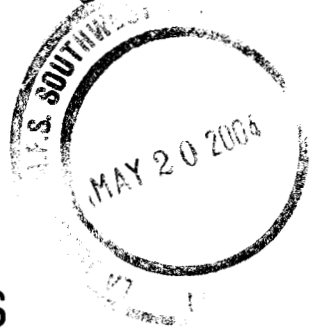


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OBSERVATIONS OF THE HAWAIIAN MONK SEAL ON LAYSAN ISLAND FROM 1977 THROUGH 1980

Brian W. Johnson
Patricia A. Johnson

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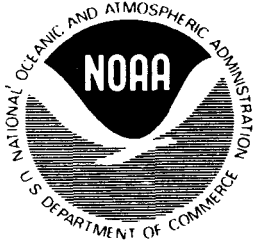
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OCTOBER 1984

**OBSERVATIONS OF THE HAWAIIAN MONK SEAL
ON LAYSAN ISLAND FROM 1977 THROUGH 1980**

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U.S. DEPARTMENT OF COMMERCE
Malcolm Baldrige, Secretary
National Oceanic and Atmospheric Administration
John V. Byrne, Administrator
National Marine Fisheries Service
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PREFACE

This report was prepared under Contract No. 80-ABC-00124 to the National Marine Fisheries Service by Brian W. Johnson and Patricia A. Johnson. The primary purpose of the contract was to summarize Hawaiian monk seal observational data collected on Laysan Island by the contractors from 1977 through 1980. The statements and findings in this report are those of the contractors and do not necessarily reflect the view of the National Marine Fisheries Service.

ABSTRACT

Behavioral observations of the Hawaiian monk seal on Laysan Island were made between 1977 and 1980. Primary objectives included determination of population size, reproductive patterns and survival rates. Individual seals were recognized by photographs of natural markings (particularly scar patterns) or by temporary bleach marks.

The 1977 mean count, 179 seals, was representative of the average count from the previous 10 years. During 1978 an unusual "die-off" of seals occurred, resulting in a 35% reduction in the mean count, to 112 by 1980. Using nondisturbance population estimation techniques developed in 1979, the mean count of 100 nonpups ashore in 1980 was shown to be well below the estimated population size of 269 seals.

From the Laysan data it appears sexual maturity (as measured by first birth) may not occur until after five years of age for females. Known-age males did not show courtship behavior until 8 or 9 years old. During the 4 years of the study an estimated 64% of the adult females produced pups. The mean weaning age for pups was 36.2 days. Females outnumbered males at birth but first year survival was significantly greater for males. Adult males outnumbered adult females by 3 to 1. Yearly survival rates of seals from birth to about age 4 was estimated at 75%, increasing to 85% for subadults and adults.

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INTRODUCTION

The Hawaiian monk seal, Monachus schauinslandi, was designated as a depleted species under the Marine Mammal Protection Act of 1972 and listed as endangered under the Endangered Species Act in 1976. As the basic biology and life history of the monk seal were incompletely known, the authors, aided by personnel from the National Marine Fisheries Service (NMFS) and U.S. Fish and Wildlife Service (FWS), designed a study to learn about population parameters and threats to survival of the Hawaiian monk seal. This report summarizes the results of 4 years investigation on Laysan Island. Information gathered on the French Frigate Shoals population of monk seals is included in a separate report (Johnson and Johnson 1984).

Funding for the project was provided primarily by the Marine Mammal Commission, with additional support and equipment provided by National Marine Fisheries Service, U.S. Fish and Wildlife Service, the U.S. Coast Guard, the Easy Rider Corporation, and the State of Hawaii.

Laysan Island was selected as the study site, with field research beginning in 1977. Laysan is a coral sand island located approximately 1350 km from Oahu (Fig. 1). As part of the Northwest Hawaiian Island Archipelago, it is included in the Hawaiian Islands National Wildlife Refuge. Access to Laysan is strictly limited. The island is home to two endemic bird species listed as endangered as well as the monk seal, and to the threatened Hawaiian green sea turtle, Chelonia mydas. Laysan is 1.7 by 2.8 km, with a circumference of about 12 km. Low vegetation and a high saline lagoon cover much of the interior. (For a more complete description of the island and its history see Ely and Clapp 1973.)

The historical use of Laysan by the monk seal is incompletely known. No information is available on the size of the seal population prior to near decimation by sealers and other visitors using the island in the 1800's. By the early 1900's seals were rarely seen on Laysan. As summarized in Fiscus et al. (1978), the population gradually recovered, with counts occasionally exceeding 300 animals in the late 1950's and early 1960's. The number of seals counted declined during the mid-1960's, but remained relatively stable during the 10 years prior to the start of this study, averaging just under 200 seals.

Past studies have shown the Hawaiian monk seal to be adversely affected by human disturbance (Kenyon 1972). With this in mind, the present study was carefully designed to record the behavior of a colony of monk seals relatively undisturbed by man. Care was taken that the natural behaviors of the species not be altered by the presence of seal or bird biologists living on Laysan, or by visitors to the island.

During each year from 1977 to 1980 5 to 7 months were spent on Laysan. Observations were limited to the months from late February through September except in 1978, when brief visits were also made in October and December. (Arrival and departure dates for all years are listed in Appendix A.) The authors were the sole human inhabitants of Laysan during 1977 and 1978. In 1979 and 1980 the size of the Laysan field party increased to five with the addition of three FWS biologists.

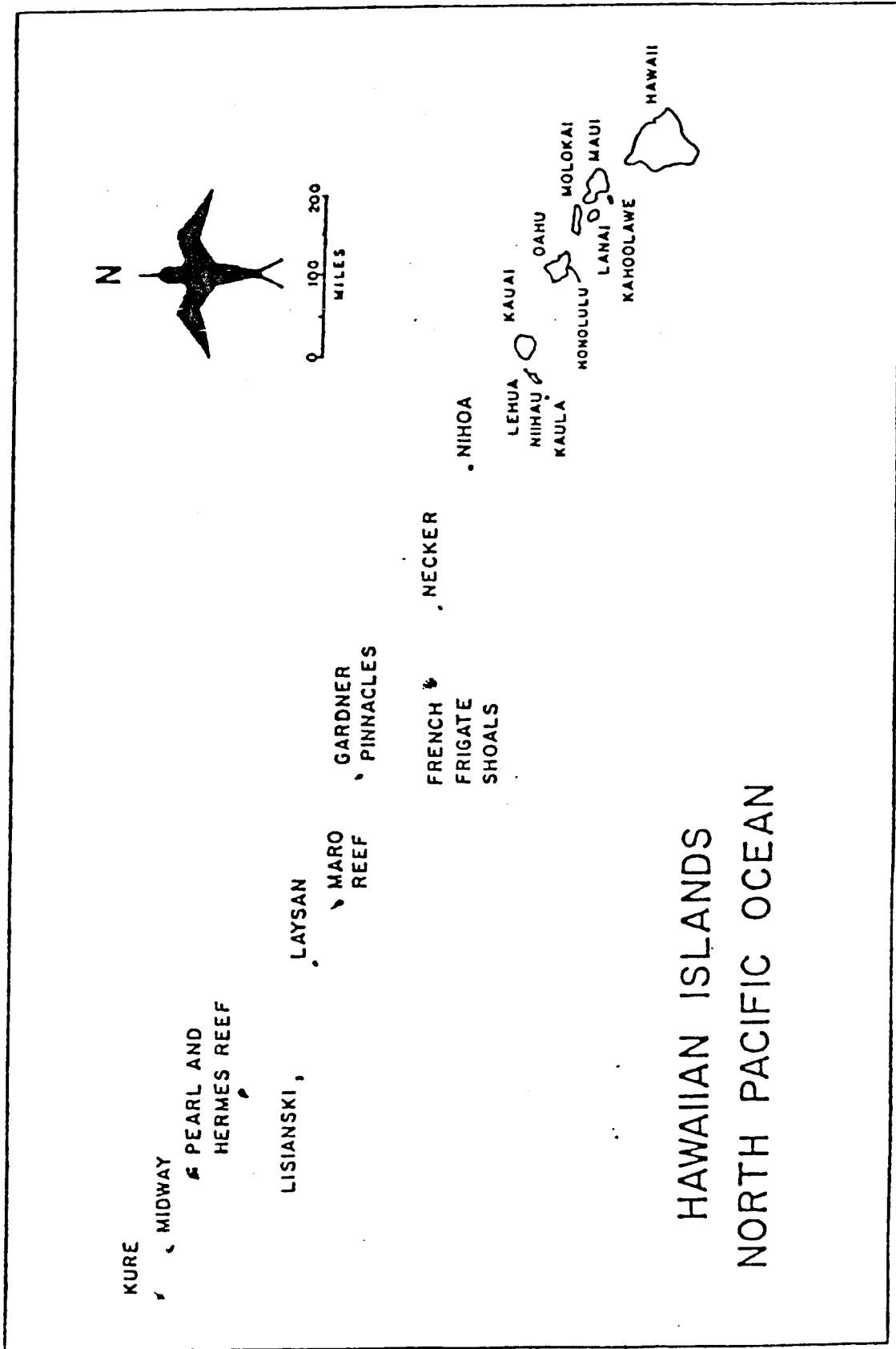


Figure 1.--Hawaiian Archipelago.

Camp was established on the northwest side of the island, east of the lone ironwood tree and well back from the beach. With the exception of the beach directly below camp, all human access to beaches was restricted and carefully monitored. No handling of seals occurred except during a 3-day visit by a team of scientists in May of 1978, when 11 seals were restrained for collection of blood samples and physical examination.

During the 1978 field season an unusually large number of seals died or disappeared on Laysan (Johnson and Johnson 1981b). Later investigation determined the probable cause was a fish toxin, ciguatera (Gilmartin 1983). Dramatic population declines of unknown etiology had been recorded for seal populations on other atolls in recent years (Gilmartin 1983). The Laysan "die-off" provided the first opportunity to study the circumstances and effects of a high mortality on what had appeared to be a relatively healthy population. Observing the affected animals, the changes in population structure, and the overall effect of the mortality became a high priority.

This report summarizes 4 years of research, but emphasizes data collected in 1980 as funding was available to computerize data from that year which allowed more complete analysis. Results from the previous years have been reported elsewhere (Johnson and Johnson 1978, 1981a, 1981b).

METHODS

Seal Identification

An extensive portfolio of photographs, sketches, and descriptions of natural scars and marks was compiled and constantly updated, allowing reliable identification of individual seals. Photographs were taken with both Polaroid and 35-mm cameras. Field identification was generally made on the basis of sketches, descriptions, or direct comparison of a photograph and the animal. Most recognizable animals were photographed repeatedly to monitor changes in scar patterns or visibility and to assess rate of acquisition of new marks.

Many adult seals had conspicuous scars or other markings which were unique. However, young seals rarely had acquired identifiable scars. To facilitate individual identification of these animals it was necessary to apply artificial identification marks to the hair of some immature seals and all pups born during the study, using a commercial hair lightener preparation (Lady Clairol Ultra Blue). The marks were applied to sleeping seals and did not result in observable adverse physical or behavioral changes. Bleach marks lasted until the next molt of the animal.

Age Determination

During the first year of the study it was difficult to reliably assign seals to any age class other than adult, immature, and pup. The adult female size class was defined by the size of the smallest animal to bear a pup. The definition of an adult male was based on the size of the smallest animals showing courtship behavior. Nonadult seals were classified as subadult, juvenile large, juvenile small (assumed to be yearlings), and pups. In subsequent years tagged seals and known-age animals were available to serve as a reference, and distinctions based on size, color, and other

features were used to age seals. The age classes were defined as follows for all observations made from 1978 through 1980.

Adult: animal of breeding size, usually over 2.0 m in nose to tail length. Minimum breeding size for females was defined as the size of the smallest female to give birth to a pup. Minimum breeding size for males was defined as the size of the smallest male to engage in courtship behavior, including the "rolling bellow" (see Kenyon and Rice 1959, p. 235).

Subadult: animal near breeding size, approximately 1.6 to 1.9 m in length. Data from the few known-age animals in this age class indicate that most 4- and 5-year-old females and most 4- to 7-year-old males would be included as subadults.

Juvenile: small seal, not a pup or identified 1-year-old animal, approximately 1.4 to 1.6 m in length. This age class includes all 2-year-old and probably most 3-year-old seals.

Yearling: approximately 1.3 to 1.4 m in length. Includes only those animals known to have been born on Laysan during the previous year. One-year-old animals born on other atolls or with marks that were unreadable during censuses would have been classified as juveniles.

Pup: young of the year, classified as "nursing" or "weaned," approximately 1.3 m in length at weaning.

Length measurements are listed as a basic guide. They are not a reliable measure of age, as there is a wide overlap in lengths of animals known to have been born in different years. For some purposes subadult, juvenile, and yearling animals were combined into a single age class and called immatures.

Because of the inherent subjectivity of the age classifications used, it is likely that the specific boundaries between age classes vary slightly from census to census. These differences are probably insignificant due to the continual check provided by the large number of identifiable animals in the population, and because the same observers conducted the counts throughout all 4 years. Further, counts conducted with other monk seal researchers (including DeLong, Fiscus, A. Johnson, Kenyon, Knudtson, and Rauzon) showed close agreement in age classification, indicating the basic age categories are relatively distinct, even when observers differ and identified animals are not used.

Sex Determination

While subtle sexual differences in face, body proportions, and coat color may be present in monk seals, we considered a good view of the posterior ventrum the only reliable method of determining sex, with three exceptions.

1. The sex of seals recognizable by natural or applied marks was routinely recorded without reconfirmation.

2. The sex of adults attending nursing (i.e., unweaned) pups was assumed to be female.
3. The sex of vocalizing adults giving the characteristic adult male "rolling bellow" during courtship displays was recorded as male, even if no ventral examination was made.

By recording the sex of an animal only if it met one of the above criteria, errors in sex determination are very unlikely, but it is also inevitable that many seals will be recorded as "sex unknown." If a significant proportion of the seals ashore are unsexed, the observed sex ratio will be biased unless the probability of sexing males and females is the same. In particular, counts of adults made during the pupping season will be strongly biased toward females (if very many seals are unsexed) because all adults attending pups will be recorded as female. Appendix B presents a discussion of other potential biases, and offers a method of correcting for the female-with-pup bias. The female-with-pup correction should be applied to counts from all studies when interpreting or comparing sex ratio data collected during the pupping season.

