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The estimation of theoretical population levels for natural populations

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University of California, San Diego, 1990

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UNIVERSITY OF CALIFORNIA, SAN DIEGO

The Estimation of Theoretical Population Levels

for Natural Populations

A dissertation submitted in partial satisfaction of the

requirements for the degree of Doctor of Philosphy

in Oceanography

by

Timothy J. Ragen

Committee in charge:

    Professor Paul Dayton, Co-Chair
    Professor Alec MacCall, Co-Chair
    Professor Ted Case
    Professor Douglas DeMaster
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1990

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1990

iii

TABLE OF CONTENTS

LIST OF FIGURES

v

viii

LIST OF TABLES

ACKNOWLEDGEMENTS

I very gratefully thank the members of my committee, Profs. Ted Case, Douglas DeMaster, James Enright, and Joseph Reid, for their helpful discussions and reviews of my dissertation. I especially thank the Co-Chairmen of my committee, Profs. Paul Dayton and Alec MacCall, for their truly invaluable guidance over the past four years.

As a student at Scripps Institution of Oceanography, I have had many opportunities to interact with individuals at the Southwest Fisheries Center. I gratefully acknowledge their significant contribution to my education, and I thank them for making me feel a part of their scientific community.

Dr. Charles W. Fowler of the National Marine Mammal Laboratory, Seattle, WA, has contributed significantly to my education in field biology and theoretical population dynamics. I thank him for many enlightening discussions, and for his interest in my work over the past four years. I thank Prof. Douglas G. Chapman for introducing me to quantitative biology and for his many pioneering contributions to the study of marine mammal population dynamics. I also thank Prof. Ian Abramson of the mathematics department for his very helpful assistance with my study of pre-exploitation abundance of three large fishes off Southern California.

I gratefully acknowledge the San Diego Supercomputer Center. Numerous analyses in this dissertation were completed using the CRAY X-MP48 and the CRAY Y-MPA/864. The study described in Chapter 2 was

Finally, I thank all the members of my family, and especially
Dr. Wendy Tada, for continuous and virtually unlimited support.

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VII. Contracts and Grants Awarded

Pacific Rim Research Program, University of California, 1989-90 ($55,000) and 1990-91 ($73,000). For the study of northern fur seal/fisheries interaction in the North Pacific Ocean.

Minerals Management Service, Department of the Interior, 1990 ($15,000). For transportation in the same study of northern fur seal/fisheries interaction in the North Pacific Ocean.

ABSTRACT OF THE DISSERTATION

The Estimation of Theoretical Population Levels

for Natural Populations

by

Timothy J. Ragen

Doctor of Philosophy in Oceanography

University of California, San Diego, 1990

Professor Paul K. Dayton, Co-Chair

Professor Alec D. MacCall, Co-Chair

The focus of this dissertation was the estimation of theoretical reference levels such as K, the environmental carrying capacity, and MNPL, the maximum net productivity level, for three fishes off Southern California and for the northern fur seal (*Callorhinus ursinus*) population of St. Paul Island, Alaska. The estimation techniques were based on computer modeling of historical population trends. The assessment of these theoretical reference levels for natural populations is fundamentally important to the development and testing of concepts in theoretical ecology and population dynamics.

In the first study, maximum-likelihood estimates of pre-exploitation biomass were made for the white seabass (*Atractoscion nobilis*) and the yellowtail (*Seriola lalandei*) by assuming that development of corresponding commercial fisheries led to a shift in size distributions of these fishes, as indicated by records of the

Avalon Tuna Club, Santa Catalina Island, California. Pre-exploitation biomass for Southern California populations of both these fishes was estimated to be about 20,000 tons. The pre-exploitation biomass of the giant sea bass (*Stereolepis gigas*) was estimated to be 1300 tons. Due to insufficient natural history information, this estimate was based on commercial catch records only.

In the second study, estimates of theoretical reference levels for the northern fur seal population of St. Paul Island were based on computer simulations of pup production from 1912 to 1970. Repetitive simulations were used to construct frequency distributions of estimates for MNPL, K, the number of pups born at MNPL and K, and the ratio MNPL/K. These distributions serve as a measure of the confidence that can be placed in single estimates of reference levels, and thereby provide a general context within which these reference levels can be evaluated.

The final study of this dissertation investigated the pelagic migration of northern fur seal pups. Results indicated that initial migration paths for these pups are more widely dispersed that previously assumed. This information contributes to the understanding of northern fur seal life histories. A fuller understanding of life history information will eventually facilitate more accurate modeling of northern fur seal population dynamics.

CHAPTER 1.   INTRODUCTION

A fundamental problem in the extension of theoretical population ecology to natural populations is the measurement of theoretical reference levels for natural or field populations. In theoretical ecology, populations are defined in relative terms, from 0 (zero) to some nominal upper limit. Natural populations, on the other hand, must be defined in absolute terms. Two reference levels of theoretical populations that have been very difficult to measure in natural populations are the equilibrium level or environmental carrying capacity (K), and the maximum net productivity level (MNPL). The main purpose of this dissertation is to consider the estimation of K and MNPL for several natural populations, including previous estimates where they exist, and to suggest additional methods for their estimation.

Determination of these reference levels in absolute terms is fundamental to the development and testing of population ecology theory. These levels are basic to concepts of growth patterns (MNPL) and limits (K). They reflect the integration of various natural history characteristics of a population and the interaction of those characteristics with the environment.

K has been defined as the population level at which the birth rate equals the death rate (i.e., the growth rate is zero) or as the largest population that can be supported by its environment. Malthus (1798) did not use the term "K" or the "environmental carrying

1

capacity", but he expressed the same concept, "...(a) population can never actually increase beyond the lowest nourishment capable of supporting it, a strong check on (a) population...." K was mathematically incorporated into theoretical ecology by Verhulst (1838) and later by Pearl and Reed (1920) in their independent derivations of the logistic equation.

Chapman (1928) suggested that K represents a kind of environmental resistance to growth, and is the end result of the interaction between population growth and environmental restraint. However, there have been substantial disagreements about the role of the population versus the environment in limiting growth. Early proponents of density-dependent regulation (Nicholson 1933, Smith 1935) emphasized the importance of the population "restorative" forces which maintain a more-or-less stable balance or constancy of populations. But Andrewartha and Birch (1954) argued that density-independent environmental forces can not be ignored, and that these generally lead to less stability in populations. An important difference between these two views is the issue of population stability.

The assumed stability of K suggested by Nicholson (1933) and Smith (1935) is a corollary of the "balance of nature" paradigm, which Egerton (1973) traces back to Greek mythology. This stability can be challenged on an evolutionary time scale (populations go extinct), and on an ecological time scale (populations vary in abundance). Again, while Nicholson (1933) and Smith (1935)

recognized some variation in population abundance, they suggested that variation is about a "steady density." But the notion of a steady density has also been challenged with evidence that for some populations either this steady density must change, or it does not exist (Ehrlich and Birch 1967).

An important consequence of this debate has been the recognition that the nature of regulation and resulting stability may vary from population to population, as is exemplified by the conceptual model of r- and K-selection (MacArthur and Wilson 1967). According to this model, r-selected populations exhibit greater sensitivity to environmental variation, and that sensitivity is reflected in large variation in abundance. K-selected populations are less sensitive and exhibit greater stability in abundance. Hence, depending on the stability of the population of interest, the concept of K may or may not be a useful measure of a natural population.

The second theoretical level that is considered in this dissertation is the maximum net productivity level (MNPL); that is, the level at which population growth rate is maximal. The concept of MNPL is closely related to the concept of maximum sustainable yield, which has been prominent in the field of applied fisheries ecology since the 1930's and 1940's (Larkin 1977), but can be traced to before the turn of the century, when it was used to manage the harvesting of timber in Europe (Nash 1982).

Determination of MNPL can be more complex than determination of K. While K can be observed directly from an equilibrium population in its natural environment, determination of MNPL requires either knowledge of the nature of the interaction between population growth and environmental limitation or observation of the growth pattern characteristic for that population. Thus, while K is the end result of the interaction between growth and limitation, MNPL reflects the nature or pattern of that interaction.

As noted above, theoretical population levels are defined in relative terms. Theoretical MNPL is generally defined as a fraction of K. For the simple logistic equation, MNPL occurs at 0.5K with population growth symmetrical about that point. However, the logistic model was generalized initially by Verhulst (1838; see Gilpin et al. 1976) and Pearl and Reed (1923,1925), and later by Richards (1959). These generalized forms allow for asymmetrical growth about an MNPL $\neq$ 0.5K. Gilpin et al. (1976) provided theoretical arguments that the selection for asymmetrical growth (which they termed "theta-selection") may result from the nature of disturbance to which the population is exposed. Fowler (1981) has also provided theoretical arguments that MNPL may not occur at 0.5K, especially for large mammals. His arguments are based largely on selection for resistance to mortality (K-selected) versus selection for large reproductive capacity (r-selected), and on trophic interactions.

Irrespective of the validity of these theoretical arguments, MNPL and K have been difficult to measure for natural populations. Marine populations are particularly difficult to assess. Fish populations, for example, are essentially invisible to unaided human observation. Fish are frequently highly mobile, and the extent to which they form discrete population units is often uncertain. Furthermore, standard assessment techniques depend on large-scale harvests or removals from the population, which can severely confound or bias the estimation of these reference levels.

Marine mammal populations are also difficult to assess. The annual cycle of pinnipeds such as the northern fur seal (*Callorhinus ursinus*) may include a land-based reproductive phase during which there are varying degrees of aggregation. However, it is difficult to know what portion of the population is present at these aggregations at any one time. In addition, aggregations may be sensitive to disturbance and commonly occur at remote sites. The combination of avoidance behavior and difficult logistics can make assessment difficult and imprecise, and it is frequently necessary to rely on various indices of population abundance.

Another major obstacle to the assessment of K or MNPL is the time required for the assessments. To assess K, the population of interest must be allowed to seek its equilibrium level in a natural environment, which may take years depending on the initial status and natural variability of the population. Similarly, assessment of MNPL may require observation of population growth from below its MNPL to

above that level. The opportunity for such observation may be rare, particularly for unharvested populations. An alternative to the investment of long periods of observation is the use of historical data.

The studies in this dissertation use historical records to estimate K and MNPL for several different populations. Each study is presented independently in a separate chapter. In Chapter 2, estimates are made of the pre-exploitation abundances of white seabass (*Atractoscion nobilis*), yellowtail (*Seriola lalandei*), and giant sea bass (*Stereolepis gigas*). For all three fishes, the estimation of pre-exploitation abundance may serve as an indication of current K, if it is assumed that the corresponding environments have not undergone significant natural changes since that time. There is little information about these fishes at the turn of the century (brief reviews are included in Chapter 2). The estimation of their pre-exploitation abundance may therefore be of use in understanding the role of these fishes in southern California marine communities before substantial alteration by human activity. This information may also be of use to organizations currently responsible for managing those marine communities.

Estimates for the white seabass and yellowtail are based on a unique data set of catch records by members of the Avalon Tuna Club of Santa Catalina, California. The estimation technique used is a form of maximum likelihood estimation that accounts for historical commercial and sport catches and produces estimates of population

parameters including abundance under presumably natural conditions at the turn of the century. This method of estimation is not applied to the giant sea bass, due to a lack of sufficient growth data. A lower bound for its pre-exploitation abundance is based on commercial and sport catch records.

In Chapter 3, MNPL and K are estimated for the northern fur seal (*Callorhinus ursinus*) population of St. Paul Island, Alaska. These estimates are important for several reasons. The northern fur seal is the most extensively studied marine mammal in the world. As such, its population dynamics frequently serve as a model for the dynamics of other, less-thoroughly studied pinnipeds. Secondly, during the past two centuries this species has experienced large changes in abundance, providing an opportunity to study density-dependent mechanisms of natural population regulation. Finally, this species is currently at a low population level after several decades of decline. The study of its dynamics and the estimation of its MNPL may provide information useful to the management of this species.

Three approaches to the estimation of MNPL are emphasized, including analytical models, numerical models, and repetitive simulations. Repetitive simulations demonstrate that results based on single analytical or numerical models fail to account for the uncertainty in natural history information and model specification, and may lead to unwarranted confidence in any particular model. In view of the uncertainty with which life history parameters and

density-dependent mechanisms of regulation are known for the northern fur seal, repetitive simulations are used to address the question of what estimates of MNPL and K are consistent with historical observations. Hence, these simulations produce frequency distributions of MNPL and K estimates rather than single "best" estimates. The distributions can serve as indicators of current MNPL and K if it is assumed that the environment of the northern fur seal has not undergone substantial natural changes, and that the specified model adequately represents the dynamic properties of this population.

Estimates of MNPL and K for the northern fur seal are based on population simulations requiring extensive natural history information. In spite of the extensive study of northern fur seals since the late 1940's, there is a critical lack of information about young animals, particularly females, from the age of about 4 months, when they leave their island of birth, until age 2 or 3, when they return to that island. Presumably, most of these animals remain at sea for this 20 - 32 month period, but their distribution is largely unknown. These age groups were underrepresented in a large pelagic collection of northern fur seals taken by Canadian and U.S. scientists from 1958 to 1974, and their early natural history continues to be a major gap in our understanding of fur seal population biology. The final chapter in this dissertation, Chapter 4, presents an investigation which characterizes the initial phase of fur seal pup migration by taking advantage of islands through which

these pups pass as they leave the Bering Sea and enter the North Pacific Ocean. The study objectives were to determine the direction and rate of travel of pups between St. Paul Island and the Aleutian Islands. As is true for marine mammals in general, study of these animals during a large portion of their annual cycle is severely limited by their highly mobile nature and their marine habitat. But it is nevertheless important that our understanding of the natural history of these animals be expanded through study of the pelagic phase of their annual cycle.

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Prentice-Hall, Englewood Cliffs, N.J.)

CHAPTER 2. PRE-EXPLOITATION ABUNDANCES OF THREE LARGE FISHES OFF SOUTHERN CALIFORNIA

INTRODUCTION

Baseline measures of abundance or biomass of fish and wildlife populations are valuable for assessment of human-induced changes in those populations. Such measures are, however, rare. Populations may be altered long before the need for baseline information is recognized. Status assessments of fish populations generally rely on corresponding fishery statistics, and hence it is difficult, if not impossible, to evaluate those populations in an unaltered state.

Commercial fisheries for the white seabass (*Atractoscion nobilis*), yellowtail (*Seriola lalandei*), and giant sea bass (*Stereolepis gigas*) were well established by the late 1910's and early 1920's, a period during which significant changes occurred in the populations of these three large predatory fishes (Figs. 1-3). Fisheries data from this period to the present suggest California populations of these fishes are in various states of depletion, but prefishery population levels have not been estimated.

A unique data set collected by the Avalon Tuna Club of Santa Catalina Island (Figs. 1-3) contains information that predates large-scale commercial fishing off Southern California (Macrate 1948). This data set contains records of the heaviest white seabass, yellowtail, and giant sea bass caught each year by a member of the club. To the extent that size composition reflects fishing pressure,

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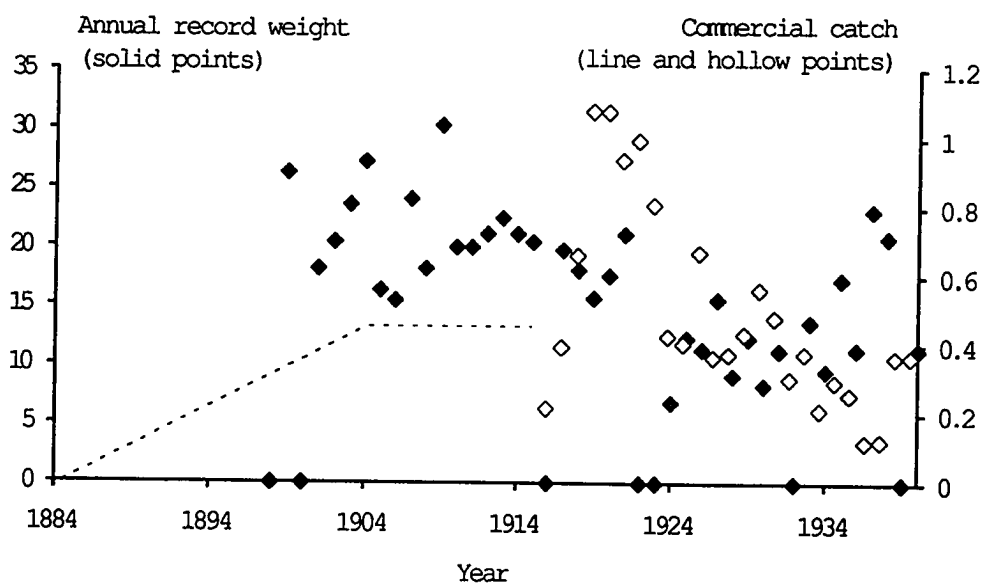
Figure 1. Commercial catch (1000 tons) and record weight (kg) of
white seabass caught by a member of the Avalon Tuna Club, 1884-1940.
Actual commercial catch data are shown as hollow points. Commercial
catch for years with no catch data were estimated by linear
extrapolation (dashed line) on the basis of Frey (1971), "Early
commercial fishery catch records indicate that by 1889 well over
250,000 pounds of white seabass were landed annually. The million
pound level was surpassed in 1904, and remained fairly constant
through 1915."

Figure 2. Commercial catch (1000 tons) and record weight (kg) of yellowtail caught by a member of the Avalon Tuna Club, 1884-1940. Actual commercial catch data are shown by hollow points. Commercial catch for years with no catch data were estimated by linear extrapolation (dashed line). Commercial catch records from Frey (1971, for period 1916-1940) and from Skogsberg (1925, for period 1889-1892 and 1895).
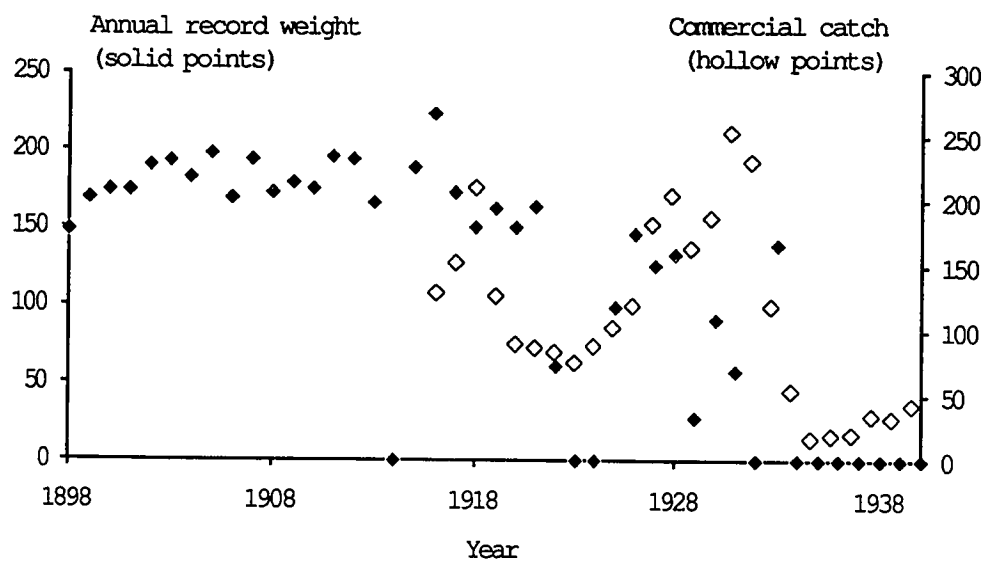
Figure 3. Commercial catch (1000 tons) and record weight (kg) of giant sea bass caught by a member of the Avalon Tuna Club, 1898-1940. Commercial catch data (hollow points) are from Frey (1971).

these data provide a means of estimating pre-exploitation biomasses for these fish populations.

Maximum likelihood estimates of pre-exploitation biomass of the white seabass and the yellowtail were made by combining a simple population model and a statistical model. The population model requires few parameters and generates year-specific weight-frequency distributions. Commercial and sport fishery catches were removed from the modeled population according to historical catch records. The statistical model provides maximum value statistics for samples taken from the weight-frequency distributions of the population. These order statistics were compared to the Avalon Tuna Club records to generate a likelihood for a given population model and its assumed parameters. Analyses were conducted to assess the sensitivity of the maximum likelihood solutions for the parameters and assumptions incorporated into the combined models.

Inadequate life history data precluded use of this maximum likelihood approach with the giant sea bass; a lower limit of its pre-exploitation biomass was estimated using catch data only.

BRIEF REVIEWS

White sea bass. The white sea bass is the largest member of the family Sciaenidae in California waters. Its distribution extends from southeastern Alaska to at least as far south as Bahia Magdalena, Baja California (Fig. 4). An isolated population is also reported for the northern portion of the Golfo de California (Fitch 1949,
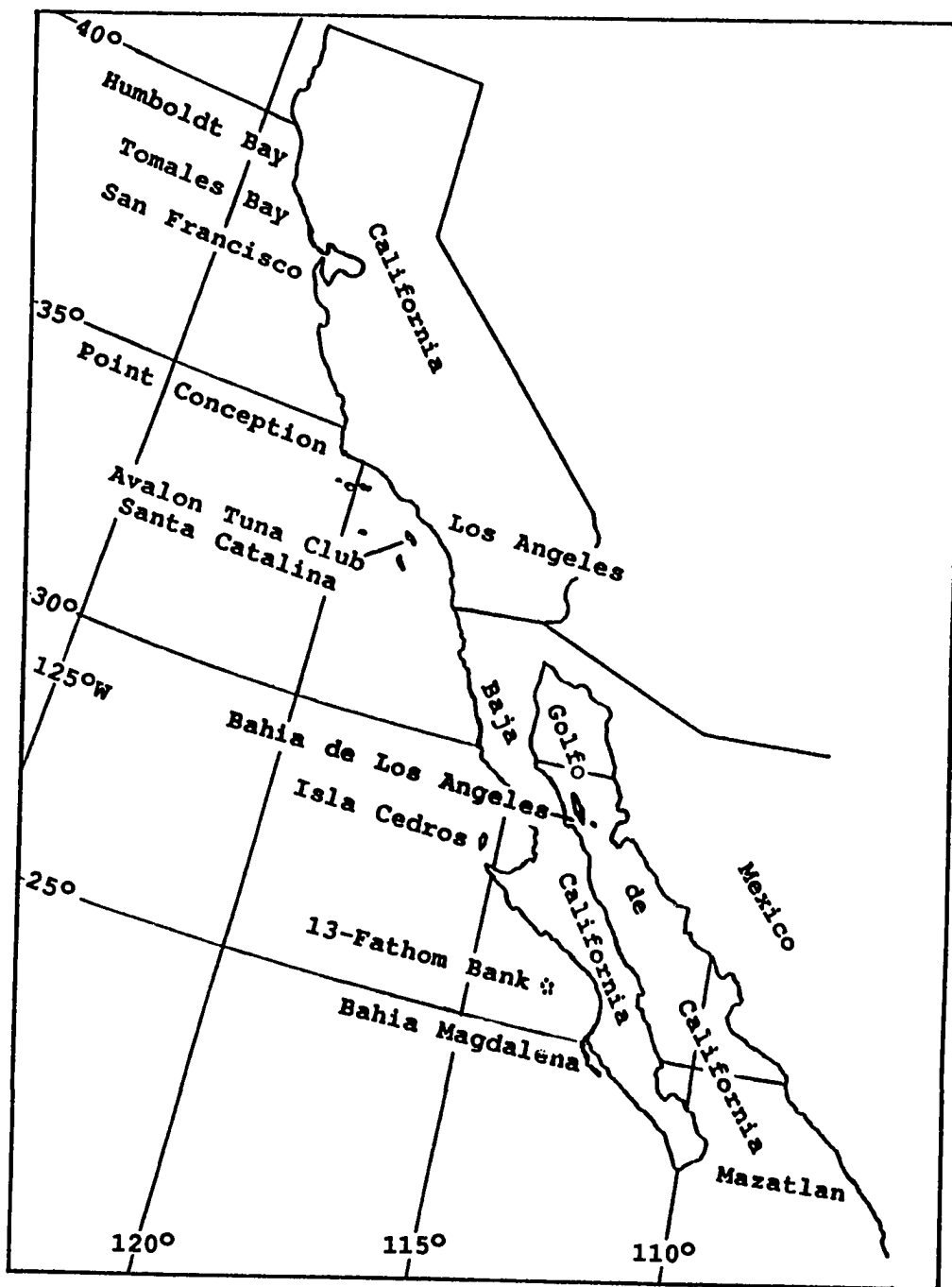
Figure 4. Oceanic area pertinent to study.

Thomas 1968). The commercial distribution of the white seabass in the early part of this century ranged from Tomales Bay in northern California to Bahia Magdalena, Baja California (Croker 1937), but has since contracted to south of Pt. Conception (Vojkovich and Reed 1983).

The habitat of the white seabass is generally described as being in or near kelp beds (Fitch 1949). Skogsberg (1939) and Frey (1971) suggest a movement of fish with age; juvenile fish tending to be in or near bays, intermediate fish near mainland kelp beds and over sandy bottoms, and older, larger fish near rocky headlands and offshore islands where there are kelp beds. These fish occur as solitary individuals and in schools (Skogsberg 1939).

White seabass are reported to be piscivorous, feeding on, among others, anchovy (*Engraulis mordax*), sardine (*Sardinops sagax caeruleus*), and herring (*Clupea harengus*), but also feeding on squid (*Loligo opalescens*) and pelagic red crab (*Pleuroncodes planipes*) (Thomas 1968). Note that these prey items are not associated with kelp beds, suggesting the habitat of white seabass is not fully understood.

Seasonal coastal migration of the white sea bass is generally inferred from catch records suggesting regular shifts in areas of abundance (Frey 1971, Vojkovich and Reed 1983). The extent of seasonal on and offshore movements is undetermined (Skogsberg 1939).

Longevity of the white seabass is unknown. Thomas (1968) reports fish over 1.4 m in length and exceeding 22 kg, but Skogsberg

(1939) suggests maximum weight may exceed 36 kg. Clark (1930) was the first to estimate the weight(W)-length(L) relation, suggesting

$$(1) \qquad W = 10.49 * L^{3.315},$$

where W is kg and L is meters (total length). This estimate was based on 78 fish only, and she regarded the resulting curve as tentative at best. Thomas (1968) also developed a (round or whole fish) relation, (W in kg and L [total] in meters),

$$(2) \qquad W = 8.919 * L^{2.92},$$

as well as a von Bertalanffy length-age(A) relation (L in meters and A in years):

$$(3) \qquad L = 1.465 * [1 - \exp\{-0.128 * (A + 0.2805)\}].$$

For this study, we estimate the standard deviation of length(m)-at-age from Thomas (1968, his Table 4):

$$\text{standard deviation}_A = 0.04757 + 0.001841 * A, \quad A \leq 12$$

(4)

$$\text{standard deviation}_A = 0.07150, \qquad\qquad A > 12.$$

Figure 5 shows the weight-age relation resulting from the combination
of Equations (2) and (3). The dashed line indicates a possible
effect of density dependence on the von Bertalanffy growth parameters
L_∞ and K; that is, the dashed line was constructed by substituting
0.95*1.465 and 0.95*0.128 for 1.465 and 0.128, respectively, in
Equation (3). It is well known that, at least in artificially reared
fish, growth rate can be slowed by the effects of density (see Brett
1979 for a review). That high densities of natural lake populations
can lead to smaller asymptotic size (length and weight) was shown by
Beckman (1941). The extent to which this is true in marine
populations is uncertain, but Prager and MacCall (1988) provide
evidence that this is the case for Pacific mackerel (*Scomber
japonicus*). Hence, this method of modeling density-dependent growth
appears to be reasonable approximation for the purpose of sensitivity
analysis.

Clark (1930) suggested that males reach sexual maturity one
year before females, larger males becoming mature in their second
year with few females becoming mature until their third year.
Spawning occurs from April to August but is most intense in May and
June (Skogsberg 1925a, 1939). Two estimates of natural mortality
rate of the white seabass can be found in the literature. Thomas
(1968) calculated instantaneous natural mortality rate to be 0.303
yr^{-1}, while MacCall, Stauffer, and Troadec (1976) estimated a value
of 0.13 yr^{-1}.
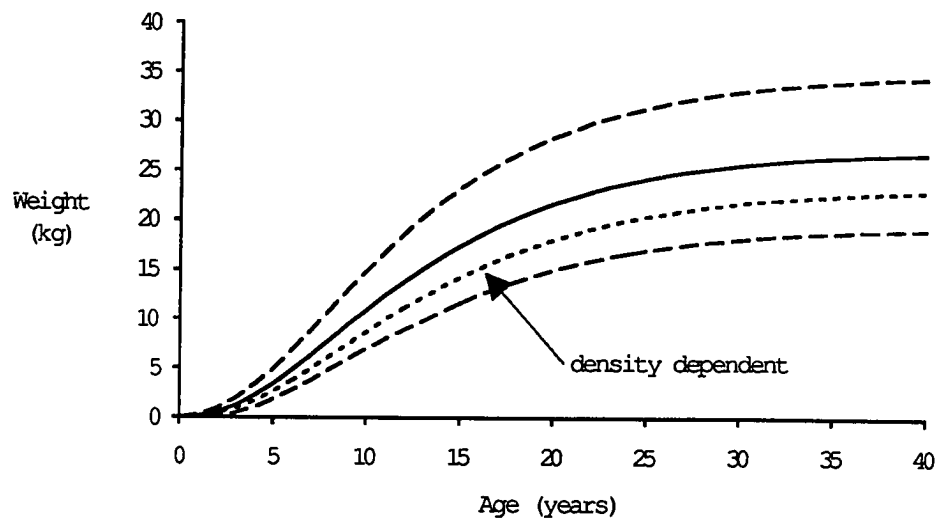
Figure 5. Modeled relation of weight to age for the white seabass. Solid line is mean relation, long-dash lines correspond to mean ± 2 standard deviations, and short-dash line corresponds to relation under density-dependent growth.

Records of commercial fishing for white seabass date back to at least 1889 (Skogsberg 1925a). Prior to the mid 1910's the center for this fishery was off San Francisco (Skogsberg, 1925a), but then shifted, perhaps as a result of a change in environmental conditions (Skogsberg 1939), to Southern California waters. With the shift, a number of changes occurred in the white seabass fishery. Between 1916 and 1921 there was a seven-fold increase of landings in Southern California. Prior to 1925 small boats could successfully fish nearshore waters and get their catch to market on the same day. Nearshore scarcity of fish, presumably resulting from harvesting, led to a change to larger boats that could keep ice on board, allowing an extension of fishing trips beyond nearshore regions. Concomitantly, the increasing scarcity of fish led to a shift in fishing gear; gill nets replaced purse seines and other round haul nets which had previously accounted for the majority of the catch. And as larger boats were used, more gill nets were tied together to form longer gangs of net. An analysis of this fishery by Whitehead (1930) suggested declining catch per unit effort during this period. Perhaps as a result of Whitehead's analysis, protective legislation was passed in the 1930's, mandating closed seasons, size limits, bag limits, gear restrictions (particularly the prohibition of round haul nets), closed areas, market restrictions, vessel limits, and licensing of anglers (Skogsberg 1939).

Records for the white seabass sportfishery were kept beginning in 1936. MacCall, et al. (1976), and Vojkovich and Reed (1983)

reviewed the sport and commercial fisheries for this fish from the 1940's and 1950's to the present. Their analyses suggested that with the exception of warm water years in the late 1950's the catch indicates a declining fishery, particularly when contributions from Mexican waters were taken into account.

Yellowtail. The yellowtail is the largest Carangid found in California waters. This pelagic fish is distributed in the North Pacific from waters off southern Washington to Mazatlan, Mexico (Fig. 4), and into the Golfo de California at least as far north as Bahia de Los Angeles (Frey 1971). In California, few yellowtail are found north of Los Angeles County (Collyer 1954). Based on tagging experiments, two main centers of abundance have been suggested; the first is located in the vicinity of Isla Cedros, and the second is found further south in the 13-Fathom Bank area (Baxter 1960). California is on the fringe of the yellowtail distribution, and a large portion of the fish present in California waters are thought to be migrants moving north in the spring and returning south to Mexican waters in the fall. The warm water event of the late 1950's is thought to have accentuated the northerly migration of yellowtail, resulting in an unusually large sportcatch (Radovich 1961). Yellowtail are thought to be opportunistic feeders.

Longevity of the yellowtail is unknown. No estimates of natural mortality rates for the yellowtail were found in the literature.

Baxter (1960) reported maximum weight to be at least 36 kg. He determined a (total) length(L)-weight(W) relation,

(5) $W = 11.96 * L^{2.85}$

(L in meters and W in kg), as well as a von Bertalanffy length-age(A) relation:

(6) $L = 1.291 * \{1 - \exp[-0.136 * (A + 1.9)]\}$

(L in meters and A in years). Equation (5) suggests a 1.291 m fish would weigh 24.8 kg, so the 36 kg maximum reported by Baxter (1960) was presumably an exceptional fish. For this study, we estimated the standard deviation of length(m)-at-age from Baxter (1960, his Table 9):

(7)
$$\text{standard deviation}_A = 0.05343 + 0.001952 * A, \quad A < 12$$
$$\text{standard deviation}_A = 0.07686, \quad A \geq 12.$$

Figure 6 shows the weight-age relation resulting from the combination of Equations (5) and (6). The dashed line indicates a possible effect of density dependence on the von Bertalanffy growth parameters L_∞ and K, where the scope for change of those parameters is 10%; that is, the dashed line was constructed by substituting 0.9*1.291 and 0.9*0.136 for 1.291 and 0.136, respectively, in Equation (6).
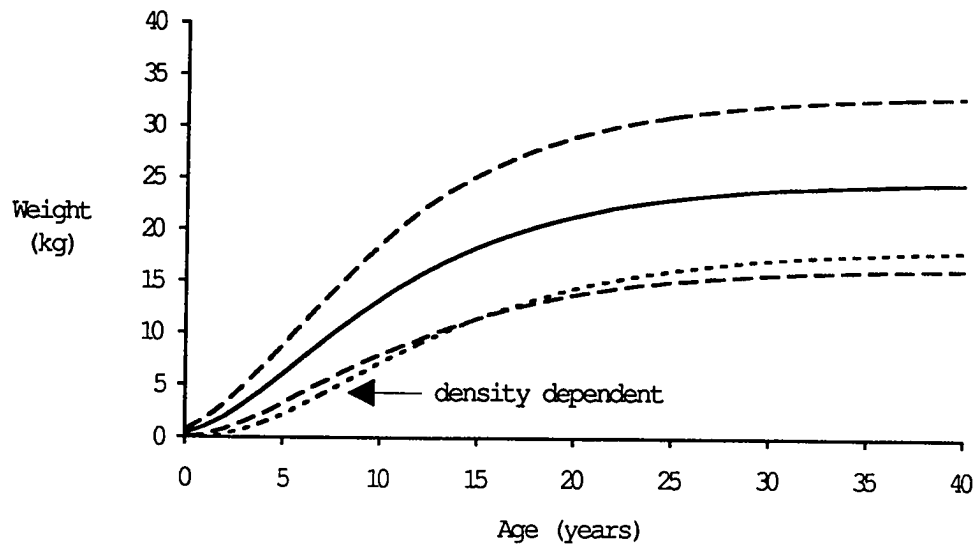
Figure 6. Modeled relation of weight to age for the yellowtail. Solid line is mean relation, long-dash lines correspond to mean ± 2 standard deviations, and short-dash line corresponds to relation under density-dependent growth.

Some yellowtail are sexually mature by age two, and all are mature by age three. In their first year of sexual maturity, they may only spawn once, but older fish are capable of multiple spawnings each season. Spawning, thought to be infrequent in California waters, occurs offshore from July to October. Baxter (1960) evaluated fecundity (F) as a function of age (A) and fit the linear equation: $F = -71 + 98 * A$, where F is thousands of eggs.

During the late 1910's and 1920's most yellowtail were taken commercially in the fall, the same period during which spawning occurs. Skogsberg (1925b) suggested that off Southern California there were no signs of overfishing at that time, but by the early 1930's there was evidence of a downward trend in catch per effort (Whitehead 1933, Fry 1937). As a result of declining local catches and a law preventing the canning of yellowtail caught in California waters, the center of commercial fishing shifted southward to the area of Isla Cedros and Bahia Magdalena off central Baja California (Frey 1971). In California, however, the yellowtail continued to be highly valued as a sport fish, and records are available for the sportcatch since 1936.

