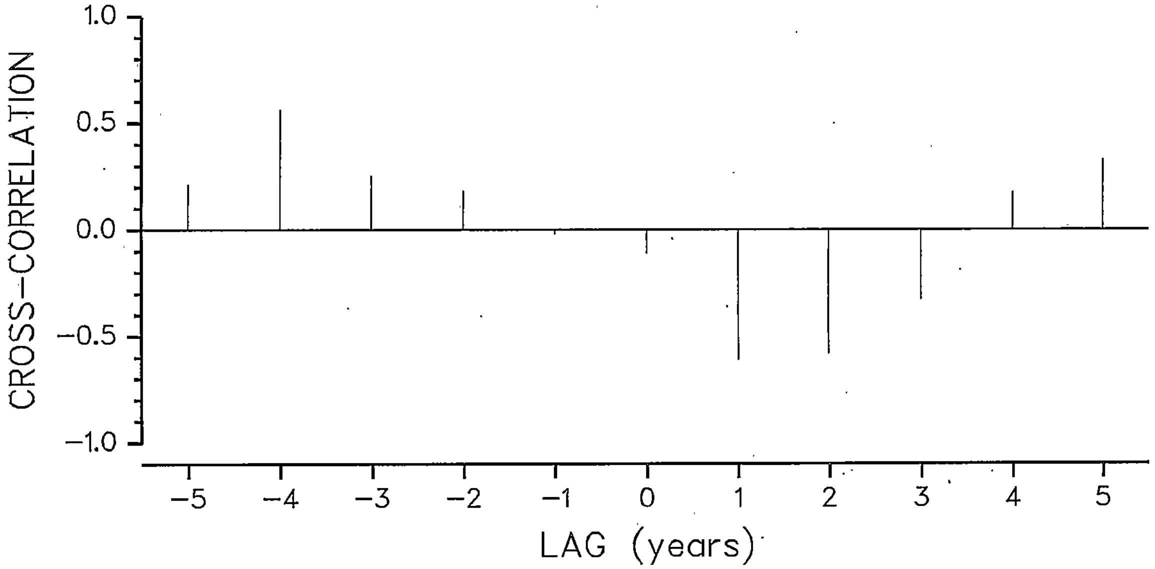

Figure 33. Cross-correlations between the modeled series of cohort strengths and the STL trend for sea ice extent. Sea ice leads cohort strength for positive lags. At an experiment-wise (all lags tested) level of α=0.05, none of the cross-correlations is significant.

Surface Air Temperature

The cross-correlations between crabeater seal cohort strength and Antarctic Peninsula surface air temperature are shown in Figure 34. Even with the relatively long time series of temperatures the hypothesized positive correlation between sea ice and cohort strength (a negative correlation between temperature and cohort strength) is not supported (ρ=-0.189, P=0.292). None of the correlations are significant when all lags are considered simultaneously.