Molt

During 1977, data collected on censuses included noting any obviously molting seals. From 1978 through 1980, all seals seen on censuses were recorded as either premolt, molting, or postmolt. Premolt seals generally had a brownish-yellow tinge to the pelage, and often had algal growth on the hind flippers or muzzle. Postmolt seals were similar in color to recently weaned pups, with a gray or silver coat color. At about 3 months postmolt, the hair began to gradually develop a brownish-yellow tinge.

In 1977 and early 1978, a seal was classified as molting once the first patch of hair was shed. In July of 1978 the molt was redefined to include animals as molting only if a patch of hair at least 2 cm square was missing from the chest of the animal. This change was necessary because some animals showed signs of molting on the hind flippers or around scars as much as a week before they began to molt elsewhere. Other animals retained a small patch of old pelage on their backs for a few days after the rest of the old hair had been shed. In the latter case, we continued to record a seal as molting until the last patch of old dorsal hair was gone. (Occasionally patches of epidermis remained attached after the last hair was shed: These animals were called postmolt.)

From 1978 through 1980, molting seals were classified by the percentage of body hair that had been shed. There were five main categories, ranging from <20% to >80%. (For additional information on the molt in Hawaiian monk seals see Johnson and Johnson 1981a.)

Censusing Techniques

Knowledge of the specific methodology used during seal censuses is extremely important when making comparisons between studies. Differences in such factors as start time, counting seals in the water, or overall time to complete a count can seriously bias comparisons. Unfortunately, these factors are sometimes difficult to identify, and are frequently ignored.

The methodology used on Laysan during the 4 years of our study was patterned after that used in previous surveys of the Hawaiian monk seal, and included counting seals in the nearshore water. Both our counts and previous ground surveys attempted to count the maximum number of seals using the area. Our methods differed slightly from previous counts in that greater precautions were taken to avoid counting individual seals more than once. Comparison of counts made by the authors with concurrent counts made by researchers visiting Laysan during the 4 years of the study period showed close agreement, despite the slight difference in methodology. Counts made by National Marine Fisheries Service personnel since 1982 have excluded all animals in the near-shore waters (Gilmartin, personal communication) and are therefore not directly comparable to our Laysan counts or to other counts made prior to 1982.

The methodology used on Laysan was consistent between 1977 and 1980. To minimize disturbance, most beaches were rarely visited between censuses. Since a major objective of the study was observation of an undisturbed population, we made every effort to remain undetected by the seals. Observations were made at the greatest distance possible, using binoculars.

A once every 4-day censusing schedule was maintained throughout all 4 years of the study. These "main" censuses were usually started between 1200 and 1600 and allowed direct comparison of haul-out parameters between years. Additional censuses, with variable start times were conducted after 1977. All censuses generally started on the west shore below camp. The two observers walked in opposite directions; one observer (BWJ) counted seals to the south while the other (PAJ) counted seals around the northern half of the island (observers occasionally switched censusing directions). Censuses normally ended approximately 3 hours after they started, when the two observers met on the east shore.

All seals onshore during the census were added to the total unless a recognizable individual seal was encountered which had been counted earlier on the census. Seals floating in the water or swimming directly toward or away from the island were included in the count, unless previously identified. Seals swimming along the shoreline presented a problem, as these animals often swam back and forth along a large section of beach, introducing the possibility of double counting. To minimize this possibility, we included all seals swimming from an area not yet censused (unless a previously identified animal) and excluded from the total all seals swimming from an area already counted (unless the animal was an identified individual which had definitely not been seen previously on the count; e.g., when all seals of that age/sex class seen previously had been identified).

Data collected on each seal during censuses throughout the 4 years included: age class, sex (when possible), identity (if known), and location on the island. Molting seals were noted in 1977; in all other years the stage of molt, including pre- or postmolt and molting (as percent molted) was recorded.

Because of the nature of the study there were slight differences between data collected in 1977 and data from later years. During the first year of the study few seals were individually recognizable; therefore, fewer seals were sexed on counts in 1977 than in subsequent years. The presence

of large numbers of identified individuals by the end of the study made sexing a large proportion of the seals easier, and increased the consistency of the age class assignment. Finally, our definition of the molt stages changed during 1978. Thereafter, a seal was not recorded as molting until hair loss began on the chest. This change meant that seals were recorded as molting for longer periods in 1977 and early 1978 than in subsequent years (Johnson and Johnson 1981a).

Population Estimation

The techniques used to estimate population size were designed to avoid any handling or disturbance to the seals. This was important for two reasons. First, earlier studies indicated human disturbance might be a major factor in the decline of the species (Kenyon 1972). Secondly, data obtained using nondisturbance methods can serve as an important control to test the reliability of future studies involving tagging of animals. Any studies which require handling of animals must assume that capture and tagging do not affect the haul-out behavior of the animal. The ratio of mean count to population estimate during our study can be compared with data collected in future years to test this assumption if counts are made in a comparable manner.

The methodology was designed so that data could be collected using binoculars at a considerable distance from the animals. The techniques which required individual recognition of animals (Petersen Estimate, Petersen/Molt, and Molt Summation) were based on detailed identification files which contained photographs, sketches, and descriptions of scars and marks.

No techniques were used to estimate the number of pups born, as regular censusing throughout the field season provided an accurate count of the total pup production. Also, no attempt was made to estimate the number of yearlings in the population, since all pups born on Laysan the previous year were bleach marked, thus identifiable.

Natality and Reproduction

As the risk of disturbance to all beaches each day was considered unjustifiable, many areas of the island were not visited on noncensus days. Accurate determination of birth and wean dates for pups was considered important, so daily visits were frequently made to a particular beach when a birth or weaning was expected. Despite these additional observations, the actual day of birth was not determined for many pups, and it was necessary to use a best-guess method to minimize the possible error in assigning a birth or weaning date. The day of birth was recorded as the day halfway between when the pup was first seen and the last time the area had been checked. The only exception occurred when tracks and/or a fresh placenta indicated the birth was very recent (same day) or definitely had not been that recent. The same approach was used to determine the day of weaning, with the day of weaning considered to be the day halfway between the date the pup was last seen with an attending female and the first day it was seen alone. Since censuses were conducted at least once every 4 days, this introduced a maximum error of plus or minus 4 days into determination of age at weaning (or lactation interval for adult females). Weaning was defined as the departure of the attending female while the pup remained.

One pup was weaned prior to our arrival in 1980, but it was possible to determine the probable mother as the physical appearance and alteration in haul-out and molt patterns for only one female fit the pattern expected for the mother of the early pup. The reproductive data for this female has been included in the calculations, classifying her as parturient in 1980. In the only other case of a weaning prior to our arrival (in 1977), no such assumption was made. Only females known to produce pups were included as parturient. To be listed as nonparturient the female had to be seen throughout the period she might be expected to pup, or be obviously not pregnant at that time (otherwise her reproductive status for that year was excluded from analysis). Although it is unlikely that any female seen regularly on Laysan Island during a field season gave birth on another atoll in that year, the possibility cannot be excluded. No seals seen during our study on Laysan Island matched the photographs, sketches, or descriptions of mothers seen in 1980 at Kure Atoll (NMFS files examined in November 1980) or French Frigate Shoals (FWS files examined in July 1981). Any female that became pregnant but aborted prior to the start of the field season would have been classified as nonparturient.

A subjective assessment of the size of most mothers was made several times during the field season, including before, during, and after lactation. A five point scale was used, with 1 being very small, and 5 very large. The mean of all recorded sizes was calculated for each female each year. The assignment of a size was based on overall length and girth.

RESULTS AND DISCUSSION

Island Counts

In 1977 the mean of all censuses conducted between mid-March and mid-August (the period allowing comparisons between all years of the study) was 179 seals. The highest count (211 seals) was as high as any count since 1965, indicating little change in the total number of seals using Laysan between 1965 and 1977.

The mean count during the mid-March to mid-August period in 1978 declined dramatically to 123 animals. Over 50 identified animals were known to have died or disappeared during what has been termed the 1978 "die-off." The mean count during 1979 was 113 seals, showing a further decline. The mean count of 112 seals in 1980 was almost identical to the 1979 mean, suggesting the Laysan population may have stabilized, but at approximately 35% below the 1977 level. (The results of all censuses conducted during the study are included in Appendix C.)

The age composition also changed with the die-off of 1978. Figure 2 shows the decrease in total seals, immatures, and adults, taken from all censuses conducted in the mid-March through mid-August period of each year. The greatest decline occurred in the immature seal counts. Field observation showed the yearling cohort was especially affected, with only 7 of the 42 pups born in 1977 known to have survived through 1978.

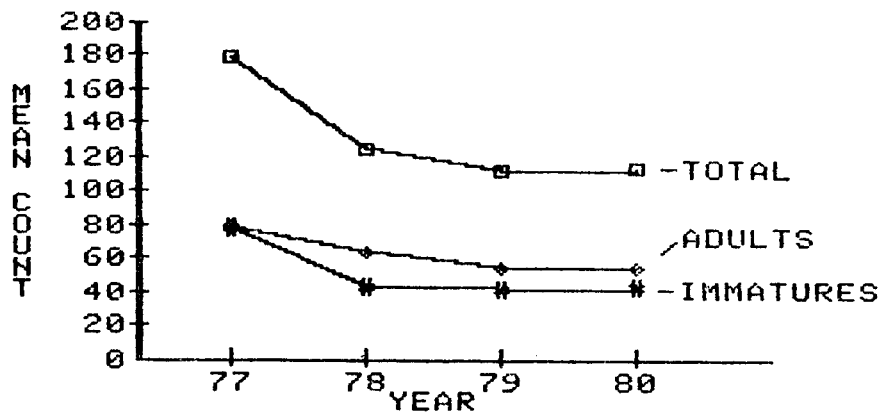


Figure 2.--The mean mid-March through mid-August seal count, 1977-80.

Changes in the sex structure were more difficult to document as 44% of the seals (excluding pups) were not sexed on counts in 1977, compared with only 8% unsexed in 1980. The increase in number of animals sexed over the study was due to the greater number of individually recognizable seals as well as to the increased experience of the observers.

To ascertain the degree of change in the sex structure of the population, it is necessary to examine potential sources of bias which could result in either males or females being easier to sex on counts. If no biases exist, then extrapolating the sex ratio of animals sexed on counts to the unsexed animals in each age class would be a valid way to compare data from 1977 with other years. Appendix B lists several potential biases, and presents data showing the effect of these biases was negligible, except for the correctable female-with-pup bias.

Figure 3 compares the mean count for the adult and immature age/sex classes from mid-March through August 1977 with the same period in 1980. The data include a correction for the female-with-pup bias (as described in Appendix B) and assume that the male:female sex ratio for unsexed animals is the same as for sexed animals. These data show similar declines in male and female numbers in both age classes, with a greater decline in the number of immature seals than adults (44% and 26%, respectively).

Seasonal changes in haul-out patterns for each age/sex class can best be shown using data from 1979 and 1980 (1977 data are excluded because of the large number of unsexed animals and 1978 data because major changes were occurring in the composition of the population throughout that year). Figure 4 compares semimonthly mean counts for 1979 and 1980. Data from both years show a similar pattern, with an initial high in April followed by a low in May and a second high in June followed by a decline in July. A difference can be seen between years in the counts during the April and June high periods. In early April the 1979 counts were about 10% below the counts, but in early July the situation was reversed with the 1979 counts higher than the 1980 counts.

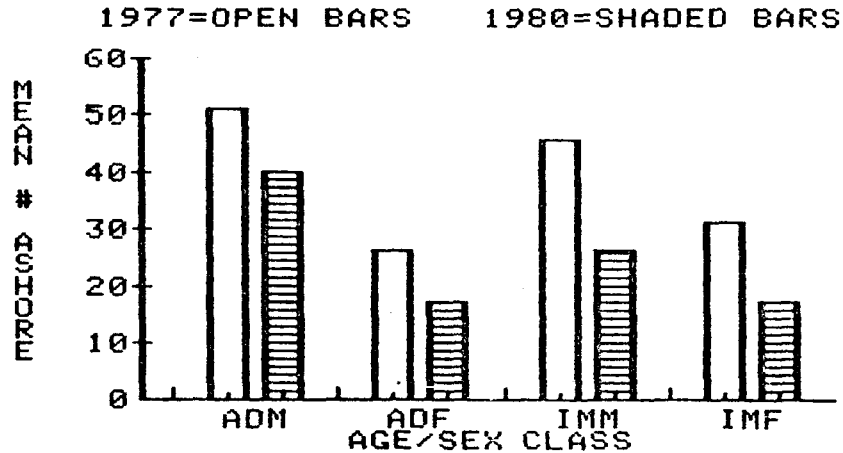


Figure 3.--Mean island count from mid-March through mid-August, based on extrapolated data from Appendix C.

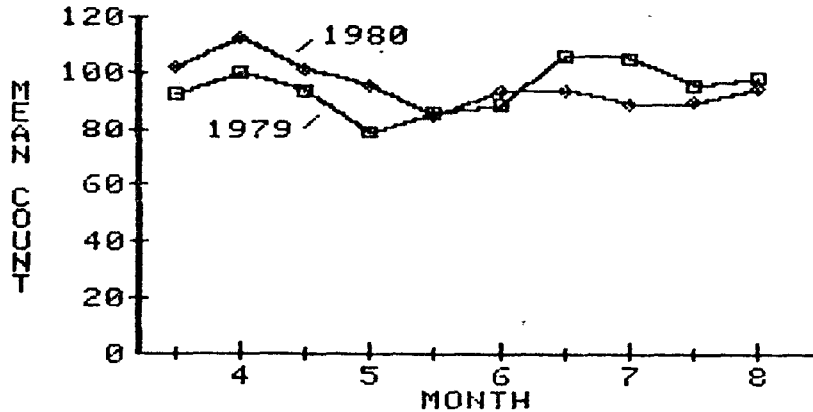


Figure 4.--Mean count (excluding pups) from mid-March through mid-August.

Figure 5 combines the data from both years to illustrate the overall pattern. Although the standard deviations for most months overlap, the count data show the lowest counts occurred in late May (at the start of the molting season) and the highest counts occurred in September (during the peak of the adult male molt). Late May, early June, and early August showed the least variance in counts and thus may be the best time to conduct year-to-year comparative counts on Laysan.

Figures 6 through 9 present seasonal haul-out patterns for the different age/sex classes, based on the combined counts of 1979 and 1980. Counts have been corrected for the female-with-pup bias, and unsexed animals have been included based on the sex ratio of seals that were sexed in each age class. Counts of adult males were lowest during June and July, and highest in September (Fig. 6). Adult female counts remained relatively stable throughout the study until a decline in August and September (Fig. 7). Counts of immature males peaked in August (Fig. 8), and immature female counts peaked in June (Fig. 9).