A large tagging program by the California Department of Fish and Game in the mid to late 1950's suggested the importance of yellowtail migrants to the Southern California sport fishery. Tag recoveries from this study also suggested significant fishing pressure in waters of Southern California (Baxter 1960), indicating an increase in catches in that area would be unlikely (MacCall, et

al., 1976). While MacCall, et al. (1976), reported the status of the yellowtail to be relatively healthy, a series of recruitment failures in the late 1970's led to a shift in age structure of the population and raised new questions about its status (Crooke 1983).

Giant sea bass. This very large Serranid is distributed from Humboldt Bay, California to the Golfo de California (Fig. 4), although Frey (1971) considered California to be on the very northern edge of its distribution. Eschmeyer, et al. (1983) reported its habitat to be "on rock bottom; near shore, outside kelp beds, and along drop-offs" at depths of about 5 to 50 meters.

Longevity of the giant sea bass is unknown, although Eschmeyer, et al. (1983) suggested it lives to at least 70 years of age, and Frey (1971) speculated the largest giant sea bass caught on record (2.26 m and 255 kg) may have been 90 to 100 years of age. Unfortunately, the information on age, length, and weight relations and on mortality rate is insufficient for the maximum likelihood method presented here. Age of sexual maturity is also uncertain, with Frey reporting first spawning at 7 to 8 years of age and elsewhere (Anonymous 1987) sexual maturity was reported to occur at 11 to 13 years of age. The only available information on fecundity is the report of a 145 kg female with ovaries weighing 21 kg and containing an estimated 60 million eggs (Frey 1971). Spawning aggregations occur from June to September.

Croker (1937) described the early commercial fishery for giant sea bass in three periods. During the first period (1916 to 1922),

local California catch was roughly 57,000 kg and the Mexican catch was about 15,400 kg. It seems reasonable to speculate that substantial catches were made before 1916, but the literature provides no guidance in this respect. During the second period (1923 to 1932) the local catch increased 33 percent while the Mexican landings increased six-fold. After 1932 the local fishery diminished substantially while the Mexican fishery increased almost another three-fold. Frey (1971) concluded that the combination of commercial fishing prior to 1945, slow recruitment in California waters, and continued sportfishing has prevented the giant sea bass from recovering to a level where commercial fishing might again be profitable. A moratorium on the taking of giant sea bass was initiated in 1982 and remains in effect to date.

THE GENERAL MODEL

Maximum likelihood estimates of the pre-exploitation abundances for the white seabass and the yellowtail were generated by combining 1) a harvested population model generating yearly weight-frequency distributions, 2) a statistical model for the probability distribution of the heaviest fish in a sample from the model population, and 3) annual observations of the heaviest fish caught by a member of the Avalon Tuna Club. The statistical model linked the records of the Avalon Tuna Club to the modeled population weight-frequency distribution, providing a basis for estimating the

likelihood of having observed the Avalon Tuna Club data given the assumed population model.

The population model. The purpose of the population model was to provide annual weight-frequency distributions of an assumed resident, self-sustaining population in California waters. Components of the model included length-at-age and weight-at-length relations, a stock-recruitment relation, an age of recruitment to the fishery, and the historical commercial and sport harvests. Fitted parameters were initial population size and instantaneous mortality rate.

By assuming a constant instantaneous natural mortality rate and an initial population size, we constructed a stable age frequency distribution. Using age-length (with variability) and length-weight relations from the literature, the age frequency distribution was converted to a weight-frequency distribution with fish summed over discrete weight categories of unit width. Constant recruitment to the model population in the absence of other extraneous perturbation led to a constant population abundance and weight-frequency distribution over time.

Such constancy ceases under conditions of harvesting, and the weight distribution subsequently varied with the removal of portions of the model population according to historical commercial and sport catch records. Commercial landings of yellowtail and white seabass from 1916 to 1940 were taken from Frey (1971). Skogsberg (1925a, 1925b) documents commercial catches for the period 1889 to 1916; and

sport landings from 1936 to 1940 were taken from Baxter (1960) and Thomas (1968) for the yellowtail and white seabass, respectively. In the model, availability of a year class to fisheries increased annually by 25% over a period of 4 years; the nominal age of recruitment was that age at which 50% of a cohort was available. Fish were removed from the model population in a manner consistent with seasonal distribution of the catch. That is, the total catch was removed at the midpoint of each year (Pope 1972), immediately after natural mortality from the first six months was subtracted from the population. Natural mortality occurring in the last six months of each year was subtracted at the end of that year. Regardless of age or size, all fish available to the commercial and sport fisheries were assumed to have an equal chance of being caught. In addition to the California resident population, migrants from Baja California could be included in the model. It was assumed that the weight-frequency distribution of the migrants was the same as the resident population, and these migrants were treated in the model as additional biomass available to the fisheries, independent of stock status. The migrants were not assumed to contribute to local reproduction.

Annual recruitment to the population was treated according to an equation explored by Cushing (1971),

(8) $R = a * B^b$,

where recruitment is either constant (b = 0) or dependent on population size (Fig. 7). Density-dependent recruitment was treated as either proportional to population biomass (i.e. without compensation, b = 1), or proportional to the square root of biomass (b = 0.5) representing intermediate compensation. Because sexual maturity for each of these fishes appears to occur at approximately three years of age, B in Equation (8) referred to the spawning biomass three years earlier. As can be seen in Figure 7, b=0 and b=1 are limiting cases.

When fish growth was assumed to be density-dependent, L_∞ and K in the von Bertalanffy growth Equations (3) and (6) were made linear functions of the population biomass. At the initial biomass level (which was the maximum biomass) these growth parameters were reduced by 5% (white seabass) or 10% (yellowtail). The scope for change in the growth parameters was different for the two fishes as the model failed to find a solution for the white seabass when the growth parameters were changed by 10%. As the populations approached zero biomass (extinction), L_∞ and K approached the values determined by Thomas (1968) and Baxter (1960) for the white seabass and yellowtail, respectively (the values given in Equations 3 and 6). For annual growth increments to reflect the influence of density dependence, length at time t+1 (L_{t+1}) was calculated as a function of length at time t (L_t) using a modified form of the von Bertalanffy equation:
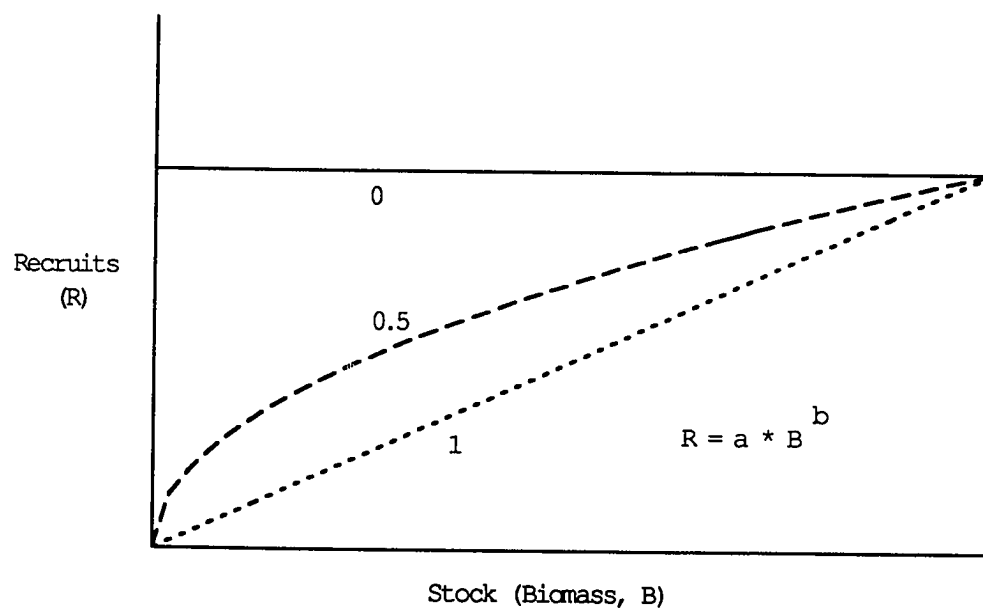
Figure 7. Stock-recruitment relations used in the model. The three lines correspond to the indicated values of b.

$$(9) \qquad L_{t+1} = L_\infty - (L_\infty - L_t) * e^{-K},$$

where, again, L_∞ and K are adjusted to correspond linearly with the biomass at time t. The population model ran from 1884 to 1940. Avalon Tuna Club records begin in 1898. The period from 1884 to 1897 was included to incorporate the effects of earlier years of commercial fishing for which records are available.

The statistical model. Based on a year-specific weight-frequency distribution from the population model, the statistical model provided a method of determining a year-specific probability distribution for the heaviest fish in a sample from the population. This extreme-value probability distribution was taken from Hogg and Craig (1965):

$$(9) \qquad f(Wmax|S) = S * [F(W)]^{S-1} * f(W),$$

where S, f(W), and F(W) were the sample size, weight-frequency distribution, and cumulative weight-frequency distribution for the model population. Recall that the year-specific weight-frequency and cumulative weight-frequency distributions (f(W) and F(W), respectively) were functions of the population model and its estimated parameters. Hence, a given year-specific probability distribution for the heaviest fish taken in a sample from the population was also a function of those parameters. While the Avalon Tuna Club records do not include sample size, and hence true sample

size was unknown, its mean can be assumed to be approximately
proportional to the year-specific abundance in numbers of fish (N)
given by the population model. The constant of proportionality (q,
where Smean = qN) was an estimated parameter. Because actual S
varied about Smean, and was a relatively small number, S was assumed
to be Poisson distributed. The density function used in the
likelihood equation was the weighted mean of the f(Wmax|S) values
from Equation (9), with weighting from the Poisson frequency
distribution p(s). Thus, if a maximum weight observation existed for
a particular year,

$$(10a) \quad f(Wmax|Smean) = \sum_{s=1}^{\infty} [f(Wmax|s) * p(s|Smean)],$$

and if there was no observation,

$$(10b) \quad f(no\ obs) = p(s=0|Smean).$$

Note that lack of a recorded maximum-sized fish for a particular year
(which occurs in these time series) is likely to indicate that
recreational catch rates, and hence available biomass, were low. The
stochastic treatment allowed this inference to be incorporated
explicitly in the likelihood function.

By comparing the observed annual records of the Avalon Tuna
Club to the corresponding probability distribution for the heaviest
fish, a year-specific probability was determined for each year of the

interval 1898 to 1940 in the model simulation. The sum of the natural logarithms of those year-specific probabilities over the period 1898 to 1940 was the log-likelihood function for the population model and its specific input.

The simplex algorithm (Nelder and Mead 1965) was combined with a parametric searching method to locate the combination of parameters which led to the maximum likelihood. Those parameters included the pre-exploitation abundance, the instantaneous mortality rate, and the constant of proportionality for sample size. The simplex algorithm adjusted all three parameters simultaneously. When it finished, the parametric searching method varied the parameters singly and in pairs, so as to examine the local response surface more carefully and assure that maximization of the log-likelihood function had been achieved.

Two methods of testing precision of the results were used. The first estimated minimum-variance bounds for the parameters using second and mixed partial derivatives (Norden 1972,1973). Derivatives of the log-likelihood function were calculated numerically following Abramowitz and Stegun (1965). As these derivatives were all negative, their absolute values were placed in a 3x3 matrix and the matrix was inverted to provide estimates of the asymptotic minimum bounds for the variances and covariances of the three estimated parameters. The second method was to vary the assumptions of the population model, including the stock-recruitment function, the age of recruitment to the fishery, the biomass of seasonal migrants to

the population and commercial fishery, the period of extensive sport
fishing, variability and density dependence in the length-age
functions, and the stability of the starting age distribution. Only
one assumption was varied for any given model run. The intermediate
stock-recruitment function (b=0.5) was used in all tests of model
sensitivity to these assumptions.

RESULTS

White seabass. Results from model simulations under various
conditions are presented in Table 1. With exceptions as indicated,
parameter settings and conditions for these simulations were: b
(exponent in the stock-recruitment relation) = 0.5, age of
recruitment to the fishery = 3, initial age distribution stable,
sportfishery records included for 1936 to 1940 only, and migration of
fish from Baja California waters not included. Under these
conditions the correspondence of model biomass to annual record
weight of white seabass taken by the Avalon Tuna Club was as
illustrated in Figure 8. Similarly, Figure 9 illustrates the
correspondence of model biomass to annual commercial catch.
Maximum likelihood estimates of M for the white seabass ranged from
0.0617 to 0.0888 yr^{-1}. Pre-fishery biomass estimates ranged from
14.87 to 26.05 million kg, corresponding to population abundance
estimates of 1.512 to 2.637 million fish. Estimates of q (the
constant of proportionality in the sample size function, Smean = qN)

Table 1. Maximum likelihood estimates for the white seabass parameters using the combined population and statistical models under various assumptions, as indicated (where not specified, age of recruitment = 3 and b = 0.5). Directly below each parameter estimate is the corresponding minimum standard error calculated from the minimum-variance bound. M is instantaneous natural mortality per year, B_0 is initial population biomass (1000 tons), N_0 is initial population abundance, and q is the constant of proportionality that determines sample size as a function of abundance. For each year from 1898 to 1940 (a period of 43 years) the statistical model generates a probability distribution for the largest fish taken in a sample from the modeled population. A probability is associated with each year by comparing the model-generated distribution to the record fish caught that year by the Avalon Tuna Club. The sum of the logs of those probabilities over the 43 years is the log-likelihood associated with any given model. The column of geometric mean probabilities is intended to give the reader a sense of the correspondence between the annual model-generated probability distributions and the record fish caught by the Avalon Tuna Club. The geometric mean probability is calculated from the maximum likelihood model as: antilog (maximized log-likelihood / 43 years).

File Description	M	B_0 $\times 10^6$	N_0 $\times 10^6$	q $\times 10^{-6}$	Geometric Mean Probability
b = 0.0	0.0788	20.94	1.945	1.693	0.0343
	0.0132	8.02	0.744	0.957	
b = 0.5	0.0837	22.27	2.171	1.636	0.0344
	0.0126	7.75	0.756	0.892	
b = 1.0	0.0888	25.71	2.637	1.427	0.0343
	0.0123	8.40	0.861	0.755	
age recruitment = 4	0.0816	20.46	1.954	1.838	0.0346
	0.0121	5.64	0.539	0.827	
density-dependent growth	0.0617	21.68	2.027	1.817	0.0281
	0.0094	7.48	0.582	0.925	
skewed age distribution	0.0733	14.87	1.512	1.962	0.0346
	0.0112	3.71	0.325	0.790	
linear increase sportcatch	0.0831	23.30	2.259	1.545	0.0342
	0.0124	8.61	0.834	0.884	
double variance in length	0.0823	21.95	2.111	1.689	0.0356
	0.0127	7.06	0.679	0.867	
effect of migrants, b = 0.5					
migrant biomass = 0 mtons	0.0837	22.27	2.171	1.636	0.0343555
100 tons	0.0837	22.27	2.171	1.636	0.0343558
200 tons	0.0837	22.27	2.171	1.636	0.0343551
400 tons	0.0837	22.27	2.171	1.636	0.0343508
600 tons	0.0837	22.27	2.171	1.636	0.0343434
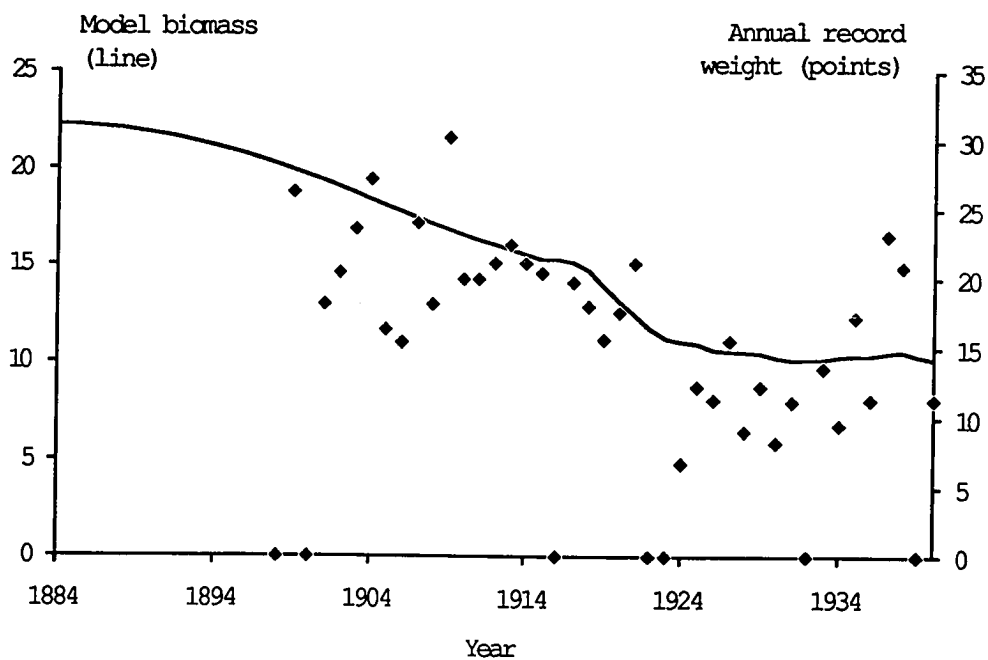
Figure 8. Model biomass (1000 tons) and annual record catch (kg) of white seabass by an Avalon Tuna Club member, 1884-1940.
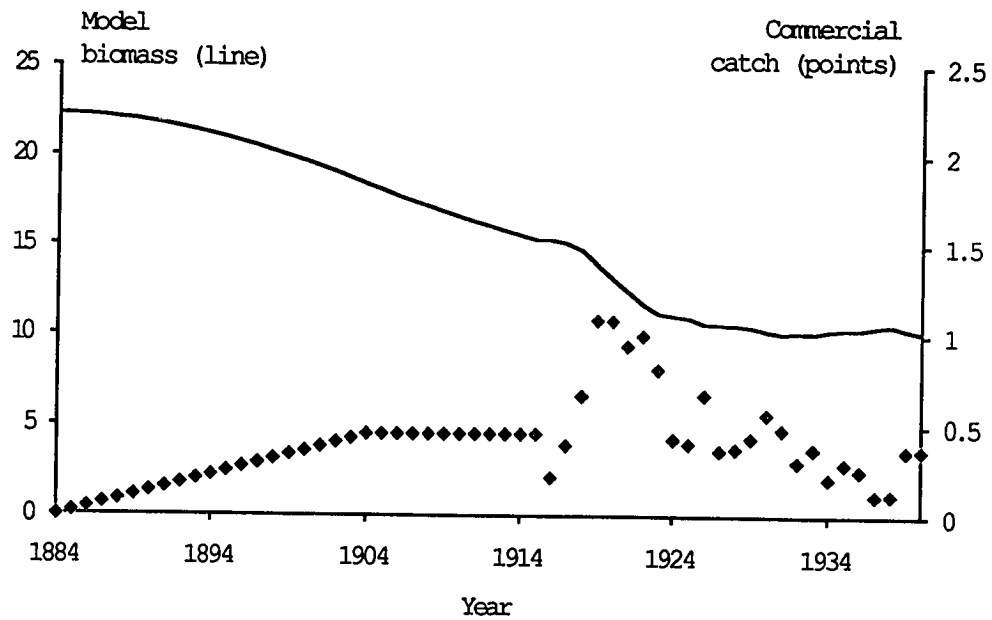
Figure 9. Model biomass and commercial catch of white seabass, 1884-1940. Both vertical axes are in units of 1000 tons.

were from $1.427 * 10^{-6}$ to $1.962 * 10^{-6}$, indicating mean sample sizes of approximately 3 to 4 fish per annual sample.

With the parameter estimates for the various simulations of Table 1 are the standard errors of these estimates calculated as the square root of the minimum-variance bounds (hence, these are "minimum" standard errors). These minimum standard errors were on the order of 15% of M estimates, 25-40% of biomass and abundance estimates, and approximately 40-60% of estimates of q. Correlations among the three parameters M, N_O, and q for all white seabass simulations were approximately as indicated in Table 2. The correlation of M with the other parameters declined somewhat in those cases where growth was density-dependent and where recruitment to the population was constant (b = 0.0).

Table 2. The correlation matrix for the white seabass simulation with b = 0.5.

	M	N_O	q
M |	1.0	-0.563	0.354
N_O |	-	1.0	-0.930
q |	-	-	1.0

The effects of the form of stock-recruitment depicted in the cases where b = 0.0, 0.5, or 1.0, were as might have been expected. As recruitment became more nearly proportional to parental stock,

there was a corresponding increase in the estimate of initial abundance (and therefore biomass) to compensate for declining recruitment as the stock was reduced by the commercial catch. The critical correspondence between the population weight-frequency distribution and the Avalon Tuna Club record weights provided a limit to how much initial estimated abundance could increase to counteract the effects of density-dependent recruitment. As abundance estimates increased due to the assumed form of stock-recruitment, estimates of q changed in a compensatory manner, maintaining approximately the same estimated annual sample size. Similarly, instantaneous mortality increased (in magnitude) to limit the longevity of the population and maintain the correspondence of the weight-frequency distribution with the Avalon Tuna Club records.

A change in the age of recruitment had little effect on the estimated parameters. Not surprisingly, the direction of change suggests that the population stock (or biomass) was more easily maintained when fishery efforts removed older individuals. Under these conditions, q increased slightly, again appearing to compensate for the decrease in biomass. There was also a slight compensatory decrease in M.

Under conditions of density-dependent fish growth, the model estimated a much lower instantaneous mortality rate without a large increase in biomass. The result was an increased average age in the model population which compensated for the slower growth rate at higher abundance. Presumably, compensation occurred in mortality

rate rather than in initial abundance because mortality rate influenced the shape of the weight-frequency distribution as well as the longevity of the fish.

Certainly unfished populations need not be in a stable or a stationary age distribution. For example, a large distortion of the age distribution would be expected in a population that had experienced a prolonged trend of greater or less than normal reproduction prior to exploitation. To examine the effect of a nonstable initial age distribution, a simulation was run starting with an age distribution corresponding to an instantaneous mortality of M * 1.2 (i.e. a 20% increase). The resulting parameter estimates were substantially lower than estimates from other simulations. However, the biomass listed in Table 1 was the initial biomass. In this simulation the biomass began increasing over time as the age distribution stabilized, and only declined after the commercial catch was sufficient to match and exceed the growth. Presumably, in the absence of a commercial catch the biomass would have attained a level comparable to that resulting in the other simulations given sufficient time. Apparently, the reduction in estimated mortality rate from this simulation allowed the model population to compensate for the initially distorted age distribution and to approach a more likely size and age structure before the start of record keeping by the Avalon Tuna Club.

As noted above, records of the sportfishery are not available for the period before 1936. To examine the effect of a sportfishery

gradually increasing over time, as opposed to a fishery starting abruptly in 1936, the model was run with the sportcatch in 1935 set at the mean of the 1936 to 1940 catches, zero sportcatch in 1925, and a linear increase in the catch between these years. The resulting parameter estimates were virtually unchanged, except to reflect the additional number (or biomass) of fish removed from the population. Hence, to get the maximum likelihood fit, the initial abundance incorporated these additional fish.

As already noted, the variance in length-at-age was taken from Thomas (1968). The estimation of that variance was based on 15 fish of each age class from 1 to 13. Variance beyond 13 was held constant in the model. To assess the sensitivity of the model to this variance, the standard error of length at each age was doubled and the model was rerun. The resulting maximum log-likelihood was the largest achieved for any model run, as indicated in Table 1. The corresponding parameter estimates were not, however, substantially different.

Finally, it is known that white seabass from Baja California waters migrate seasonally into Southern California waters (Collyer 1954). To assess the affect of these migrants on model results, migrants were added in the form of additional biomass available to the commercial catch. The amount of biomass added was independent of current resident stock size. These migrants were assumed to have the same weight-frequency distribution as the resident population and therefore should not have altered that distribution or the resulting

Table 3. Maximum likelihood estimates for the yellowtail parameters using the combined population and statistical models under various assumptions, as indicated (where not specified, age of recruitment = 3 and b = 0.5). Directly below each parameter estimate is the corresponding standard error calculated from the minimum-variance bound. M is instantaneous natural mortality per year, B_0 is initial population biomass (1000 tons), N_0 is initial population abundance, and q is the constant of proportionality that determines sample size as a function of abundance. See Table 1 caption for explanation of the geometric mean probability.

File Description	M	B_0 $\times 10^6$	N_0 $\times 10^6$	q $\times 10^{-6}$	Geometric Mean Probability
b = 0.0	0.0816	21.67	1.902	2.092	0.0493
	0.0121	2.05	0.180	0.512	
b = 0.5	0.0915	21.31	2.017	2.877	0.0544
	0.0178	1.71	0.162	0.628	
b = 1.0	0.1218	21.60	2.533	3.548	0.0612
	0.0186	1.43	0.167	0.845	
density-dependent growth	0.0427	22.97	2.062	4.367	0.0383
	0.0081	1.19	0.075	0.919	
age recruitment = 4	0.0894	20.75	1.933	2.834	0.0547
	0.0145	1.44	0.134	0.602	
skewed age distribution	0.0854	14.98	1.537	3.124	0.0553
	0.0207	1.14	0.103	0.649	
linear increase sportcatch	0.0967	21.81	2.146	2.732	0.0551
	0.0121	1.21	0.119	0.623	
double variance in length	0.0933	21.07	2.022	2.922	0.0555
	0.0260	2.35	0.226	0.649	
effect of migration, b = 0.5					
migrant biomass = 0 mtons	-0.0915	21.31	2.017	2.877	0.054439
100 mtons	-0.0915	21.31	2.017	2.877	0.054338
200 mtons	-0.0915	21.31	2.017	2.877	0.054131

calculated order statistics (Eqn 10). As can be seen in Table 1, the effects of migration on the model likelihood were negligible. Moreover, the maximum likelihood solution was achieved with a migration parameter of zero.

Yellowtail. Model results for the yellowtail are summarized in Table 3. Unless otherwise noted, model parameters were: b = 0.5, age of recruitment to the fishery = 3, initial age distribution stable, sportfishery records included for 1936 to 1940 only, and migration of fish from Baja California waters not included. (Default parameters were the same for the yellowtail and white seabass.) Under these conditions the correspondence of model biomass to annual record weight of yellowtail taken by the Avalon Tuna Club was as illustrated in Figure 10. Figure 11 illustrates the correspondence of model biomass to annual commercial catch.

Parameter estimates for the yellowtail were generally similar to those for the white seabass, both in magnitude and in sensitivity to various model assumptions. Estimates of M for the yellowtail under various model assumptions ranged from 0.0427 to 0.1218 yr^{-1}. Pre-fishery biomass estimates ranged from 14.98 to 22.97 million kg, corresponding to initial abundance estimates ranging from 1.537 to 2.533 million fish. Estimates of q ranged from 2.092 $* 10^{-6}$ to 4.367 $* 10^{-6}$, indicating annual mean sample sizes for the Avalon Tuna Club on the order of 3 to 9 fish. The main differences between the results for the two fishes appeared to be with the estimation of q, which was more sensitive to model assumptions for the yellowtail, and
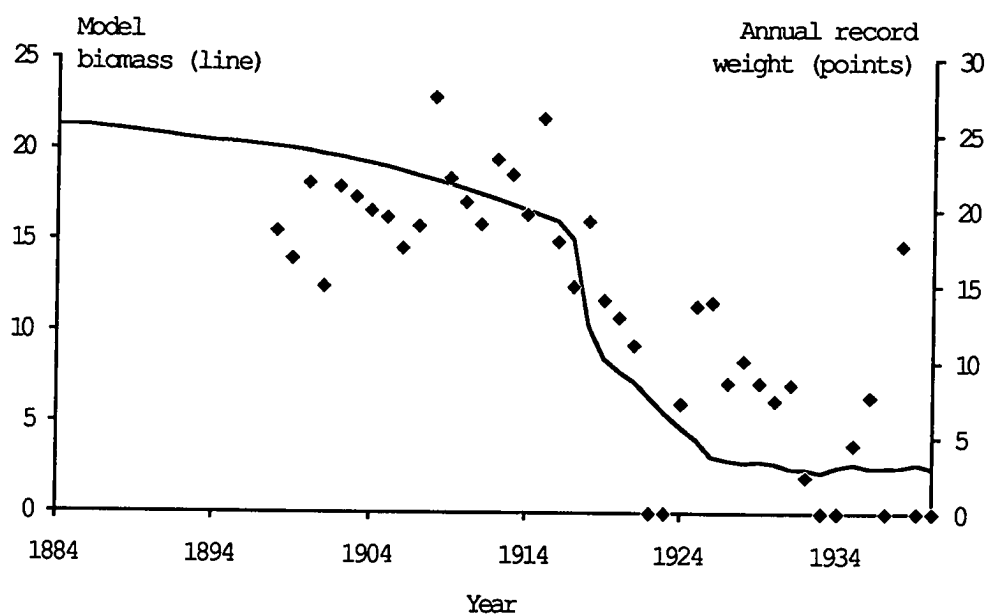
Figure 10. Model biomass (1000 tons) and annual record catch (kg) of yellowtail by an Avalon Tuna Club member, 1884-1940.
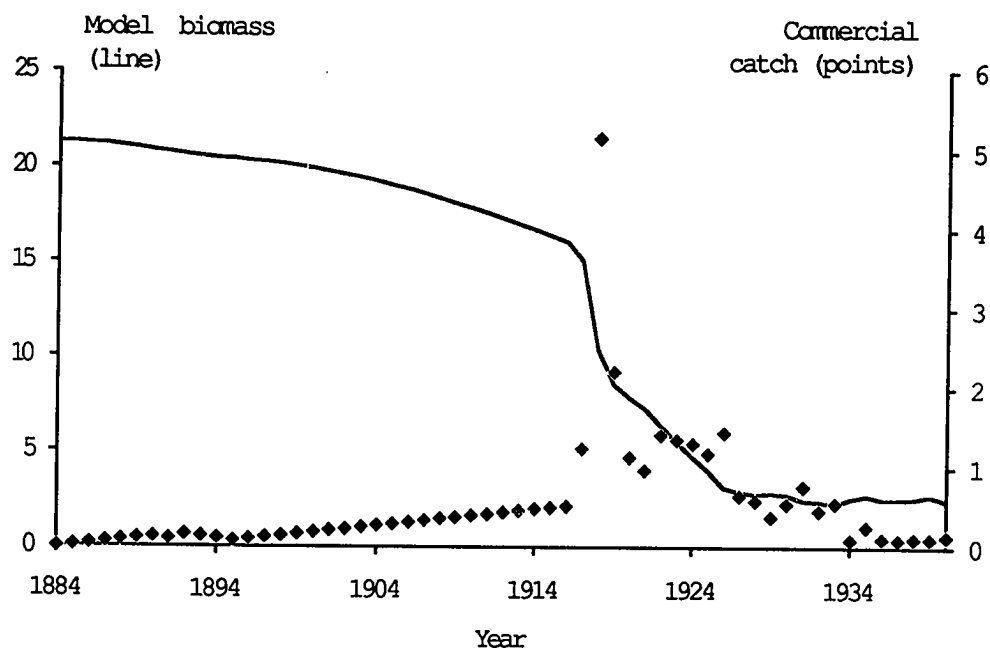
Figure 11. Model biomass and commercial catch of yellowtail, 1884-1940. Both vertical axes are in units of 1000 tons.

in the precision with which initial abundance and q were estimated. With respect to M , minimum standard errors were approximately 12-28% of the estimates, which is similar to the case for the white seabass. However, minimum standard errors for initial abundance (and therefore biomass) were substantially smaller for the yellowtail, on the order of 5-11% of the estimates. The estimates of initial abundance were relatively precise because a very large portion of the stock was removed over a very short period at the beginning of the fishery. Similarly, minimum standard errors for q were also smaller, ranging from 20-24% of q estimates. An additional difference between the two fishes was the slightly greater estimated mortality rate for the yellowtail.

The correlation matrices resulting from the yellowtail model under the various assumptions tended to be more variable than was the case for the white seabass. Correlations for the case of b = 0.5 are shown in Table 4. The correlation between N_O and M was generally strongly negative. The correlation between M and q was variable, but weakly negative in all but the case where b = 0.0. The correlation between N_O and q showed large variation, ranging from -0.98 in the case of a skewed initial age distribution to 0.26 in the case where b = 1.0.

Initial biomass estimates were remarkably consistent under all conditions except in the case where the starting age distribution was skewed. Similarly, estimates of M were robust to all conditions

Table 4. The correlation matrix for the yellowtail simulation with b=0.5.

	M	N_O	q
M |	1.0	-0.908	-0.156
N_O |	-	1.0	-0.120
q |	-	-	1.0

except where b = 1.0 and where there was density-dependent growth.

Giant sea bass. As noted earlier, insufficient information on giant sea bass life history parameters, particularly with respect to age-length-weight relations, precluded the estimation of pre-exploitation biomass for this fish with the model used here. However, if Frey (1971) correctly concluded that the combination of commercial fishing, slow recruitment, and continued sportfishing inhibited the recovery of the giant sea bass, then a first approximation for that biomass can be estimated by summing the total commercial catch of giant sea bass during the period from 1916 (when records begin for the commercial fishery) to 1940. The yearly landings in California were found in Frey (1971), and the sum of those landings for this period is approximately 1.3 million kg. Certainly, this approximation could be improved with knowledge of giant sea bass growth, recruitment, and mortality, and with estimates of the sportcatch during this period. Still, the sportcatch prior to 1940 probably is negligible relative to the commercial catch, and

regardless of growth and mortality, recruitment is sufficiently low to prevent rapid turnover of the population.

DISCUSSION

In searching the likelihood response surface for the peak, there was at least one major constraint on the parameters searched; the initial abundance and mortality rate had to allow for an initial population sufficiently large to withstand the removal of the biomass taken in the commercial catch. On the response surface this constraint manifested itself in the form of a boundary beyond which any solution was infeasible. Figure 12 illustrates likelihood response surfaces for the white seabass and the yellowtail when q was held constant, b=0.5, and M and N_0 were varied over a range of possible values. In the case of both the white seabass and the yellowtail the peak of the surface was located close to this boundary of feasible solutions, suggesting that these populations were fished to very low levels during the early part of this century.

Another prominent feature of these response surfaces was suggested by the oblong nature of the isobars of likelihood; that is, there was a ridge running nearly parallel to the boundary of feasible solutions. The sharpness of this ridge was determined by the covariance of the parameters involved, and can have a marked effect on the performance of the searching algorithm. To confirm that the simplex algorithm used to search for the maximum likelihood did not prematurely stop if following this ridge, and had indeed continued
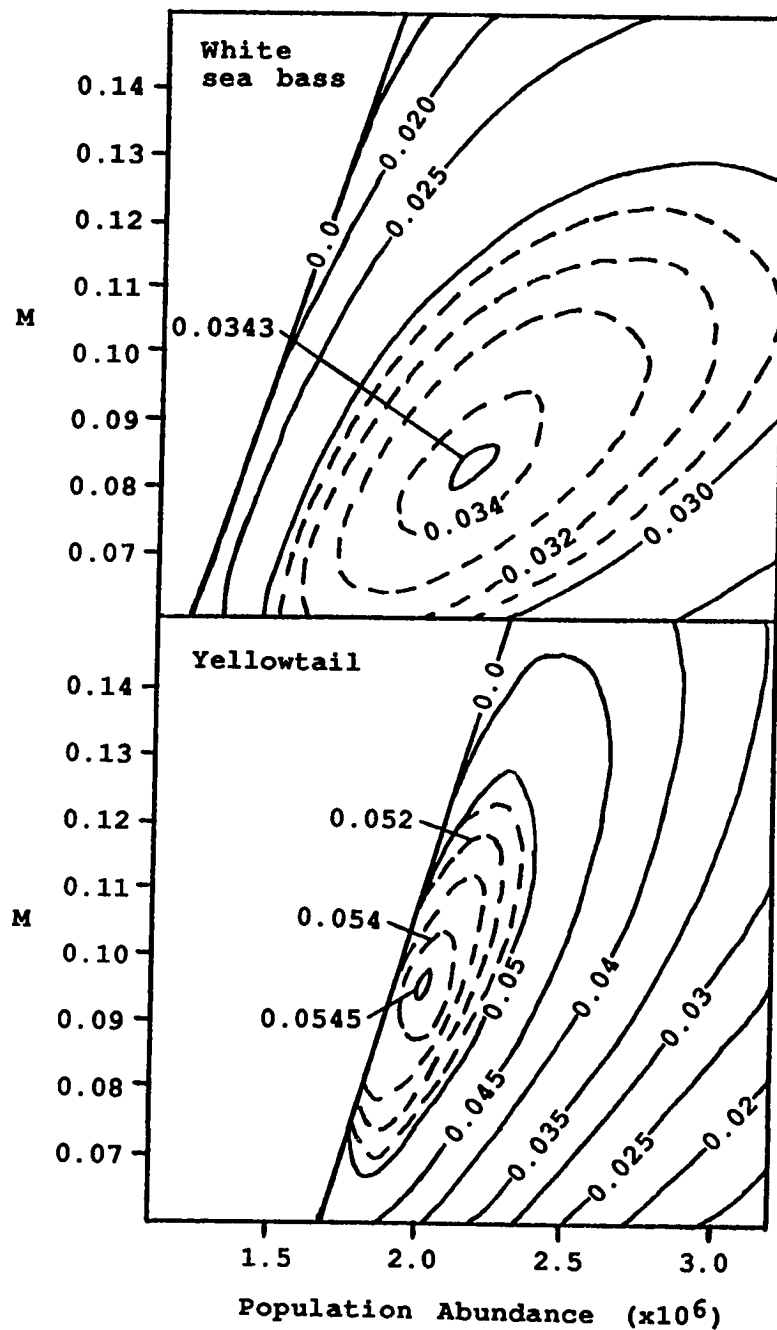
Figure 12. Contour plots of model response surfaces for the white seabass and the yellowtail. Isobars are of geometric mean probabilities, determined as: antilog (log-likelihood / 43 years).

until it found the peak, additional single-parameter and paired-parameter searches were made in the region where the simplex algorithm was satisfied. The results from these single- and double-parameter searches were also used in estimating the second and mixed partial derivatives of the log-likelihood, and these derivatives were, in turn, used to estimate the minimum-variance bounds for the parameters.