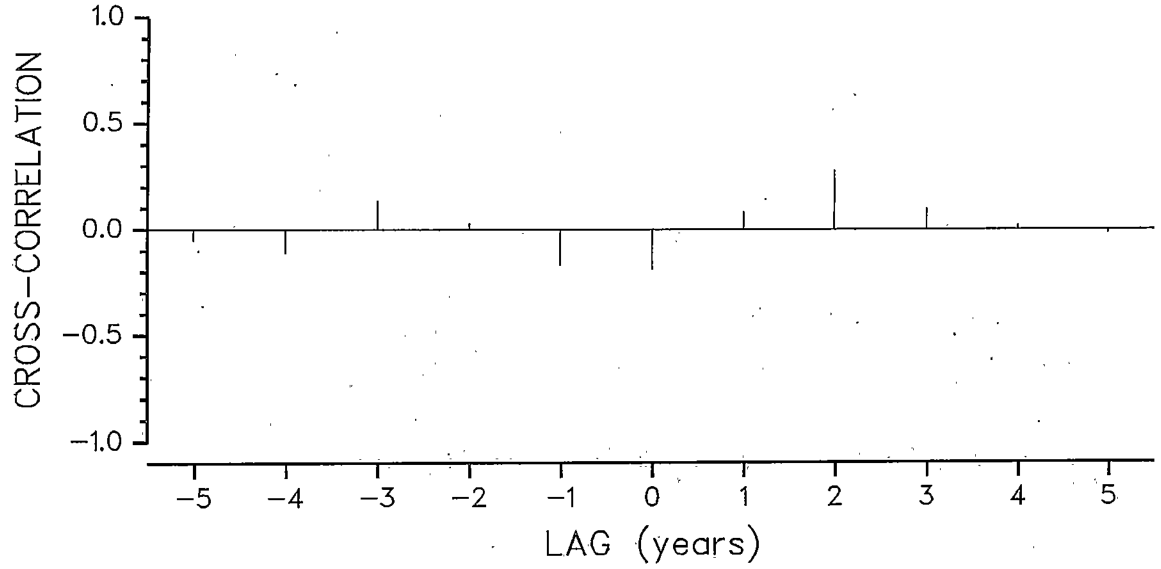

Figure 34. Cross-correlations between the modeled series of cohort strengths and the STL trend for Antarctic Peninsula surface air temperature. Temperature leads cohort strength for positive lags. At an experiment-wise (all lags tested) level of $\alpha=0.05$, none of the cross-correlations is significant.

Darwin Sea-Level Pressure

The cross-correlations between crabeater seal cohort strength and sea-level pressure at Darwin, Australia are shown in Figure 35. None of the correlations are significant when all lags are considered simultaneously.

Leopard Seal Sightings

The cross-correlations between crabeater seal cohort strength and log-transformed annual sightings of leopard seals at Macquarie Island are shown in Figure 36. None of the correlations are significant when all lags are considered simultaneously.

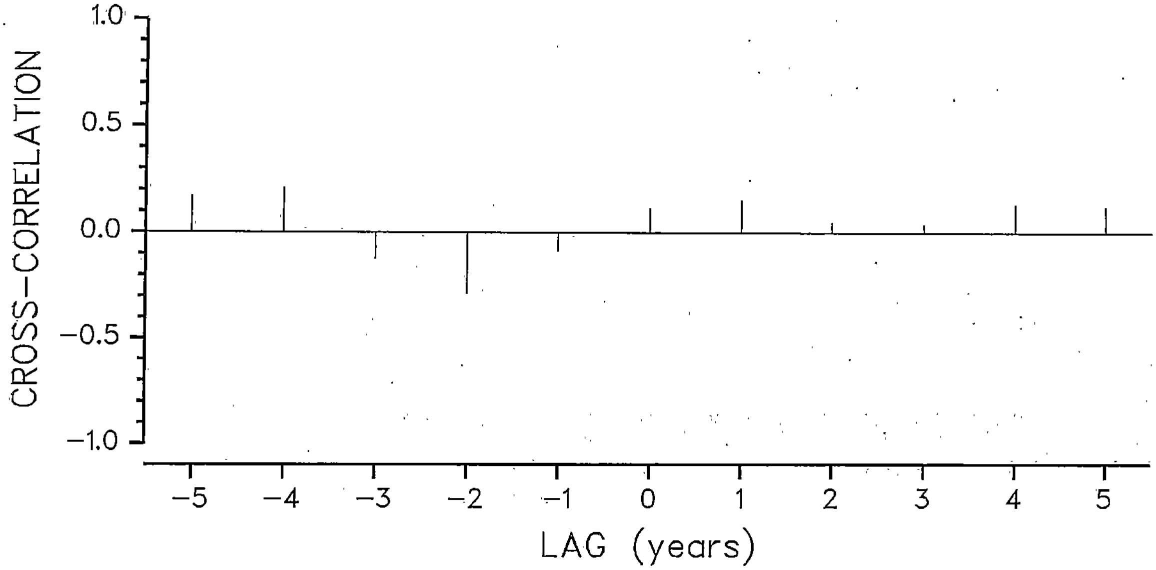

Figure 35. Cross-correlations between the modeled series of cohort strengths and the STL trend for Darwin sea-level pressure. Pressure leads cohort strength for positive lags. At an experiment-wise (all lags tested) level of $\alpha=0.05$, none of the cross-correlations is significant.