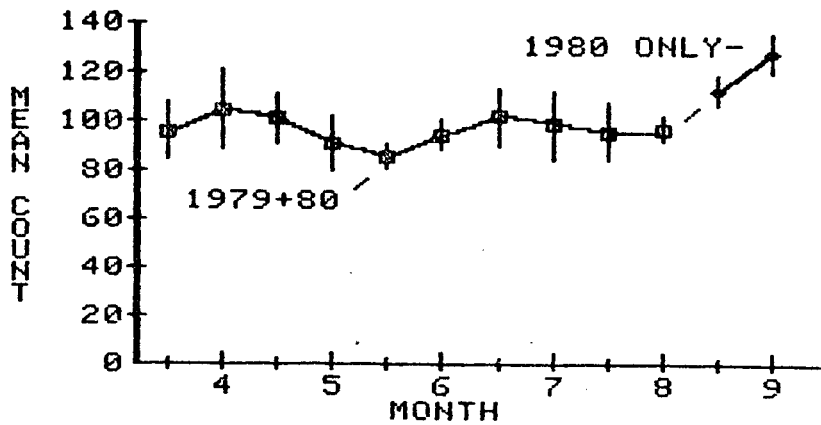


Figure 5.--Semimonthly counts (mean and standard deviation) for 1979 and 1980 combined.

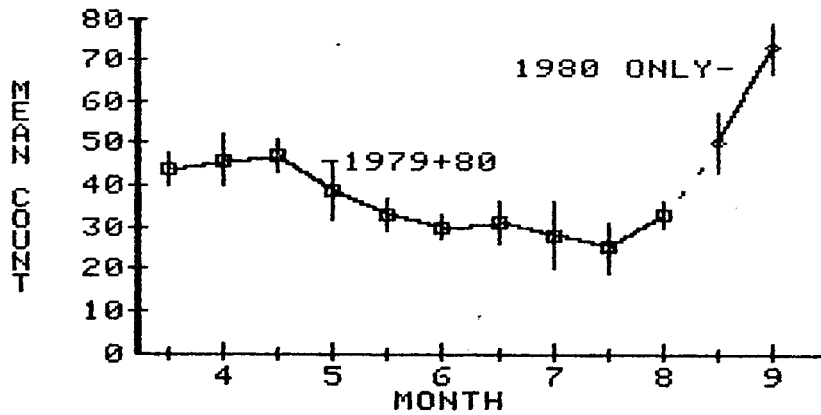


Figure 6.--Adult male counts (mean and standard deviation) for 1979 and 1980 combined.

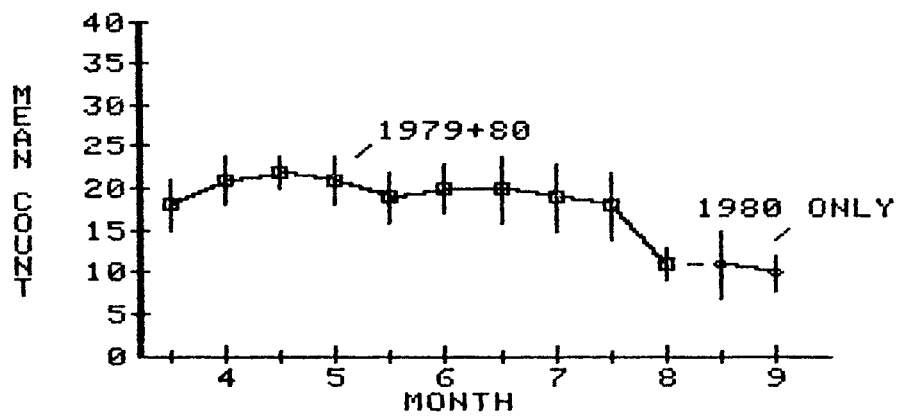


Figure 7.--Adult female counts (mean and standard deviation) for 1979 and 1980 combined.

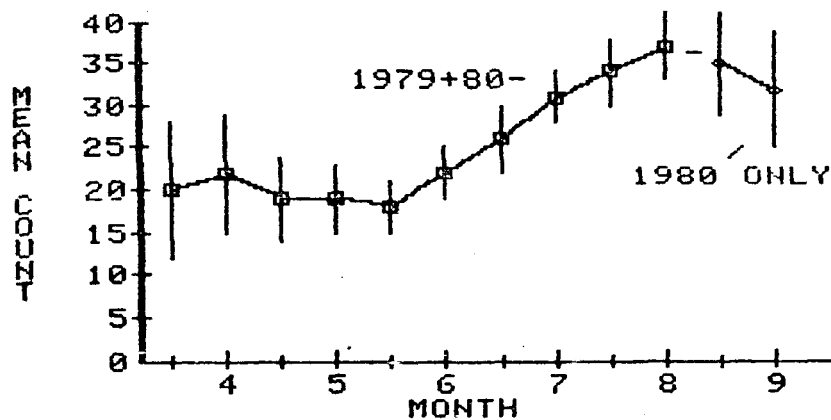


Figure 8.--Immature male counts (mean and standard deviation) for 1979 and 1980 combined.

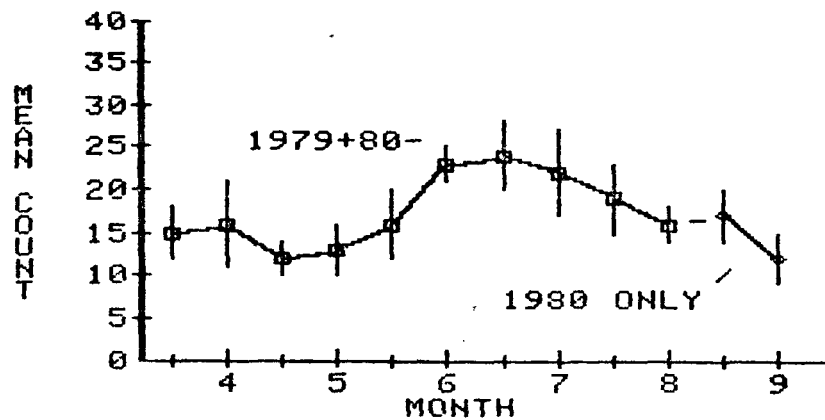


Figure 9.--Immature female counts (mean and standard deviation) 1979 and 1980 combined.

Population Estimation

In 1979 several methods for estimating the size of the monk seal population on Laysan Island were devised and tested, all using nondisturbance techniques exclusively. The methodology used and the 1979 results have been reported elsewhere (Johnson and Johnson 1981a). One of the techniques (the 8-day Molt Estimate) was tested at French Frigate Shoals during 1980 (Johnson and Johnson 1984). These sources should be consulted for detailed discussion of assumptions, methods, inherent biases, and results. The following summary reviews each technique as it applies to data collected on Laysan during 1980.

Molt Summation

Since all Hawaiian monk seals undergo a conspicuous annual molt, during which they remain on or near shore, counting each molting seal would result in a total population count for that atoll, discrete from all other atoll

populations (Johnson and Johnson 1981a). In 1979 and 1980, frequent censusing during the molting season allowed us to identify and count each individual seal that molted during each study period. Most molting seals had been previously identified on the basis of natural or applied marks. Because of the extended molting season, relatively few seals molted at any one time, thus animals without identifiable marks could still be differentiated on the basis of age/sex category, stage of molt, and location on the island. Occasionally molting seals were marked with bleach to facilitate identification. In 1979 the study period ended well before the end of the molting season, thus a complete count of molting seals was not possible. In 1980, the field season extended throughout most of the molting season for all age/sex classes except adult males, allowing a total population count of the other age/sex classes. Summing the animals in all age classes, the Molt Summation data suggest a total of 158 seals, excluding adult males, used Laysan during the summer and fall of 1980. The number of molting seals in each age/sex class was as follows.

Pups.--Of the 33 pups born on Laysan during 1980, 28 survived through weaning (and their postnatal molt) including 9 males and 19 females.

Yearlings.--Twenty-four yearlings (seals born on Laysan in 1979) molted on Laysan during the 1980 field season (14 males and 10 females). One yearling female was seen regularly throughout the field season but had not molted by our departure, resulting in a total yearling count of 25. Two other yearlings (one male and one female) were seen on Laysan early in the field season but not after the start of the molting season, and are therefore excluded from the yearling total.

Juveniles.--A total of 8 juvenile males and 11 juvenile females molted during the study period. This includes all the identified juveniles seen in 1980 except one male which died on 23 April and another male which was not resighted after 26 July.

Subadults.--A total of 30 subadult males and 18 subadult females molted during the field season. This included all identified subadults seen in 1980 except one male, last seen on 22 April, and one female, last seen on 3 April.

Adult females.--Thirty-five adult females molted during the study period. Three additional females which pupped late in the pupping season had not molted by mid-September, resulting in a total adult female count for the summer and fall in 1980 of 38. An additional 11 adult females identified during 1980 were not seen molting, thus were excluded from the molt total. (The unusually large number of adult females disappearing during 1980 is a matter of concern, needing further study and careful monitoring.)

The Molt Summation count is an ideal method for determining population size as it provides an actual count of the total number of animals in each age/sex class and defines a population discrete from all other populations (eliminating the problem of interatoll movement). The major drawback to the technique is the requirement for frequent censusing over many months. (Although the 1980 field season lasted over six months, it was not long enough to encompass the entire adult male or yearling molting season.) Therefore, future studies may have to rely on other population estimation techniques.

The sighting data from Laysan indicate seals that molt on the island are probably year-round residents. However, other populations could be less stable, with the molting population not the same as the population using the area at other times of the year. To test this, population estimating techniques using data gathered in spring or winter months can be compared to the Molt Summation results.

Petersen Estimate

The Petersen Estimate (also known as the Lincoln Index) is a simple method for estimating N , the number of animals in a closed population. As described by Seber (1973), a sample of marked animals (n_1) is released into a population. After sufficient time has elapsed to allow for random mixing of marked and unmarked animals, a second sample of animals (n_2) is taken, a subset (m_2) of which were previously marked. Assuming that the proportion of marked animals in the second sample is a reasonable estimate of the proportion of marked to unmarked animals in N , we can equate the two and obtain an estimate of N . Thus:

$$\frac{m_2}{n_2} = \frac{n_1}{N} \quad \text{or} \quad \hat{N} = \frac{n_1 n_2}{m_2}$$

Specifics of the methodology used in 1979 and a discussion of assumptions can be found in Johnson and Johnson (1981a). The major methodological difference between 1979 and 1980 was an attempt in 1980 to increase the reliability of the estimate by increasing the number of marked animals in each age/sex class, and by increasing the number of recapture censuses. The following reviews the methodology as it applies to the 1980 data.

Marked animals.--Prior to the start of the Petersen Estimate censuses, a list was compiled of all seals with identifiable scars or marks that were seen on Laysan during the previous 2 months (15 March to 15 May). The seals were listed by age/sex class and ranked according to the conspicuousness of their markings. (Yearlings and pups were excluded from the lists as the actual number of animals in both age classes was known.) Excluded from the list were two animals which died before 15 May and three seals which were intermediate in size, sometimes being classed as subadult, sometimes as adult.

The seals chosen as the marked sample included the 40 adult males and 25 adult females with the most conspicuous markings, and all 23 immature males and 19 immature females on the list.

Census procedure.--The procedure was designed to ensure that any marked animals onshore would always be recognized. The perimeter of the island was divided into three roughly equal sections. Each section was censused nine times between 17 May and 5 June. The date and time of each census are listed in Table 1.

Each census involved two observers walking one of the three sections of the island perimeter together. An observer stopped at each seal, positioning him/herself so as not to be observed by any seals, and waited until the seal

Table 1.--Date and time of Petersen Estimate censuses on Laysan Island, 1980.

Time*	North	Southeast	Southwest
0730-1115	5-17	5-20	5-22
	5-26	5-28	5-30
	6-01	6-03	6-05
1130-1515	5-22	5-17	5-20
	5-30	5-26	5-28
	6-05	6-01	6-03
1530-1915	5-20	5-22	5-17
	5-28	5-30	5-26
	6-03	6-05	6-01

*Hawaii Standard Time.

had moved sufficiently to allow a good view of all sides. Scars or marks on the animal were compared with photographs and sketches of identified seals carried by the observer. Animals in the water were not included in the count. All animals which entered the water during the observation period, including identified seals, were excluded, unless the observer had clearly seen all sides of the animal. To increase the reliability of age classification, one of the observers (PAJ) was responsible for recording age/sex data on all seals.

Results.--The formulas used to estimate population size and variance (Seber 1973, p. 61) are:

$$\hat{N} = n_1(n_2+1)/(m_2+1)$$

$$V = \frac{n_1^2(n_2+1)(n_2-m_2)}{(m_2+1)^2(m_2+2)}$$

The results of the Petersen Estimate (N), standard deviation (SD), and upper (NU) and lower (NL) 95% confidence limits (from Pearson and Hartley 1966, p. 228) for each age/sex class are shown in Table 2. An estimate of the total population (excluding pups) and confidence limits were obtained by summing the separate age/sex class values.

Petersen/Molt Estimate

The presence of animals marked prior to the molting season provided another opportunity for estimating the 1980 Laysan monk seal population. Since the actual number of seals which molted before our departure from

Table 2.--Petersen Estimate for each age and sex class at Laysan Island, 1980.

	Adult male	Adult female	Immature male	Immature female	Yearling male*	Yearling female*	Total
n1	40	25	23	19			
n2	246	154	136	125			
m2	74	86	83	85			
\hat{N}	132	45	38	28	14	12	269
SD	12.6	3.1	2.5	1.6			
NL	110	39	33	25	14	12	233
NU	160	53	44	32	14	12	315

*The size of the yearling population was known, thus $N = NU = NL$.

Laysan was known, and the proportion of a "marked" sample of seals which had molted was also known, then the total resident population (all seals molting on Laysan) can be estimated by:

$$\frac{m2}{n1} = \frac{n2}{N} \quad \text{or} \quad \hat{N} = \frac{n1n2}{m2}$$

where:

- n1 = total number of marked animals
- n2 = total number of seals known to have molted
- m2 = marked animals known to have molted
- \hat{N} = estimated resident population.

This is the same formula for calculation of the Petersen Estimate, discussed in the previous section.