Hence, the estimation of the minimum-variance bounds was, at least partially, a function of the coarseness of the search for the response surface peak. These bounds reflect the curvature of the response surface in the region of the peak. If the surface was asymmetrical or had substantial higher derivatives near the peak, as was the case for some of these estimates, then estimated minimum-variance bounds must be viewed with caution.

A second caution in interpreting the asymptotic minimum-variance bounds pertains to the weight-frequency distributions from which samples were drawn. Maximum likelihood techniques are commonly applied to cases where samples are taken from an assumed stationary distribution. In the approach used here, the estimated weight-frequency distributions (from which samples were presumed to have been drawn by the Avalon Tuna Club) change with the size and age structure of the model population. The sensitivity of minimum-variance bound estimation to fluctuation in the population weight-frequency distribution was not determined, and again, these bounds must be viewed with caution.

The close correspondence between the parameter estimates for the white seabass and the yellowtail suggests these two fishes were very similar in population size and have somewhat similar life histories. An alternative explanation is that the correspondence was a function of the modeling approach and the model failed to distinguish between what may be substantially different life history features and population sizes. However, in addition to differences in historical data entered into the model for the white seabass and the yellowtail, there were several differences in the outcome of the models for the two fishes. Solution likelihoods for the yellowtail were substantially larger than those for the white seabass, indicating much better agreement with the assumed model. In part, this may have been due to the increase in annual record weight of white seabass caught by an Avalon Tuna Club member during the late 1930's. There may have been changes in Avalon Tuna Club effort devoted to white seabass, which could have increased sample size, but there is (to our knowledge) no evidence for or against this supposition. This same increase in the record fish (Fig. 1) may have been responsible for the larger minimum standard errors for white seabass parameters. Also, there could have been differential environmental effects on migration of the two fishes; the influence of the environment is well known for El Niño years. One possible reason for the rather low geometric mean likelihood, particularly for the white seabass, may have been the model's inability to explain year-to-year fluctuations due to environmental perturbations. In

addition, if q is any indication, mean annual sample size was larger for the yellowtail than for the white seabass. And, as noted above, instantaneous mortality estimates were slightly larger for the yellowtail.

In the construction of the model, one controversial issue was the possibility of change in the mortality rate with age. For example, is there a senility component to instantaneous mortality? In the model it was assumed that the mortality rate is constant with respect to age, and as a consequence, these fish are long-lived. With a constant mortality rate of 0.10, 1% of a year class is still alive (in the absence of fishing) at the age of 46 years. This increases to age 57 when the mortality drops to 0.08. Whether these are reasonable estimates of longevity for the white seabass and the yellowtail is unknown.

A second, rather nebulous issue was the designation of the model "population" and the extent to which the model population reflects reality. There were at least three populations to be considered in this investigation. The first was the population fished by Avalon Tuna Club members, the second was the population(s) from which the commercial harvest was taken, and the third was the generic population assumed in the model. To what extent the populations fished by the Avalon Tuna Club and fished commercially overlapped was unknown; in the model it was assumed that they were one and the same. To complicate this issue, there was a known seasonal migration of both species into Southern California waters

from the waters of Baja California. The effect of these migrants on the maximum likelihood, indicated in Tables 1 and 3, appeared to be relatively small. When a model population was near extinction due to intense fishing, the effect of migration was to reduce the fishing pressure and thereby allow the "resident" population to persist. If the migrants had a weight-frequency distribution similar to the resident population, then those migrants would not have affected the likelihood of fish of given sizes being caught by the Avalon Tuna Club. However, if the migrants were larger fish, they would have altered the weight-frequency distribution of fish available to the Avalon Tuna Club and this modeling approach would be correspondingly compromised. Migration of larger fish into Southern California waters might possibly explain the increase in record catch of white seabass by Avalon Tuna Club members in the late 1930's.

In spite of the multiple assumptions required, this modeling approach generates the only available estimates of pre-exploitation abundance for the white seabass and yellowtail. As such, these provide the only indication of the severity of historical exploitation, and the extent of recovery that would be necessary to return these populations to their natural state. Clearly, however, these estimates apply to the natural state in the late 1800's. To suggest that in the absence of exploitation these fish populations would be at similar levels today requires the assumption that the overall influence of the pertinent demographic and environmental conditions has not changed. In the absence of information on such

changes, the estimates generated here provide our best indication of the natural state of these fishes.

As such, this information should be useful as a guide for programs such as California's OREHP, the Ocean Resources Enhancement and Hatchery Program. One of the projects funded by OREHP has been development of a cost-benefit assessment model of hatchery performance and stock rehabilitation, with particular emphasis on the white seabass. As the population dynamics of the white seabass have heretofore not been well known, the OREHP investigation has necessarily relied on many assumptions regarding vital rates and related population properties. Although the white seabass is thought to be depleted, data have been insufficient to obtain clear results from standard fishery assessment models (MacCall et al. 1976). One of the most serious shortcomings in the data is lack of information on fishing effort or abundance during the early years of the fishery, data which would provide a clear slope or abundance-effort relation in a production model.

To the present time, assessment and management of the white seabass, the yellowtail, and the giant sea bass have been based on the assumption that California's catches are taken from the seasonal northward migrants, which has largely been the case over most of the last half-century. Managers have understandably hesitated to impose restrictions on harvests from a resource over which they would seem to have little real control. Management based on conservation of a strictly resident stock would require much greater restrictions on

fishing effort. In addition, these results indicate natural mortality is low, which also suggests fishing mortality must be kept low if a resident stock is to be sustained. Presumably a population composed of both resident and migrant fish would allow intermediate levels of fishing. Until now, lack of sufficient information on the early resources and fisheries has prevented quantitative consideration of resident Southern California stocks of these species. The estimates provided by this study give managers a new view of the potential productivity of these stocks in Southern California . For example, the results allow the Gulland potential yield rule-of-thumb, $Y_{pot} = MB_0/2$, to be applied, in these cases indicating a Y_{pot} on the order of 500 to 900 metric tons. Indeed, the recent interest in artificial propagation of white seabass would seem to be more consistent with a management of a resident rather than a migrant resource. If artificial propagation is to be attempted seriously, it is desirable and perhaps essential that management of these populations in Southern California be made consistent with conservation of a resident population. This study provides information which will help fishery scientists to evaluate and managers to decide whether the benefits of resident-based population management are worth the restrictions which would have to be imposed on fisheries.

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CHAPTER 3. PROBLEMS IN MAXIMUM NET PRODUCTIVITY LEVEL ESTIMATION FOR THE NORTHERN FUR SEAL (*CALLORHINUS URSINUS*) POPULATION OF ST. PAUL ISLAND, ALASKA.

INTRODUCTION

From 1957 to 1984 the International Convention for the Conservation of North Pacific Fur Seals provided the legal structure for management of northern fur seal (*Callorhinus ursinus*) populations by Canada, Japan, the U.S.S.R., and the U.S. In 1985 the U.S. Congress chose not to renew the Convention. As a consequence legal authority for fur seal management was transferred to the Marine Mammal Protection Act of 1972 (MMPA). The MMPA requires that populations or stocks of marine mammals not be allowed to diminish below their optimum sustainable population level. The National Marine Fisheries Service (Gehringer 1976) interpreted the "optimum sustainable population" as occurring "...within a range from the population level of a given species or stock which is the largest supportable within the ecosystem to the population level that results in maximum net productivity. Maximum net productivity is the greatest net annual increment in population numbers or biomass resulting from additions to the population due to reproduction and/or growth less losses due to natural mortality."

By this interpretation, the lower bound of the optimum sustainable population is the maximum net productivity level (MNPL). Due to the change in jurisdiction over northern fur seals, an important management objective has become the identification of their

MNPL. Fowler (1984, 1988) has suggested that MNPL for Pribilof Island populations may be on the order of 60% of the environmental carrying capacity (K), and as they are currently thought to be below this level, they have been designated as "depleted" under the MMPA. However, the precision of Fowler's (1984, 1988) estimate is not known, and there is uncertainty regarding the absolute abundance at which MNPL occurs and how to measure that abundance.

While the concept of MNPL is straightforward, its quantitative determination for natural marine mammal populations has proven to be difficult. Gerrodette and DeMaster (1990) reviewed methods for determining the status of a population relative to its MNPL, and divided them into those methods which require estimation of the MNPL, and those that do not (for an example, see Goodman 1988). The methods considered here involve estimation of MNPL as an absolute abundance, or, when K is known, as a fraction of K. The simple (non-generalized) logistic growth equation predicts that MNPL occurs when the population is 0.5K, but there is theoretical evidence that it occurs at greater than 0.5K for large mammals (Gilpin et al. 1976, Eberhardt and Siniff 1977, and Fowler 1981).

The purpose of this chapter is to consider three approaches to estimating MNPL or the ratio MNPL/K for the northern fur seal population of St. Paul Island in the Bering Sea. The first approach is based on analytical stock-recruitment models which can be fit to fur seal data and manipulated algebraically to provide estimates of these theoretical population levels. Such analytical models have

been used in the past primarily to estimate the population size producing the maximum sustainable yield (MSY). The second approach is based on previous numerical models of northern fur seal population dynamics. These numerical models attempted to simulate the recent history of the northern fur seal (Fig. 1) by creating model populations which are moved through time and subjected to hypothetical schemes of density-dependent regulation. The third approach is based on the numerical model of Smith and Polacheck (1984). This approach uses a series of numerical simulations to generate distributions of MNPL and MNPL/K estimates, where the distributions are functions of the uncertainty in the parameters and regulating mechanisms of the model.

ANALYTICAL MODELS

The concept of maximum productivity is not new to northern fur seal management (North Pacific Fur Seal Commission 1962). From 1956 to 1968 nearly 300,000 females on the Pribilof Islands were killed to reduce these populations to a level intended to produce the maximum number of juvenile males for the commercial harvest. This effort to achieve MSY was based on the assumptions that the Pribilof Island populations are regulated by density-dependent mechanisms and that those populations were too large in the 1950's to produce the MSY. MSY remained the goal of management until the International Convention for the Conservation of North Pacific Fur Seals expired in 1985, at which time attention shifted to MNPL.
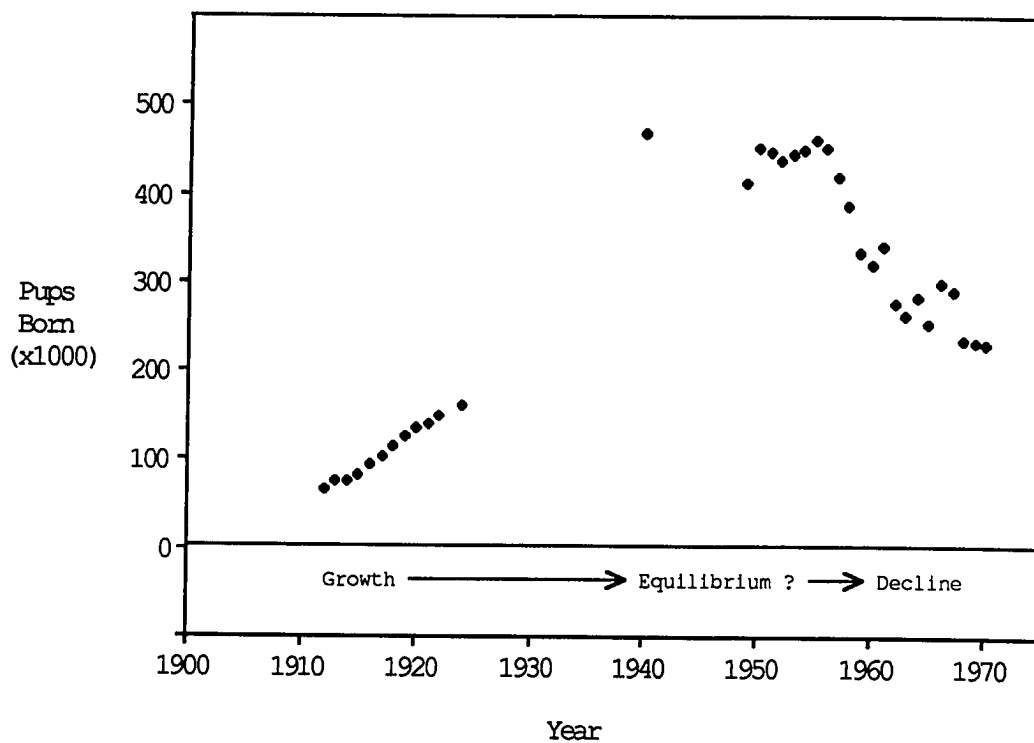
Figure 1. Number of northern fur seal pups born annually on St. Paul Island, Alaska from 1912 to 1970. Simulations discussed later in this chapter attempt to reproduce this trend, filling in the large gap in the time series between 1925 and the late 1940's. Data are from Briggs and Fowler (1984).

difference between MSY and MNPL is that in principle, MNPL is a whole-population measure determined under natural conditions without confounding by age- or sex-selective harvests or other forms of human influence, either direct or indirect. MSY is used with reference to a harvested population and varies with the nature and selectivity of the harvest (DeMaster 1984a). If harvests are taken randomly with respect to age and sex, then MNPL corresponds to the population level producing MSY. If harvests are selective, then MSY may be defined in terms of a single age and/or sex group, rather than the whole population.

Previous MSY analyses for northern fur seal populations were based on the relationship between the number of pups born in a cohort (stock) and the number of males or females in that cohort surviving to age 3 (recruitment). The use of this type of stock-recruitment relationship to estimate MNPL presumes that the pup abundance leading to maximum net recruitment of 3-year-olds (or MSY) coincides with the pup abundance when there is the greatest net annual increment in the total population (MNPL) (Fig. 2). Berkson and DeMaster (1985) have shown that pup numbers may be biased indicators of whole population trends, depending on the nature and timing of density-dependent regulation of the population. MSY analyses using pup numbers and the number of animals surviving to age 3 may contain a similar bias as indicators of MNPL, perhaps by neglecting important density-related mechanisms of regulation other than juvenile survival, or by neglecting undetected effects of the commercial harvests on the
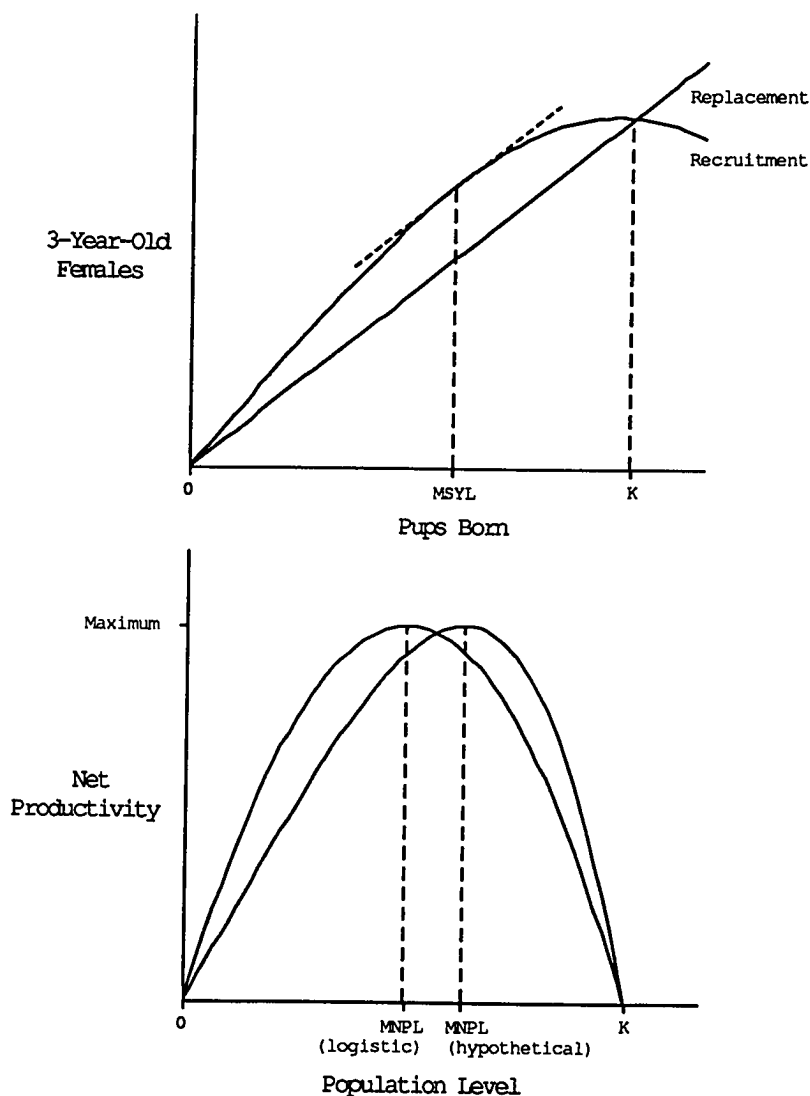
Figure 2. A. Hypothetical maximum net recruitment of 3-year-old northern fur seals as a function of the number of pups born. The distance between the replacement and recruitment lines corresponds to net recruitment. Maximum net recruitment occurs where the slope of the recruitment line is equal to the slope of the replacement line. If 3-year-olds are harvested, then MSY coincides with maximum net recruitment. Note that maximum net recruitment and MSY are defined in terms of a specific portion of the population. B. MNPL as predicted by the simple logistic, and as may occur (hypothetically) for the northern fur seal. MNPL is defined in terms of the whole population. MSY and maximum net productivity do not necessarily occur at the same population level; hence, the population producing MSY may be a biased indicator of MNPL.

dynamics of these populations. In spite of the potential for bias, the difficulty of assessing changes of total abundance suggests that to estimate MNPL, it may be necessary to utilize various population indices such as the number of pups born and the number of recruits to the adult population. The purpose of this section is 1) to review stock-recruitment models previously used to estimate MSY, and 2) to illustrate weaknesses (other than bias) associated with this approach to MNPL estimation.

Estimates of MSY for northern fur seals are generally for the St. Paul Island population and come primarily from the work of Chapman (1961, 1964, 1973). Chapman (1961) compared two analytic models, the logistic (Eqn. 1) and a nonlinear variant based on the notion that density-induced food limitation to nursing females is the regulating mechanism for the dynamics of fur seal populations in the Bering Sea (Eqn. 2).

(1) $R = A * S - B * S^2$

(2) $R = A * S^{3/2} - B * S^2$

In these equations A and B are parameters, R is recruits, and S is stock. With these models Chapman estimated that MSY, or the maximum return of 3-year-old males to St. Paul Island, would occur from a pup population near 480,000. He also suggested that when both males and females are harvested the maximum harvest would occur from a pup

population just under 400,000. Nagasaki (1961) used a generalized Ricker model (Ricker 1954) (Eqn. 3, where C is an added parameter)

$$(3) \qquad R = A * S * e^{-B} * S^C$$

with estimates of fall pup numbers (pups alive after the initial period of high on-land mortality) and numbers of 3-year-old males harvested from 1947 to 1956, and concluded that the maximum harvest of 3-year-old males occurs when the fall pup number is about 400,000. When summer pup mortality is added to Nagasaki's (1961) estimate, it is consistent with Chapman's estimate of 480,000 pups born.

These analyses were based on annual pup estimates from the late 1940's and 1950's. The estimates were derived by mark-recapture techniques. Large numbers of pups were tagged with metal Monel tags, and pup population estimates were calculated from the ratio of tagged to untagged males found 3 years later in the commercial harvest. In this application of the mark-recapture technique, equal survivorship of animals tagged and not tagged was assumed. Both Chapman (1961) and Nagasaki (1961) raised the question of possible bias in these estimates, and Chapman (1964) argued that they may have been inflated due to tag-induced mortality. After adjusting estimates of the number of pups born from 1947 to 1959, Chapman (1964) recalculated the pup population level which resulted in maximum number of males surviving to age 3 as 351,000 pups (food limitation model) or 366,000 pups (logistic model). All of these estimates supported the idea

that in the 1950's and early 1960's fur seal populations were too large to produce MSY.

Chapman (1973) began by reviewing several stock-recruitment curves, including those of Ricker (1954), Beverton and Holt (1957), and a model adapted from Robbins (1945, hereafter referred to as the Robbins-Chapman model) (Eqns. 4-6, respectively), as well as the

$$(4) \qquad R = A * S * e^{-B * S}$$

$$(5) \qquad R = 1 / (A + B / S)$$

$$(6) \qquad R = A * (1 - e^{-B * S})$$

logistic and food-limitation forms (Eqns. 1 and 2, respectively) he had used in his earlier papers. He concluded that stock-recruitment models may have different biological derivations but may be empirically indistinguishable: "It would appear therefore that if we pick a particular stock-recruit model...to fit to real data, we are merely picking a convenient empirical curve which may have, but probably does not have, biological meaning." He derived a nonparametric approach to estimate the population level which results in MSY, and concluded that, at least by this method, MSY would occur when the population produced about 283,000 pups. Eberhardt (1981) reviewed Chapman's (1973) nonparametric model and showed how, with

slight modification, that model would predict MSY from a population producing just over 360,000 pups.

Eberhardt (1981) also multiplied Chapman's (1973) juvenile male survivorship data by 1.1 to estimate juvenile female survivorship, and then fit the female estimates to the survivorship curve

(7) $S = S_{max} * (1 - e^{-A} * (N_{max} - N))$,

where S is female survival to age three, S_{max} is the maximum survivorship, A is a shape parameter, N_{max} is the number of female pups born at equilibrium, and N is the total number of female pups in the cohort. On the basis of his results, Eberhardt (1981) suggested that MSY should occur when approximately 400,000 pups (females and males) are born on St. Paul Island.

In addition to the potential for bias, these earlier studies reveal other problems with the use of analytical MSY models for MNPL estimation. These problems are illustrated by fitting a variety of stock-recruitment models to juvenile survival data adapted from Chapman (1973) (Table 1 and Fig. 3). His data are for males, but are multiplied by 1.1 to estimate survival of females from birth to age 3 (female survival to age 3 assumed proportional to male survival by a factor of 1.1; see Chapman (1973)). To determine MNPL and K using these models, it is necessary to estimate the replacement rate (Fig. 2) in terms of the ratio of 3-year-old females to pups born

Table 1. Fitted stock-recruitment curves, including modification of the Robbins-Chapman, Ricker, and Beverton and Holt models. MNPL and K are given in thousands of pups born. The data fitted are from Chapman (1973, p. 331, his Table 112). Models followed by an asterisk incorporate the additional parameter as suggested by Paulik (1973). Values under parameter estimates are standard errors. VAR @ REG is the sum of squared errors divided by the degrees of freedom.

MODEL (R =)	A	B	C	MNPL	K	MNPL /K	VAR @ REG
Robbins-Chapman							
$A(1-\exp(-BS))$	105.9 61.27	2.375e-3 2.217e-3	--------	206	452	0.46	317.2
$A(1-\exp(-(B+CS)S))$	72.28 15.90	1.422e-3 3.901e-3	1.180e-5 2.278e-5	280	445	0.63	329.6
$A(1-\exp(-(B\exp(CS))S))$	69.72 10.34	1.870e-3 1.927e-3	3.576e-3 4.715e-3	299	445	0.67	327.2
$A(1-\exp(-BS^C))*$	72.91 20.12	1.210e-4 6.969e-4	1.649 1.130	277	445	0.62	330.4
Ricker							
$AS\exp(-BS)$	0.2484 0.07996	1.061e-3 8.188e-4	--------	211	450	0.47	316.4
$AS\exp(-(B+CS)S)$	0.2265 0.2372	4.529e-4 6.448e-3	9.059e-7 9.458e-6	234	448	0.52	333.1
$AS\exp(-(B\exp(CS))S)$	0.2269 0.1583	3.610e-4 2.761e-3	2.063e-3 0.01351	242	436	0.56	330.9
Beverton and Holt							
$1/(A+B/S)$	5.769e-3 4.498e-3	3.856 1.711	--------	198	456	0.43	318.2
$1/(A+(B\exp(CS))/S)$	0.01329 3.953e-3	8.662 14.55	-6.112e-3 9.110e-3	277	445	0.62	330.5
$1/(A+B/(S^C))*$	0.01160 6.973e-3	387.5 3.920e+3	1.932 1.996	262	446	0.59	332.4
Richards (as suggested by Eberhardt (1981))							
$AS[(B/S)^{(1-C)}-1]/(1-C)$	10.68 0.9506	466.8 6.513	60.01 47.97	422	452	0.93	286.3
Generalized Allen (from Chapman 1981)							
$AS^B(K-S)^C$	6.127e-3 0.02114	1.448 0.5025	0.1741 0.1033	365	464	0.79	286.3
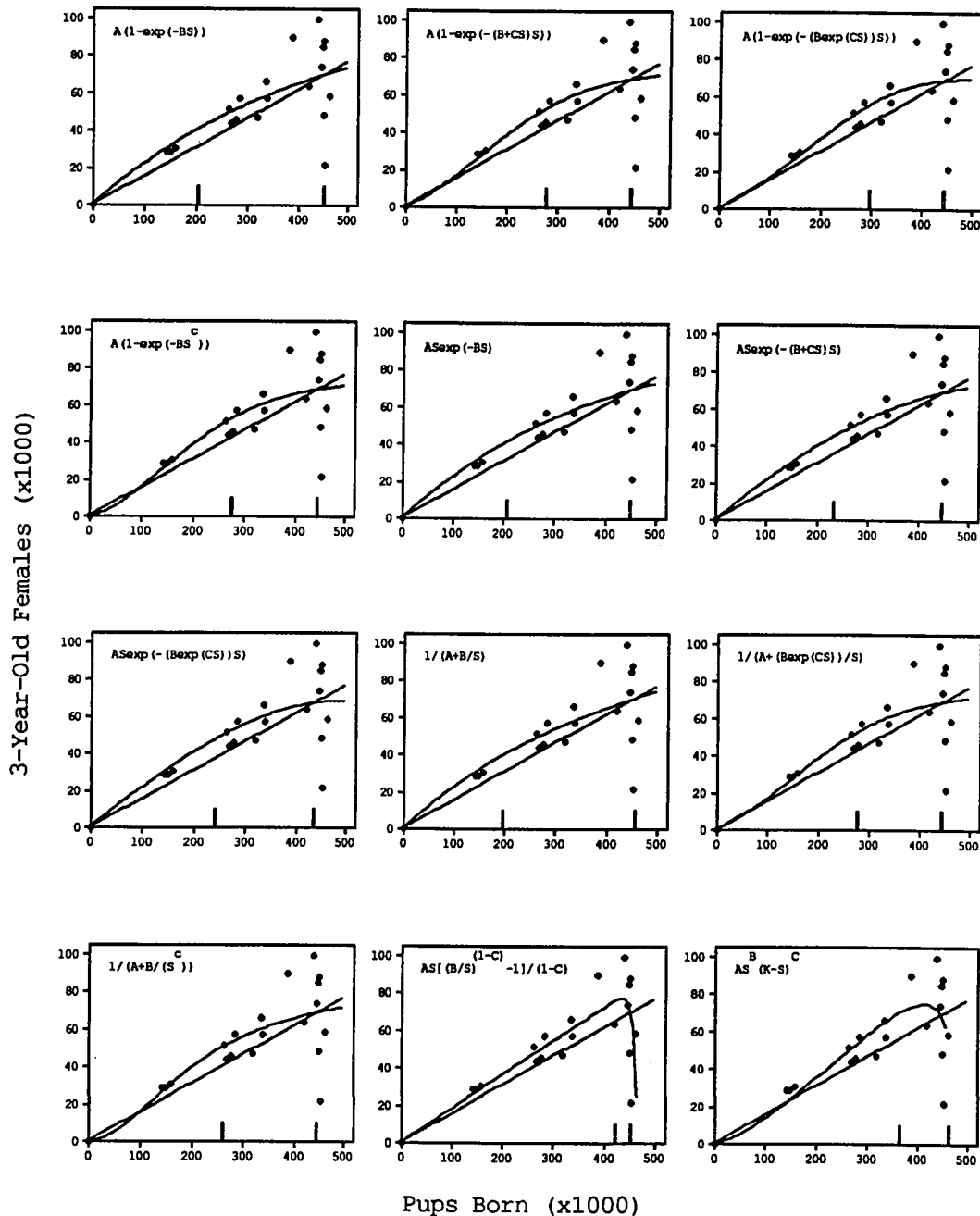
Figure 3. Stock-recruitment models from Table 1, used to fit estimated recruitment of 3-year-old females (Y-axes) to number of pups born (X-axes). Data are adapted from Chapman (1973) and are for the years 1920-22, and 1950-65. Except for the generalized logistic and Allen models (middle and right of bottom row, respectively) the fitted models are visually similar. However, these models result in substantially different estimates of MNPL (left bars just above X-axes). Estimates of K (right bars) are much less variable.

(See Appendix). The life table information necessary to estimate replacement rate is more reliable for females; thus, the conversion of the data to female survival. In the Appendix, the replacement rate is estimated to be 0.154, which is similar to the estimate of 0.123 by Chapman (1973). In Table 1, the estimates of K are derived algebraically or iteratively by setting the number of recruits equal to the replacement (replacement rate * number of pups born) and solving the respective stock-recruitment equations for S, the number of pups born. Similarly, the MNPL estimates are calculated by taking the first derivatives of the stock-recruitment equations, setting them equal to the replacement rate (number of 3-year-old females / number of pups born), and solving for S.

The first problem apparent in Table 1 and Figure 3 is the question of which model most nearly reflects the dynamics of fur seal populations. Clearly there are many stock-recruitment forms, only a small portion of which are included here. As noted above, Chapman (1973) suggests the model which best fits the real data may or may not have biological meaning; the "best" model may simply be the one that gives the best empirical fit. In Table 1, Richards' (1959) form of generalized logistic and Chapman's (1981) generalized Allen (1972) equation give the best fits, as indicated by variance about the regression. However, these models have strongly descending right-hand limbs (Fig. 3), suggesting that juvenile survival rapidly approaches zero as the population approaches K. This is questionably realistic; hence, the "best fit" may reflect some degree of

statistical artifact. Note also that the generalized Allen (1972) model includes a fourth parameter, K. The value of K used in Table 1 and Figure 3 was determined by finding the best fit of the other three parameters for a range of different values of K, and then using the value of K which resulted in the smallest variation about the regression. Thus, for this model, K is a fourth fitted parameter.

Estimates of K from these analytical models are relatively consistent, ranging from populations which produce 436,000 to 464,000 pups. But estimates of MNPL vary widely, ranging from populations which produce 198,000 to 422,000 pups. Thus, the choice of model has a marked effect on the estimate of MNPL. For example, the MNPL estimated from the basic Beverton and Holt model occurs when 198,000 pups are born. When this model is made more flexible by changing the shape parameter (B) to an exponential function of stock size (Bexp(CS)), the new MNPL estimate is 277,000 pups, an increase of 40%.

A second problem is that while several of these models may fit the data reasonably well, they are mathematically biased and inappropriate for predicting MNPL (Fowler 1981). For example, the familiar Beverton and Holt stock-recruitment model (Eqn. 5) and the Robbins-Chapman model (Eqn. 6) are mathematically constrained to predict MNPL to be below 0.5K. Because there is theoretical evidence that MNPL for marine mammal occurs at greater than 0.5K, these models are inappropriate for this use. However, this inflexibility can be reduced by the addition of a third parameter to the models. Paulik

(1973), for example, suggested "asymptotic exponential regression" to make these models more flexible. Additional methods include changing the shape parameter in each of these basic models (the B parameter in Table 1) to a linear or exponential function of stock size.

Addition of a third parameter to the basic Robbins-Chapman, Ricker, and Beverton and Holt models, consistently leads to large increases in estimated MNPL, as well as small decreases in the estimates of the number of pups born at K. Thus, the ratio MNPL/K increases, suggesting that the bias inherent in the basic models is reduced by adding a third parameter.

However, addition of a third parameter also leads to an increase in variability about the regression. While the total sums of squared errors is reduced for the more flexible models, they lose a degree of freedom, and the estimated variance about the regression increases. More importantly, adding a third parameter often leads to increased estimates for the standard errors of the parameters. Thus, while the parameter estimates may be less biased, they are also less certain. As a consequence, estimates of MNPL and K based on the more flexible models are also less certain. The determination of the most appropriate model requires an evaluation of this uncertainty relative to the bias of the simpler models.

A third problem is the nature of the data used to obtain the model fits. There are two elements to this problem, the first being the often overlooked errors-in-variables. That is, for these stock-recruitment models, the independent variable (number of pups) is not

known without error, but that error is not taken into account by standard regression techniques. As indicated by Walters and Ludwig (1981), "Errors in measuring ... stocks can have a profound effect on the appearance of stock-recruitment relationships." In addition to the ignored error in the independent variable, these data may also be substantially biased. As Chapman (1964) pointed out, changes in pup production during the 1950's appeared to be unreasonable large, and pup estimates may have been substantially inflated due to failure to account for tag-induced mortality. Chapman (1973) provided new estimates of pups born from 1950 to 1965, although it is difficult to know how much bias may remain in those numbers. Other survival estimates for the approximately same period have been calculated by Lander (1975), Smith and Polacheck (1984), and Trites (1989) (Fig. 4), demonstrating the lack of agreement with respect to juvenile survival values.

Given these problems with analytical models, it is difficult to determine where MNPL occurs. From these models only, it would appear that a minimal estimate would be when approximately 235,000 pups are born on St. Paul Island, and a maximal estimate may be well over 300,000 pups. But clearly, other methods of estimating this level are desirable. A second means of MNPL estimation for this northern fur seal population is through the use of numerical models of fur seal population dynamics. These models are addressed in the following section.
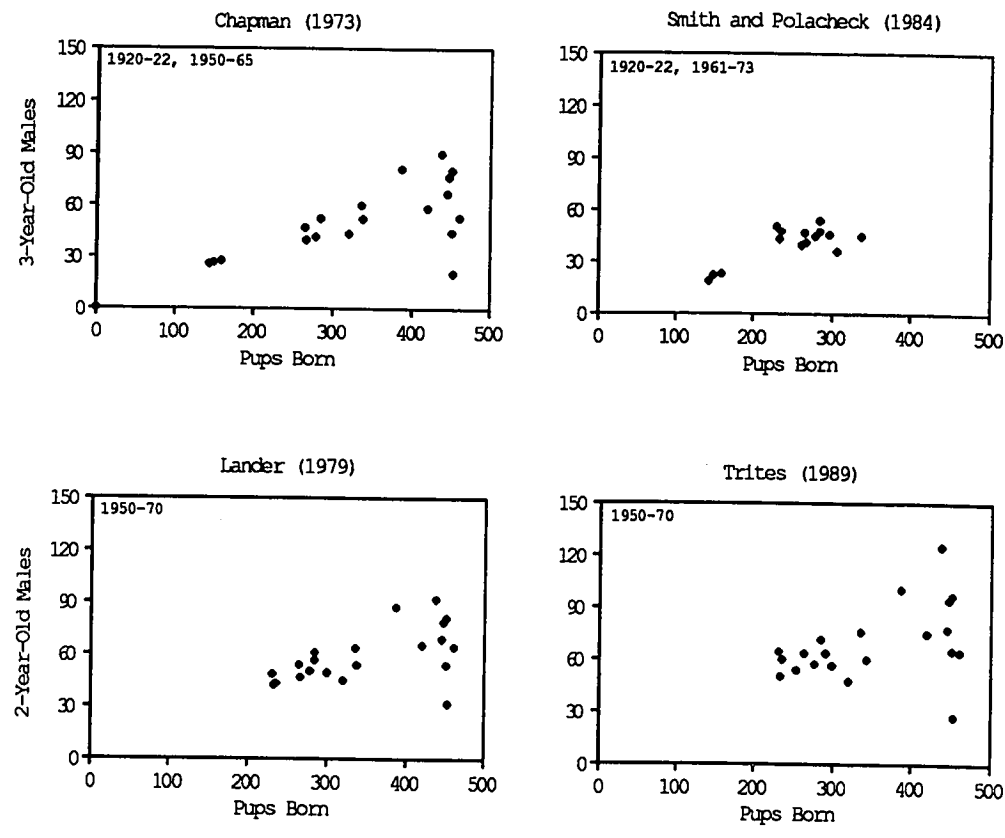
Figure 4. Estimates of male survival from birth to age 3 in Chapman (1973) and Smith and Polacheck (1984), and from birth to age 2 in Lander (1979) and Trites (1989).