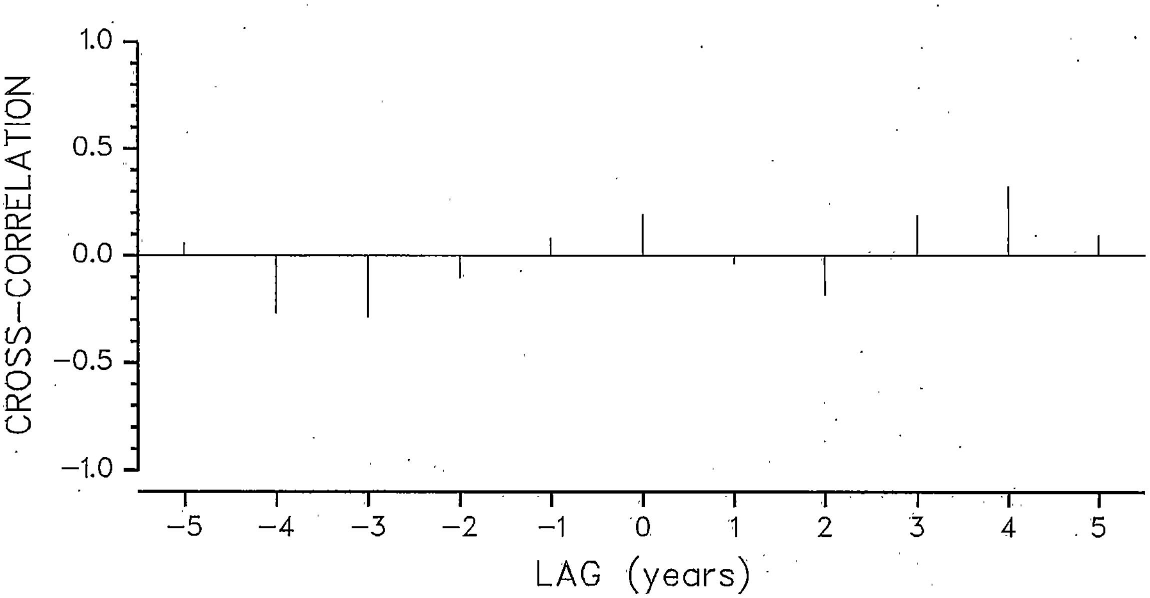

Figure 36. Cross-correlations between crabeater seal cohort strengths and sightings of leopard seals at Macquarie Island. Leopard seal sightings lead cohort strengths for positive lags. At an experiment-wise (all lags tested) level of $\alpha=0.05$, none of the cross-correlations is significant.

Discussion

The failure to detect significant correlations — i.e., the lack of power to explain variability in the crabeater cohort strengths — could be due to a variety of causes. One is, of course, that the hypothesized relationships simply do not exist, or they exist only in rare circumstances not well represented in the data set. Although crabeater seals may be dependent on sea ice, for example, ice may have always been plentiful enough that the effect was not manifested in the data used here. Another possibility is that cohort strengths vary with some combination of environmental and ecological factors in a way that cannot be approximated by the variability in a single parameter of the type I tested. It is also possible that true correlations were masked or reduced to insignificance because the variables were measured incorrectly or with too much error. For example, the index of sea ice extent used here (negative latitude of the northern edge of the sea ice measured at four longitudes near the Antarctic Peninsula; Chapter 3) may not capture the aspects of sea ice variability most important to crabeater seals; the index takes no account of the ice characteristics nor the amount of ice-covered area south of the ice edge. As was acknowledged in Chapter 2, the age estimates from which the cohort strengths were computed contain errors. It is perhaps noteworthy that the peak correlations were higher — though not necessarily at the same lag — in every test (cohort strength vs. sea ice, air temperature, Darwin pressure, and leopard seal sightings) when the "age-error corrected" series of cohort strengths (Figure 21) were used in place of the modeled series. As indicated in Chapter 2, however, there is sufficient uncertainty regarding the process used for estimation of ages of seals in the early half of the collections that I chose not to draw conclusions about whether the "age-error corrected" series is truly a better representation of cohort strength than the modeled series. Finally, the approach taken here, namely to use trends in the explanatory variables that resolve events of durations similar to the durations of fluctuations in the cohort series (two to four years, say), would likely not detect relationships that occur on shorter time scales. Perhaps, for example, anomalous temperatures during just one critical month of the seals' annual cycle affect the cohort strength in that year or the following year. The STL decompositions that I used would relegate such anomalies to the noise term, which was not tested for potential to explain cohort strengths (because the necessary hypotheses would be much more detailed and were envisioned as a logical next step from the present study).