Methodology.--For calculation of the Petersen/Molt Estimate, the n1 sample of marked animals was comprised of all uniquely scarred or marked seals seen by both observers during May. (Because adult males molted later than the other age/sex classes, and because some adult males stayed away from the island for over a month at a time, the marked sample of adult males was taken from all adult males seen during May and June.) Of the total number of animals which had started the molt by 16 September (n2), all were examined for scars or marks, and the number of molted marked animals determined (m2). Sampling was considered without replacement, as each molting seal (whether marked or not) could only be counted once in the n2 sample. The formula for an unbiased estimate of N (from Seber 1973, p. 60) is:

$$N^* = \frac{(n1+1)(n2+1)}{(m2+1)} - 1$$

with a variance of:

$$V^* = \frac{(n1+1)(n2+1)(n1-m2)(n2-m2)}{(m2+1)(m2+2)}$$

Results.--The results of the Petersen/Molt Estimate, with standard deviation (SD), upper (NU), and lower (NL) confidence limits, are listed in Table 3.

Table 3.--Petersen/Molt estimate for each age/sex class at Laysan Island, 1980.

	ADM	ADF	IMM	IMF	YM*	YF*	TOTAL
n1	51	31	30	20			
n2	78	37	36	27			
m2	30	27	30	20			
N	132	42	36	27	14	12	263
SD	11.6	1.5	0	0			
NL	100	37	36	27	14	12	226
NU	182	55	45	34	14	12	342

*The size of the yearling population was known, thus N = NU = NL.

Summary of Estimates

Table 4 compares the results of the 1980 Petersen and Petersen/Molt estimates with the 1980 Molt Summation count, and also presents the best population estimate from 1979 (from Johnson and Johnson 1981a).

The best estimate (the one with the narrowest confidence limits) for the 1980 Laysan monk seal population is the Petersen Estimate. The reliability of the estimate is strengthened by its close agreement with the Petersen/Molt estimate results and the close agreement of both estimates with the Molt Summation count. Further, the Molt Summation count for immatures was within two animals (for each sex) of both estimates, indicating the resident population (defined as the seals which molted on Laysan) is the same as the number of seals using Laysan during earlier months.

Table 4.--Comparison of results from estimation techniques used in 1980 with the best population estimate from 1979 on Laysan Island. Numbers for each age/sex class include the estimate with the lower and upper confidence limits, when available. The yearling totals are not estimates, as the actual size of that age class was known.

	ADM	ADF	IMM	IMF	YM	YF	TOTAL	IMM+YM	IMF+YF
Petersen Estimate	132 110-160	45 39-53	38 33-44	28 25-32	(14)	(12)	269 233-315	52 47-58	40 37-44
Petersen/Molt	132 100-182	42 37-55	36 36-45	27 27-34	(14)	(12)	263 226-342	50 50-59	39 39-46
Molt Summation	---	38	38	29	(14)	(11)		52	40
1979 Estimate	148 103-241	44 38-58	46 34-72	35 25-58	(8)	(9)	290 217-446	54 42-80	44 34-67

When compared with the 1979 estimates, the adult numbers fall well within the confidence limits of both years, indicating no significant change in the adult population. But within 1980, the lower confidence limit for the Petersen Estimate of adult females (early spring) was higher than the Molt Summation count (summer), indicating a serious decline occurred in the number of adult females using Laysan in 1980.

Although the immature male and female confidence limits for both years overlap, the 1979 immature estimates for both sexes are greater than the upper confidence limits for 1980. But when the yearling count is added to the immature estimate for both years, there is no significant difference between years.

Like the earlier 1979 data, the 1980 data indicate adult males outnumber adult females by approximately 3:1, while the immature sex ratio is almost equal. (Although immature males appear to outnumber immature females, sighting records of tagged animals indicate that most 7-year-old females are called adults, while most 7- and 8-year-old males are still classed as immatures. Further, even if an equal sex ratio were expected, a Chi-square analysis indicates that no significant difference exists between the observed frequencies ($X^2 = 1.2$, $df = 1$, n.s.).)

Percentage Ashore

The Petersen Estimate indicates the total 1980 Laysan seal population, excluding pups, was 269 seals. The mean count (excluding pups) for all censuses was 100 seals. Thus, on the average, just slightly more than one-third of the Laysan population was counted on censuses. The maximum count during 1980 was 137, or approximately one-half the actual population.

Figure 10 presents the semimonthly percent of the total population which was ashore during afternoon censuses. Figures 11 through 14 present the semimonthly percent ashore for each age/sex class. The total population estimates were taken from the 1980 Petersen Estimate except for adult females which were estimated at 42, the mean of the Petersen Estimate and

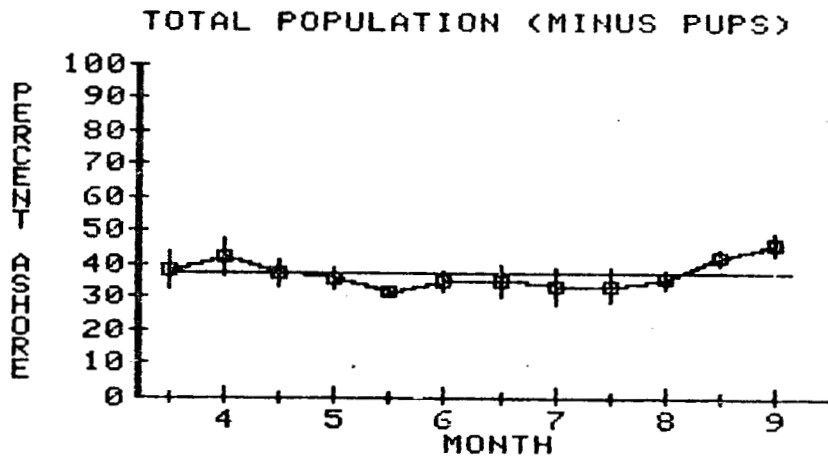


Figure 10.--Percent of total population ashore on counts, 1980 (mean and standard deviation).

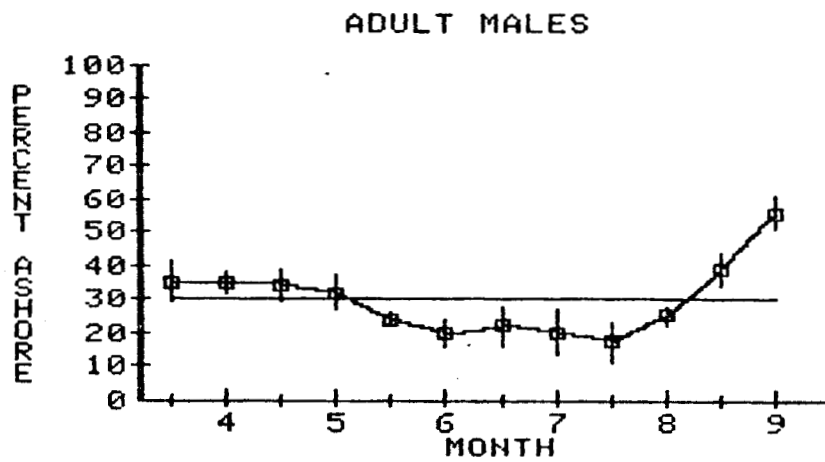


Figure 11.--The percent of adult males ashore on counts, 1980 (mean and standard deviation).

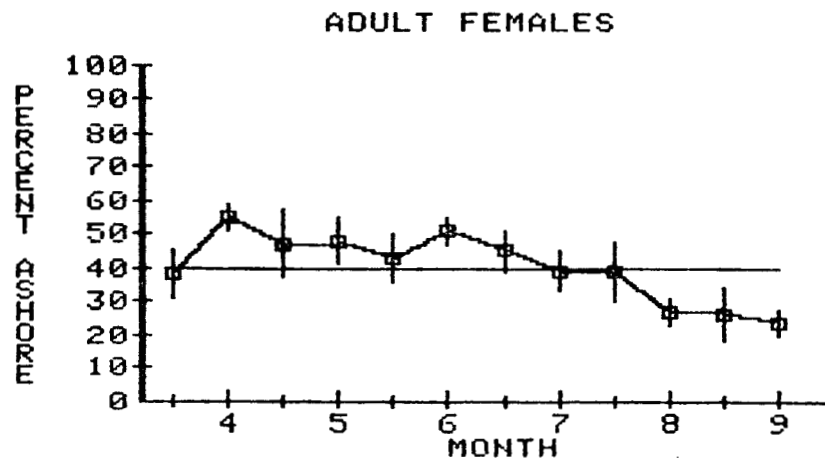


Figure 12.--Percent of adult females ashore on counts, 1980 (mean and standard deviation).

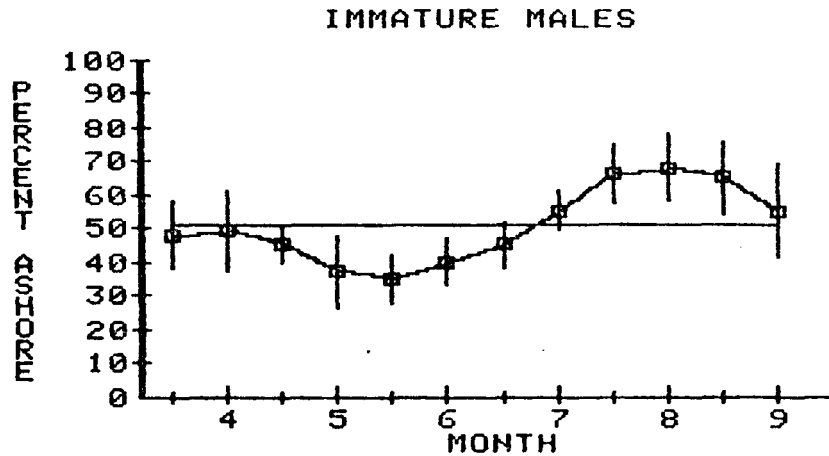


Figure 13.--Percent of immature males ashore on counts, 1980 (mean and standard deviation).

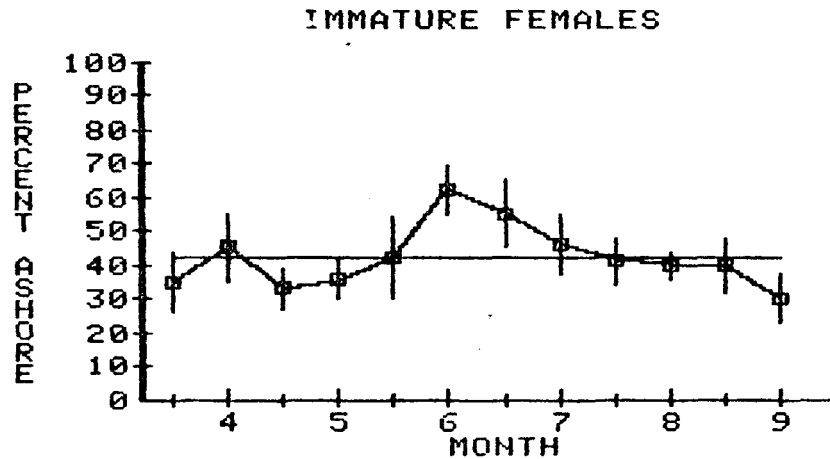


Figure 14.--Percent of immature females ashore on counts, 1980 (mean and standard deviation).

the later Molt Summation (this was done to compensate for the large number of adult females disappearing during 1980). The mean semimonthly counts (with standard deviations) were taken from censuses started between 1200 and 1600 (Hawaii standard time). An average of 8% of the seals were unsexed on these censuses. For the purposes of this summary, the sex of unsexed animals was estimated, by first correcting for the female-with-pup bias, and then by assuming that the proportion of males to females in the sexed animals was the same in the unsexed animals (with adults and immatures calculated separately, see Appendix C).

For the period covered by the 1980 field season, adult males spent proportionately the least time ashore (30%), while immature males spent the most time ashore (51%). Adult females spent about 42% of their time ashore, while about 40% of the immature females were ashore on counts. If data from the entire year were available this pattern might change, as seasonal variation in percent ashore was seen in each age/sex class.

Distribution

Seals did not use all haul-out areas around Laysan Island equally. The choice of haul-out area varied with age, sex, and time of year.

The beaches around Laysan differed in several ways, including: amount of vegetation; exposure to trade winds; nearshore substrate (sand or reef) and water depth; onshore substrate (sand or rock), and other less obvious characteristics.

During the 1977 field season the circumference of the island was subdivided into four "ecological" units, roughly equal in size. The divisions were based primarily on availability of vegetation and the type of nearshore substrate. The areas and descriptive characteristics were:

- NORTH - wide beaches, exposed to trade winds, with little or no vegetation at the beach crest.
- WEST - narrow beaches, on the leeward side of the island, with numerous shallow reef areas in the nearshore waters, and vegetation at the beach crest.
- EAST - wide beaches, with a shallow rock ledge extending the length of the nearshore area and no vegetation near the beach crest.
- SOUTH - sand beaches interspersed with rock ledges, rough surf, and some cover at the beach crest.

Figure 15 shows the proportion of seals which used each area from March through August 1977, based on census counts. Figure 16 presents comparable data from 1980. The use of the south shore was similar in both years. Use of the east shore increased about 10% in 1980, while both the west and north areas showed a 5% decrease in use. The significance of this shift, if any, is unknown.

Detailed data on the haul-out patterns for each age/sex class are available only for 1980. With a high proportion of seals sexed on censuses and the island circumference divided into 14 areas, it was possible to identify haul-out patterns unique to different segments of the population. Figure 17 presents a map of Laysan (from an FWS aerial photograph taken in May of 1980) showing the area breakdowns. Table 5 presents the percentage of seals in each age/sex class utilizing each of the 14 areas. These data indicate that all age/sex classes, except pups, preferred the northeast beaches (areas 5 and 6) but the second most utilized haul-out area varied for each age/sex class.

Over 30% of the adult males hauled out along the southwest corner of the island (areas 11, 12, and 13). This same part of the island was used by less than 4% of the adult females and about 10% of the immature seals. A substantial number of adult males also used area 14, which was a preferred haul-out area for mothers attending pups. However, males used this area mostly during August and September (during the adult male molt), well after the pupping season.

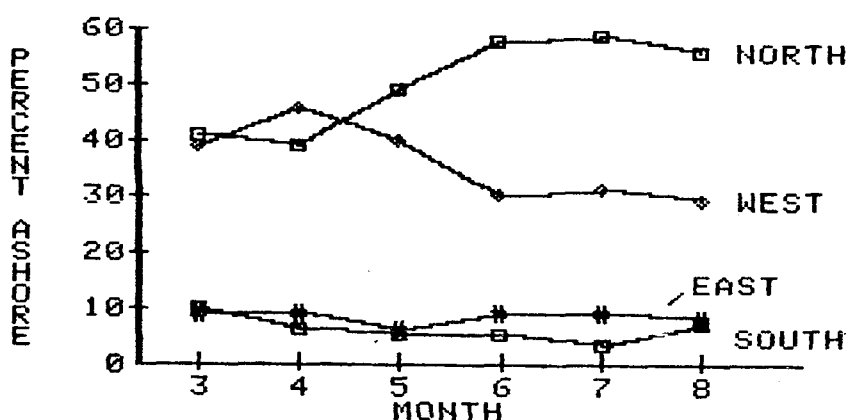


Figure 15.--Mean percent ashore in each of four areas on Laysan Island, 1977.