NUMERICAL MODELS

Numerical models have been developed to duplicate recent trends in northern fur seal abundance and to study the effects of various extrinsic influences (e.g., harvests or fisheries interactions) on their populations (Smith 1973, Eberhardt 1981, Goodman 1981, Smith and Polacheck 1984, Swartzman 1984, Gerrodette et al. 1985, Reed et al. 1987, Trites and Larkin 1989, Eberhardt 1990). Goodman (1981), Gerrodette et al. (1985), and Trites and Larkin (1989) did not include mechanisms of density dependence in their models and will not be considered here. Eberhardt (1990) included the same mechanism as in his earlier study (Eberhardt 1981), and only the earlier study will be considered here.

In this section numerical models by Smith (1973), Eberhardt (1981), Swartzman (1984), and Reed et al. (1987) will be briefly described and modified, when necessary, to estimate MNPL. A fifth model by Smith and Polacheck (1984) is the basis for the third section of this chapter, and will be considered in detail there. The basic elements of these models are the life tables of age-specific survival and fecundity parameters and the mechanisms relating changes in those parameters to some measure of population abundance.

Smith (1973). Smith used a variable projection matrix model to simulate the Pribilof Island northern fur seal population from 1911 to 1970. The only density-dependent factor in the model was pup survival, which was a nonlinear function of the number of females age

1 and older (Fig. 5). However, the nonlinearity resulted from the linking of two linear functions (Eqn. 8):

$$(8) \quad \begin{aligned} S_0 &= 0.7, & N_F &< 714,500, \text{ or} \\ S_0 &= 1.174 - 6.637 * 10^{-7} * N_F, & N_F &> 714,500, \end{aligned}$$

where S_0 is pup survival to age 1, and N_F is the total number of females age 1 and older. That is, pup survival was constant at 0.7 yr^{-1} until the number of females reached 714,500, and then declined linearly to a rate of 0.48 yr^{-1} at a female population of 1,046,000. The life table for Smith's model was based on data from the first four years of the pelagic collection (i.e., 1958 to 1961), when the population was assumed to be at equilibrium.

To validate his model, Smith compared growth rate in the model to historical records from 1920 to 1924. The growth rate was too low, but by increasing all fecundity rates by 10%, it increased to 0.072 yr^{-1}, which is consistent with historical records. Smith then fit the growth rate from his adjusted model to a form of the Richards' (1959) function, which he suggested could approximate growth in a matrix model. The parameters of the Richards' (1959) function include K, which Smith estimated to be 1,233,000 females, and an additional parameter which allows the calculation of the ratio MNPL/K (Richards 1959, p. 293). Smith does not make this calculation, but provides the parameter, and the resulting estimate of MNPL/K is 0.61 for his adjusted model. This ratio and the estimate of K suggest the MNPL occurs at approximately 752,000
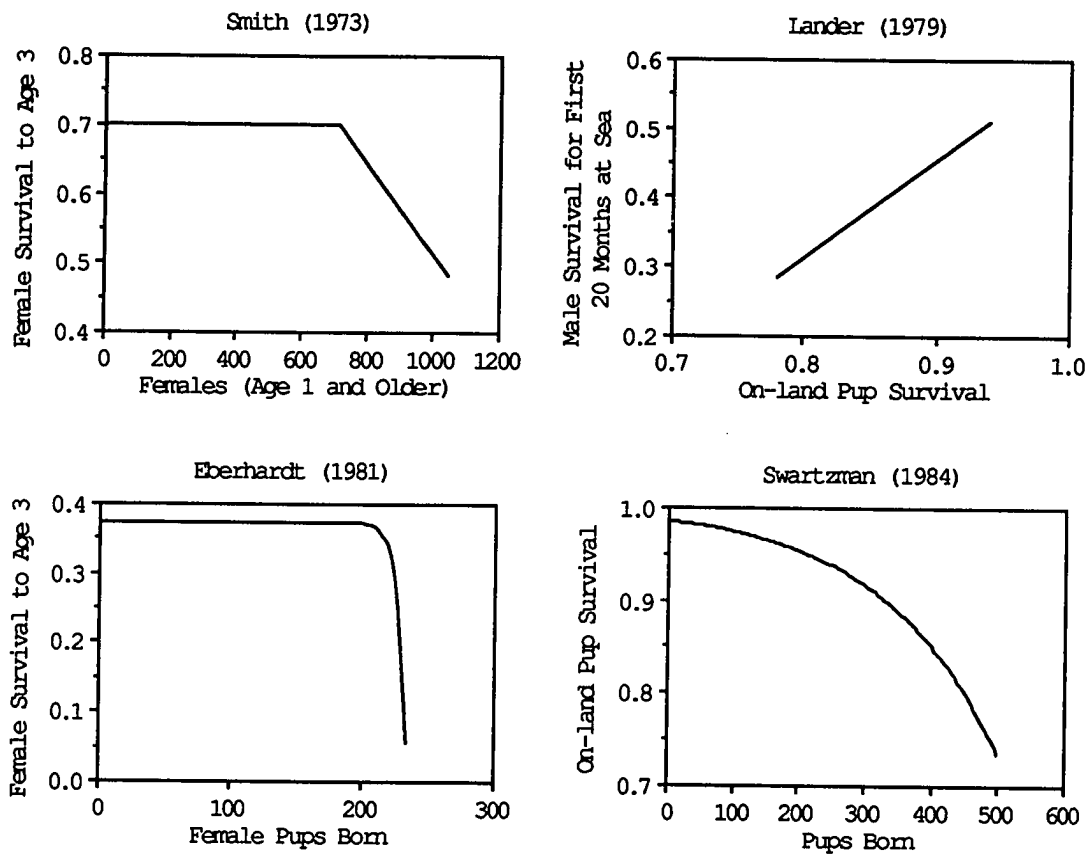
Figure 5. Density-dependent mechanisms used in numerical modeling of northern fur seal population dynamics, including female survival from birth to age 3 (Smith 1973 and Eberhardt 1981), on-land pup survival (Swartzman 1984), and survival for the first 20 months at sea as a function of on-land survival (Lander 1979).

females. Smith also used 500,000 as the equilibrium number of pups. A population with 752,000 females (MNPL) and Smith's adjusted fecundity schedule should produce just over 300,000 pups.

Eberhardt (1981). Eberhardt argued that the Pribilof Island population of northern fur seals reached an equilibrium in the late 1940's, and he constructed a life table accordingly. With this life table and Equation (7) above, he simulated the population from 1951 to 1976. However, the parameters Eberhardt suggested for Equation (7) (S_{max} - 0.40, A = 0.0333, and N_{max} = 300,000; see Fig. 5), used in combination with his life table, result in population growth of about 2%, well below the realized growth rates recorded between 1912 and 1924. Under these conditions the model does not appear to be appropriate for simulating population growth in the early part of this century. Realistic growth rates and growth patterns can be achieved by adjusting the parameters S_{max} and A. For example, with S_{max} and A set to 0.65 and 0.01, respectively, the population grows in a manner consistent with historical records, reaching K at a total population of 1,842 million with 461 thousand pups, and achieving MNPL at 1,327 million with 343 thousand pups. But the parameter adjustments to obtain these estimates are arbitrary and other combinations of parameters provide equally plausible results. Hence, there is little basis for confidence using this model.

Swartzman (1984). Swartzman added age structure to a model developed by Fowler (1982) to examine the effects of entanglement on northern fur seal population dynamics. Swartzman used the life table

from Lander (1980) and included density dependence in the survival of pups from birth to weaning only (Fig. 5):

(9) $S_{0,on-land} = 1 - 0.01477 * e^{(5.792 * 10^{-6} * N)}$,

where $S_{0,on-land}$ is the survival rate of pups from birth to weaning, and N is the total number of pups born.

Swartzman focused on analytical solutions for population equilibrium with varying levels of entanglement-induced mortality of different age groups. He did not attempt to simulate a period of growth such as occurred during the first half of this century. If, however, a simulation is run with a matrix model incorporating the life table (Lander 1980) and density-regulating mechanism used in Swartzman's model (Eqn. 9), the simulated population reaches equilibrium at an abundance of 2,269,000 animals with 494,000 pups. The MNPL, determined numerically, occurs at an abundance of 1,559,000 (69% of K) with 344,000 pups (70% of pups at K).

Reed, French, Calambokidia, and Cubbage (1987). Reed et al. combined a detailed model of northern fur seal dynamics and migration with an oil spill trajectory model to predict possible effects of an oil spill on the Pribilof Island populations. The population dynamics segment of the model was also used to reproduce historical changes in fur seal population levels, and to study possible effects of entanglement in marine debris (French and Reed 1989).

Life table information for this model included pregnancy rates from York (1979, based on the pelagic collection 1958-74) and mortality rates from Lander (1981). With the exception of survival from birth to age 2, all vital rates were held constant. On-land survival of pups was a function of the number of pups born as determined by Swartzman (1984, Eqn. 9), and was equal for females and males. Survival for the first 20 months at sea (from the age of about 4 months to 2 years) was estimated from Lander's (1979) relationship between survival for this period and survival of pups on land (Fig. 5). When used with the migration model and oil spill trajectory models, the population dynamics model did not include differential survival of males and females for the first three years. However, the model more closely approximated the historical records from the early 1900's to the 1950's when a differential survival of 1.74 was included (female survival to age 3 = 1.74 * male survival). Under these conditions, the modeled population (total Pribilof population) reached K at 1,950,000 animals and was maximally productive at approximately 74% of K, or 1,440,000 animals (D. French, pers. comm.).

Problems with the numerical approach. Development of these numerical models involved choosing a life table of vital parameters and a mechanism of density-dependent regulation, then running a simulation and comparing it to historical observations (validation criteria), and finally adjusting one or more elements of the model until the comparison was satisfactory and thus provided a basis for

confidence in the model. The problems with this approach to MNPL estimation stem from uncertainty in the information required by the models. Uncertainty in model input (i.e., life table parameters and mechanism(s) of density dependence) suggests that there may be many combinations of parameters and density dependence which, when entered into a model, lead not only to satisfaction of the validation criteria, but to different estimates of MNPL. The results from each of the above models are based on a single combination of input information, and therefore cannot reflect the uncertainty with which life table parameters and density dependence are known.

Uncertainty in life table parameters for the northern fur seal is indicated by the number of published survival and fecundity schedules (Kenyon et al. 1954, Chapman 1964, Eberhardt 1981, Goodman 1981, Lander 1981, Smith and Polacheck 1981, York and Hartley 1981, Barlow and Boveng [in press]). With the exception of Kenyon et al. (1954), survival and fecundity schedules have been developed primarily from data gathered in the extensive pelagic collection taken from 1958 to 1974 by Canadian and U.S. scientists. But these schedules differ with respect to assumptions of population equilibrium and methods of estimating survival of young females, which were underrepresented in the pelagic collection. Figure 6 illustrates the variability among four of these life tables with respect to estimates of equilibrium survival rates of females.

Similarly, there is uncertainty about which of these parameters respond to changes in population abundance, and how they
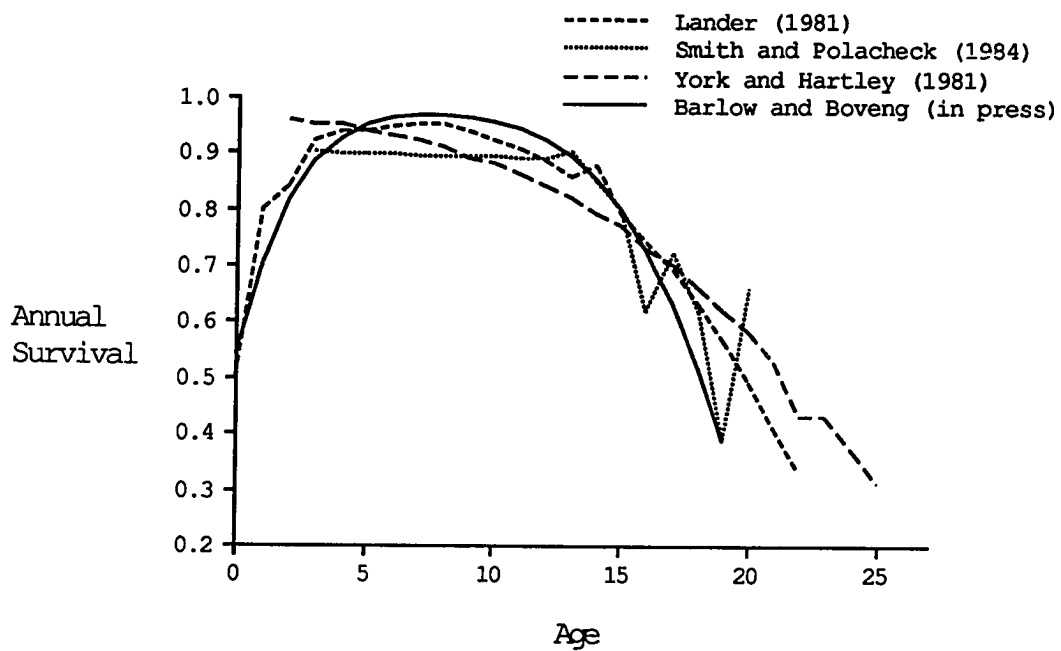
Figure 6. Female northern fur seal survival rates by age from the life tables of Lander (1981), York and Hartley (1981), Smith and Polacheck (1984), and Barlow and Boveng (in press).

change. Each of the four models described above incorporated density-dependent change in juvenile survival only; fecundity rates and survival rates of older animals were held constant. Yet, Smith and Polacheck (1981) argued that changes in juvenile survival alone could not account for the 8% change in population growth rate that occurred between 1912 and the 1950's. They point out that if two or more density-related mechanisms were responsible for the pattern of growth seen, then change in any one mechanism may have been small and therefore difficult to detect. Small changes in adult female survival can have large regulatory effects (Eberhardt and Siniff 1977). But adult female survival is very difficult to measure, and previous estimates are imprecise relative to the degree of change necessary to substantially modify population growth. While there may not yet be clear evidence for density-related changes in fecundity and adult survival, the lack of evidence may reflect an inability to detect those changes when they occur. Density-dependent fecundity and adult survival should be considered as possible regulatory mechanisms in models of northern fur seal population dynamics.

When numerical models are used to estimate MNPL, three questions must be addressed. The first is whether the results of any given model satisfy the validation criteria and can therefore be used to estimate MNPL. The second is whether other models also produce results that satisfy the criteria. And the third is whether there is any basis for selecting more appropriate models from the set of models that satisfy the criteria. The second and third questions are

critical if numeric models are to be used with confidence to estimate MNPL. The purpose of the final section of this chapter is to address the second and third questions: what other models satisfy the criteria, and whether there is a basis for preference among those models.

REPETITIVE SIMULATIONS

The preceding sections were intended to illustrate the nature of the problems with the estimation of MNPL for northern fur seals. Both the analytical and numerical approaches require data of uncertain accuracy and precision, and utilize either stock-recruitment models or models of density dependence which vary in their theoretical derivations and in their predictive properties. Consequently, it is difficult to judge the level of confidence that can be placed in the resulting estimates.

To circumvent these problems, this study extended the modeling approach of Smith and Polacheck (1984). Their approach begins by estimating the range of possible values for each model parameter. The combination of all the parameters constitutes a "parameter space," which they systematically partitioned to form a large number of parameter combinations. Smith and Polacheck (1984) used these parameter combinations in separate simulations to study the effects of age structure and density dependence on the harvesting of females. In the present study, separate simulations using different parameter combinations were used to estimate possible

values of MNPL. The results from the subset of simulations satisfying predetermined validation criteria created a distribution of MNPL estimates, which provides a measure of confidence in these estimates.

Simulated populations began in 1912 with the population in stable age distribution and producing 70,000 pups (Kenyon et al. 1954). As the model advanced from year to year in any one simulation, its results were compared to the validation criteria. If any of the criteria was not met, that simulation was discontinued and the next one was begun.

Five validation criteria were used (Fig. 7). The first was the growth rate achieved during the period 1912 to 1924. Historical records suggest that the number of pups born annually during this period was growing at the annual rate of about 8% (Kenyon et al. 1954). Pups were enumerated in these early years, and while these counts are generally accepted, the possible error may be substantial. Gerrodette et al. (1985) estimated the growth rate of a northern fur seal population under conditions similar to those in the 1910's and determined the 99% confidence interval for the growth rate to fall between $0.048 \ yr^{-1}$ and $0.115 \ yr^{-1}$. In this study growth rate values of $0.05 \ yr^{-1}$ and $0.11 \ yr^{-1}$ (which corresponds to approximately 15% error in counting) were used as lower and upper limits to the growth rate between 1912 and 1924. Simulations with lower or greater growth rates were not continued.
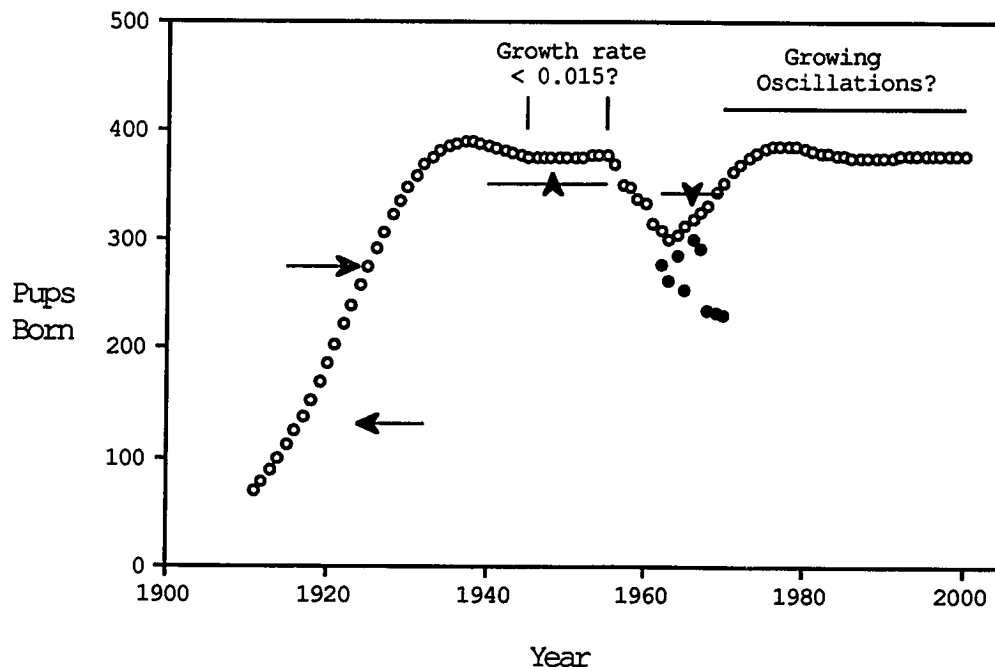
Figure 7. The five validation criteria used to accept or reject simulations. The first criterion is the growth rate between 1912 and 1924. If the growth rate is within acceptable limits, the pup numbers pass between the two arrows on the left. The second criterion is the lower limit (350 thousand) for the maximum annual pup number between 1940 and 1955. The third criterion is the annual growth rate during the period 1945 to 1954, which must decrease to less than 0.015 for at least one year. The fourth criterion is the number of pups born between 1962 and 1970, which must be less than 342.7 thousand for at least one year. The final criterion rejects the simulation if there are growing oscillations after 1970. Hollow circles are the pup numbers from a simulation. Also shown (filled circles) are the observed pup estimates for the period 1962 to 1970 (Briggs and Fowler 1984).

The second criterion was the number of pups born annually from 1940 to 1955. Smith and Polacheck (1984) estimated a lower limit of pup population size during that period as 350 thousand. If the maximum pup number in the model during this period did not reach 350 thousand, the simulation was discontinued.

The third criterion was based on the generally accepted idea that the population was near equilibrium by the late 1940's or early 1950's. If growth rate for the population did not decline to less than 0.015 yr^{-1} (arbitrarily chosen) during the period 1945 to 1955, the simulation was stopped.

The fourth criterion was the number of pups born from 1962 to 1970. The shear-sample (mark-recapture) technique for counting pups (Chapman and Johnson 1968) was used during this period and the counts are considered relatively reliable. These pup estimates have been used to validate models in numerous earlier studies (Smith 1973, Eberhardt 1981 and 1990, Smith and Polacheck 1984, Reed et al. 1987, and Trites and Larkin (1989). The maximum number of pups estimated for this period was about 298 thousand (Briggs and Fowler 1984, Smith and Polacheck 1984). Allowing for 15% error in this estimate, the fourth criterion stopped the simulation if the minimum count during this period (1962-70) was greater than 343 thousand.

The fifth criterion was the presence of oscillations in population abundance. If a simulation passed the other criteria, it was allowed to run until the year 2000, and any tendency for

oscillation was observed. Simulations with oscillations were rejected only if the oscillations were growing.

Five population measures, including MNPL, K, the number of pups born at the MNPL and K, and the ratio MNPL/K, were recorded for each simulation that passed the validation criteria. MNPL was determined numerically by recording the total population size resulting in the maximum net annual increment in population growth; the number of pups born at that population size was also recorded. The number of pups born at equilibrium was a simulation parameter, which was used with the equilibrium life table to calculate the population size at K; K was not determined numerically. Simulation pup abundances were recorded to compare with observed pup estimates, which are the most reliable measures of the population in the field.

All simulations were based on the model of Smith and Polacheck (1984). Their model is a variant of an age-structured Leslie matrix (Lewis 1942, Leslie 1945, 1948) where both reproductive and survival parameters may be density-dependent according to the general function (Allen 1976)

$$(10) \quad X_{i,t}(N_{1+,t}) = X_i^* + (X_i' - X_i^*)\,(1 - (N_{1+,t}/N_{1+}^*)^Z),$$

where $X_{i,t}(N_{1+,t})$ = the value of parameter X for age i, year t, as a function of the number of females age 1 and older at the beginning of year t,

X_i^* = the value of the parameter X_i at population equilibrium,

X_i' = the realized maximum value of the parameter X_i,

$N_{1+,t}$ = the number of females age 1 and older at the beginning of year t,

N_{1+}^* = the number of females age 1 and older at population equilibrium, and

Z = a positive constant (shape parameter).

The term $(X_i' - X_i^*)$ in Equation (10) is the difference between the realized maximum value of a fecundity or survival parameter and its value when the population is at equilibrium; hence, it is the scope for density-dependent change in that parameter. However, realized maximum values for these parameters are unknown. Biologically possible maximum values are 1.0 yr^{-1} for adult female survival and 0.5 yr^{-1} for fecundity, but it is unlikely that these values are ever reached. In this study a range of realized maximum values were considered in the manner described by Smith and Polacheck (1984). They set their realized maximum values as the equilibrium values plus some portion of the maximum possible scope for change (Fig. 8). For any given simulation, the realized maximum values of adult female survival (S_i) and fecundity (F_i) were determined by

(11) $S_i' = M_a (1.0 - S_i^*) + S_i^*$, and
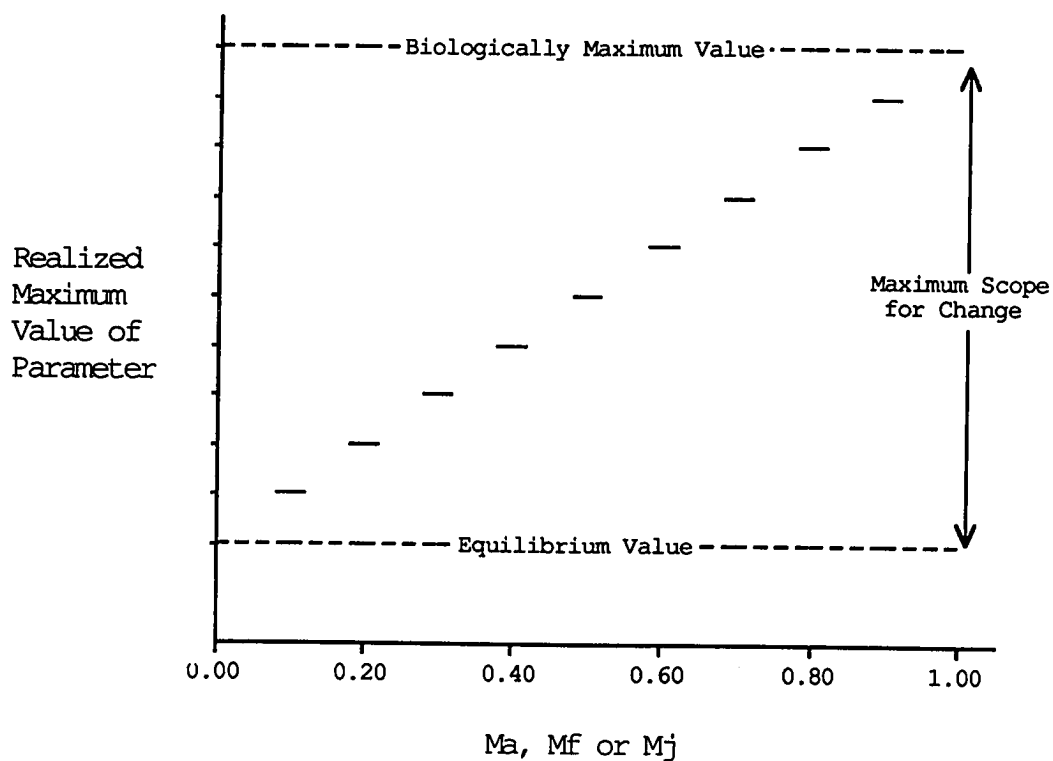
Figure 8. Maximum realized values and scope for density-dependent change of life table parameters as determined by the parameters M_j, M_a, and M_f (from Smith and Polacheck 1984). See text for maximum possible parameter values and Table 2 for equilibrium values.

$$(12) \quad F_i' = M_f (0.5 - F_i^*) + F_i^*,$$

where M_a and M_f are the proportion of the maximum possible scope for change. Note that the value 0.5 yr^{-1} in Equation (12) is based on the assumptions of a 1:1 sex ratio at birth and no more than a single pup per year per adult female. Note also that M_a and M_f apply simultaneously to all adult female survival values and all fecundity values, respectively.

Smith and Polacheck (1984) also set the biologically possible juvenile survival values at 1.0 yr^{-1}. However, it is clear that this is never realized, and biologically possible maximum survival values in this study were set for female pups at 0.8 yr^{-1}, for 1-year-old females at 0.9 yr^{-1}, and for 2-year-old females at 1.0 yr^{-1}. Hence, realized maximum survival values for female pups, 1-year-olds, and 2-year-olds were determined by

$$(13) \quad S_0' = M_j (0.8 - S_0^*) + S_0^*,$$

$$(14) \quad S_1' = M_j (0.9 - S_1^*) + S_1^*, \text{ and}$$

$$(15) \quad S_2' = M_j (1.0 - S_2^*) + S_2^*,$$

where M_j determined the realized maximum survival for all three age groups simultaneously in any simulation. The use of 0.8, 0.9, and 1.0 yr^{-1} as biologically possible maximum values means the maximum

possible survival of females from birth to age 3 is 0.72, which is consistent with the model of Smith (1973) and with the life table used by Goodman (1981) and Gerrodette et al. (1985).

The third term of the regulating function $(1-(N_{1+,t}/N_{1+}*)^Z)$, determines the extent of parameter change between the realized maximum value and the equilibrium value as a function of the ratio of number of females age 1 and older at the beginning of year t $(N_{1+,t})$ to the number of females age 1 and older when the population is at equilibrium $(N_{1+}*)$. Smith and Polacheck (1984) used the number of pups born instead of the number of females age 1 and older. However, trial simulations suggested that the use of the number of pups born as the density-independent factor leads to unnatural oscillations in population abundance; hence, the change to number of females age 1 and older. Z, the shape parameter, determines the concavity of the density-dependent regulating function. When Z is 1.0, the resulting function is linear. If Z is increased above 1.0, the function becomes nonlinear and concave downward, and the nonlinearity increases as Z becomes larger (Fig. 9). As mentioned earlier, Fowler (1981) presents evidence that density-dependent changes for marine mammals are nonlinear (Z > 1.0), and the linear function (Z = 1.0) is considered to be the limiting case for marine mammals (for example, see DeMaster 1984b).

The annual cycle for the simulated population began with the birth of a new cohort, followed by population census, and determination of survival and life history parameters for the coming

$$X(N) = X* + (X'-X*) (1-(N/N*)^Z)$$
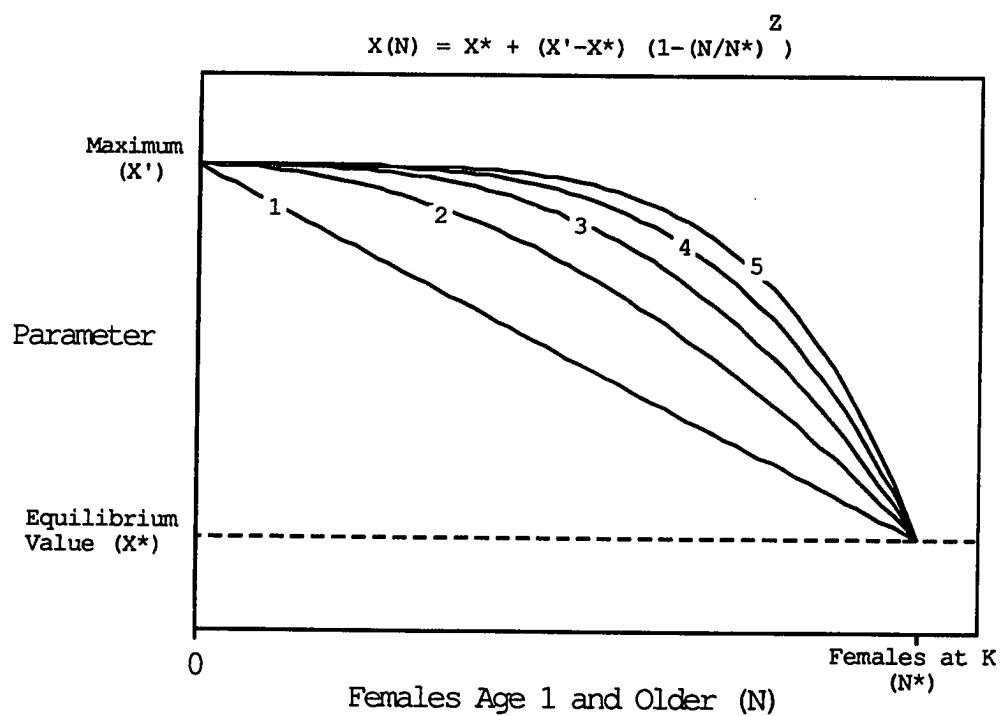
Figure 9. Density dependence of vital parameters determined by the general Allen (1976) function, and used by Smith and Polacheck (1984). Each line is labeled with the Z value used to generate that line.

year (Fig. 10). At the end of the year, the simulated population was reduced according to age-specific survival rates determined at the beginning of the year. The birth of the new cohort marked the end of one year and the beginning of the next.

Smith and Polacheck (1984) limited their model to females only. However, as the purpose here was to estimate MNPL, males were included. Survival for juvenile males was determined as a function of female juvenile survival. Chapman (1961, 1964, 1973) suggested survival of males and females from birth to age 3 can be related with the function

$$(16) \qquad S_{0-3,m} = S_{0-3,f} \ / \ Lambda,$$

where $S_{0-3,m}$ and $S_{0-3,f}$ are survival from birth to age 3 for males and females, respectively, and Lambda is a constant (set to 1.1). Determined in this manner, survival of males for this period was density-dependent in the same manner as survival of the same age group of females. Survival of males older than age three was held constant in all simulations. The commercial kill of juvenile males was not included in the model. Males were subjected to natural sources of mortality only, and were counted as part of the total population. The female kill from 1956 to 1968 was included, and females were removed by age according to records from the kill (Smith and Polacheck 1984). The removal of females during any simulation occurred after MNPL was determined, and was an important aspect of

Annual cycle begins with birth of new cohort

Population census includes new cohort

Determination of survival (t=0 to t=1) and
birth rates (t=1) as a function of number of
females age 1 and older

time

t=0

t=1

Mortality occurring during the year removed
from the population. Females removed according
to records of female kill 1956 to 1968
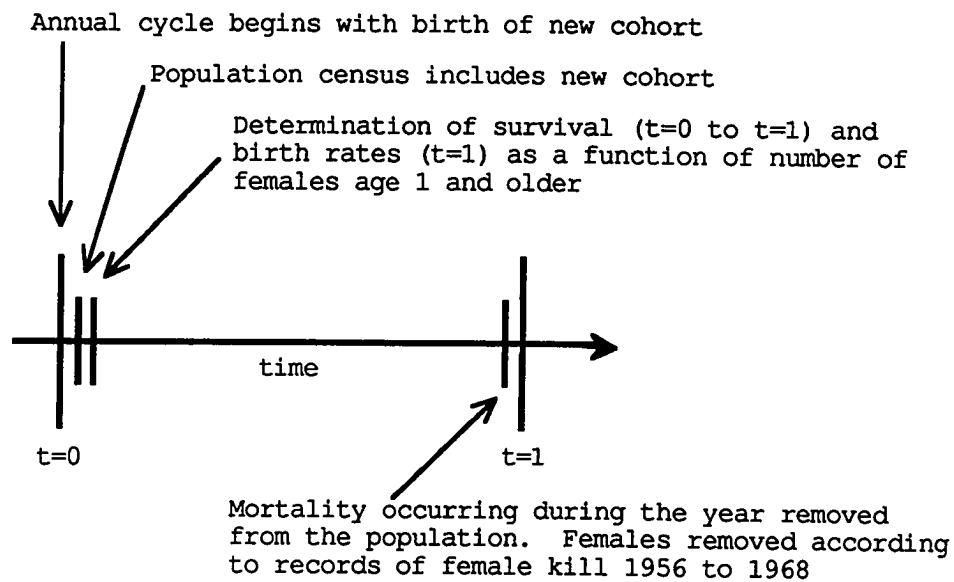
Figure 10. The annual cycle of the northern fur seal as modeled in
these repetitive simulations.

model validation. Smith and Polacheck (1984) did not remove the pups of those females, but virtually all of them must have perished due to starvation. Hence, they were also removed from the simulated population (York and Hartley 1981).

Each simulation used a different combination of model parameters. Input for the model included 1) $\{X_i\}$, the set of equilibrium survival and fecundity values, 2) M_a, M_f, and M_j, the portions of the maximum possible scope for density-dependent change in adult survival, fecundity, and juvenile survival, respectively, 3) Z, the shape parameter in the regulatory function, and 4) P^*, the number of pups born at equilibrium.

The set of equilibrium female survival and fecundity values were taken from Barlow and Boveng (in press) and Smith and Polacheck (1981), respectively, and male survival values were taken from Lander (1981) (Table 2 here). Equilibrium life table values were the same for all simulations; changes in vital parameters were restricted to the density-dependent scope for change from the equilibrium values.