The crabeater seal catch-at-age data used in this study are perhaps the only data available that might allow a detailed view into the past four decades of population variability of an Antarctic ice-breeding seal. Estimates of abundance of ice-breeding seals from ship and aerial surveys (Erickson and Hanson 1990) are too few and too variable to reliably estimate trends, even over the relatively short period covered (1968-1983). The series of leopard seal sightings at Macquarie Island (Rounsevell and Eberhard 1980; Rounsevell 1988; Testa *et al.* 1991) is comparable in length to the crabeater seal cohort series, but the relationship of the sightings to leopard seal population variability is not apparent. Reproductive rates of Weddell seals in McMurdo Sound (Testa and Siniff 1987; Testa *et al.* 1990; Testa *et al.* 1991) have great potential for recording population variability but the time series is presently only about one-half the length of the crabeater seal series.

The population represented by the crabeater seal catch-at-age data witnessed the near extinction of several stocks of large whales, an increase of about 15% in the global atmospheric CO_2 concentration and the onset of annual disruptions of the Southern Hemisphere ozone layer. The polar regions have been identified as the areas where global warming will be most pronounced and possibly most easily detected (Manabe and Stouffer 1980; Sansom 1989; Gloerson and Campbell 1991; Walsh 1991). The Global Ocean Ecosystem Dynamics (GLOBEC) Southern Ocean Program includes, as part of its research plans, population studies of Antarctic top predators and their prey (GLOBEC 1991). The GLOBEC Program, noting that global warming may disrupt life cycles of marine animals at several trophic levels and that the shortness of some Antarctic marine food chains implies close coupling of trophic levels, suggests that long-term studies of these predator-prey relationships may eventually form the basis for monitoring human-induced impacts.

Because of the uniqueness of the crabeater seal catch-at-age data and the prominence of Antarctic marine top predators in efforts such as GLOBEC, it seemed appropriate to begin this research with simple questions about crabeater seal cohort variability, even though searches for simple relationships between mammal populations and environmental variables are notoriously unrewarding. In Chapter 2 it was found that the sampling scheme used to obtain the catch-at-age data was probably sufficient to detect fluctuations in cohort strength of the magnitude estimated in this and previous studies. It was found that the series of cohort strengths could reasonably be modeled by an ARIMA process with some tendency toward periodicity, but that the conclusions and analysis in earlier studies that treated the series as periodic are perhaps not justified. In Chapter 3, fluctuations in environmental parameters, of similar duration to those in the cohort series, were shown to be coherent among several sites representing the locations from which the seals were collected. Correlations among the environmental parameters were documented. This spatial coherence and correlation among parameters, along with known aspects of crabeater seal life history led to simple hypotheses tested in Chapter 4 about whether a significant fraction of the variation in seal cohorts could be explained by variation in sea ice, surface air temperature, the Southern Oscillation, or numbers of leopard seals sighted annually at Macquarie Island. It was found that none was capable of explaining a significant fraction of the variance in crabeater seal cohorts.

The lack of power to explain seal cohort variability by the environmental and ecological factors tested here may be cause for concern about efforts such as GLOBEC that propose to use Antarctic seals or other top predators in their schemes to monitor climate or other environmental changes. The wide distribution and remote habitats of these species make sampling and detecting (significant) changes difficult. If these species are to be included in such efforts, existing data such as the catch-at-age data used here and the associated reproductive data should be thoroughly evaluated to assist in identification of population parameters that are most sensitive to environmental change and most efficient to measure. This study suggests that cohort strengths of crabeater seals near the Antarctic Peninsula may not meet those criteria, though further analysis, particularly with refinements to the sea ice data and the statistical model for age estimation error, might alter this conclusion.

In further research on the demography of crabeater seals it would be desirable to include the following objectives: (1) to form more detailed hypotheses about sources of cohort variability based on critical times and components of crabeater seal life history; (2) to obtain, if possible, raw data used to derive final age estimates for the 1964-1976 samples (Chapter 2) and estimate new series of cohort strengths accounting for errors in age estimation; (3) to obtain an improved index of sea ice extent; and (4) to devise experiments that might help to distinguish between environmental and ecological sources of cohort variability.

With respect to objective (4), one experiment in particular may prove useful. It was suggested in Chapter 2 that crabeater seals of the Antarctic Peninsula may be subject to unusually high first-year mortality. If so, this feature of the life history might be used to distinguish between leopard seal predation and any factor that affects more than the first age class. For example, if evidence — perhaps in the fine-structure of the teeth — can be found to show that all age classes experienced difficult conditions in years associated with weak cohorts, leopard seal predation on young-of-the-year would seem unlikely to be the primary cause of cohort variability. Such an experiment may require new developments in methods of preparing tooth samples and identifying and measuring indicators of seal growth and condition.

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