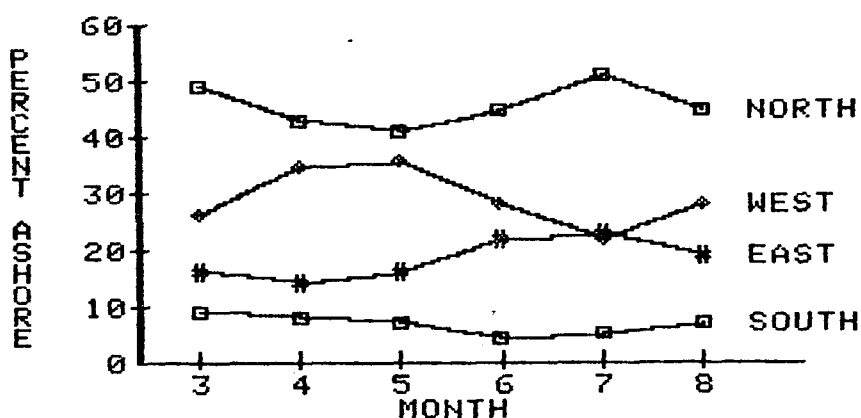


Figure 16.--Mean percent ashore in each of four areas on Laysan Island, 1980.

In addition to areas 5 and 6, adult females were found primarily in areas 2, 3, 4, and 14. If all sightings of females attending pups are excluded, the percentage of females using areas 2 and 14 (the major pupping areas) decreased while the percentage of adult females using areas 5 and 6 increased. It appears that the selection of rookery areas is not based on the same factors affecting choice of haul-out area at other times of the year.

Immature males used areas 5 and 6 primarily, with the next highest numbers found in areas 4, 9, and 10. The immature males were the only age/sex class to haul out in substantial numbers on exposed rocks, 10 to 40 m away from the beach along the shallow rock ledge area of the east shore (areas 9 and 10). Seven percent of the subadult male sightings, 4% of the juvenile male sightings, and 10% of the yearling male sightings were of animals on offshore rocks. Overall, 7% of immature male sightings were of animals

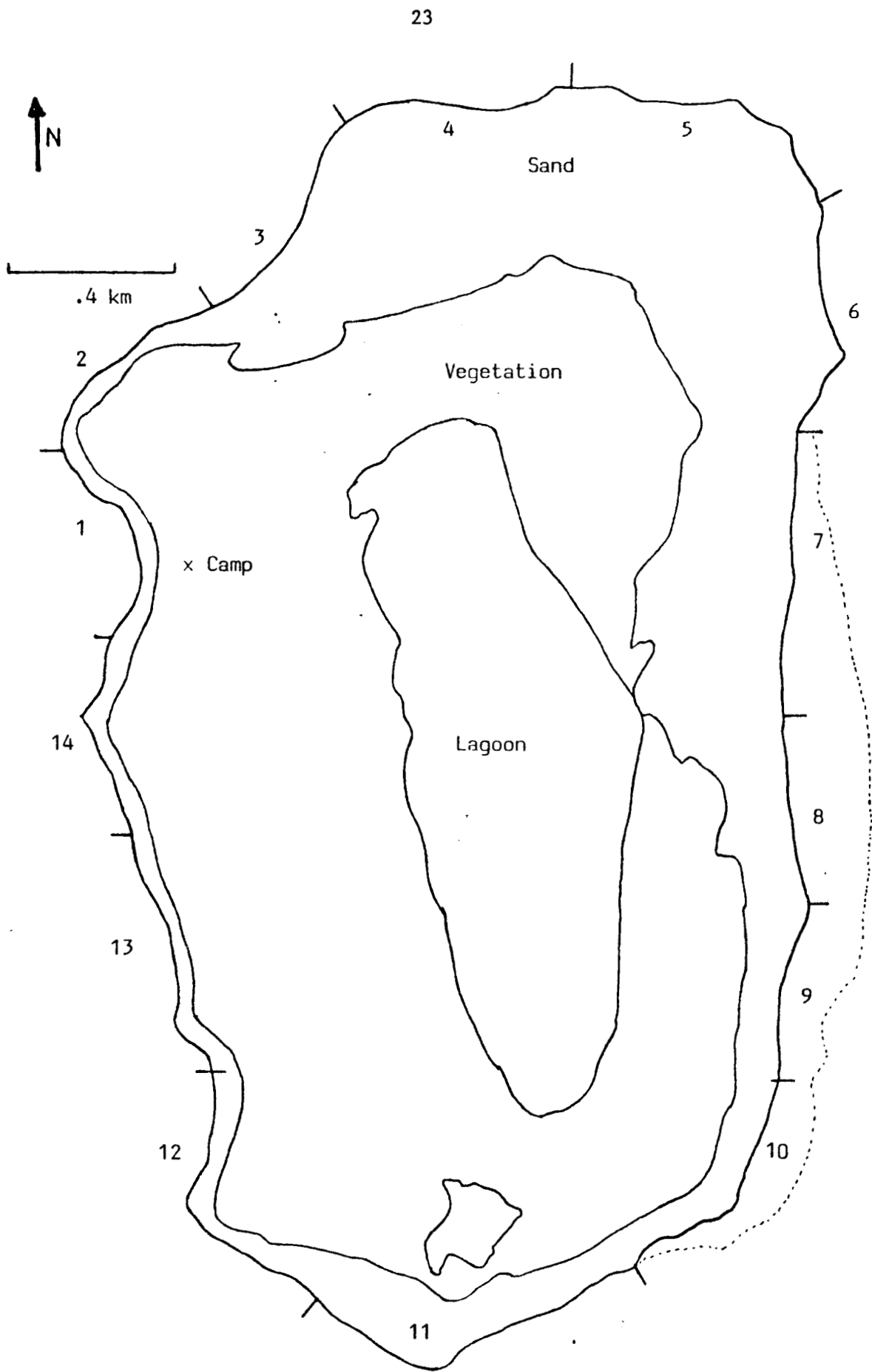


Figure 17.--Map of Laysan Island taken from aerial photograph (FWS 1980) showing circumference divided into 14 areas.

Table 5.--Percentage of each age/sex class and the total number of seals using the various areas on Laysan Island; based on mean monthly census counts in 1980.

AREA	ADM	ADF	ADF*	IMM	IMF	NURS PUP	WEAN PUP	ALL SEALS
1	5	4	3	4	5	5	6	5
2	4	13	8	3	5	23	12	6
3	5	11	10	3	4	13	10	6
4	4	10	12	11	8	7	15	9
5	11	13	18	18	27	3	9	15
6	15	21	29	17	24	6	8	16
7	2	6	4	6	6	11	3	5
8	1	2	2	3	2	2	2	2
9	2	2	2	10	3	1	4	5
10	6	3	3	12	6	5	6	7
11	14	1	1	4	4	0	1	7
12	10	1	2	2	3	0	1	4
13	10	2	1	5	2	2	15	7
14	11	12	7	3	3	24	9	8

*Mean percentage of adult females when mothers with pups are excluded.

hauled out on offshore rocks or sleeping in the water beside the rocks. Age/sex structure data based on counts which include animals using the offshore rocks should therefore not be compared with data which exclude these animals.

Over 50% of the immature females hauled out in areas 5 and 6. Area 4 was the only other area used by more than 6% of the immature females. (Only 1% of immature female sightings were of animals resting on or near exposed offshore rocks.)

Areas 2 and 14 were the areas most often selected by females attending pups, but a substantial number of mothers with nursing pups were also found in areas 3 and 7. After weaning, pups continued to use the same areas (with the exception of area 7) and also began to congregate in areas 4 and 13. These latter areas had protected pools of water near shore which attracted many newly weaned pups. Pups, both suckling and weaned, were the only age/sex class not found in substantial numbers in areas 5 and 6.

Other than the seasonal changes just mentioned, the haul-out patterns for the different age/sex classes were generally consistent throughout the field season.

Molt

Seasonal Patterns

The molting season began in April when the first adult and subadult females started to molt and continued at least into December when a few

molting adult males and yearlings were seen (no visits were made to Laysan in January or early February). It is possible that seals molted in all months of the year as the molt was delayed in some animals with injuries or apparent illnesses, and adult females having pups late in the year would molt 2 to 3 months after weaning their pups (the normal delay for parturient females).

The molt for individual seals (the period of visible hair loss) averaged 9 days. The molting season for the various segments of the population differed, with little overlap between some age/sex groups. Molt dates for every seal molting on Laysan are available for the April through early August period of 1979, and the April through early September period of 1980.

The following 10 figures present data on the number of molting seals seen through mid-September. Each data point represents the number of seals which reached the midpoint of their molt (50% of the old hair shed) during a particular semimonthly period. (Using a midmolt date reduced the chance of missing seals at either the beginning or final stages of the molt.)

Because of the relatively small number of seals which molt during each semimonthly period (particularly when the age/sex classes are separated), considerable variation is likely from year to year. To increase sample size, molt data from 1979 and 1980 have been combined. (Data from 1980 are also presented separately to show the pattern through mid-September as no data are available after mid-August of 1979.)

Figure 18 presents the semimonthly sightings of molting seals on Laysan. Few seals of any age/sex class molted in April or May. The number of molting seals increased rapidly during June, showed a slight decline in July, and then increased again in August. The August rise was due primarily to adult males. Figure 19 shows that excluding adult males changes the upward trend.

The timing of molt for adult females was somewhat dependent on their reproductive status. The overall pattern for adult females is shown in Figure 20. Nonparturient females began to molt in April, with the majority molting in late June (Fig. 21). Parturient females did not molt until after their pups were weaned, with the majority molting in late July and early August (Fig. 22).

Subadult females showed a molting season similar to that of the nonparturient females, with the greatest frequency of molters seen in June (Fig. 23). Subadult males molted later than subadult females, with the onset of molt in June and the peak occurring in July and early August (Fig. 24).

Juvenile seals and yearlings showed less sex difference in molting season than other age classes. Juveniles of both sexes began molting in early June, with the greatest number of molting juveniles seen in late June (Fig. 25 and 26). The sample size of molting yearlings was too small to separate males from females. Adding the molt data for both sexes shows a later molt than the older animals already described, with the highest number of molting yearlings not seen until August (Fig. 27). The only age class still molting in large numbers when the yearlings molted were the adult males.

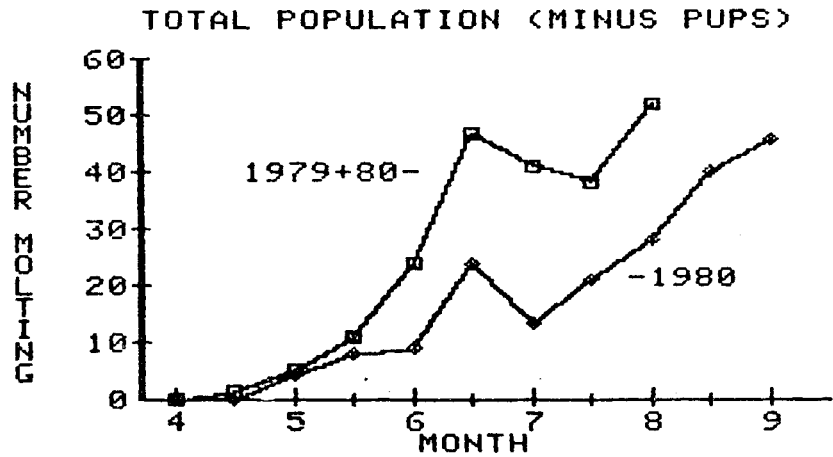


Figure 18.--The number of seals which molted (based on midmolt dates) during each semimonthly period.

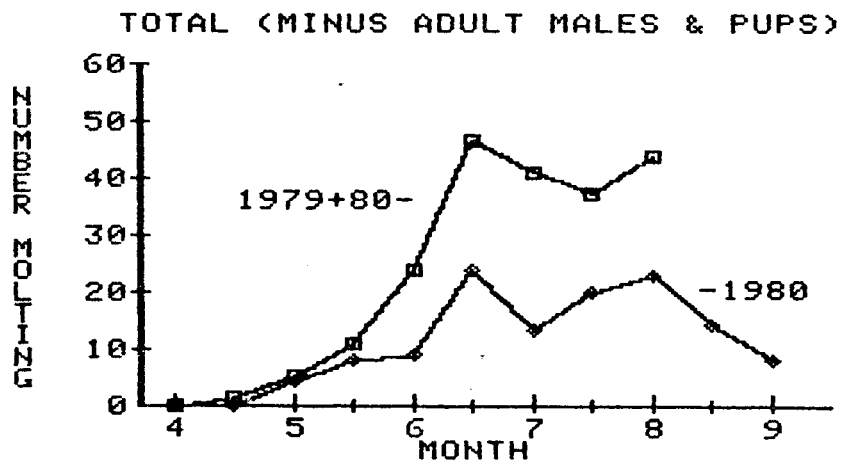


Figure 19.--The number of seals which molted (based on midmolt dates) during each semimonthly period.

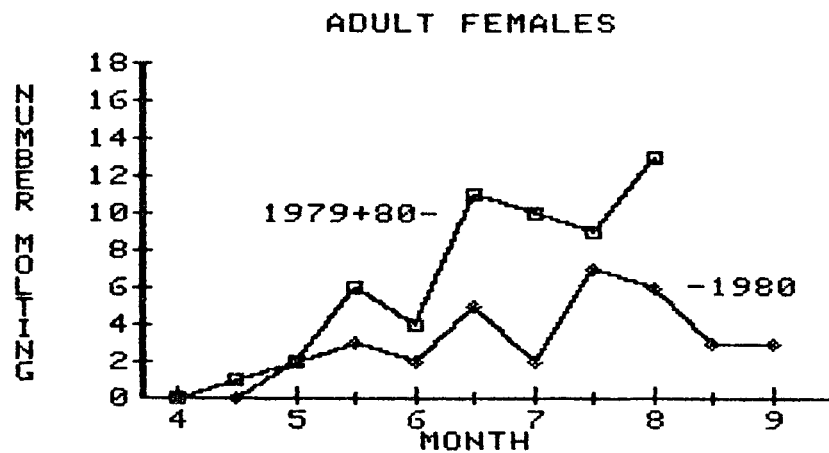


Figure 20.--The number of seals which molted (based on midmolt dates) during each semimonthly period.