The parameters M_a, M_f, and M_j in Equations (11-15) determined the realized scope for change in adult survival, fecundity, and juvenile survival, respectively, in any given simulation. As argued by Smith and Polacheck (1984), adult survival and fecundity appear to be near their biologically maximum values, and the maximum possible change of these parameters is relatively restricted. Juvenile survival is not near that maximum, and the scope for change is large.

Table 2. Equilibrium life table values used in the simulations. Female survival rates taken from Barlow and Boveng (in press), pregnancy rates modified from Smith and Polacheck (1984), and male survival rates modified from Lander (1981).

	Females			Males	
Age (years)	Annual Survival Rate P_x	Survival from Age 0 l_x	Annual Pregnancy Rate m_x	Annual Survival Rate P_x	Survival from Age 0 l_x
0	0.539	1.000	0.000	0.522	1.000
1	0.702	0.539	0.000	0.680	0.522
2	0.814	0.378	0.000	0.789	0.355
3	0.885	0.308	0.010	0.800	0.280
4	0.928	0.273	0.015	0.800	0.224
5	0.951	0.253	0.220	0.800	0.179
6	0.964	0.241	0.395	0.800	0.143
7	0.969	0.232	0.395	0.800	0.115
8	0.969	0.225	0.425	0.800	0.092
9	0.964	0.218	0.460	0.760	0.073
10	0.956	0.210	0.445	0.730	0.056
11	0.943	0.201	0.450	0.700	0.041
12	0.923	0.189	0.440	0.650	0.029
13	0.894	0.175	0.430	0.590	0.019
14	0.854	0.156	0.420	0.540	0.011
15	0.799	0.133	0.410	0.430	0.006
16	0.726	0.107	0.390	0.000	0.003
17	0.631	0.077	0.350	0.000	0.000
18	0.515	0.049	0.305	0.000	0.000
19	0.384	0.025	0.264	0.000	0.000
20	0.000	0.010	0.025	0.000	0.000

For any simulation, the lower and upper limits for M_a, M_f, and M_j were 0.0 and 1.0. A value of 0.0 for one of these parameters meant that the corresponding vital parameters were constant, rather than density-dependent. Between simulations these parameters were changed in increments of 0.1. Given the natural history of northern fur seals, it is unlikely that density-dependent changes in adult survival are greater than changes in fecundity, and for any given simulation, M_a was not allowed to exceed M_f.

The value of Z determines the shape of density-dependent change in the vital parameters. While the numerical models described above restricted density effects to juvenile survival, density may also influence adult fecundity and survival (see, for example, Eberhardt and Siniff 1977). But density does not necessarily influence these vital parameters in a similar manner, and separate Z values were used for juvenile survival, adult female survival, and fecundity (i.e., Z_j, Z_a, and Z_f, respectively). The tested range for each of these exponents was from 1.0 to 5.0, varying between simulations in increments of 0.5.

The number of pups born at equilibrium is unknown. Early estimates of pups born in the 1950's (Chapman 1961) suggested the number could be well in excess of 500 thousand, but after revisions (Chapman 1964, 1973) it appears that the number born was less than 500 thousand. A range of estimates was examined, beginning with 350 thousand and increasing in increments of 10 thousand to the maximum estimate of 500 thousand. These are the same lower and upper limits

used by Smith and Polacheck (1984). The number of pups born at equilibrium and the equilibrium survival rates for females were used to determine the number of females age 1 and older used in the regulating function (Eqn. 10).

The model was programmed in FORTRAN, and "do-loops" were used to scan all the parameter combinations; each do-loop changed the value of a single parameter in the increments described above. The partitioning of parameters just described resulted in 8,468,064 parameter combinations, each of which was tested in a separate simulation.

The approach, then, was to partition the parameters of the Smith and Polacheck (1984) model, run a simulation with each of the resulting combinations of parameters, submit the simulation to validation criteria, and then record the 5 population measures for each successful simulation. In addition to comparing the simulations to the original criteria, simulations were also compared to modified criteria to assess the influence of changes in those criteria on the distributions of estimates for the 5 population measures. Finally, to select those simulations which were most consistent with historical records, an error was calculated for each successful simulation. The error was based on observed and modeled pup estimates from 1962 to 1970. Assuming that the standard error in pup estimates from this period is proportional to the size of the pup population, the error was calculated as

$$(17) \qquad \text{error} = \sum_{t=1962}^{1970} [\ ln(N_{0,t,m}) - ln(N_{0,t,o})\ ]^2,$$

where ln is the natural logarithm, $N_{0,t,m}$ is the year-specific pup production in the model, and $N_{0,t,o}$ is the observed annual pup production reported in Briggs and Fowler (1984). Error calculations do not extend beyond 1970 as there is evidence that population trends, including pup production, were substantially confounded by entanglement after 1970 (Fowler 1985).

RESULTS

Results with original validation criteria. A total of 931,821 (11.0%) of the 8,468,064 attempted simulations passed the validation criteria. Estimates of MNPL, pups born at MNPL, K, pups born at K, and the ratio MNPL/K from these simulations were used to construct the frequency histograms shown in Figure 11. MNPL in these successful simulations ranged from a total abundance of approximately 0.8 to 1.4 million, with the mode at 1.08 million (Fig. 11A). The distribution of MNPL estimates appeared to be nearly normal.

Corresponding estimates of pups born at MNPL (Fig. 11B) ranged from approximately 220 thousand to over 310 thousand with a mode at 265 thousand pups born. Again, the estimates formed a distribution which was nearly normal. Estimates of the ratio MNPL/K(Fig.11C) ranged from just over 0.5 to just less than 0.9, with
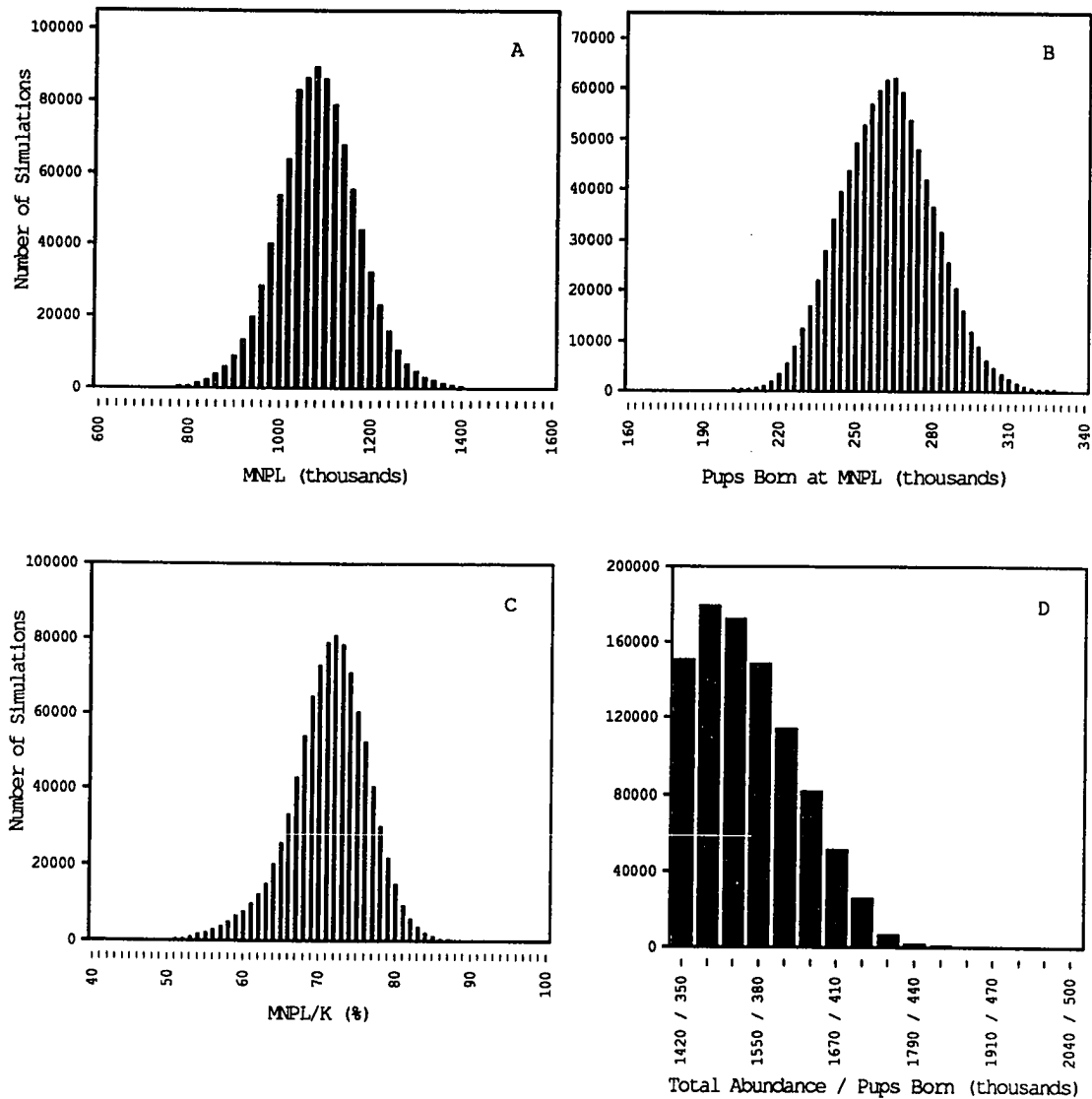
Figure 11. Frequency distributions for five population measures for
simulations satisfying original validation criteria (n = 931,821).
Population measures include A) MNPL, B) pups born at MNPL, C) MNPL/K,
and D) K and pups born at K.

a mode at 0.72. The distribution of estimates for MNPL/K appeared to be slightly skewed to the left.

Estimates of total abundance at K and pups born at K had identically shaped frequency distributions (Fig. 11D) because K was calculated from the equilibrium life table and the number of pups born at K (an input parameter). In general, estimates of K ranged from 1.42 to less than 1.9 million animals, with a mode at 1.45 million. Associated estimates of pups at K ranged from 350 to 500 thousand with a mode at 360 thousand. The left truncation of this shared distribution corresponds to the lower limit of pups born at equilibrium entered in the model.

Results with modified validation criteria. Single validation criteria were modified in order to test the sensitivity of this modeling approach to those criteria. The first modification consisted of narrowing the acceptable range of population growth rates for the period 1912 to 1924. The second modification was a lowering of the acceptable growth rate between 1945 to 1955. The final modification was an increase in the minimum pup population size for the period from 1940 to 1955. Note that only one of these criteria was changed at a time.

Reducing the acceptable range for the growth rate from 1912 to 1924 to $0.06 - 0.10$ yr^{-1} (from $0.05 - 0.11$ yr^{-1}) resulted in fewer simulations being accepted (n = 685,525). However, the ranges and the modes of the resulting distributions were essentially unchanged

and the reductions in the distributions appeared to be proportional (Fig. 12).

Decreasing the upper limit for the minimum annual growth rate during the period 1940 to 1955 from 0.015 yr^{-1} to 0.01 yr^{-1} resulted in only a slight reduction in the number of successful simulations (n = 921,287), and as used in this study, this validation criterion had almost no effect on the outcome of these distributions (Fig. 13).

Increasing the lower limit for the maximum number of pups born annually between 1945 and 1955 from 350 thousand to 381 thousand had a substantial effect on the distributions of the population measures (n = 427,159), as indicated particularly by the modes of the distributions (Fig. 14). As might have been predicted, all distributions were shifted to the right. The modal values for MNPL and pups at MNPL increased to 1.12 million animals and 268 thousand pups, respectively. Similarly, the abundance at K and the number of pups born at K increased to 1.55 million animals with 380 thousand pups born. The mode of MNPL/K was unchanged, suggesting the increase in MNPL was proportional to the increase in K.

Additional results. A preliminary test of the sensitivity of this modeling approach to the method of partitioning the parameter space was conducted by changing the increment size for M_a and M_f from 0.1 to 0.2. That is, these parameters were allowed to assume only 6 values (0.0, 0.2, 0.4,...,1.0) instead of 11 (0.0, 0.1, 0.2,...,1.0). This adjusted partitioning resulted in a 70% reduction in the number

Figure 12. Frequency distributions for five population measures (n = 685,525), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Growth rate limits for period from 1912 to 1924 narrowed to 0.06 and 0.10. The dotted line in these illustrations corresponds to the results from Fig. 11, with the original validation criteria.

Figure 13. Frequency distributions for five population measures (n = 921,287), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Upper limit for minimal annual growth rate between 1945 and 1954 lowered to 0.01 from 0.015. The dotted line in these illustrations corresponds to the results from Fig. 11, with the original validation criteria.

Figure 14. Frequency distributions for five population measures (n = 427,159), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. Lower limit for maximum annual number of pups born from 1940 to 1955 increased to 381 thousand. The dotted line in these illustrations corresponds to the results from Fig. 11, with the original validation criteria.

of successful simulations (n = 278,462). Again, the distributions of population measures appeared to decrease proportionately (Fig. 15).

Weighting the population measures by the inverse of the error in pup counts during the period 1962 to 1970 did not change the mode for the distribution of MNPL/K, or for the combined distribution of K and pups born at K (Fig. 16, C and D). The mode of the MNPL distribution decreased slightly to 1.02 million animals (Fig. 16A), and the distribution for the number of pups born at MNPL shifted to the left with a new mode at about 260 thousand animals (Fig. 16B).

However, when only those simulations with errors in the lowest 10% of the error range were considered (n=5907), there were large downward shifts for the distribution of the number of pups born at MNPL, and the combined distribution of K and the number of pups born at K (Fig. 17, B and D). The mode of MNPL/K shifted slightly upward (Fig. 17C), probably due to the decrease in the mode of the estimates of K.

The parameters M_a, M_f, and M_j determined the scope for change for adult survival, fecundity, and juvenile survival, respectively. For each successful simulation corresponding to the original validation criteria (Fig. 11, n=931,821), values of M_a, M_f, and M_j were recorded. The distributions of M_f and M_j were strongly skewed to higher values, while the distribution of M_a values was strongly skewed to lower values (Fig. 18). Recall, however, that the value of M_a in any given simulation was never allowed to exceed M_f; hence, relatively fewer simulations were run with larger values of M_a.
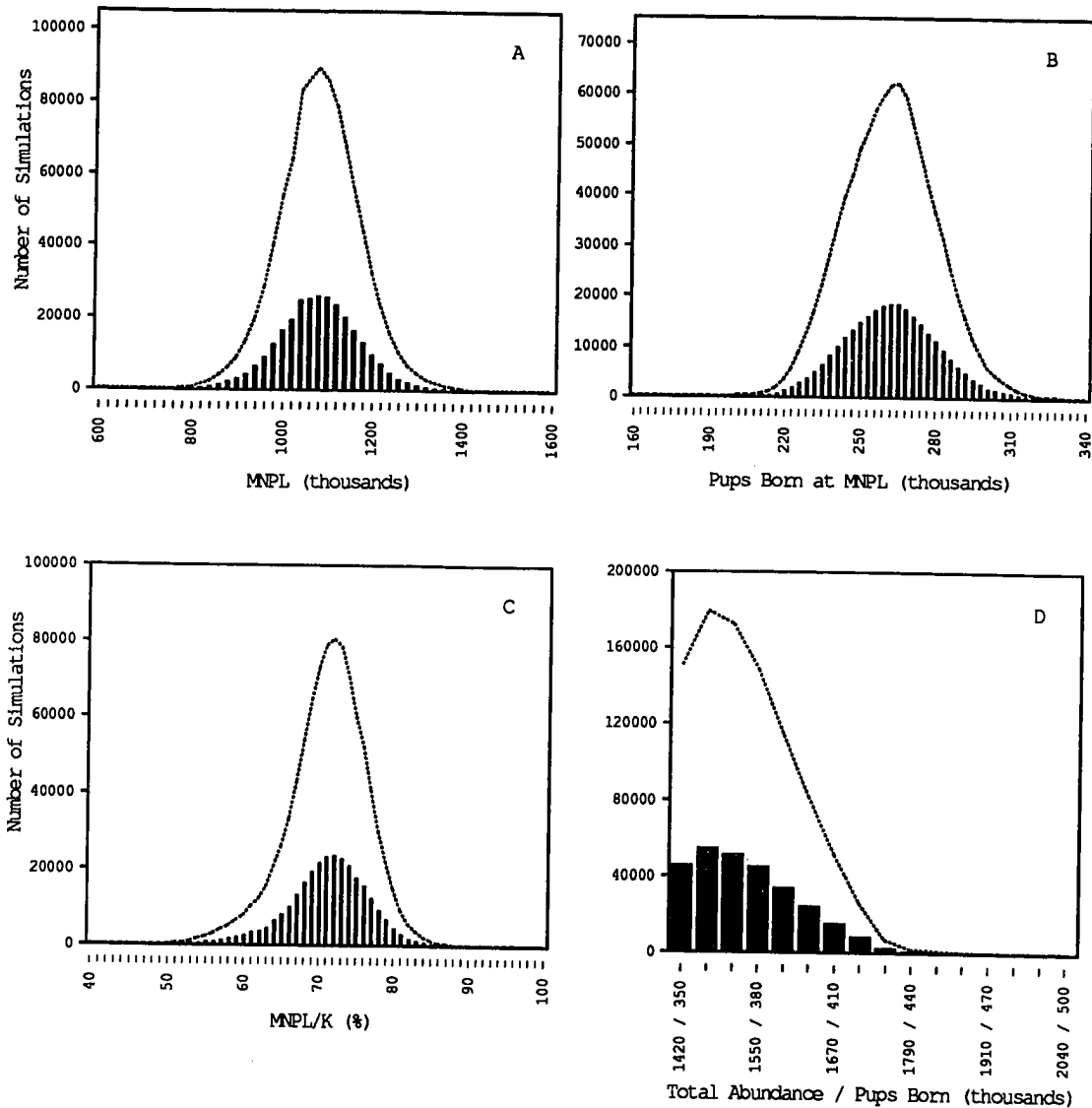
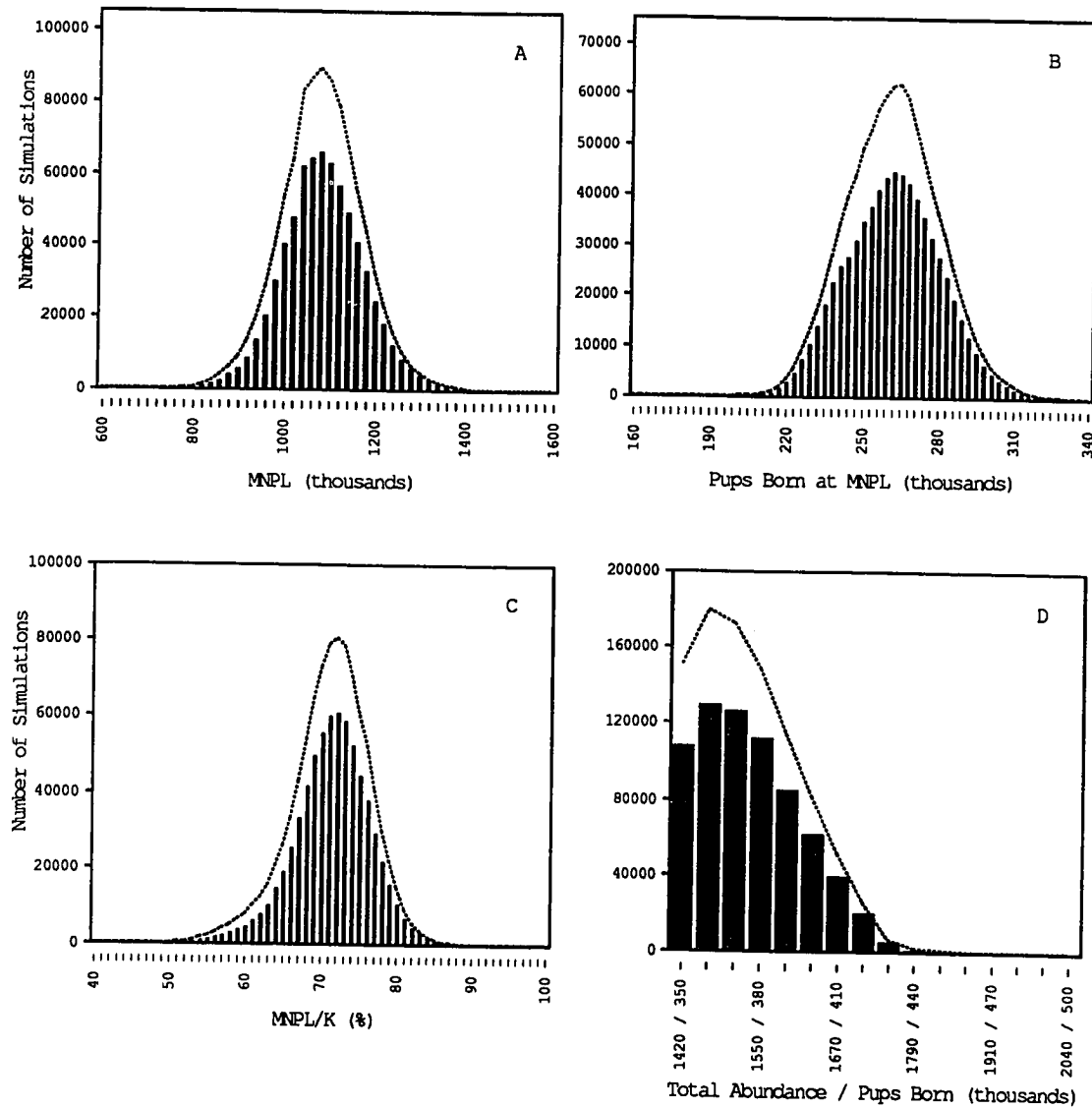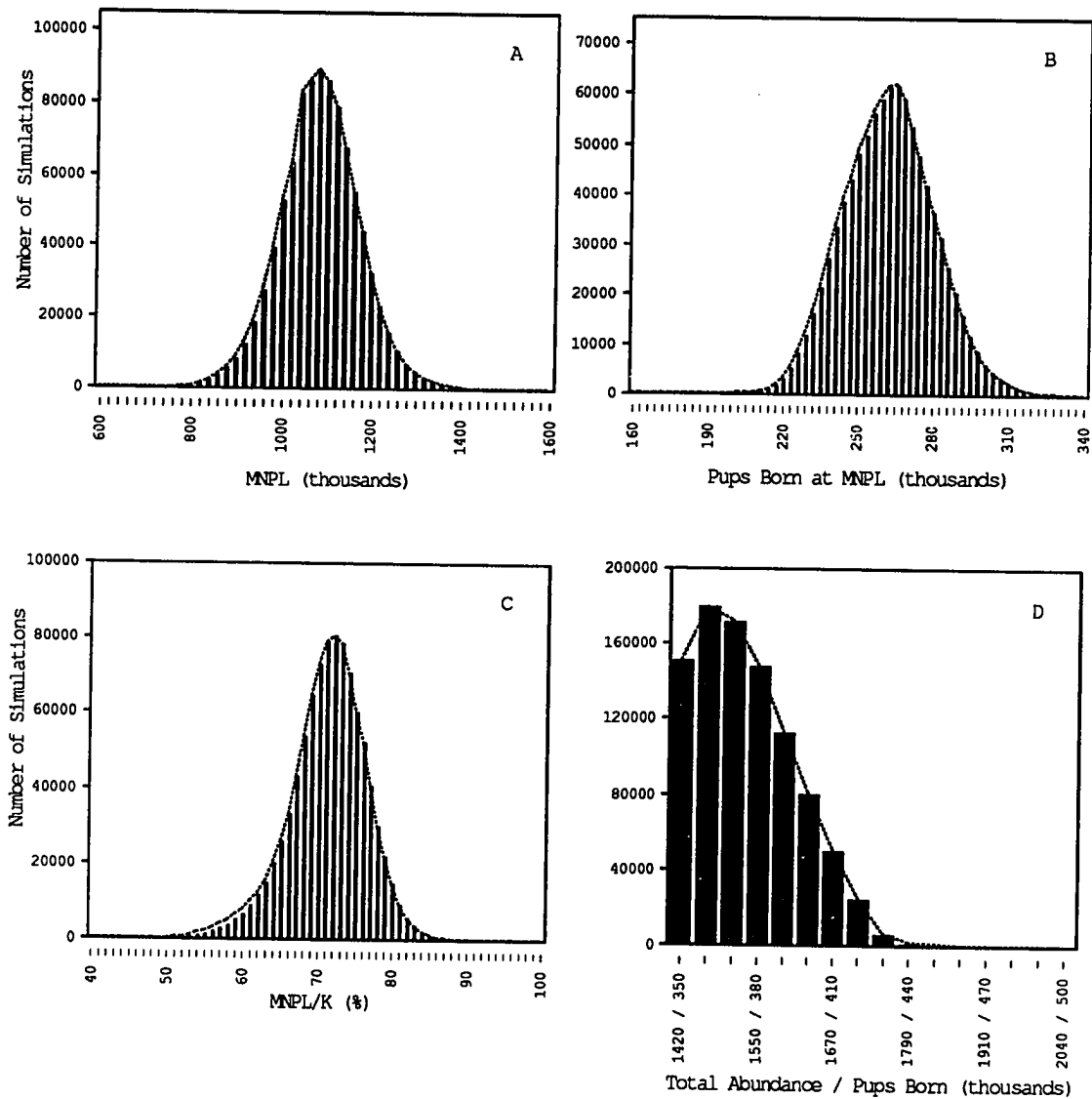Figure 15. Frequency distributions for five population measures (n = 278,462), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. M_a and M_f parameters limited to 6 values (0.0, 0.2, 0.4,..., 1.0) rather than 11 values (0.0, 0.1, 0.2,..., 1.0). The dotted line in these illustrations corresponds to the results from Fig. 11, with the original validation criteria.
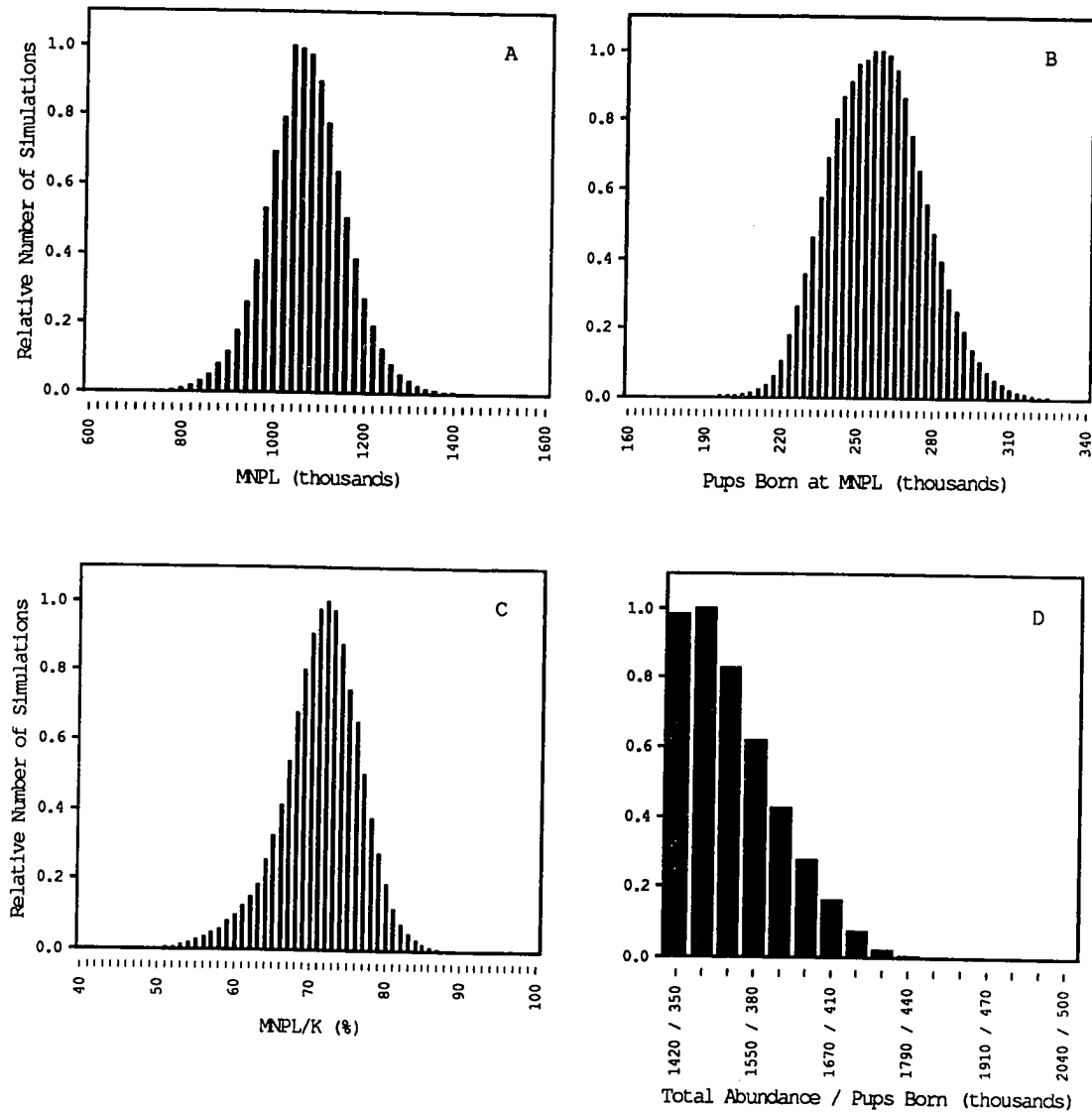
Figure 16. Relative frequency distributions for five population measures (n = 931,821), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. All distributions are weighted by the error between observed pups born annually (1962 to 1970) and pups born in the model.
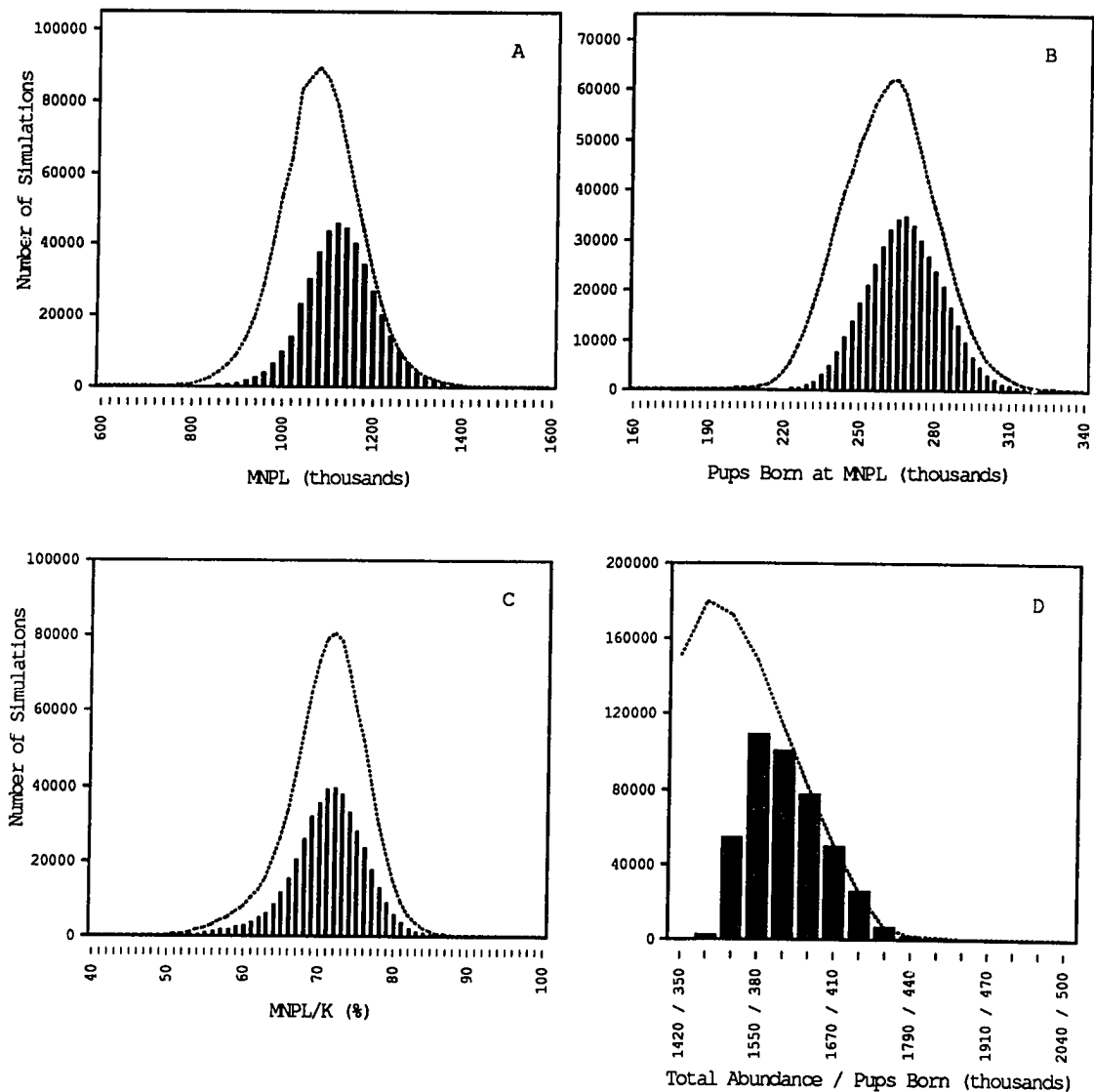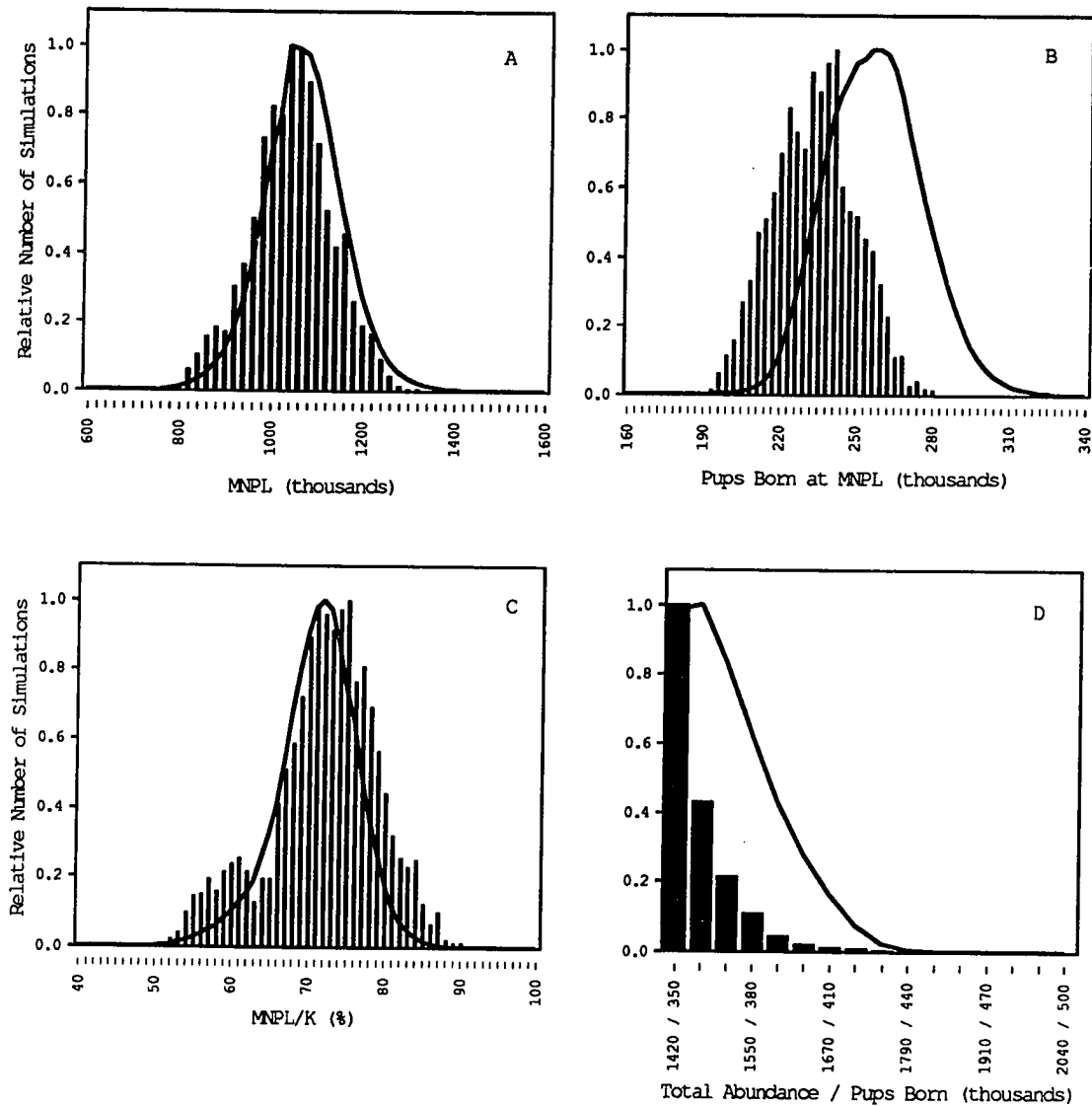
Figure 17. Relative frequency distributions for five population measures (n = 5907), including A) MNPL, B) pups born at MNPL, C) MNPL/K, and D) K and pups born at K. All distributions are weighted by the error between observed pups born annually (1962 to 1970) and pups born in the model. Only simulations with errors in the lower 10% of the error range are included. The lines correspond to the relative weighted frequency distributions in Figure 16.
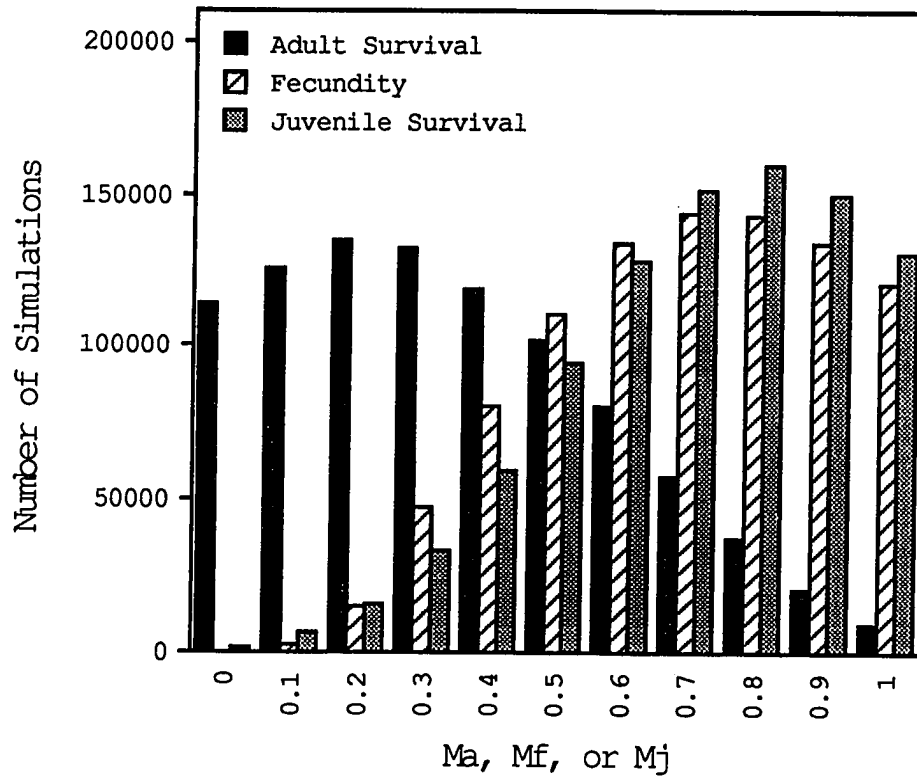
Figure 18. Frequency distributions for values of M_a, M_f, and M_j recorded from successful simulations (n=931,821).