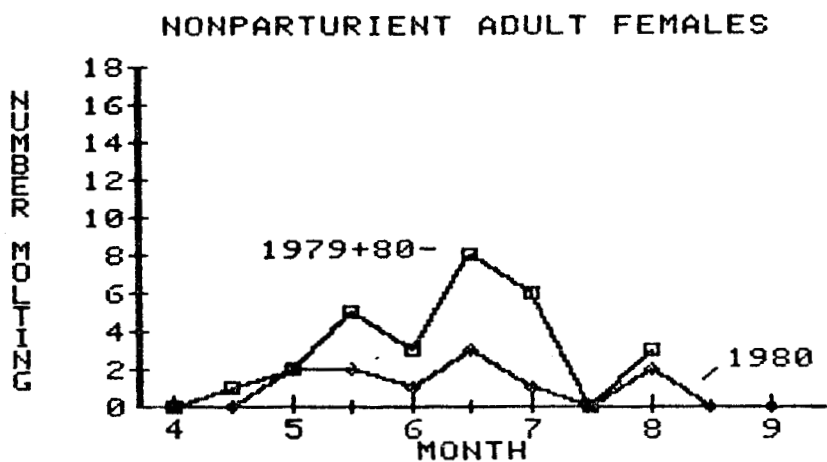


Figure 21.--The number of seals which molted (based on midmolt dates) during each semimonthly period.

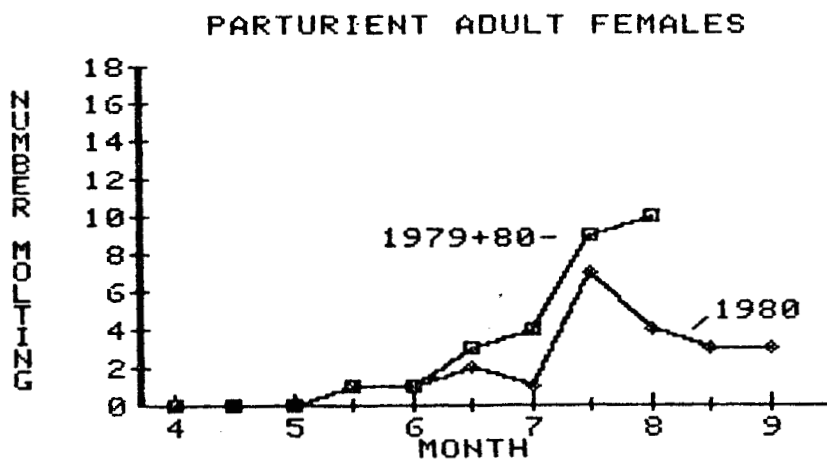


Figure 22.--The number of seals which molted (based on midmolt dates) during each semimonthly period.

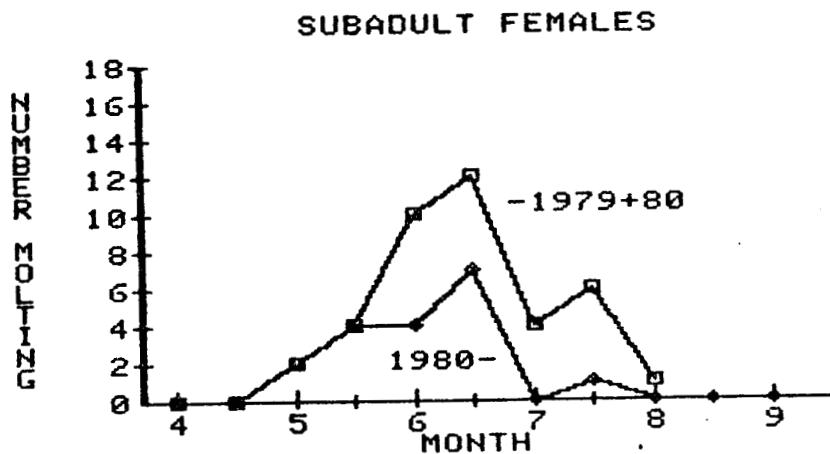


Figure 23.--The number of seals which molted (based on midmolt dates) during each semimonthly period.

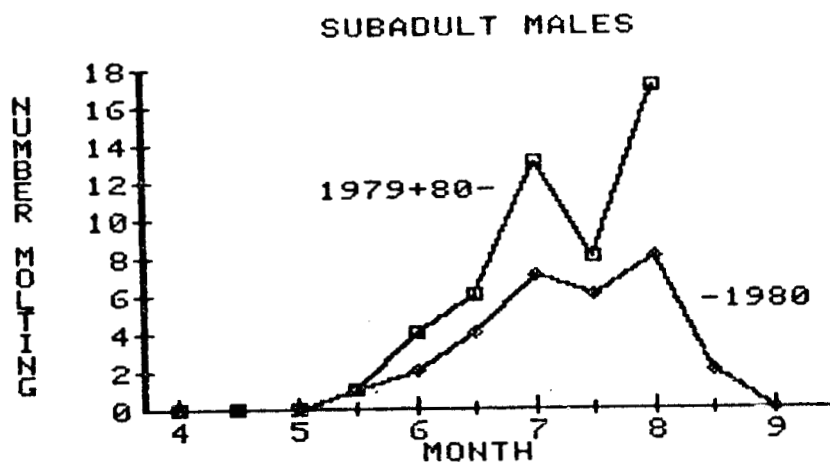


Figure 24.--The number of seals which molted (based on midmolt dates) during each semimonthly period.

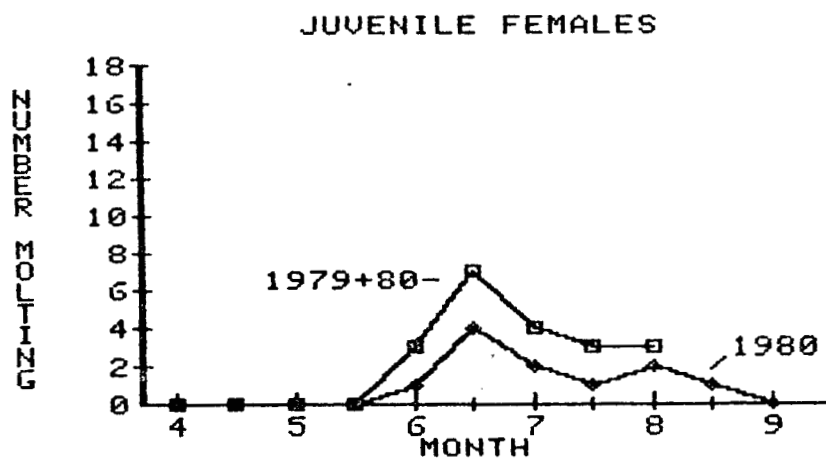


Figure 25.--The number of seals which molted (based on midmolt dates) during each semimonthly period.

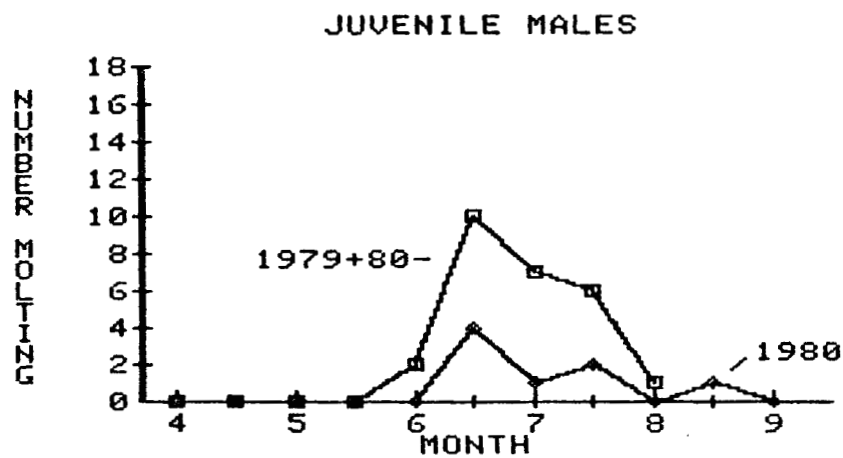


Figure 26.--The number of seals which molted (based on midmolt dates) during each semimonthly period.

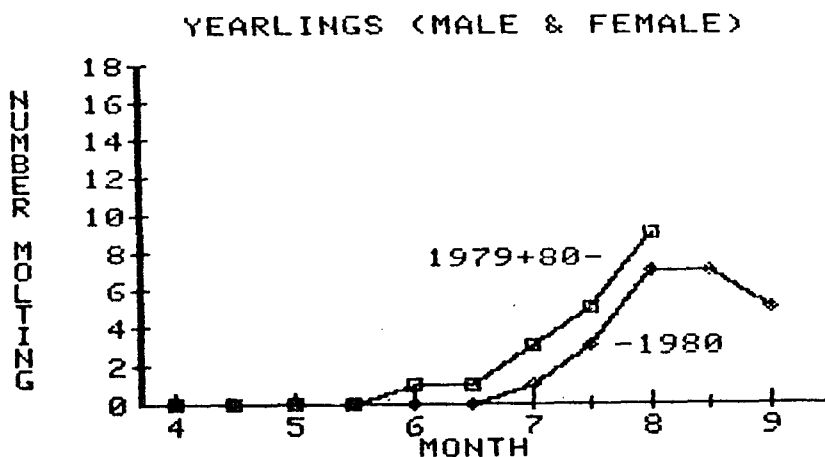


Figure 27.--The number of seals which molted (based on midmolt dates) during each semimonthly period.

The 1979 and 1980 field seasons did not continue through the adult male molting season, so data from 1978 are presented in Figure 28. Unlike the data presented for the other age/sex classes, these numbers are based on the mean number of molting seals seen on the censuses (a complete listing of all molting seals was not collected in 1978). Adult males did not begin to molt until August, with the number of molting seals reaching a peak in late September. (The early October "mean" is based on a single count made on October 13.) Unlike the similarity in molting patterns seen between subadult and adult females, there was little overlap in molting season for adult and subadult males. This difference (reflected in the coat color) can potentially be useful in distinguishing between reproductive and nonreproductive males.

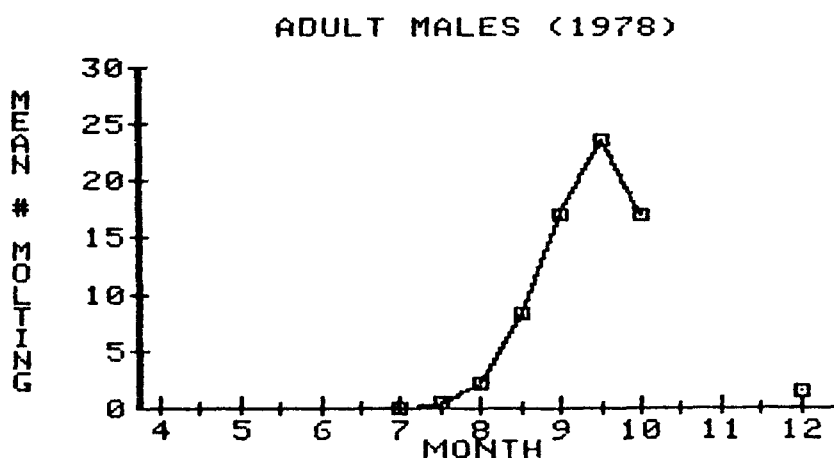


Figure 28.--Mean number of molting adult males seen on censuses, 1978. (October data based on one count.)

Island Usage

Table 6 presents data on the percentage of each age/sex class which molted in the various areas around Laysan (based on 1980 counts).

Table 6.--Comparison between the percentage of each age/sex class molting in the various areas of Laysan with the distribution throughout the year, 1980.

Areas	Adult-Males		Adult-Females		Immature-Males		Immature-Females	
	Molt	Total	Molt	Total	Molt	Total	Molt	Total
1+2	8	9	8	16	4	7	11	10
3+4	0	9	20	21	10	13	10	12
5+6	14	26	43	34	42	35	43	52
7+8	2	3	7	8	15	9	12	7
9+10	7	8	9	5	7	22	14	9
11+12	26	24	0	2	7	6	3	6
13+14	42	21	14	14	15	8	8	5

Over 40% of all sightings of molting adult females, immature males, and immature females occurred in areas 5 and 6. Areas 5 and 6 were also the areas most frequently used by these age/sex classes for haul out in 1980. Overall, with the exception of a substantial reduction in the usage of areas 9 and 10 by molting immature males, the distribution of molting adult females and immatures of both sexes was similar to their distribution throughout the year.

This was not true for adult males. The greatest number of adult males molted in areas 13 and 14 (42%), twice the percentage of adult males normally hauled out in those areas. The increased use of areas 13 and 14 corresponded to a reduction in use of areas 3 through 6, the areas used by the greatest number of molting seals from the other age/sex classes.

Reproduction

Sexual Maturity: Females

No pups born during the study had reached reproductive size by 1980. Only two females from the 1977 pup cohort were still alive and recognizable in 1980 (as 3-year-old seals); one was consistently classified as a juvenile and the other was generally classed as a subadult.

Tag numbers of 10 females marked prior to 1972 were read in 1977. Data from one of these females have been excluded as the animal was not resighted after the first day of the study. (Tag numbers are listed in Appendix D.) The ages of the remaining animals ranged from 5 to 11 years old in 1977. As Table 7 shows, neither of the two females seen when 5 or 6 years old produced pups, while one of the two 7-year-old seals did have a pup. All tagged females 7 or older were consistently classified as adult size when observed, whereas the females seen when 5 or 6 years old

Table 7.--Number of births to known-age females between 1977 and 1980 on Laysan Island.

	Age of Female									
	5	6	7	8	9	10	11	12	13	14
With Pups	0	0	1	1	1	3	3	3	0	1
Without Pups	2	1	1	1	3	3	2	0	1	0
Total Sample	2	1	2	2	4	6	5	3	1	1

were recorded as subadult size. Additionally, of the six small juvenile females (probably 1- or 2-year-old seals) identified in 1977 and seen through 1980, none had produced pups by 1980.

From these limited data it appears age at first reproduction for female Hawaiian monk seals (as measured by the birth of the first pup) may not occur until age seven or later. (Materials from subadult and adult females which died on Laysan during the study, including a known-age 4-year-old female were given to NMFS for analysis. Additional information on sexual maturity will become available when analysis of reproductive tracts and tooth sections from these animals is completed.)

Sexual Maturity: Males

It was more difficult to measure age at first reproduction for male monk seals as sexual maturity of males did not result in an observable event such as a birth. A subjective age was recorded for the six tagged males seen during the study, based on size and the presence or absence of reproductive behaviors normally shown by adult males (tag numbers are included in Appendix D). As Table 8 shows, males generally did not exhibit typical "courtship" behavior until 8 or 9 years old, although it is possible that physiological maturity occurred earlier. Of the three males still sighted from the 1977 pup cohort in 1980, one was generally listed as a subadult, while the other two were usually classified as juveniles.

Table 8.--Subjective age classification of tagged, known-age males between 1977 and 1980 on Laysan Island.

	Age of Males				
	5	6	7	8	9
Subadult	2	3	3	3	0
Adult	0	0	1	1	3

A potentially useful means of identifying sexual maturity in males is by the timing of their molt. Subadult and adult males showed minimal overlap in molting seasons, as all but 5% of the subadult males had completed their molt by the end of August, when the first adult males were beginning to molt.

Reproductive Rate

Ovulation and pregnancy rates could not be determined from observations of monk seals on Laysan, therefore reproductive success for females was measured by the birth of a pup. In comparisons with other species, care should be taken to compare only similar data.

There are several ways to estimate the reproductive rate of the Laysan population. Four different approaches will be presented.

Tagged-females.--The reproductive status was determined for nine tagged females, ranging in age from 5 to 11 years old in 1977. Of the four females still being seen in 1980, the youngest was 10 years old, the oldest 14. Sighting records presented in Table 7 show the change in frequency of pupping with age. Of the 14 sightings of females aged 7 through 10, 43% had pups (5- and 6-year-old animals were excluded as they were classified as subadult in size). Of the 10 sightings of females 11 through 14, 70% pupped. While this difference indicates an increased fertility with age, the sample size is too small to tell if the trend is significant. The overall reproductive success was 13 pups to 24 adults, or 54%. As the Tagged-female sample is small, and includes only animals up to age 14, it is probably not representative of the total population.

Estimated-females.--Population estimates for adult females during the pupping season provide another means of calculating reproductive rate. Population estimates are only available for 1979 and 1980 (the estimates with the narrowest confidence limits were used for each year). During 1979, 32 pups were born to an estimated adult female population of 44 (Table 4). In 1980, 33 pups were born to an estimated adult female population of 45 animals (Petersen Estimate, Table 4). Using these numbers, the estimated reproductive rate for 1979 was 73%, with a range of 55 to 84% (using the lower and upper confidence limits for the adult female estimate). The estimate was also 73% for 1980, with a range of 60 to 89%. The disadvantages of this approach include: the wide range of the estimate (due to the confidence limits of the adult female estimate); a certain degree of subjectivity inherent in deciding which females to class as adult; and the availability of the estimate for only 2 years.

Identified-females.--Table 9 presents yearly reproductive rates for well-identified females seen, and classed as adult size, in at least 3 years of the study (data taken from Appendix E). The overall reproductive rate for the 4 years was 64%. The data for the individual years indicate an increase in reproductive success occurred during the study. When data from 1977 are combined with 1978 (for a 57% reproductive rate), and data from 1979 with 1980 (for a 72% rate), Chi-square analysis shows a significantly lower pupping rate for the first 2 years of the study than for the last 2 years ($\chi^2 = 4.01$, $p < 0.05$). The Identified-female sample has the advantage of a large sample size and covers the entire 4-year study

period. One disadvantage of this sample is the subjectivity of size classification. A second disadvantage is the increased age over time, as animals had to have known reproductive histories in at least 3 years. This requirement did not allow recruitment after 1978 or mortality before 1980. As a check on the degree of this latter problem, a pupping rate was calculated, based on the number of pups born to well-identified females seen in 1980. This sample includes all females of reproductive size in that year, not just animals of adult size in previous years. The resulting reproductive rate of 75% (30 pups born to 40 adult females) is only slightly lower than the 79% presented in Table 9 for 1980, indicating the increased age of the Identified-female sample was not solely responsible for the increased reproductive rate.

Table 9.--Yearly reproductive rates for females seen and classed as adult in at least 3 years on Laysan Island.

Year	Births	Total Females	Rate
1977	23	39	0.59
1978	24	44	0.55
1979	29	44	0.66
1980	27	34	0.79
Totals	103	161	0.64

Mature-females.--Some variability due to the subjectivity of age classification can be eliminated by including only those females known to be mature by a previous birth. The Mature-female sample included all females pupping in 1977, 1978, or 1979 that were seen in at least one additional year. The data for the first observed birth (year 1) are excluded from the calculations. Table 10 presents the sample size and the percentage pupping in years 2 through 4. Animals first observed pupping in 1977 have up to 3 years data, whereas females first observed pupping in 1979 are included in

Table 10.--Reproductive status of females in years following the first observed birth. Data for each year include number of pups born (No.), number of adult females (N), and percentage pupping (%).

First Birth	Year 2			Year 3			Year 4			Totals		
	No.	N	%	No.	N	%	No.	N	%	No.	N	%
1977	15	27	56	18	23	78	15	19	79	48	69	70
1978	6	12	50	8	9	89	----	----	----	14	21	67
1979	2	3	67	----	----	----	----	----	----	2	3	67
Totals	23	42	55	26	32	81	15	19	79	64	93	69

only 1 year. The reproductive rate increased dramatically from year 2 to years 3 and 4, with an overall reproductive success for years 2 through 4 of 64 births to 93 female sightings, or 69%. (Reproductive patterns for individual seals are listed in Appendix E.)

Previous observation of Hawaiian monk seals had suggested that a large proportion of monk seal females missed pregnancy in the year following a birth (Rice 1960). If true, then the year 2 reproductive rate would be lower, as all females in the sample pupped in year 1. Testing whether the probability of pupping in year 2 is independent of reproductive status in year 1 is possible by comparing the observed frequency of pupping (for females seen in 3 consecutive years) against the expected frequencies of a binomial distribution. As can be seen in Table 11, there is no significant difference; thus reproduction in year 2 can be considered independent of previous reproductive status.

Defining maturity by the actual birth of a pup guarantees that all animals in the sample are capable of reproduction; however, it also raises the age of the animals used to calculate the reproductive rate, and eliminates infertile animals, resulting in a higher reproductive rate than for the population as a whole.

Table 11.--Observed and Expected number of females showing each of four reproductive patterns, including only females known to be mature which were seen in at least 3 years on Laysan Island (P = pup, N = no-pup).

	Observed	Expected
PPP	13	12.7
PPN	2	7.8
PNP	13	7.8
PNN	5	4.5
X ² = 4.7 p = n.s.		

Discussion.--Table 12 summarizes the results from the four reproductive rate estimates. Of the four, the Tagged-female estimate is the least reliable due to small sample size and nonrepresentative age structure. Of the other three estimates, the one most likely to be representative of the pupping rate between 1977 and 1980 is the Identified-female sample. The overall reproductive rate for the sample, 64%, was based on a large sample size covering all 4 years of the study.

Support for the accuracy of the Identified-female estimate is provided by comparisons with the other estimates. Comparison with the Mature-female estimate (69%) shows the Identified-female estimate to be slightly lower. This is reasonable as nulliparous females (young adults and infertile animals) are excluded from the Mature-female sample but are included in the Identified-female sample. Comparing the Identified-female estimate for 1979

Table 12.--Reproductive success estimates for the Hawaiian monk seal population on Laysan Island, 1977 through 1980.

Sample	Range	N	Overall Rate
Tagged-females	7-10 years = 43%	14	54%
	11-14 years = 70%	10	
Estimated-females	1979 = 55 - 84%	44	73%
	1980 = 60 - 89%	45	
Mature-females	Year 2 = 55%	42	69%
	Years 3+4 = 80%	32	
Identified-females	1977 = 59%	39	64%
	1978 = 55%	44	
	1979 = 66%	44	
	1980 = 79%	34	

and 1980 combined (72%) with the estimate from the Estimated-female sample for the same years (73%), shows the two estimates are very close.

Data from the Identified-female sample show a significant increase in reproductive success between the first 2 years of the study and the last 2 years. If increased age were responsible for the increased reproductive rate, the Identified-female sample should overestimate the reproductive success in 1979 and 1980. The close agreement between the Identified-female and the Estimated-female rates for these years, however, indicate the effect of increased age within the sample was negligible.

Further evidence for an increase in pupping rate during the study is provided by the crude birth rate (calculated by dividing the yearly pup production by the mean mid-March through mid-August census counts, excluding pups). These data show a change from 0.27 in both 1977 and 1978 to 0.34 and 0.35 in 1979 and 1980 respectively (Table 13).

Table 13.--Yearly crude birth rate (births/mean count) for 1977 through 1980 on Laysan Island.

Year	No. of Births	Mean count	Birth rate
1977	42	156	0.27
1978	29	106	0.27
1979	32	94	0.34
1980	33	95	0.35

Factors which could have resulted in an increased fertility rate include the following.

1. Illnesses associated with the 1978 die-off could have increased the number of missed pregnancies or abortions during 1977 and 1978 (although only one aborted fetus was found in 1977 and none in 1978).
2. The die-off of 1978 could have resulted in changes in the age distribution of adult females. If the animals affected by the 1978 die-off were primarily the youngest and the oldest animals (the females that would be expected to have the lowest fertility rates), this could have contributed to the increase in reproductive rate seen in 1979 and 1980.
3. The changes in reproductive success could be density dependent, with the higher reproductive rates in 1979 and 1980 a response to the 35% decrease in seal numbers from 1977 levels.

Additional research is needed to identify which factors affect reproductive rates in the monk seal. Taken as a whole, the data from Laysan indicate pupping rates for the species are variable and may have the potential to respond quickly to changes in the environment.

Interval Between Births

Based on observations at Midway from 1957 to 1959, Rice (1960) reported that a high proportion of monk seal females missed pregnancy following a birth. As shown by the Mature-female sample previously described, this was not the case on Laysan. Data from Laysan show a variety of reproductive patterns. One female pupped in all 4 years and was photographed with a pup in 1976 (by DeLong, NMFS, Seattle) for a total of five consecutive births. Another female was known not to have pupped in any of the 4 years of the study, although appearing adult size in a photograph from 1976 (DeLong, NMFS, Seattle), as well as fully adult size throughout our study.

On Laysan, females pupping in consecutive years generally pupped later in the second year. The mean interval between births was 380.7 days (SD = 20.62, N = 60). All identified females pupping in consecutive years were included in this sample. The mean interval between the end of lactation for the female (whether due to pup's death, disappearance, or normal weaning) and birth the following year was 347.3 days (SD = 20.64, N = 60). Six females had full term pups in 4 consecutive years (one additional female pupped in 3 years, but aborted in the fourth). For these six females, the birth dates in 1980 ranged from 38 to 99 days later than in 1977. The mean change in birth date between 1977 and 1980 was 62 days, with each successive birth averaging 15.5 days later. Wirtz (1968) reported a mean interval between births of 382 days for Kure in 1964 and 1965.

Another way to look at the interval between births examines data from females seen during all years of the study. Twenty-nine females were classed as adult in 1977 and seen in all 4 years (data in Appendix E). The largest proportion, 45%, pupped twice during the 4 year period; 24% pupped in all years; 21% pupped in 3 of the 4 years; 7% pupped only once; and one female did not pup in any year.

Pupping

Sex ratio at birth.--Between 1977 and 1980, 136 pups were born on Laysan Island. Seventy-five were females and 58 were males. The sex of three pups was not determined as they disappeared before weaning. There was no significant difference between the observed and the expected sex ratio at birth. Table 14 lists the sex ratio at birth for each year of the study and shows considerable variability between years. Pups born early in the field season tended to be male, while pups born later were more likely to be female ($t = 1.994$, $p < 0.05$).

Table 14.--Sex ratio at birth for all pups born from 1977 through 1980 on Laysan Island.

Year	Male	Female	Unknown	Total
1977	17	23	2	42
1978	12	17	0	29
1979	19	13	0	32
1980	10	22	1	33
Total	58	75	3	136

Timing of births.--Births were known to occur in all months from January through August. If any pups were born during the September to December period, they had disappeared by the time the next field season began. No attended or recently weaned pups were seen during winter visits made in 1978 (BWJ) or 1980 (Knudtson, personal communication).

Figure 29 shows the semimonthly distribution of births. More pups were born in April than in any other month. The yearly patterns are shown in Table 15. The mean pupping date was 17 April, ranging from 13 April in 1977

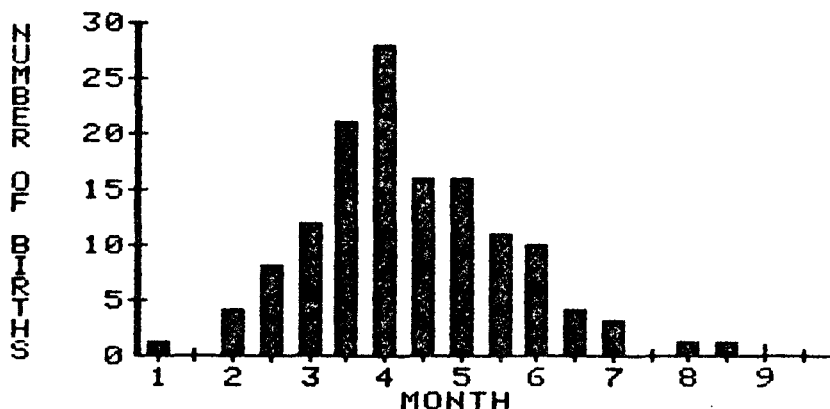


Figure 29.--Semimonthly distribution of births on Laysan Island, 1977-80.

to 20 April in 1979. (For a discussion of the pupping season as defined by counts of mother-pup pairs see Johnson and Johnson 1984.)

Table 15.--Number of pups born during each month on Laysan Island from 1977 through 1980.

Year	J	F	M	A	M	J	J	A	Total
1977	1	5	12	12	7	2	1	2	42
1978	0	2	7	10	7	3	0	0	29
1979	0	3	7	9	9	3	1	0	32
1980	1	1	7	13	4	6	1	0	33
Total	2	11	33	44	27	14	3	2	136

Rookery areas.--Pups were born on most beaches of Laysan, but pupping activity was not evenly distributed around the island. The majority of pups (76%) were born on the northwest quarter (areas 1 through 3 and area 14). Most of the northwest corner of the island was characterized by relatively narrow beaches with vegetation above the beach crest. Mothers with pups tended to congregate near shallow water reefs in these areas. Twenty-two percent of the births occurred on the beaches along the east shoreline (areas 7 through 10) where little cover was available above the beach crest. A rock ledge extended 20 to 30 meters from the shoreline along the east side of the island, with the water depth rarely exceeding one-half meter. Eight percent of the pups were born on the northeast quarter (areas 4 through 6), and 3% on the south and southwest beaches (areas 11 through 13).