Values of Z_a, Z_f, and Z_j determined the degree of nonlinearity of density-dependent change in adult survival, fecundity, and juvenile survival, respectively. These values were also recorded for each successful simulation, and the effect of nonlinearity on the ratio MNPL/K is presented in Figures 19-21 for several values of M_a, M_f, and M_j. When M_a was 0.3 (i.e., relatively small scope for density-dependent change), the effect of increasing nonlinearity in the density-dependent function on the estimation of MNPL/K was relatively small (Fig. 19). The mode of MNPL/K increased from 0.71 to 0.72 as Z_a increased from 1.0 to 5.0. When M_a was 0.7, the effect of nonlinearity on MNPL/K was larger; MNPL/K increased from 0.70 to 0.74 as Z_a increased from 1.0 to 5.0 (Fig. 19).

In general, increasing nonlinearity in the density-dependent function regulating changes in fecundity also increased the estimate of MNPL/K (Fig. 20). However, the increase was not constant, and the mode for MNPL/K with Z_f equal to 2.0 was less than the mode when Z_f was 1.0. This was true whether M_f was 0.3 or 0.7. As shown in Figure 20, the modal values for MNPL/K were generally larger (up to 0.77) than they were for similar changes in adult survival (Fig. 19).

Finally, there was a similar effect of increasing estimates of MNPL/K as nonlinearity in juvenile survival increased; again, this was true whether M_j was 0.3 or 0.7 (Fig 21). Note, however, that estimates of MNPL/K were much lower when M_j was 0.3.
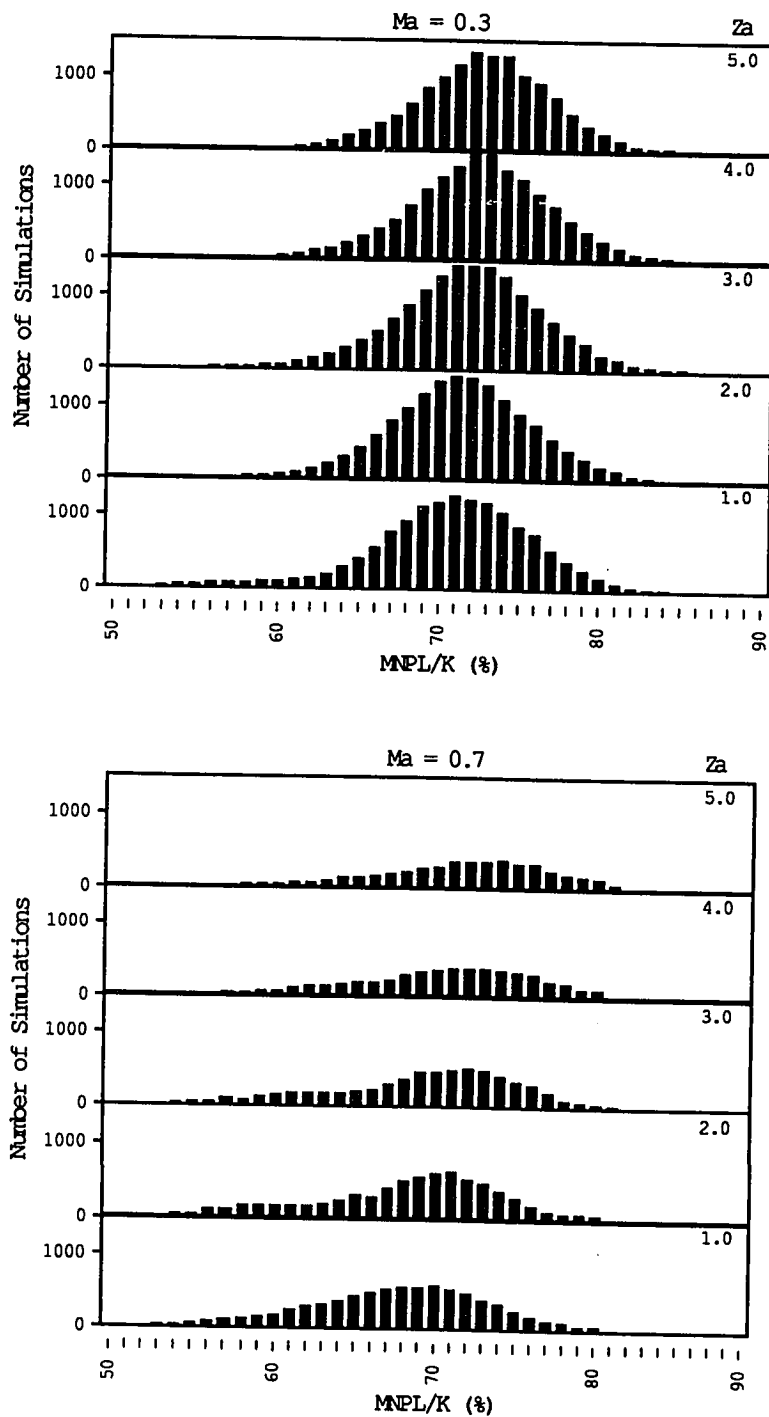
Figure 19. Frequency distributions for values of MNPL/K corresponding to different degrees of nonlinearity in adult survival (Z_a increasing from 1 to 5) when M_a is equal to 0.3 and 0.7.
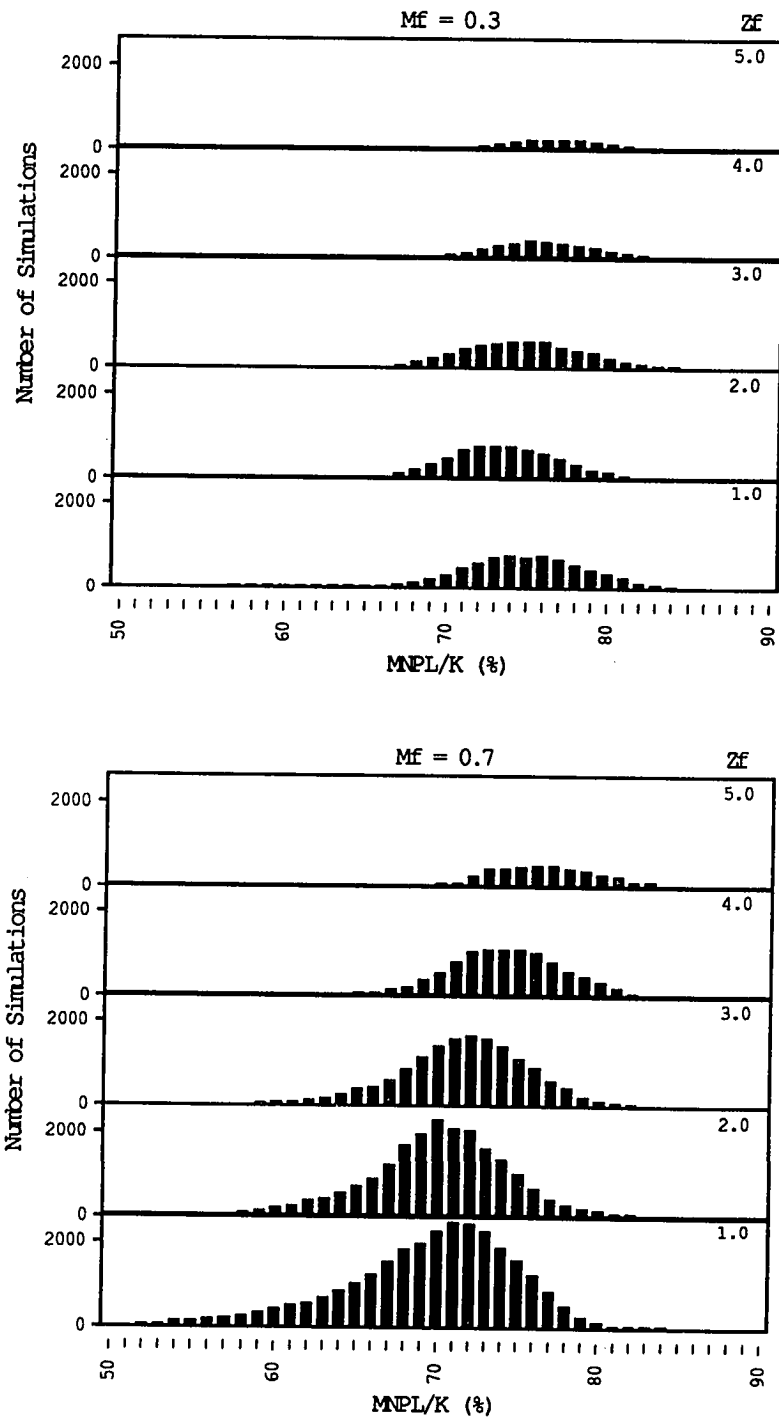
Figure 20. Frequency distributions for values of MNPL/K corresponding to different degrees of nonlinearity in fecundity (Z_f increasing from 1 to 5) when M_f is equal to 0.3 and 0.7.
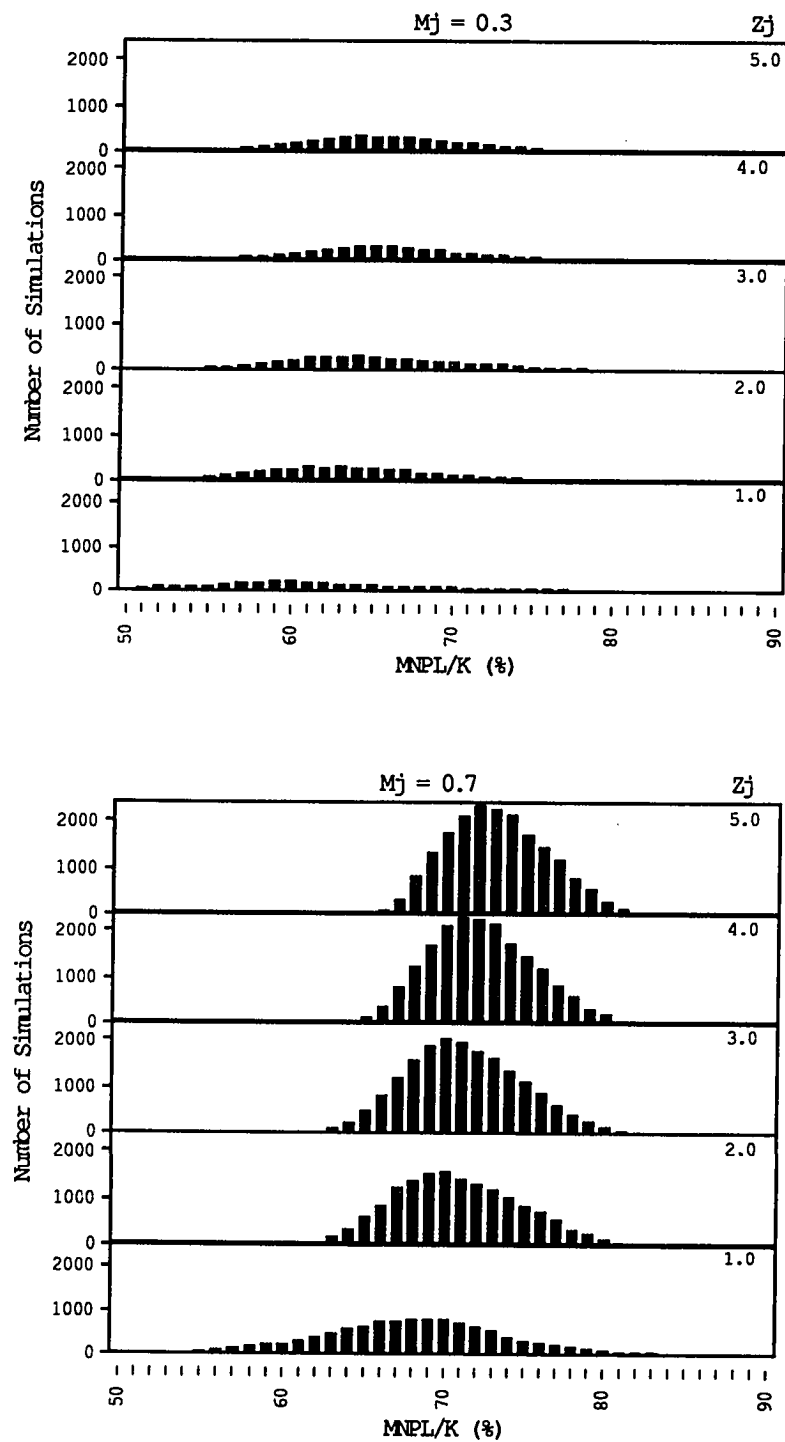
Figure 21. Frequency distributions for values of MNPL/K corresponding to different degrees of nonlinearity in juvenile survival (Z_j increasing from 1 to 5) when M_j is equal to 0.3 and 0.7.

DISCUSSION AND CONCLUSIONS

The approach used in this study has several important advantages over previous modeling attempts to determine these theoretical population measures. First, it recognizes the fundamental problem of uncertainty in northern fur seal life history parameters and mechanisms of density-dependent regulation. Second, it uses repetitive simulations to illustrate that there are many combinations of these parameters and regulating mechanisms that satisfy the validation criteria, even though these combinations represent only a small portion of the parameter space. Thus, satisfaction of the validation criteria is not, in and of itself, a basis for confidence in any given model. The confidence that can be placed in the estimates from any single simulation must be evaluated with respect to the estimates from the larger set of successful simulations. This is analogous to a statement of conditional probability; given that a certain model passes the validation criteria, what is the probability that the model accurately depicts the population dynamics of the northern fur seal population on St. Paul Island? And third, this approach provides frequency distributions which may, after further testing, provide a basis for more confidently identifying critical theoretical population levels.

The four main components of this approach included: the validation criteria, the equilibrium life table parameters and scope for density-dependent change in those parameters, the regulating

function, and the method of partitioning parameters to create parameter combinations for testing in simulations. Each of these components is discussed below.

The validation criteria. Five validation criteria were used in this study. By modifying single criteria, the sensitivity of this modeling approach to possible error in these criteria was tested.

Narrowing the range of acceptable annual growth rates from (0.05,0.11) to (0.06,0.10) for the period 1912 to 1924 reduced the number of successful simulations by one-fourth (Fig. 12). However, changes in the distributions of the five population measures appeared to be proportional, and the ranges and modes were essentially unchanged. This suggests that this modeling approach may be robust to changes in the growth rate during this period.

Decreasing the upper limit for the minimum annual growth rate from 0.015 to 0.01 had almost no effect on the outcome of these repetitive simulations (Fig. 13). Hence, it appears that this validation criterion is not particularly important to the results presented here.

An increase of 8.9% in the lower limit for the maximum number of pups produced annually from 350 thousand to 381 thousand during the period 1940 to 1955 had a significant effect on the distributions of the population measures (Fig. 14). Not only was there a 54% reduction in the number of successful simulations, but also, there was a clear shift in the distributions of MNPL and pups at MNPL, and in the combined distribution of K and pups at K. The distribution of

MNPL/K did not shift, suggesting the changes in MNPL and K distributions were proportional. Unfortunately, there is great uncertainty about true pup production during this period, and this uncertainty has been problematic regardless of the approach taken to estimating these theoretical population measures. But clearly, the sensitivity of these distributions to the estimated lower limit for pup production from 1940 to 1955 indicates the need for careful selection of the validation criteria.

The fourth validation criteria was the number of pups born annually during the period 1962 to 1970. Because estimates of pup populations during this period are considered relatively reliable, they were not used to test the sensitivity of the distributions of the five population measures. Instead, they were used to weight individual successful simulations on the basis of the error between simulated and observed numbers. As can be seen by comparing Figures 11 and 16, the effect of this weighting did not change substantially the distributions of the population measures, except for a slight shift to the left in the mode of the distribution for number of pups born at MNPL.

This weighting of simulation results provided a means for identifying "best" estimates of parameter combinations if it was assumed that those simulations with the smallest error between observed and simulated pup counts for this period were "most likely" to represent the dynamics of the northern fur seal. The results shown in Figure 17 were based on the simulations with errors in the

lowest 10% of the range of errors (n = 5907). These simulations were the most consistent with observed pup populations from 1962 to 1970, and suggested that the number of pups born at MNPL, as well as K and the number of pups born at K, may have been overestimated by the distributions presented in Figures 11-16. Importantly, the "best" simulations, or those with the least error in pup numbers for 1962 to 1970, indicate smaller total and pup population sizes at MNPL and K.

The fifth validation criterion was the presence or absence of growing oscillations. One of the most difficult aspects of this approach involves the characterization of oscillations in population abundance, and the separation of oscillations which may be "natural" from those which occur as an artifact of the modeling approach. For example, trial simulations using the number of pups as the density-independent factor resulted in 2.2% of the simulations passing the validation criteria (compared to 11.0% when the number of females age 1 and older was used). Presumably the difference was due largely to unnatural oscillations resulting from fluctuating pup numbers and the effects of that fluctuation on fecundity and adult survival rates as calculated annually in the model. When millions of simulations are run, the behavior of all individual simulations can not be visually monitored. However, visual inspection of random samples of the rejected simulations should indicate the nature and complexity of oscillatory behavior possible using this repetitive approach.

Life table parameters and scope for density-dependent change. There is substantial uncertainty in life table parameters for the

northern fur seal, as illustrated in Figure 6. However, all simulations in this study used the same equilibrium life table. The equilibrium life table determines the age structure of the population at equilibrium, and as used here, also determines the scope for density-dependent change in parameters. Hence, it is reasonable to ask whether the distributions might change if another equilibrium life table was used.

The survival schedule of Barlow and Boveng (in press) was used in this study because it includes survival rate estimates for all ages. In addition, this survival schedule seems more reasonable, at least theoretically, because it changes with age in a smooth, rather than abrupt, fashion. This survival schedule combines relatively low juvenile survival with high adult survival, allowing greater scope for density-dependent change at younger ages. Again, a different equilibrium survival schedule with relatively lower adult survival and higher juvenile survival might have changed the results from this repetitive simulation approach.

The information in Figures 18 and 19 suggests that the scope for density-dependent change in adult survival rates is more likely to be small; that is, the number of successful simulations was much larger when the scope for change of adult survival rates was small. But again, recall that in any given simulation, M_a was not allowed to exceed M_f, and consequently many more simulations were attempted with low M_a values. A series of simulations where Ma is not constrained by the value of Mf will be necessary to confirm this tendency for Ma

to be small. If M_a is really on the order of 0.2, then the corresponding change in adult survival is on the order of 1%. Given present methods of assessing adult survival in the field, a 1% change is probably undetectable (Smith and Polacheck 1981, 1984).

The information in Figures 18 and 20 suggest that the scope for density-dependent change in fecundity is more likely to be large relative to the biologically possible scope for change, which is on the order of 5% for fully mature females. Hence, change in fecundity may also be difficult to detect unless relatively large, representative samples are taken from populations over a wide range of abundance.

Changes in juvenile survival should be easier to detect, and the information in Figures 18 and 21 suggest that the scope for change is more likely to be large. However, it does not necessarily follow that because the scope for change is larger for juvenile survival, then juvenile survival is more important as a regulating mechanism for this population. To determine the relative significance of juvenile survival, adult survival, and fecundity to population regulation, the sensitivity to population growth rate to each of these parameter groups must be determined. Eberhardt and Siniff (1977) have suggested that marine mammal populations appear to be most sensitive to changes in adult survival.

The regulating function. A single regulating function (Allen 1976) was used in this study. However, by varying the scope for density-dependent change and the exponent (Z) controlling the degree

of nonlinearity, this function becomes very general and exhibits a wide range of possible behaviors (Fig. 9). The function's relative continuity over the tested values of Z was a useful property for the purpose of compiling frequency distributions. Still, this single function may be too restrictive, and additional functions should be tested. For example, density-dependent parameter change corresponding to a Z value of 5.0 (Fig. 9) is not as nonlinear as is the function of Eberhardt (1981) for female juvenile survival (Eqn. 7, Fig. 5). An altogether different function might not easily be included in the frequency distributions reported here, but perhaps could be compared with results for a particular value of Z.

The effect of the nonlinearity in the regulating function can be seen in Figures 19-21. As the exponent Z becomes larger, there is a general increase in the ratio of MNPL/K. However, these increases in MNPL/K are not large, and it appears that the estimation of the ratio MNPL/K is "conserved" in this modeling approach (i.e., the estimation of MNPL/K appears to be relatively robust). The effect of increasing nonlinearity should increase as the scope for density-dependent change increases. This appears to be the case for adult survival and fecundity (Figs. 19 and 20), but is not as apparent for juvenile survival (Fig. 21).

Another important element of the regulating function is the density-independent factor. The actual mechanism of density-dependent change in life table parameters has not been determined. Hence, it is difficult to know what portion of the population best

serves as an index of the density-independent factor. For example, if food is the limiting factor, then it is important to know how food availability limits population growth and what age and sex groups are competing for the same limiting food resource. This information is not currently available. In this study, the number of females age 1 and older was used as the density-independent factor, but the results may change if some other index of the population is used.

Partitioning of the parameter space. The presentation of results in Figures 11-15 assumed that each simulation outcome was equally likely. This implies the probability distributions for the parameters in the life table and regulating mechanisms were also equally likely, which seems unrealistic. But because probability distributions were not known for the model parameters, and the nature of regulation was uncertain, the assumption of uniform or equal probability for all simulations was used as a first approximation.

This also assumes that the true parameter values and regulating mechanisms were encompassed in the ranges tested, and that the method of partitioning the parameter space did not distort the resulting frequency distribution. A test of the method of partitioning the parameter space was conducted by reducing the number of values M_a and M_f could assume from 11 (0.0, 0.1,..., 1.0) to 6 (0.0, 0.2,..., 1.0). If the range of values for these parameters were equally likely, then the corresponding reduction in the number of successful simulations was expected to be 45%. However, the observed reduction was 70% (Fig. 15). This was consistent with the

results in Figures 18, 19, and 20, which also suggested the tested values of M_a and M_f were not equally likely.

Whether parameter combinations were unweighted or were weighted by the error between observed and simulated pup numbers, the end results of the approach used in this study were frequency distributions. While they may appear to resemble probability distributions, these distributions are functions of the modeling approach. The degree to which they approximate true probability distributions is unknown, but they clearly demonstrate that MNPL, K, pups born at MNPL and K, and MNPL/K may occur over a wide range of population levels, and that definitive estimates cannot be obtained without making unwarranted assumptions regarding density-dependent mechanisms. Importantly, these distributions more realistically reflect our uncertainty regarding the natural history of the northern fur seal, and thereby provide a realistic perspective from which individual estimates of these critical theoretical reference levels can be evaluated.

APPENDIX

The following calculation of replacement rate is based on an earlier derivation by Chapman (1973).

For a stable population at equilibrium, the number of new 4-year-old females equals the number of adult females (age 4 and older) dying during the previous year,

(A1) $N_{4,t} = N_{A,t-1} * Mmean_A$,

where $N_{4,t}$ is the number of new 4-year-old females at time t, $N_{A,t-1}$ is the number of females aged 4 and older at the beginning of the previous year, and $Mmean_A$ is a weighted mean annual mortality of females aged 4 and older. (Note that for a stable population at equilibrium, the time subscripts are unnecessary; they are included here for clarity.) However,

(A2) $N_{4,t} = N_{3,t-1} * (1 - M_3)$,

where $N_{3,t-1}$ is the number of 3-year-old females one year earlier, and M_3 is their annual mortality rate. Hence,

(A3) $N_{3,t-1} * (1 - M_3) = N_{A,t-1} * Mmean_A$, or

(A4) $N_{3,t-1} / N_{A,t-1} = Mmean_A / (1 - M_3)$.

$N_{A,t-1}$, the number of adult females at time t-1, can be estimated from the number of pups born at time t-1. That is,

(A5) $N_{A,t-1} = Pups_{t-1} / (Fmean_A * 2.0)$,

where $Fmean_A$ is the weighted mean annual fecundity (female pups per adult female, multiplied by 2 to include male pups). From Equations (A4) and (A5),

$$(A6) \quad \frac{N_{3,t-1}}{Pups,t-1} = \frac{Mmean_A}{Fmean_A * 2.0 * (1 - M_3)} .$$

If the stock-recruitment models are fit to the number of surviving 3-year-old females versus the number of pups born, and if the replacement line is assumed to be linear, then Equation (A6) provides the slope of the replacement line. For this study, $Mmean_A$ is calculated from the survivorship schedule in Barlow and Boveng (in press) and $Fmean_A$ from the pregnancy rates in Smith and Polacheck (1981). The estimated replacement rate is 0.154.

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CHAPTER 4. MIGRATION OF NORTHERN FUR SEAL (*CALLORHINUS URSINUS*) PUPS IN THE BERING SEA

INTRODUCTION

The northern fur seal (*Callorhinus ursinus*) is arguably the most extensively studied marine mammal in the world. Nevertheless, significant elements of northern fur seal population biology and history remain poorly understood largely because of the difficulty of studying these animals at sea. The annual cycle of this fur seal includes a land-based phase from approximately June to November and a pelagic phase from December to May. Although the land-based phase has greatly facilitated the study of its behavior, biology, and population dynamics, our knowledge of this species' life history will remain incomplete until we have expanded our understanding of the pelagic phase.

There is some information on fur seal distribution during the pelagic phase, obtained primarily from records of pelagic sealing in the last half of the 19th century. Townsend (1899) charted the location where 304,713 northern fur seals were killed and collected by sealers from 123 sealing vessels (Fig. 1). This information was used in 1952 to guide research collections by Canadian, Japanese, and U.S. researchers (Taylor, et al. 1955), and again from 1958 to 1974 by the four signatories of the Interim Convention for the Conservation of Fur Seals of the North Pacific Ocean: Canada, Japan, the U.S., and the U.S.S.R (Kajimura 1980). From these research

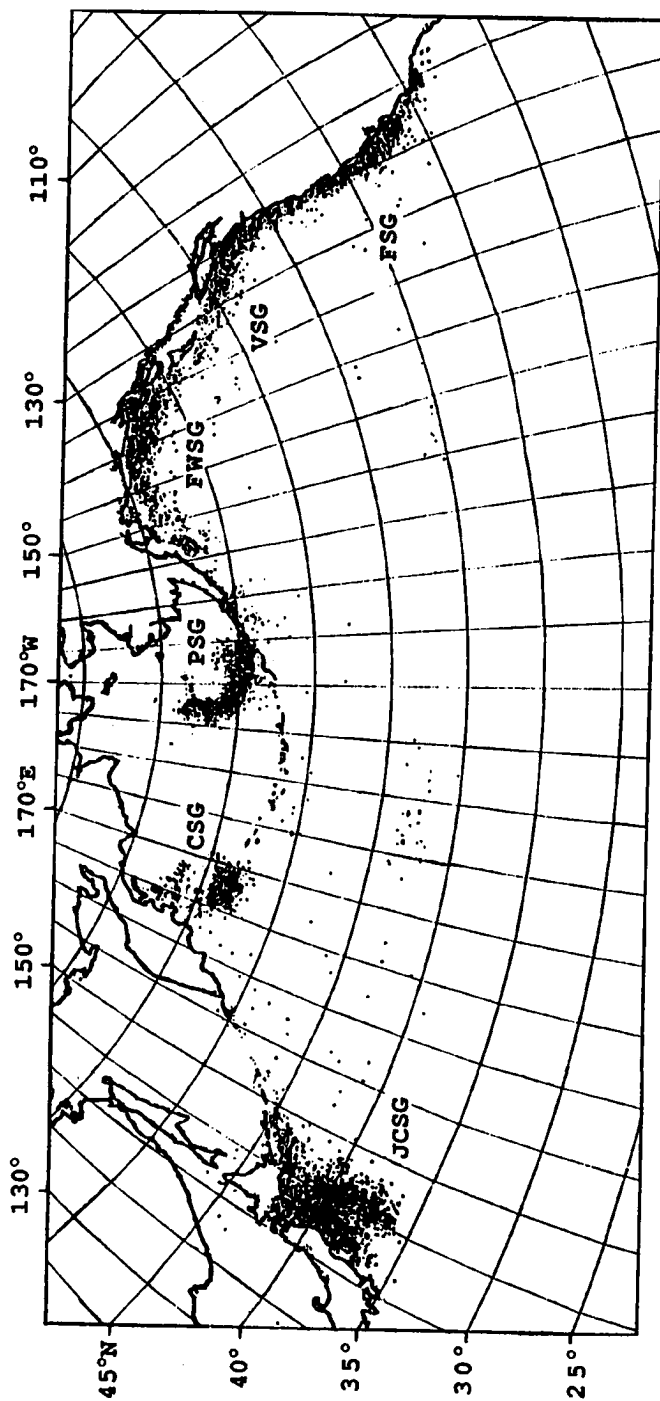Figure 1. Location where 304,713 northern fur seals were killed and collected by 123 sealing vessels in the late 1800's (modified from Townsend 1899). Areas of heavily concentrated sealing were known as the Japan Coast Sealing Ground (JCSG), The Commander Sealing Ground (CSG), the Pribilof Sealing Ground (PSG), the Fairweather Sealing Ground (FWSG), the Vancouver Sealing Ground (VSG), and the Farallon Sealing Ground (FSG).

collections food habits, pregnancy rates, survival rates for adult females, and movement patterns at sea for some age and sex groups from different island populations are available (Taylor et al. 1955, Kajimura, et al. 1979, 1980).

These collections did not determine the pelagic distribution of northern fur seals. As Bigg (1982) points out, pelagic sealers were motivated by economic profit and had to consider such factors as seal size, molting season, distance from port, and sealing regulations. Similarly, Kajimura (1980) notes that researchers during the 1958-74 pelagic collections were charged with killing and collecting a quota of seals each season and, "Effort was therefore directed toward collecting seals and away from systematic surveys to determine the density, distribution, or relative abundance of fur seals by time and area." Loughlin, et al. (1987) evaluated the feeding distribution of fur seals in the Bering Sea and their movement patterns between feeding locations and St. Paul Island. However, this study focused on adult females during summer months and did not address the question of fur seal distribution during the pelagic phase of their annual cycle. Hence, certain aspects of this pelagic phase remain poorly understood.

Little is known about the migration and distribution of young fur seals from the time they are weaned (or wean themselves) and enter the pelagic phase until they return to rookery or haul-out areas at age 2 or 3. There is information on the survival of males from birth to age 3, due to extensive commercial harvesting of

juvenile males from 1918 to 1984. Juvenile females were not harvested (except from 1956 to 1968) and their survival from birth to age 3 is poorly understood. In addition, young females were conspicuously underrepresented in the pelagic collections taken in 1952 and from 1958 to 1974. Thus, it is apparent from the life table for northern fur seals that our understanding of the life history of young animals, particularly females, is poor. The potential significance of early life history information is underscored by the view that juvenile survival may be of major significance in the natural regulation of marine mammal populations (Eberhardt and Siniff 1977).

Survival of fur seals during their first two to three years must be determined, at least proximally, by events that occur at sea, because they spend relatively little time on land. Natural factors affecting the survival of young animals at sea include their ability to capture prey, avoid predators, resist disease and parasites, and withstand the rigorous climate of the North Pacific (Scheffer 1950). Factors influencing their distribution at sea may include the availability of prey, water temperature, currents, bathymetry, and other climatic or oceanographic features.

Knowledge of the distribution of fur seals in their first year of life can be summarized as follows. In this report animals in their first year of life will be referred to as "pups"; the term "yearling" (North Pacific Fur Seal Commission 1984) will not be used. It generally is assumed that pups from the Pribilof Islands leave the

Bering Sea and enter the North Pacific primarily through Unimak Pass
(Kenyon and Wilke 1953, Kajimura 1979, Bigg 1982, French et al.
1989). They appear to segregate by sex less than older age classes
(Kajimura 1979). Large numbers of pups have been observed off the
coasts of Washington and British Columbia in the months of March and
April (Townsend 1899, Bigg 1982), but they generally are
underrepresented in coastal regions where seals have been taken by
pelagic sealers (Fig. 1) and, later, by researchers (Kenyon and Wilke
1953, Wada 1969 and 1971, Kajimura 1979, Bigg 1982, Aschepkov and
Kuzin 1987). Because pups have been less frequently seen on
traditional sealing grounds, they are assumed to disperse more widely
at sea (Kenyon and Wilke 1953; Wada 1969, 1971; Bigg 1982). Kenyon
and Wilke (1953) reported that "...pelagic sealers took young seals
in June and July as far south as Latitude 40° in mid-Pacific areas."
Finally, pups may not return to their islands of birth at the end of
their first year, but instead may remain at sea (Kajimura 1980).

These points suggest at least two hypotheses for the pelagic
distribution of northern fur seal pups originating from the Pribilof
Islands. First, the vast majority of pups may follow the apparent
path of older fur seals through Unimak Pass into the North Pacific,
then eastward to the waters offshore of western Canada and the U.S.
Thus, their distribution would be similar to the assumed distribution
of older animals, which is primarily confined to the continental
margin of the eastern North Pacific. While this hypothesis does not
appear to be consistent with the underrepresentation of juveniles in

the various pelagic kills, the apparent discrepancy may have resulted from the failure to survey systematically offshore waters along the western coasts of Canada and the U.S., or from nonrandom selection of animals to be killed.

Alternatively, pups may exhibit greater dispersal in their migration. Rather than adhering to a well-defined migratory path consistent with that of older animals, pups may enter the North Pacific through many Aleutian Island passes, and then disperse widely into the North Pacific. This hypothesis was suggested by Kenyon and Wilke (1953) and is consistent with the underrepresentation of young animals in the pelagic kill, as well as with the sealers' records of young animals taken in the mid Pacific.

These hypotheses (Fig. 2) suggest substantially different life histories for young fur seals, including food habits, exposure to oceanic and climatic conditions, and interactions with human activities such as fisheries and oil and gas exploration and drilling. In view of the need to understand the early life history of fur seals, and its relationship to the natural regulation of fur seal populations, and the need to describe and quantify the interaction of fur seals with human activities such as fisheries activities in the Bering Sea and the North Pacific Ocean, it is critical that the pelagic distribution of young northern fur seals be determined.

Following animals at sea over long periods of time poses immense difficulties. However, the geography of the North Pacific
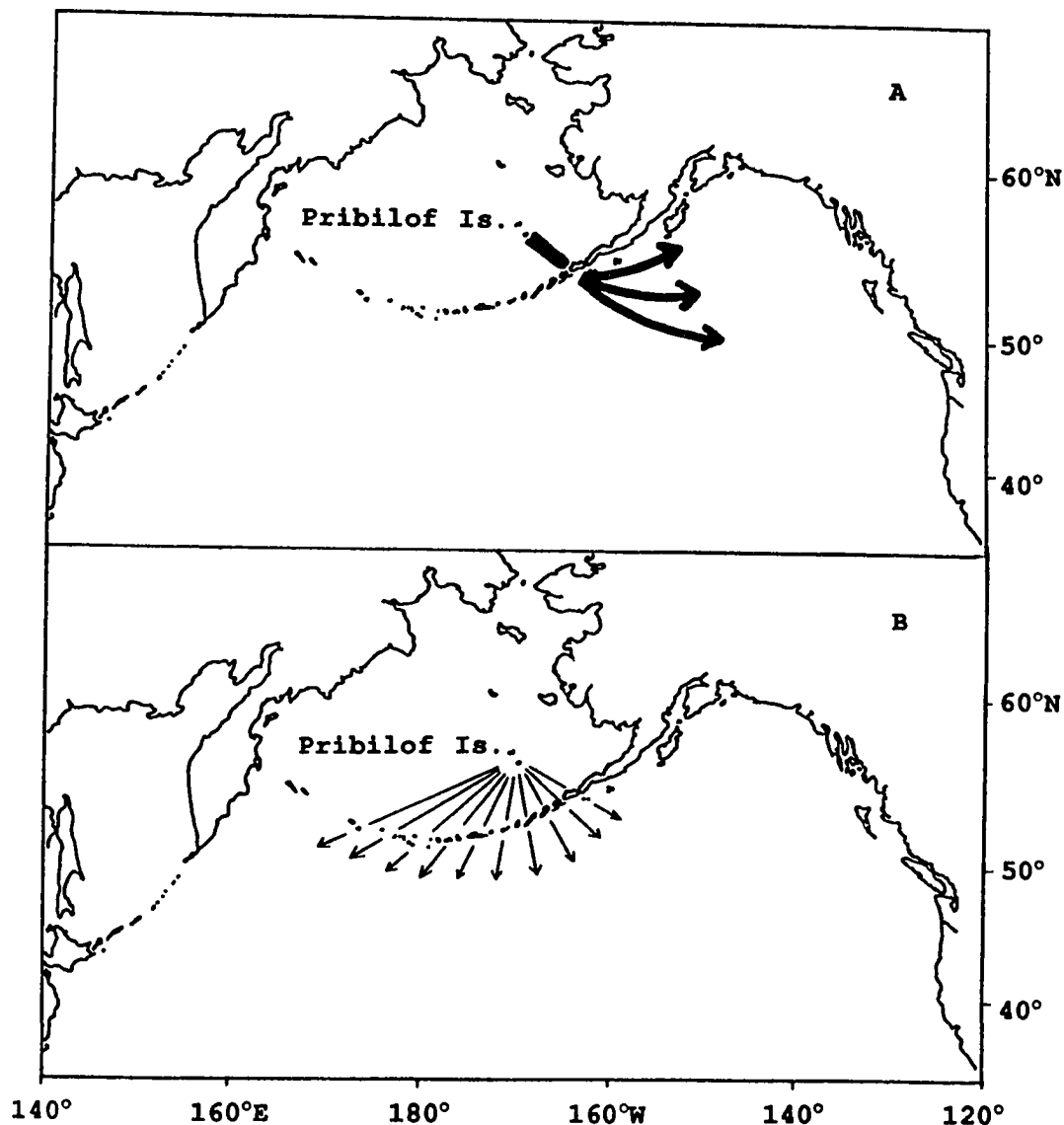
Figure 2. Two hypotheses of northern fur seal pup migration from the Pribilof Islands in the Bering Sea into the North Pacific Ocean. The first hypothesis (A) suggests pups enter the North Pacific primarily through Unimak Pass, and then migrate toward the eastern margin of the North Pacific and waters off western North America. The second hypothesis (B) suggests pups disperse widely, entering the North Pacific through many Aleutian Island passes.

region, and particularly the Aleutian Island arc, divides the migration into two stages: southward movement from the Pribilof Islands to the region of the Aleutian Islands, and migration south of the Aleutian Islands into the North Pacific Ocean. This study focused on the initial phase of fur seal pup migration. The specific objectives of the study were to determine 1) the length of time for migration from St. Paul Island (of the Pribilof Islands) to the Aleutian Islands, and 2) whether Unimak Pass is the principal migratory corridor through which pups enter the North Pacific Ocean.

METHODS

In October 1989, six automated VHF radio receiver stations were erected at locations along the eastern Aleutian Islands, including Scotch Cap of Unimak Island, Ugamak Island, Jackass Point of Akun Island, Unalga Island, Konet's Head of Unalaska Island, and Adugak Island (Fig. 3). These stations provided coverage of Unimak Pass, Akun Strait, Akutan Pass, Umnak Pass, and Samalga Pass (partial coverage). Receivers were programmed to scan 101 frequencies, including a reference frequency emitted by transmitters located on land near each receiver station. Receivers scanned continuously, switching frequency every 4 seconds unless a transmitter pulse was detected, in which case the receiver continued to listen to that frequency for an additional 10 seconds. Data loggers were programmed to record frequency, date, time, and number of pulses heard whenever the receiver detected a transmitter signal.
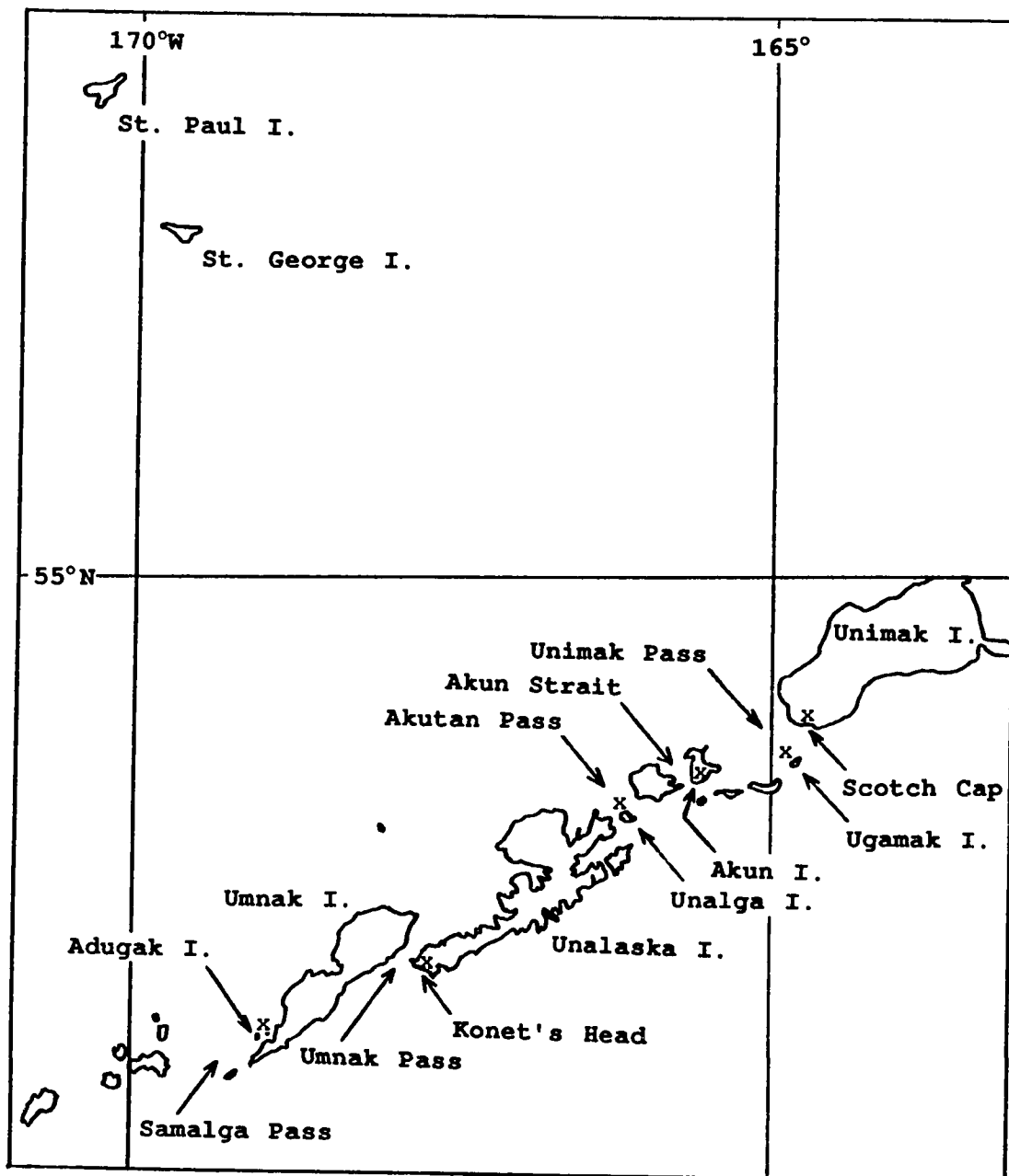
Figure 3. Approximate location of six automated VHF radio receiver stations (indicated by x) at Scotch Cap (Unimak Island), Ugamak Island, Jackass Point (Akun Island), Unalga Island, Konet's Head (Unalaska Island), and Adugak Island and the Aleutian Island passes these receiver stations were intended to cover. Distance from St. Paul Island to Unimak Pass is approximately 420 km.

In November 1989, prior to the onset of their pelagic migration, 90 northern fur seal pups (45 females and 45 males), 10 of which were from known mother-pup pairs, were instrumented with VHF radio transmitters. The ten mothers were also instrumented with transmitters. Transmitters were approximately 70 grams, with base dimensions approximately 4 x 6.5 cm, and height approximately 2 - 2.5 cm. Transmitters were equipped with a single antenna approximately 30 cm long projecting 15° back from vertical. Transmitters emitted 85 to 90 pulses per minute and were expected to have a battery life of 2.5 months minimum. Transmission range was measured at 12-15 miles with line of sight reception.

All study animals were captured at Reef rookery on St. Paul Island, except for three mother-pup pairs captured at Gorbatch rookery (also on St. Paul Island). Pups were chosen by weight; male pups less than 16 kg and females less than 15 kg were excluded (with the single exception of a male pup weighing 15.25 kg). Large animals were chosen to minimize possible effects of the transmitter on behavior or swimming. Qualitative observation of the pups on land and in the water did not reveal any changes in behavior or hydrodynamics, but no measurements or tests were conducted to confirm this.

Weight ($\pm$ 0.25 kg) and length ($\pm$ 1 cm) were determined for each pup. Prior to transmitter attachment each pup was manually constrained and the fur on the upper back between the scapuli was cleaned and dried with acetone. Neither length nor weight was

determined for adult females, and these animals were held in a constraint board (Gentry and Holt 1982) during transmitter attachment. Transmitters were attached to the fur using Devcon 5-Minute epoxy. Transmitters emitted 85-90 pulses per minute, and each transmitter was set to a different frequency to allow identification of individual animals. Animals equipped with transmitters but remaining on St. Paul Island were monitored by a stationary receiver at Reef rookery which scanned individual frequencies for 30 seconds each half hour, and by a hand-held receiver used to scan each rookery on the island on a daily basis from 12 November until 1 December, when all animals had been away from the island at least three days.

The Aleutian Island receiving stations were recovered in mid April 1990, well after migrating fur seals were expected to pass through the Aleutian Islands and enter the North Pacific Ocean.

RESULTS

Data storage problems resulted in the loss of 14, 5, 19, and 20% of the data from Scotch Cap (Unimak Pass), Unalga (Akutan Pass), Konet's Head (Umnak Pass), and Adugak (Samalga Pass), respectively. Similar problems resulted in loss of 100% of the data at Ugamak (Unimak Pass) and Jackass Point (Akun Strait). The following results are based on 80 to 95% of the records from 4 Aleutian Island stations and the St. Paul station.

Male pups used in the study had a mean weight of 18.2 kg ($\pm$ 1.48 kg standard deviation, range 15.25 - 21.0 kg, n = 45) and length

(tip of snout to base of tail) of 81.5 cm (± 2.43 cm standard deviation, range 75 - 86 cm). Mean female weight was 17.0 kg (± 1.22 kg standard deviation, range 15.0 - 19.75 kg, n = 45) and length was 79.9 cm (± 2.35 cm standard deviation, range 74 - 85 cm).

Radio-tagged pups remained on St. Paul Island an average of 11.0 days (± 5.7 days standard deviation, range 0 - 29 days, n = 90, no significant difference between male and female pups). Adult females remained on St. Paul Island 3.5 days (± 1.6 days standard deviation, range 2 - 6 days, n = 10). Daily manual scanning did not detect movement of tagged animals to rookeries other than Gorbatch and possibly Ardiguen. These two rookeries are located on the same peninsula and are contiguous to Reef rookery. Thus, there was no indication of extensive interrookery movement of pups during November. The day of departure for the 100 animals (45 female pups, 45 male pups, and 10 adult females) is shown in Figure 4. In 7 of the mother-pup pairs, the pup departed first, in 2 pairs the mother departed first. Records of the tenth mother-pup pair show departure of these animals was within 26 minutes of each other, indicating they may have departed together. The mother of this pair was relocated 12 days later at Akutan Pass; the pup was not relocated.

Thirty-four successful relocations of 30 different animals were recorded in the Aleutian Islands. These relocations were widely dispersed, including 3 in Unimak Pass, 16 in Akutan Pass, 5 in Umnak Pass, and 8 in Samalga Pass (Fig. 5). Presence on St. Paul Island and time of location in the Aleutian Islands is given for all 30
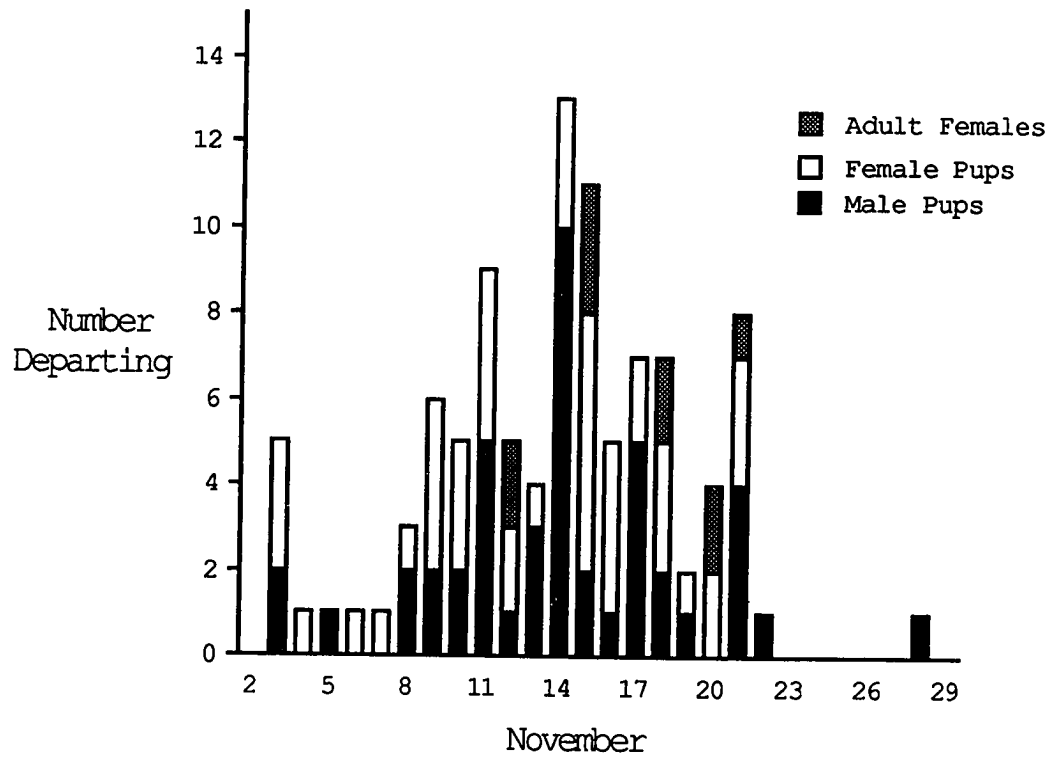
Figure 4. Histogram of departure dates for 90 northern fur seal pups and 10 adult females.
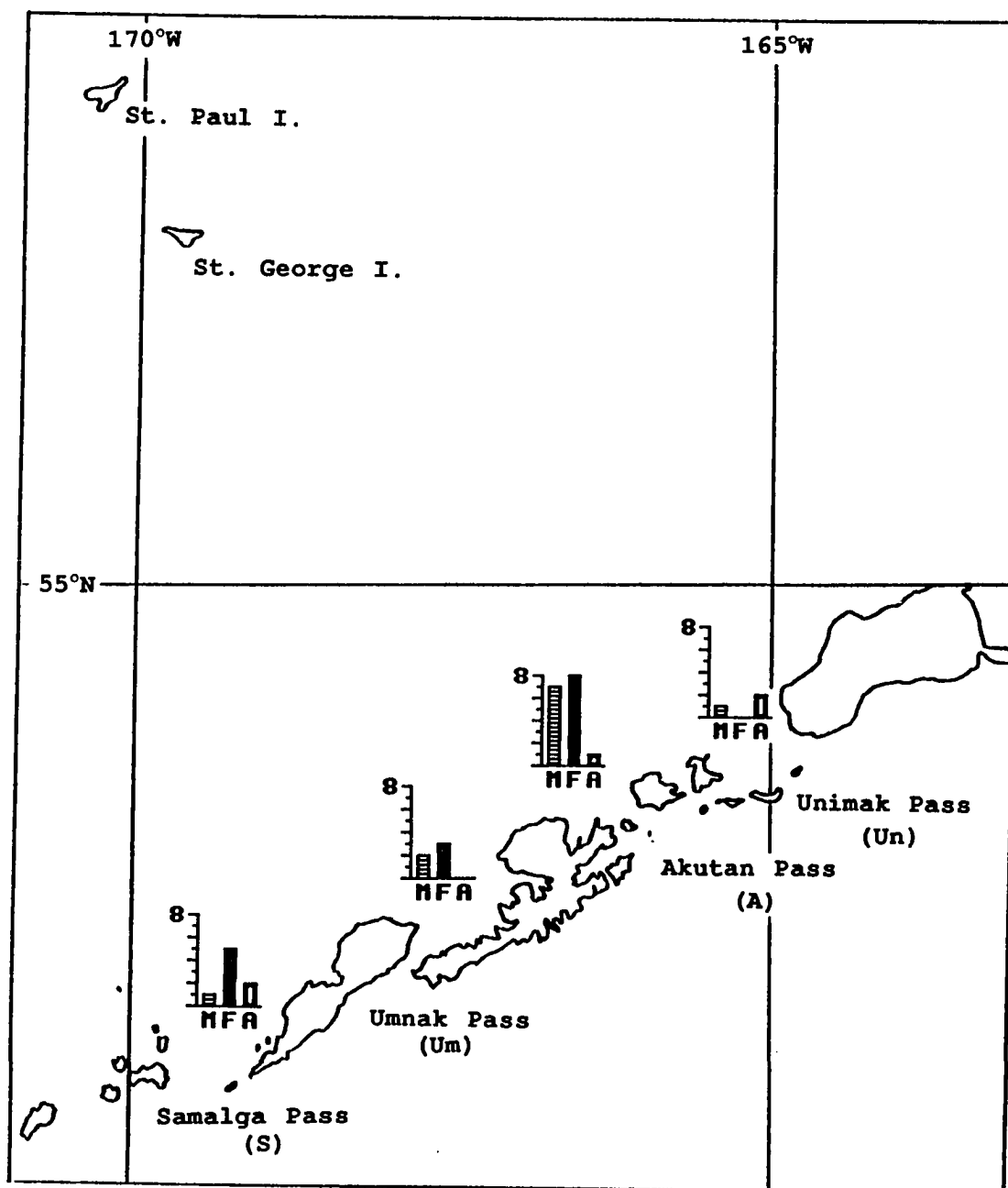
Figure 5. Distribution of pups (F = females, M = males) and adults (A) located in Unimak Pass, Akutan Pass, Umnak Pass, and Samalga Pass. Two pups were seen at 2 different passes, hence the figure is based on 32 successful relocations.

animals in Figure 6. Successfully tracked animals included 15 female pups, 10 male pups, and 5 adult females. None of the pups from the mother-pup pairs was relocated. On 3 occasions there were concurrent relocations of tagged animals in the same pass, but these animals did not appear to be traveling together as either their departures from St. Paul Island differed by at least one day, or they departed from the vicinity of the Aleutian Island stations at different times. One male pup was located at Akutan Pass on 15-17 November and Umnak Pass on 20 November. A second male pup was located three times at Akutan Pass on 22 November, 10 December, and 30-31 December. A female pup was located at Samalga Pass on 24 November and again at Umnak Pass on 13-14 January. Of the five adult females located in the Aleutian passes, two were found at Unimak Pass, one was found at Akutan Pass, and two were found at Samalga Pass.

Mean number of days spent traveling from St. Paul Island to first detection in the vicinity of the Aleutian Island receiver stations in the Aleutian Islands was 10.4 days ($\pm$ 5.1 days standard deviation, range 4 - 24 days, n = 25) for pups and 7.2 days ($\pm$ 3.1 days standard deviation, range 4 - 12 days, n = 5) for adult females. The distance from St. Paul Island to Akutan Pass, for example, is about 420 km. To swim this distance in 10.4 days requires a mean speed of about 40.4 km per day, or 1.7 km per hour. The mean length of the data record for animals in the vicinity of the receiver stations was 15.1 hours (range 0.2 - 63.1 hours, n = 29) for pups and 8.3 hours (range 1.5 - 21.6, n = 5) for adult females.
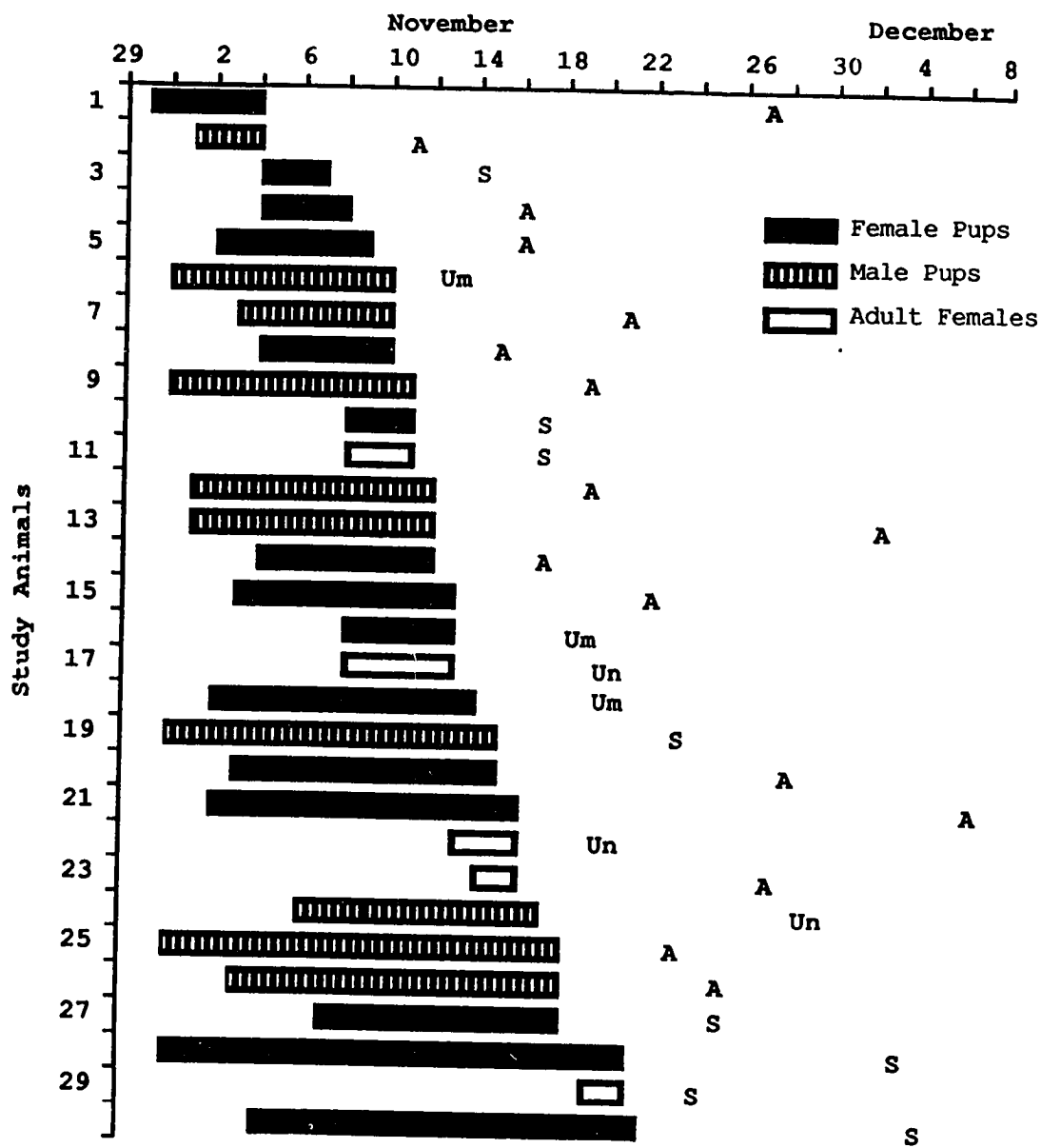
Figure 6. Presence on St. Paul Island of 25 northern fur seal pups and 5 adult females instrumented with radio transmitters, and date of first detection in the Aleutian Islands by receivers at Unimak Pass (Un), Akutan Pass (A), Umnak Pass (Um), and Samalga Pass (S).

DISCUSSION

The distribution of pups at the four Aleutian Island passes that were monitored successfully is not consistent with the commonly assumed migratory route through Unimak Pass (Fig. 5). Of the 30 relocated animals, only 3 were in Unimak Pass; 2 of those were adult females. In contrast, 27 animals were located at passes farther west, and importantly, 8 of those were as far west as Samalga Pass. Assuming that pups do, in fact, leave the Bering Sea, then failure to relocate the remaining 70 animals could have resulted from mortality prior to arrival at the Aleutian Islands, equipment failure (including failure of the transmitter attachment), or passage of these animals to the west of Samalga Pass (out of range of this westernmost receiver station).

It is doubtful that mortality accounts for more than a few animals because large ("healthy") pups were chosen and the time interval for migration from St. Paul Island to the Aleutian Islands is relatively short. Transmitter failure is possible, but there was no indication of failure while the animals remained on St. Paul Island, even though they were monitored for a period of time as long, on average, as the time required to migrate from St. Paul Island to the Aleutian Islands.

Data storage was a significant problem at two receiver stations. The station located on Ugamak Island in the middle of Unimak Pass was intended to provide primary coverage of the western half of Unimak Pass, as well as corroborate the results of the

station at Scotch Cap on the eastern side of Unimak Pass. Still, had many pups used Unimak Pass, more than one of them should have been detected by the station at Scotch Cap if they were widely distributed within the pass. The significance of information lost at Jackass Point (Akun Strait) is unknown, although this strait is relatively narrow compared to the other passes in the area.

Aside from the possibilities of mortality and equipment failure, the low number of fur seal relocations suggests that a large number of pups left the Bering Sea and entered the North Pacific Ocean to the west of the region covered by our receiver stations. This is consistent with the hypothesis of wider dispersal of pups into the North Pacific, which is also supported by the low number of animals found in Unimak Pass. Although the sample size was small, it should also be noted that only two of the five adult females located in the Aleutian passes were at Unimak Pass, the previously assumed main corridor for adults from the Bering Sea into the North Pacific Ocean.

Because pups were chosen nonrandomly by size, and because many pups probably had already departed when radio tagging began, departure dates from St. Paul Island are not considered representative of departure dates for all pups. If pups must reach a certain physiological state related to weight or age before they begin their migration, larger/older pups may tend to leave the island at an earlier date. In addition, the stress of capture and tagging procedures may have induced pups to leave earlier than normal,

although this is not apparent in the attendance record collected on St. Paul Island. Only one pup left the island on the day she was tagged. The earlier departure date for 7 of 10 pups in mother-pup pairs suggests that in most cases pups may wean themselves, which is consistent with Macy (1982), but not with Peterson (1961). Peterson (1961) observed simultaneous departure of mother-pup pairs to be most common, followed by mother-initiated weaning, and finally pup-initiated weaning.

There is no indication that size is related to migratory heading, and we assume direction is representative for this age group. The degree to which oceanographic or meteorological factors influence their migratory path is unknown. Adult female fur seals are known to dive to depths greater than 200 m (Gentry, et al. 1986). If pups dive to half that depth, then it is reasonable to assume that bottom topography of the shallow southwestern Bering Sea (Fig. 7B) may influence migration in this region. Once migrating animals leave the Bering Sea and the margin of the North Pacific Ocean, bathymetry is presumably less significant in guiding migration (Fig. 7A).

These young fur seals are making their first transition to a pelagic existence. Because they are small, and probably not strong swimmers, the currents in the Bering Sea and North Pacific may substantially influence their distribution and migratory paths (Fig. 8). The currents depicted in Figure 8 are, however, estimates of yearly averages. Seasonal variation is likely to be significant, particularly in the region between the Pribilof Islands and the

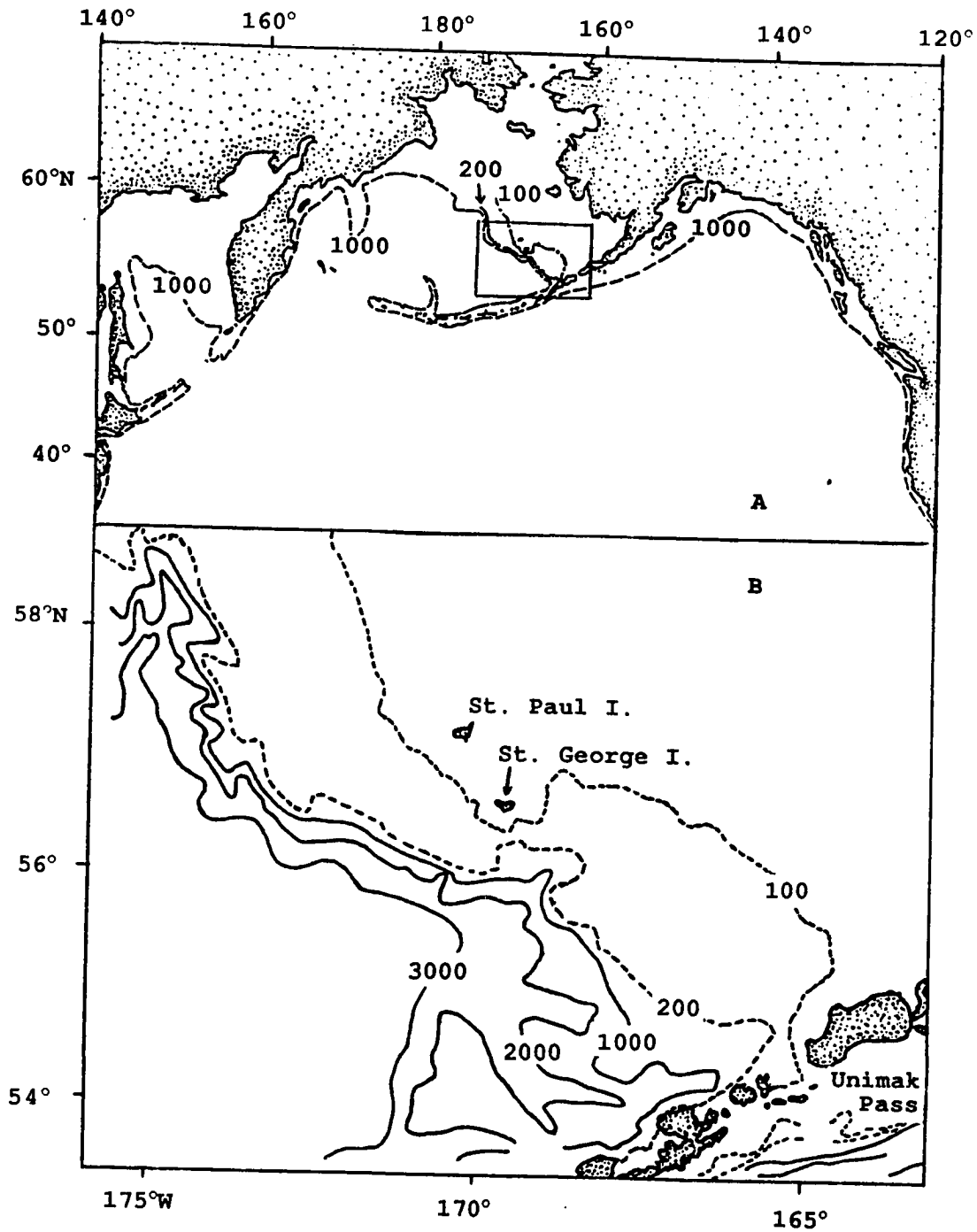Figure 7. Bathymetry in the North Pacific Ocean (A) and Pribilof Islands – Aleutian Islands region of the Bering Sea (B) to indicate regions sufficiently shallow to be of possible use to migrating fur seals (from Dodimead, Favorite, and Hirano 1963). Illustration B is an enlargement of the framed area in illustration A.
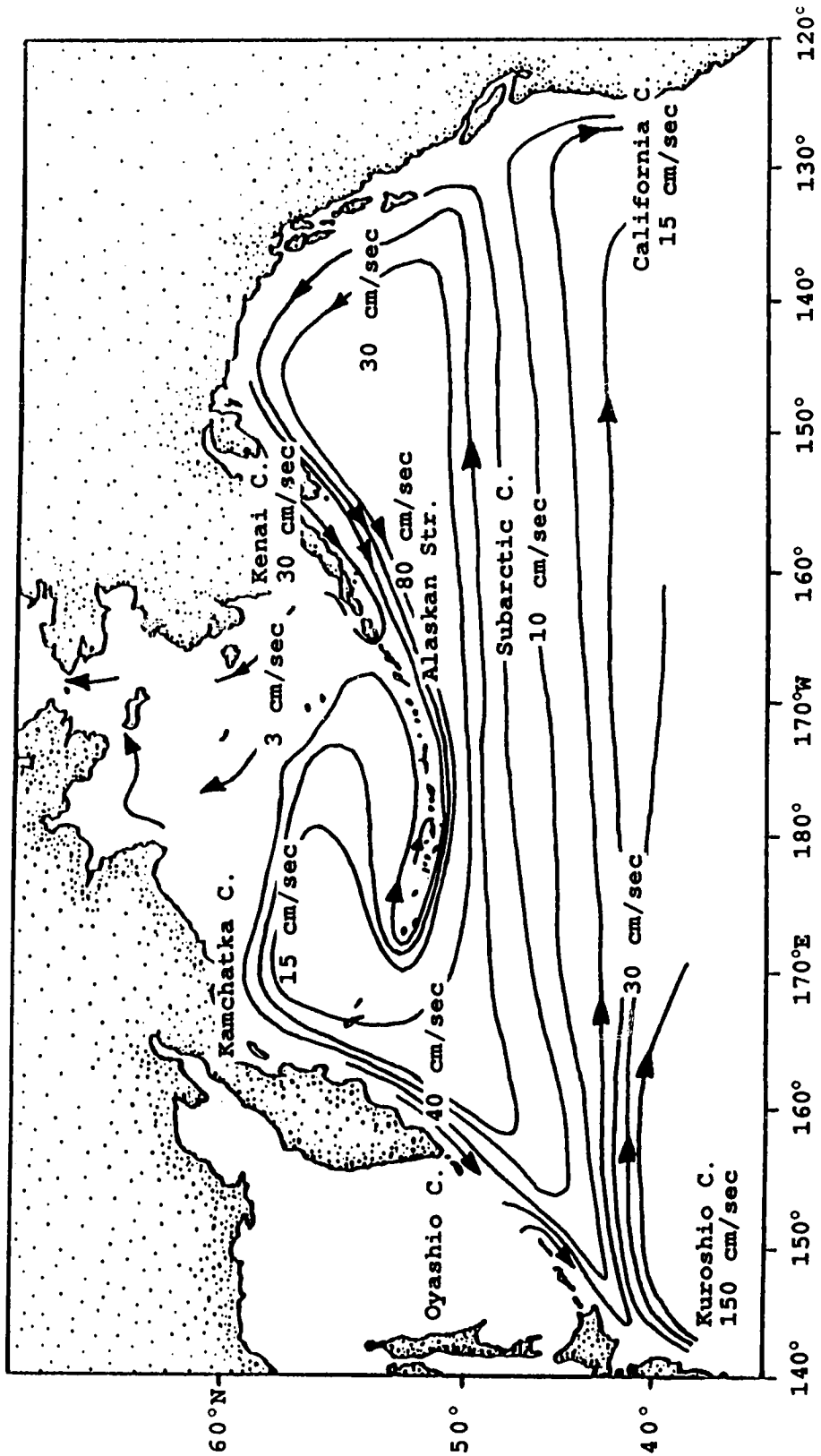
Figure 8. An estimate of average current patterns in the North Pacific Ocean (from Reed and Schumacher 1985).

Aleutian Islands. On the basis of atmospheric pressure gradients, Ingraham (National Marine Fisheries Service, January 1990, pers. comm.) suggests surface currents in the Pribilof Island region may be changing from primarily eastward (toward the continental shelf) to primarily westward (off the continental shelf) in the autumn. However, the estimated average current flows in this region are not strong relative to the westward-flowing Alaskan Stream, which the seals encounter once they are through the Aleutians. If they maintain a southern heading they leave the Alaskan Stream and enter the slower eastward-flowing Subarctic Current.

Prey distribution may also determine migratory routes. The heavy concentration of fur seals killed by sealers (Fig. 1) near the Bering Sea shelf break suggests this is the main summer feeding area, which was confirmed by Loughlin, et al. (1987). If prey concentrate in areas where they are available to recently weaned pups, then this food availability may determine the direction of migration. How prey distribution influences migration and distribution in the North Pacific is less obvious. In studies of fur seal feeding and distribution in the western Pacific, Taylor et al. (1955) noted the highest concentrations of fur seals in waters with an abrupt gradient in temperature, such as where the cold Oyashio Current meets the warm Kuroshio Current off northeastern Japan (Fig. 9). They suggested, however, that the distribution and abundance of prey, rather than water temperature, is more significant in determining fur seal distribution in these mixing waters.
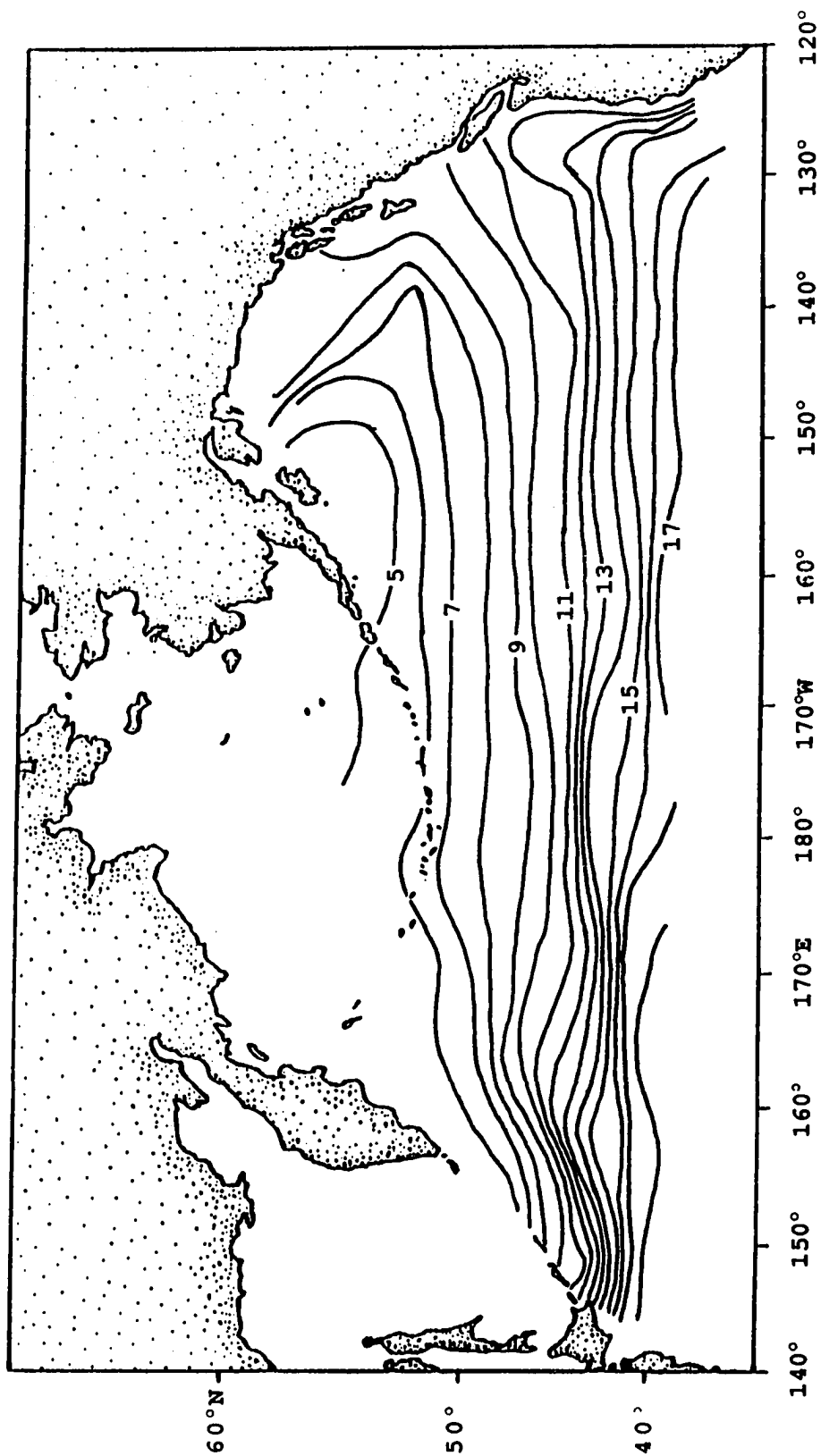
Figure 9. Surface water isotherms in the North Pacific Ocean in November 1956 (from Dodimead, Favorite, and Hirano 1963).

Direction of migration, particularly if strongly affected by prey distribution, should influence the nature of interaction of these pups with human activities. Movement within the Bering Sea may lead to interaction with various fisheries as well as oil and gas exploration and drilling activities. Exploratory drilling has already begun in Norton, Navarin, St. George, and North Aleutian Basins of the Bering Sea (Fig. 10). Unimak Pass is the major traffic lane for vessels leaving or entering the Bering Sea to or from the eastern North Pacific, and increased oil and gas activities could dramatically increase vessel traffic and pollution in this region. The results of this study suggest that vessel traffic through Unimak Pass may not be the main source of interaction of migrating pups with oil- and gas-related activities.

Migration patterns beyond the Aleutian Islands and into the North Pacific Ocean determine the potential for interaction of pups with fisheries in the North Pacific. Northern fur seal pup numbers declined severely from the late 1950's into the 1980's, and during that same period, trawl and gill net fisheries in the Bering Sea and North Pacific Ocean expanded rapidly. The significance of fur seal/fisheries interactions in this decline is uncertain. Development of these fisheries is reviewed extensively in Shomura and Yoshida (1985; see contributions by Uchida; Gong; Low, Nelson, and Narita; Merrel; Fredin; Shima; and Chen). Locations of groundfish, salmon, and squid fisheries are presented in Figures 11-14. Interactions detrimental to northern fur seals are of three types.
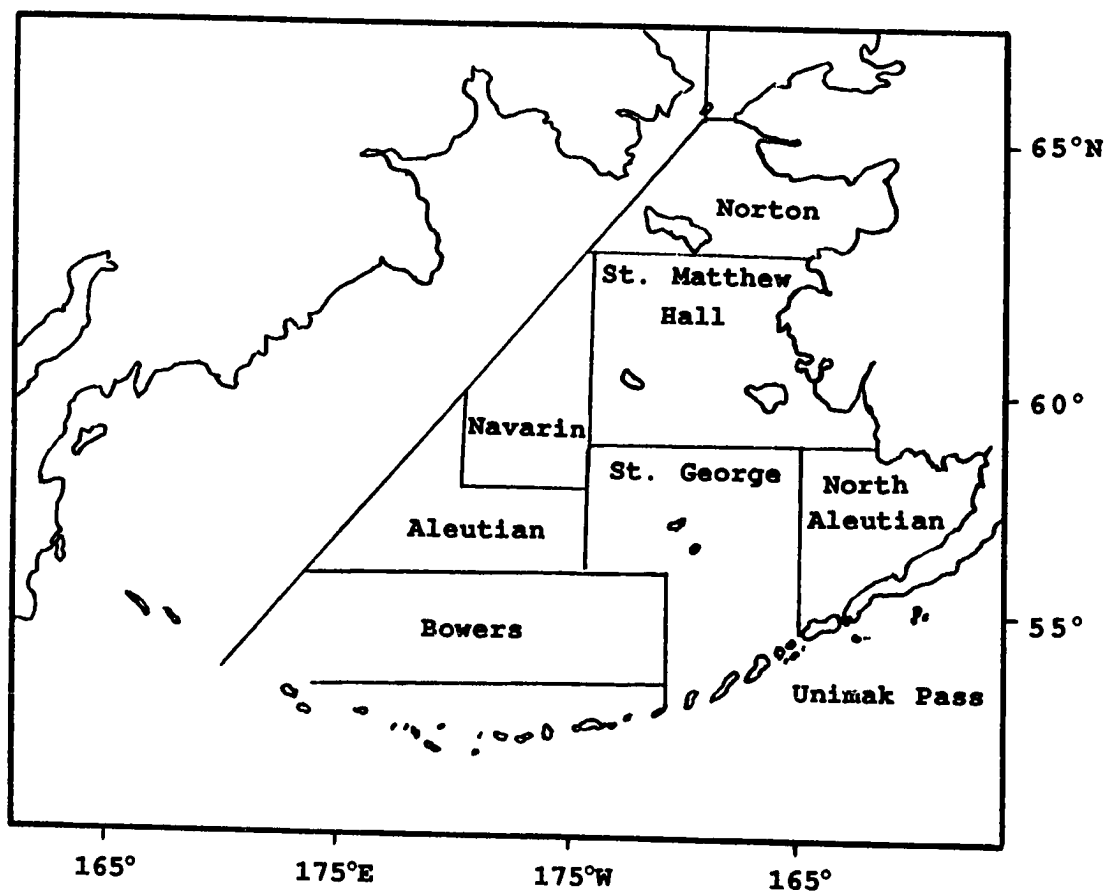
Figure 10. Oil and gas planning areas (Basins) in the Bering Sea (from Houghton, Blaylock, Zeh, and Segar 1987).
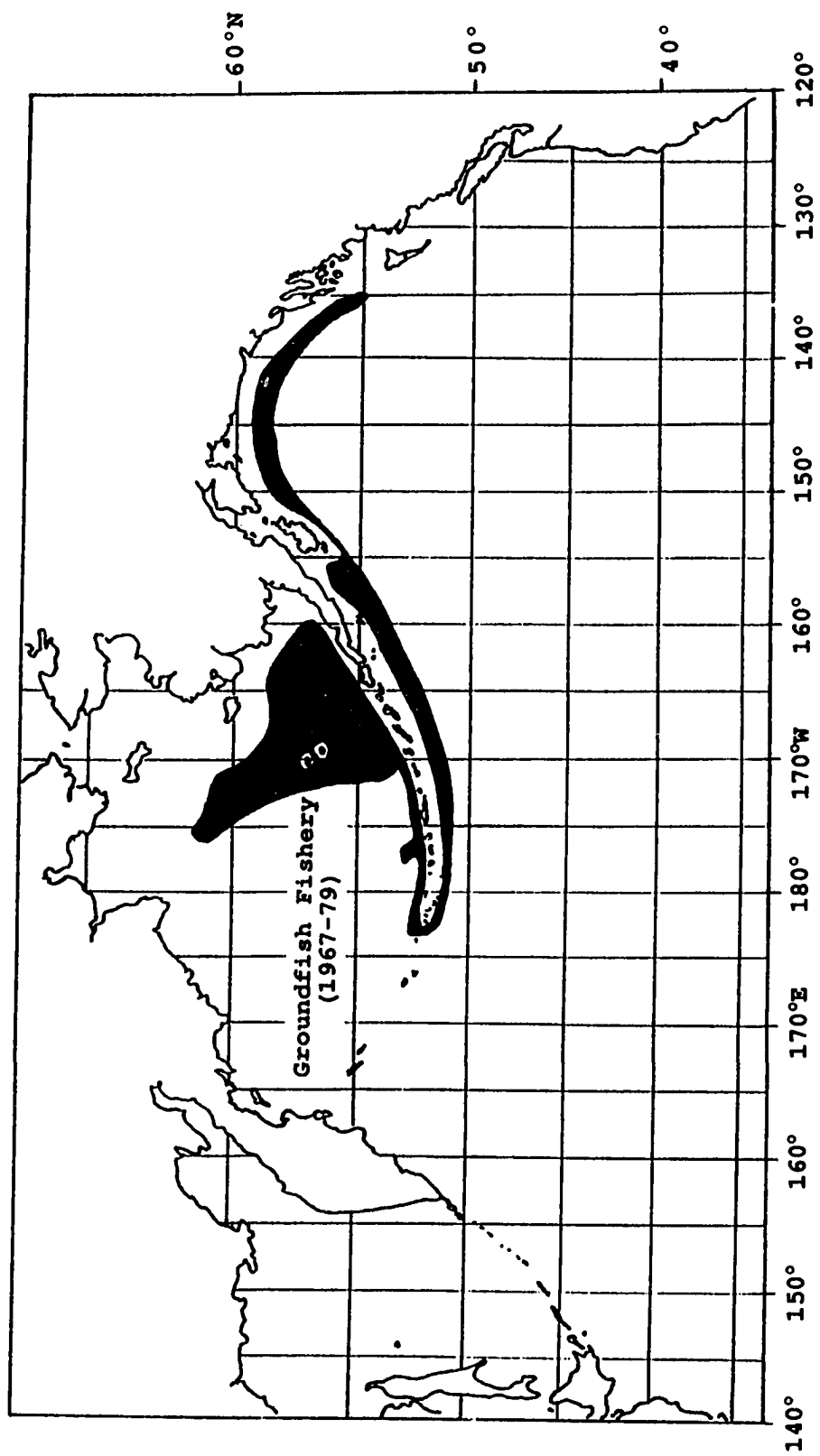
Figure 11. Location of the groundfish fishery in the Bering Sea and Gulf of Alaska, 1967–1979 (from Low, Nelson, and Narita 1985).
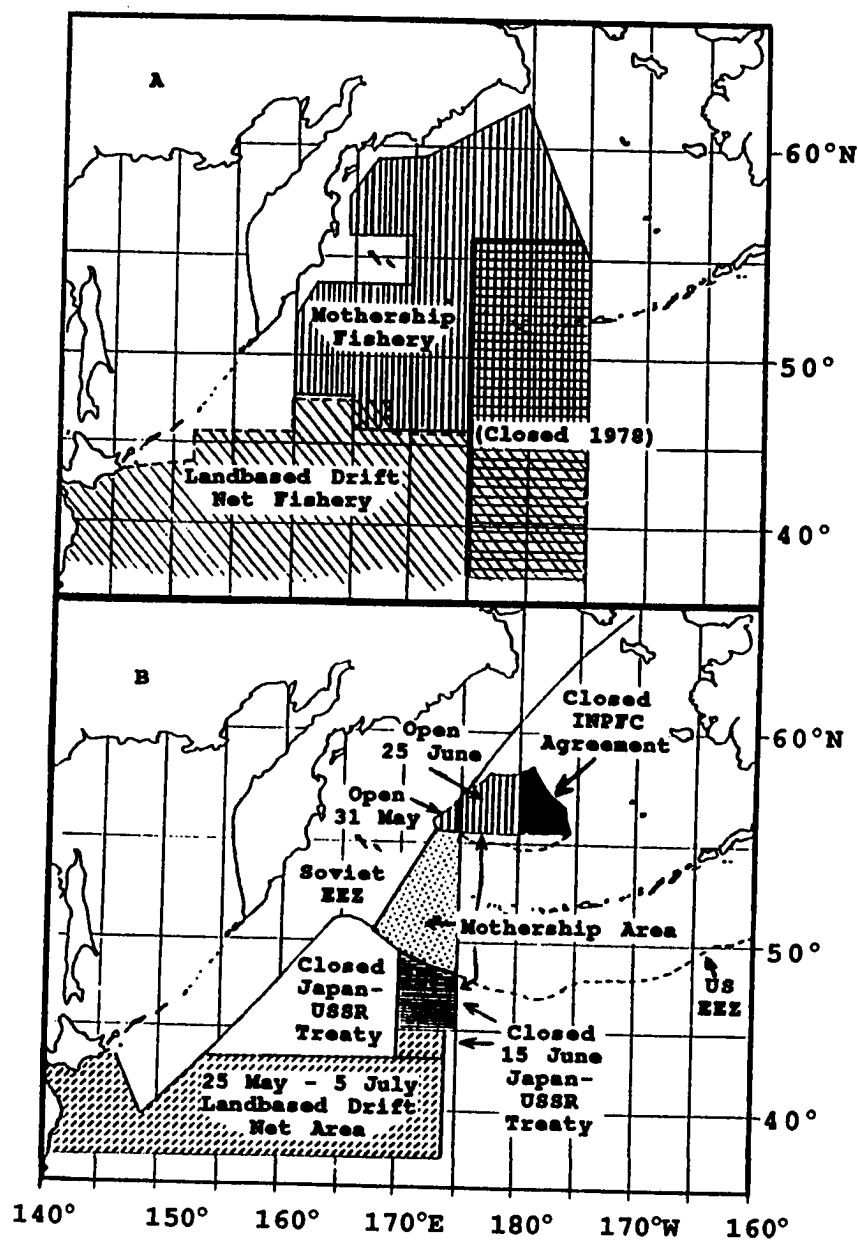
Figure 12. Location of the Japanese mothership and landbased salmon fisheries in the early 1980's (A, modified from Fredin 1985), and currently (B, modified from U.S. Dept. of Commerce 1989). Time-area restrictions including by not limited to those in illustration B were established by the International North Pacific Fisheries Commission Treaty of 1978 (amended 1986) and by bilateral agreement of Japan and the U.S.S.R. in 1988.
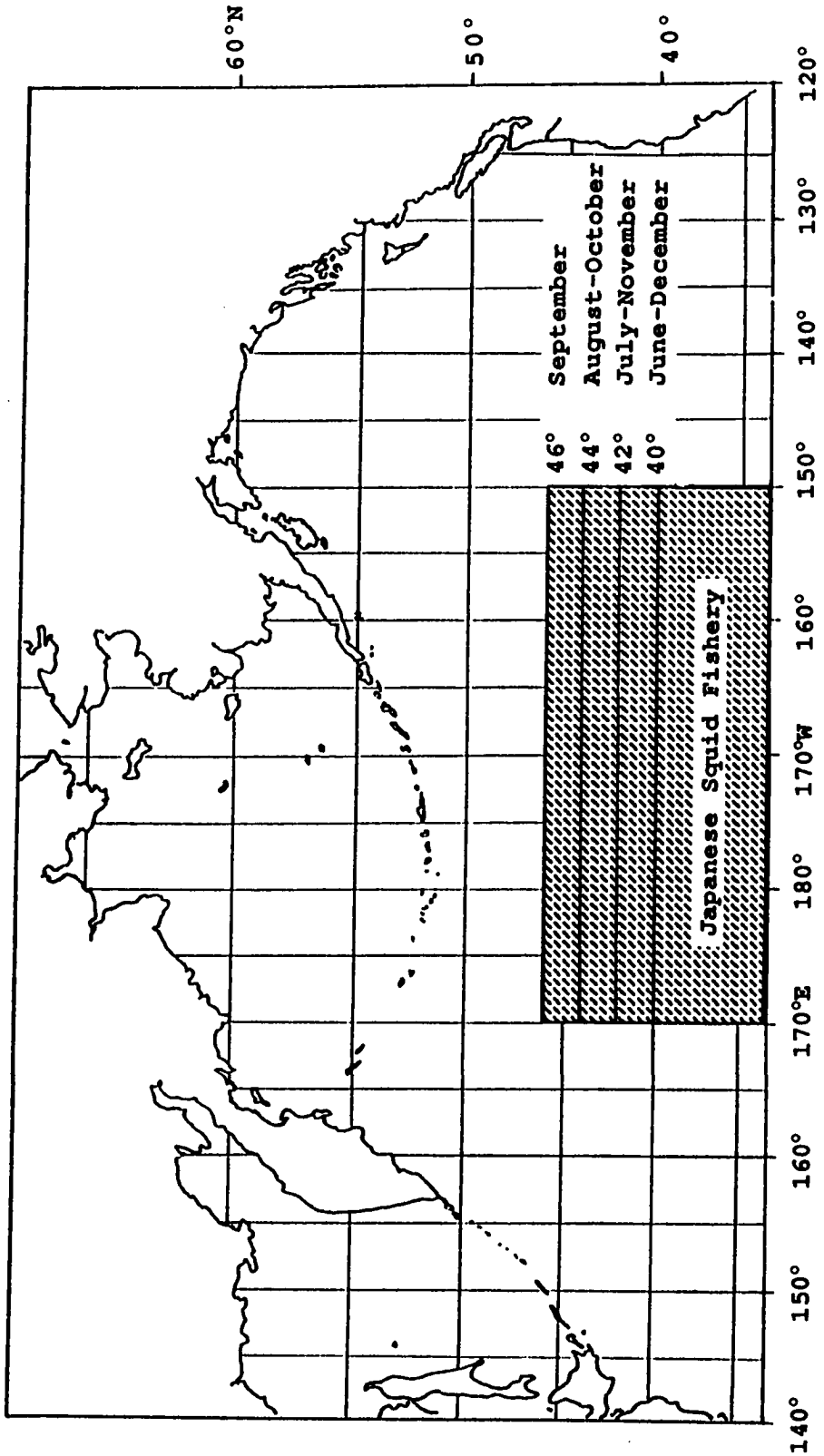
Figure 13. Location of the Japanese drift net squid fishery (modified from Merrell 1985), as established by Japanese regulations in 1981. The northern boundary varies with month in a manner intended to allow the fishery to track the 15° isotherm.
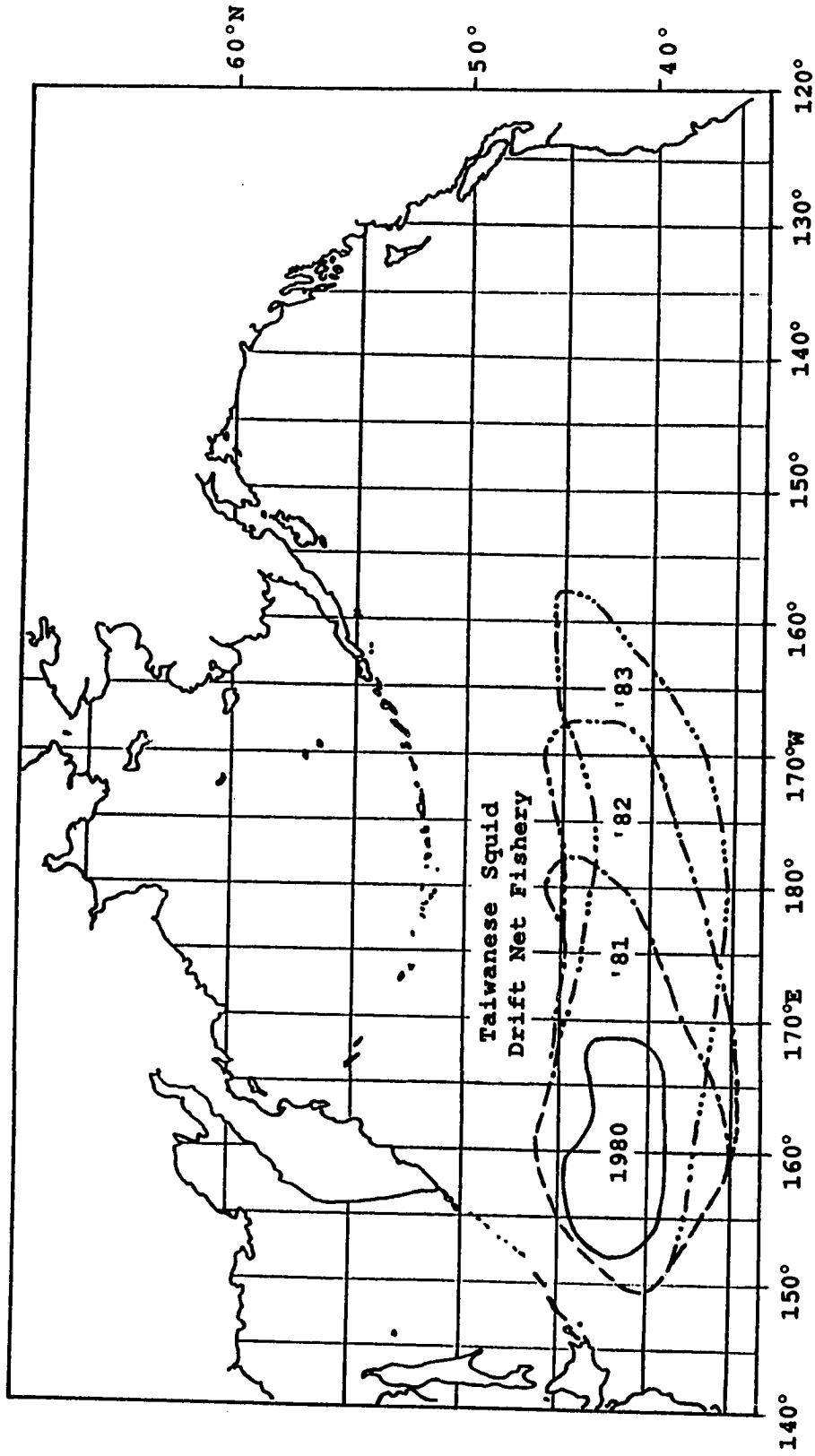
Figure 14. Location of the Taiwanese high seas drift net squid fishery, 1980-83 (from Chen 1985). The corresponding Korean fishery (1979-83) was located in the same general area, but extended further west to the waters offshore of eastern Japan (Gong 1985). In 1985 the Taiwanese established time-area restrictions on drift net squid fishing similar to the regulations of Japan (Fig. 13). The Korean fishery has no time-area restrictions.

Fur seals are killed incidentally in actively fishing gear (Jones 1982), they are injured or killed by entanglement in marine debris, a large portion of which originates with fisheries (Fowler 1985), and they lose prey to competing fisheries. A current and growing concern is the development and impact of high seas drift net squid fisheries, particularly by Japan, Taiwan, and the Republic of Korea since the late 1970's (Figs. 13 and 14). The nonselective nature of these fisheries is well known; catches include marine birds, turtles, and mammals. Importantly, extensive regions of the North Pacific are being fished, and monitoring has been inadequate to determine effects on target and other species. If the distribution of young fur seals in the North Pacific is similar to adults, they may seldom interact with high seas drift net fisheries. If, on the other hand, these young fur seals widely disperse throughout the North Pacific, then interactions may be substantially greater. Due to the potential increase in mortality from high seas fisheries, it is apparent that more information should be obtained concerning the migration of pups from the Aleutian Island passes into the North Pacific. Such tracking will be constrained by the time and expense required to follow pups far out to sea. However, shore-based tracking stations, a vessel, and a fixed-wing aircraft in the vicinity of the Aleutian Islands should be able to determine the direction of migration of pups as they depart the Aleutian Islands, thus indicating the extent of their dispersal into the North Pacific. A follow-up study

including such monitoring, with increased tracking effort, is planned for the migration of 1990-91.

The telemetry systems for this second study will be modified to provide additional means of verifying telemetry results. The telemetry system used in this first study provides only a single indicator (the transmitter frequency) of the source of a radio signal. This leads to uncertainty in the interpretation of receiver records. In the second study, receivers will also be programmed to evaluate the time interval between signal pulses, thereby providing a secondary means of signal verification. Monitoring individual frequencies and interpulse interval should substantially increase confidence in relocation records.

SUMMARY

The life history and distribution of young northern fur seals at sea are poorly understood. These parameters are, however, critical to our understanding of the natural regulation of northern fur seal populations. Due to the difficulty of studying these animals at sea, the migration of fur seal pups was divided into two stages; the first stage consisting of migration from St. Paul Island to the Aleutian Islands, and the second stage consisting of migration from the Aleutian Islands into the North Pacific Ocean. This investigation began to characterize the first stage of that migration, and demonstrates that it is possible to investigate the

early part of this migration through the use of radio telemetry and land-based receiver stations.

One hundred fur seal pups and adult females were radio-tagged prior to their departure from St. Paul Island. Thirty animals were subsequently located in the eastern Aleutian Islands between Samalga Pass and Unimak Pass 10 days (on average) after their departure from St. Paul Island. A single pup was located in Unimak Pass, and 24 others were located further west, suggesting that 1) Unimak Pass is not the primary migratory corridor for pups from the Bering Sea into the North Pacific Ocean, and 2) pups disperse more widely than assumed to be the case with older northern fur seals. Wide dispersal of fur seal pups into the North Pacific Ocean has significant implications for their early life history, as well as for the nature of interactions with human activities such as North Pacific fisheries and oil and gas exploration and drilling. Clearly, additional study is needed to confirm these results and fully characterize the migration of northern fur seal pups into the North Pacific.

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CHAPTER 5. CONCLUDING REMARKS

To relate theoretical ecology or theoretical population dynamics to the natural world, it is necessary to assess natural populations. Initially that assessment consists of conceptually simple questions such as what size is a population, and how does it change over time. However, answering those conceptually simple questions has proven to be very difficult for many natural populations. Marine populations are particularly difficult to assess because they are often highly mobile, widely dispersed, and, in the case of fish populations, invisible to unaided human observation.

A variety of techniques have been developed to assess marine populations, including simple enumeration, mark-recapture techniques, catch analysis, use of historical data, use of various population indices, and so on. But there is error associated with each of these techniques; that is, there is a degree of uncertainty associated with the assessment of natural populations. This error is a major obstacle to the understanding of population dynamics. When large, such error obscures natural growth patterns and the natural stability or instability of a population over time. The resulting uncertainty must be recognized in the conceptual formulation of theoretical ecology and population dynamics, and must also be incorporated into the application of ecological principles to the natural world.

The studies in this dissertation estimate important theoretical reference levels for several natural populations and

170

attempt to account for the degree of uncertainty associated with these estimates. This uncertainty is accounted for in various ways, depending on the population studied and the information available to estimate the reference levels.

In Chapter 2, pre-exploitation biomass for the white seabass (*Atractoscion nobilis*) and the yellowtail (*Seriola lalandei*) populations off Southern California was estimated from natural history information (i.e., growth patterns with respect to age), commercial catch records, and catch records of the heaviest fish caught annually by a member of the Avalon Tuna Club of Santa Catalina Island, California. These are the only available estimates of equilibrium biomass for these fishes. As such, they provide the only basis for measuring change in these populations since the turn of the century, prior to the onset of extensive commercial fishing. A maximum-likelihood approach was used in this study. This approach implicitly recognizes the uncertainty associated with the estimates by seeking the solution "most consistent" with record catches of the Avalon Tuna Club. In addition, standard errors for these pre-exploitation biomasses were estimated to indicate the precision of the estimates, and thereby the confidence that might be placed in them. With the exception of natural history information, it is unlikely that additional data on the pre-exploitation status of these fishes will become available. More natural history information, particularly data dealing with the instantaneous natural mortality

rate of these fishes, may provide the best means of improving these estimates of pre-exploitation status.

In Chapter 3, MNPL (the maximum net productivity level), K (the environmental carrying capacity or equilibrium level), the number of pups born at MNPL and K, and the ratio MNPL/K were estimated for the northern fur seal (*Callorhinus ursinus*) population of St. Paul Island, Alaska. The approach was substantially different from the maximum-likelihood approach taken with the fish populations. The estimation of theoretical reference levels for this population was largely a search for a method which was both consistent with historical observations of the population and which provided some measure of confidence in the resulting estimates. Extensive data are available on the life history and historical trends of the northern fur seal population of St. Paul Island, and there have been important efforts to evaluate the dynamics of this northern fur seal population using analytical and numerical approaches.

Chapman (1961, 1964, 1973) pioneered the use of analytical stock-recruitment functions to evaluate the dynamics of marine mammal populations, but he also recognized that the use of these equations was largely an empirical exercise. Hence, the choice of a particular equation was arbitrary. But as demonstrated in Chapter 3, the choice of stock-recruitment function can have a dramatic effect on the estimation of theoretical reference levels, particularly MNPL or the number of pups born at MNPL. The large range of estimates from the different stock-recruitment functions evaluated in this study,

combined with the associated problems discussed in Chapter 3, did not inspire confidence in any particular stock-recruitment model.

There were similar problems using numerical models to estimate northern fur seal reference levels. The numerical approach is largely the result of computer technology. The development of computers allowed earlier investigators to simulate growth of a northern fur seal population, and thereby attempt to determine the major elements of fur seal natural history. Importantly, these earlier investigators also recognized the need for confidence in their simulation results. They compared their results to empirical observations of the real population (validation criteria) to determine the realism of any given simulation. Replication of earlier models provided a means of estimating theoretical reference levels, particularly MNPL, but a number of estimates were generated. As with the analytical stock-recruitment approach, multiple estimates were generated without an indication of which was the best estimate. Importantly, the different estimates of MNPL and other reference levels were generated because the examined numerical models used varying combinations of life history parameters and density-dependent controlling functions.

Chapter 3 explores the use of a new approach to estimating northern fur seal reference levels. Based on Smith and Polacheck (1984), this approach was to 1) create a large parameter space based on current knowledge of northern fur seal life history and density-dependent parameters, 2) partition that parameter space into millions

of parameter combinations, 3) run a simulation with each parameter combination, 4) compare the results of each simulation to pre-determined validation criteria, and 5) use the acceptable simulations to construct frequency distributions of the various theoretical reference levels. Importantly, this approach and the resulting distributions reflect the uncertainty in our understanding of northern fur seal vital parameters and density dependence, and thus in the resulting reference level estimates. Most importantly, these distributions provide measures of confidence that can be associated with single estimates of these reference levels. That is, this very general approach provides a broad perspective within which particular estimates can be evaluated. This broad perspective is necessary because of the uncertainty in our understanding of northern fur seal life history and population regulation.

The final study of this dissertation focused on the uncertainty in life history information for young northern fur seals. The least known life history parameters are annual survival rates for young animals, particularly females. These animals leave their islands of birth at about the age of 4 months, and may not be seen again until the age of 2 or 3 when they start returning to those islands. For that intermittent period of 2 to 3 years, their distribution and migratory paths are virtually unknown. Unfortunately, this life history information is vital to the study of northern fur seal population dynamics. This third study provided information on the early migration of northern fur seal pups in the

Bering Sea between St. Paul Island and the Aleutian Islands. The results indicated that these pups disperse more widely than previously assumed.

This information is vital to an understanding of the pelagic phase of the northern fur seal annual cycle. Understanding of northern fur seal population biology will remain incomplete until this pelagic phase is more thoroughly studied. The most important questions about northern fur seal life history and population trends must be addressed by studying these animals at sea. The means for conducting this pelagic study is perhaps the greatest challenge to the study of northern fur seals, and all pinnipeds.

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