Age at weaning. The calculation of weaning age of pups was the same as that used for lactation interval of females, except in cases where a pup was exchanged or adopted. Twelve pups were known to have been nursed by at least one female other than their natural mother; two in 1977, nine in 1978, and the last in 1979, when a deserted pup was adopted by a female that had lost her pup. While at least 11 pups were involved in pup exchanges in 1977 and 1978, no known pup exchanges took place in either 1979 or 1980.

The mean weaning age for pups born during the study was 36.2 days (range 27 to 50 days). Statistical analysis showed that the mean wean age for male pups (36.6 days) and for female pups (35.8 days) did not differ significantly ($t = 1.25$, $df = 118$, *n.s.*).

The overall size and condition of pups at weaning generally depended on the number of days the pup suckled. Pups weaned at more than 36 days were generally fatter and larger than pups weaned at less than the mean weaning age. Some exceptions did occur, and the range in size of pups showed considerable overlap.

The number of days a female remained with a pup depended on her size and on the behavior of the pup (some pups weaned themselves by moving away

from the female). Females ate little or nothing during lactation, so the larger the female, the longer she could afford to stay with a pup. (Occasionally mothers chased fish and spent long periods submerged in reef areas, but no actual feeding behavior was seen.) A t-test was run comparing the number of days smaller-than-average and larger-than-average females remained with their pups. Excluding pups which died or disappeared before weaning, the larger females remained with pups for a significantly longer time than the smaller females ($t = 3.59$, $df = 117$, $p < 0.001$).

Factors affecting pup survival.--Of the 103 pups born in 1977, 1978, and 1979: 13% died or disappeared prior to weaning; another 6.5% died or disappeared before the fall of their birth year (when the field season ended); and an additional 18% disappeared before the next field season began (a few of these pups had insufficient markings to insure recognition as yearlings). The remaining 63% of the pups were resighted at least once during their yearling year. Chi-square analysis (2x2) showed no significant differences in the overall tendency of pups to survive to the end of the field season of their yearling year when compared to area of birth (prime versus other), size of mother (small versus large), season of birth (early versus late, mid versus early and late), or wean age (greater than versus less than mean). However, a significant difference was found between males and females. The 103 pups born during 1977 through 1979 included 48 males and 53 females (with 2 pups of undetermined sex). Of the 50 pups known to be alive at the end of the field season of their yearling year, 30 were males and 20 females. These data suggest males have a significantly greater survival during their yearling year than females ($X^2 = 6.18$, $df = 1$, $p < 0.05$).

Breeding

Breeding can occur throughout much of the year for the Hawaiian monk seal as births are not limited to one season or time period. Males showed typical courtship behaviors throughout the field season, although a marked reduction in the tendency to haul-out with, or defend adult females took place from mid-August through October, corresponding to the adult male molting season. Based on haul-out patterns of adult females, estrus appears to occur between the time the pup is weaned and when the female comes ashore to molt. Females remain highly aggressive toward all seals, including adult males, throughout lactation. When ashore for the molt, approximately 3 months after weaning, adult females are rarely accompanied by adult males.

Actual breeding encounters were seen on only three occasions. Two of these observations were described in detail in Johnson and Johnson (1981b). The third involved a female and consort observed on 18 and 19 April 1980. Seen first in late afternoon, the female appeared unusually tolerant of the attentions of the consort, allowing the male to grasp her back and attempt to mount her while on dry sand. The pair moved into shallow water just before sunset and the female remained passive while the male repeatedly mounted her, but we could not confirm whether intromission occurred. After about 20 minutes in the nearshore water the male followed the female into the vegetation. The pair was watched until midnight, remaining in the vegetation. Near sunrise the following morning the pair could not be located. As dawn approached their shapes could be made out in shallow water. By the time it was light enough to see, the male followed the female back up to the vegetation. It appeared she had again been passive during

the time in shallow water. When the pair returned to the shoreline 2 hours later, the consort was driven off by another adult male. The female immediately showed the characteristic aggressive behavior toward the new male, resisting all attempts by the male for close approach. She remained onshore for most of the day, moving out to sea in the late afternoon, unaccompanied. The female had last pupped on 16 March 1979 and did not have a pup in 1980.

Survival

Well-identified seals disappeared from Laysan throughout the 4 years of the study. As bodies of dead animals were rarely found, it was not known if the disappearances were due to death of the animal or to emigration. Records of tagged Hawaiian monk seals (Johnson et al. 1983) indicate that 5% of resightings occur on atolls different from the tagging site. Therefore we assume that some of the identified seals that disappeared during the study could have emigrated to another atoll, but that most disappearances resulted from mortality. The abbreviation M/D (mortality/disappearance) will be used to describe unexplained disappearances. With this uncertainty unavoidable, we concentrated on rates of known survivorship, which undoubtedly underestimate the actual survivorship for the population.

Pups

One emphasis of the study was to follow known-age cohorts as long as possible. Marking pups soon after weaning and yearlings soon after their molt made this possible. For most pups, the bleach mark allowed reliable identification throughout the first year of life. When the mark was lost during the molt, about 15 months after weaning, animals were re-marked. The identification of the entire pup cohort each year made collection of detailed data on rates of survivorship possible.

Survival through weaning.--A total of 136 pups were born during the study. One pup was not weaned by the time we left the field in 1977 (therefore unmarked and unidentifiable). Four pups were stillborn, one in each year. One of these was premature; the cause of death was not determined for the other three.

Of the remaining 131 pups, 120 (89%) survived at least 27 days (the minimum age at weaning for the study) and were resighted after the departure of their mother. Survival to weaning ranged from a low of 82% in 1980 to a high of 97% in 1978. The age and circumstance of death for the 11 pups dying or disappearing before weaning, excluding those born dead, are listed in Table 16.

Survival through 4 months.--After weaning, pups were generally seen at least once each census period (4 days) for several months. Only rarely were pups not seen for more than a week during their pup year. Because of this tendency to remain near shore, any pup that was not sighted during the last 2 weeks of the study (and not resighted during the following year) was listed as having disappeared. Of the 120 pups surviving through weaning, one was found dead and seven disappeared before the end of their pup field season. Information on these pups is listed in Table 17.

Table 16.--Pre-weaning disappearance and mortality on Laysan Island between 1977 and 1980, excluding pups born dead.

Year	Sex	Age (days)	Notes
1977	?	23	Appeared healthy 3 days before death
	?	22	Disappeared at night, mother remained
	M	8	Mother may not have produced milk
1978			None
1979	M	33	Disappeared, mother remained
	M	3	Mother lost pup to another mother hours before death
	F	8	Mother may not have produced milk
1980	M	6	No observable cause of death
	F	6	No observable cause of death, stomach empty
	F	7	Wedged in bird burrow when found
	F	16	Appeared weak day before death
	?	1	Alive at birth. Pup gone while female remained ashore the next morning

Survival data for the first 4 months postbirth are presented in Figure 30. All pups born during the study were included in as many data points as their sighting data permitted. For example, data from a pup born 40 days before the end of a field season could only be included in the Birth through 40-day period. (Yearly sample sizes are included in Appendix F.)

Table 17.--Weaned pups which died or disappeared during their pup year on Laysan Island.

Year	Sex	Wean Age	Condition when last seen
1977	F	47 days	Healthy
	F	40 days	Small dorsal infection
	M	37 days	Dead, massive dorsal infection
1978	M	35 days	Small for wean-age
	F	28 days	Small seal
	F	38 days	Healthy
1979	M	47 days	Healthy
	M	33 days	Healthy
1980			None

As Figure 30 shows, 92% of the pups born on Laysan survived the first 10 days postbirth. The M/D rate was low during the next 70 days, with 88% of the pups known to be alive by 80 days postbirth. After 80 days the M/D rate increased. By 140 days postbirth, 80% of the pups were still being resighted.

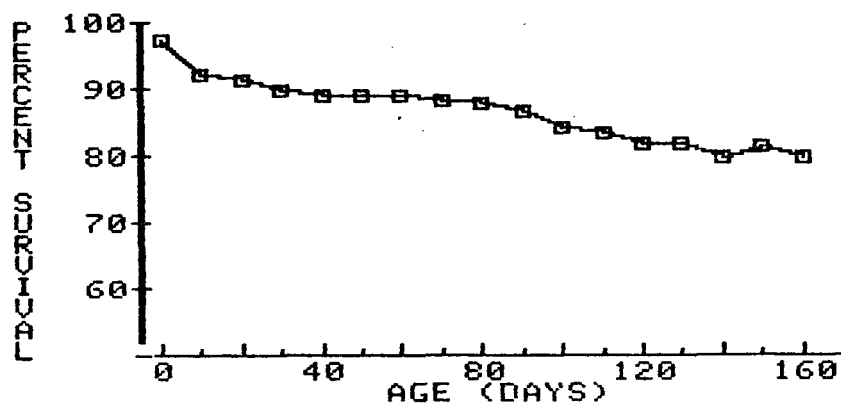


Figure 30.--Pup survival on Laysan Island, 1977 through 1980.

The survivorship patterns seen on Laysan differ markedly from data obtained during previous studies on Midway (Rice 1960) and on Kure (Wirtz 1968). Figure 31 compares pup survivorship on Laysan with that reported for Midway and Kure (see Appendix F for specific data). On Kure, early pup mortality was similar to Laysan, with approximately 90% of the pups still alive at 10 days postbirth. However the M/D rate through weaning was very high on Kure, with only 5% of the pups still being sighted at 50 days. Rice suggested that shark attack could have been responsible for the loss of pups, while Wirtz (1968) mentioned that attacks by adult male monk seals may have played a part in early pup mortality. The pups at Kure generally disappeared before the mother left the area, a pattern not seen with normal weaning on Laysan.



Figure 31.--Pup survival (# = resighted/births) for Laysan (1977-80), Kure (1964-65), and Midway (1958-59).

Data from Midway during the late 1950's also showed a higher M/D rate than Laysan, but the pattern was not the same as that seen at Kure. On Midway, approximately 30% of the pups were either born dead or died within the first 10 days. For pups that survived past 10 days the M/D rate was much lower than at Kure, with 35% of the original cohort still sighted after 70 days. Kenyon and Rice (1959) suggested that the higher rate of stillbirths could have been due to underwater explosions which were used to clear a channel at Midway during that time period. Apparently the pups which were born alive and healthy at Midway were not being subjected to the same factors causing the high postbirth mortality seen at Kure.

Survival through 16 months.--The best data for calculating minimum survivorship to 1 year of age are the resighting records for pups born in 1978 and 1979. Data from 1977 are excluded as a few pups were not marked well enough to guarantee reliable resighting the following year, and because approximately 80% of the 1977 pups recognized as yearlings in 1978 died or disappeared during the unusual 1978 "die-off."

Figure 32 presents survivorship data to 16 months for the 61 pups born in 1978 and 1979. All pups disappearing during their pup year were given a disappearance date of 1 day after their last sighting. Many pups were seen throughout their pup year, but not resighted as yearlings. For these animals the M/D age was recorded as the mean between the last day of the pup field season and the start of the following field season. (Data for each animal are included in Appendix F.)

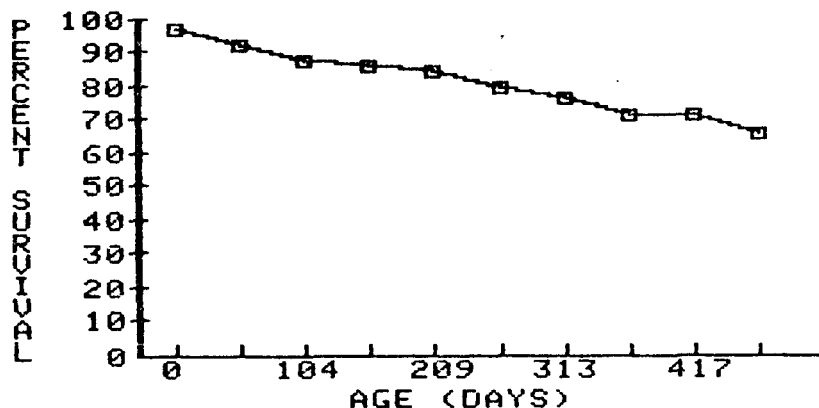


Figure 32.--Pup survival on Laysan Island, 1978 and 1979 pup cohorts.

Of the 61 pups born in 1978 and 1979, 46 (75%) were seen during the following year. However, only 43 (70%) were resighted 1 year after their actual birthday. This should be considered a minimum survival estimate, as the fate of the 18 pups which disappeared after weaning is unknown. A few of the pups born in 1978 and 1979 were poorly marked as pups. It is possible that one or two could actually have survived on Laysan, but were unrecognizable as yearlings. Three previously unidentified juvenile seals

were seen on Laysan which did not have visible bleach marks, two in 1979 and one in 1980. Although unlikely, if all three are assumed to be pups born on Laysan the previous year which had "lost" their marks, this would increase the 12-month survivorship to 75% (46 of 61).

Yearlings

The survival rate for yearlings was similar to that of pups. Eleven of the fourteen yearlings seen regularly throughout 1979 were also seen throughout 1980 as 2-year-old seals (79%). For the 1977 pup cohort, of the seven yearlings still seen regularly by the end of the 1978 field season (after the die-off), five were seen as 2-year-old seals in 1979. Combining the data from the 1977 and 1978 pup cohorts gives a survival rate for yearling seals of 76% (16 of 21).

Other Age Classes

Of the five 2-year-old seals seen in 1979, all were seen throughout 1980. However, only 23 of 29 (73%) identifiable juvenile seals (both known-age and others) seen in 1979 were also seen in 1980. (Seals classed as juveniles averaged about 3 years old, with a range of 2 to 4 years for known-age animals.)

The survival rate was higher for older seals. Table 18 presents data on 1 year of survivorship for all reliably identifiable seals older than yearlings that were seen in 1979.

In summary, yearly survival rates were about 75% for animals up to 4 years of age (birth through juvenile size). The survival rate for seals over 4 years of age (subadults and adults) increased to about 87%. As mentioned in the Reproductive section, there was a significantly greater survival of male pups through their yearling year than of females. Chi-square analysis of the data presented in Table 18 showed no significant difference in male versus female survival for juvenile, subadult, or adult animals; but the data from the small sample of juveniles indicate a tendency toward lower survival for young female monk seals. The reason for this apparent sex difference in the M/D rate is unknown, and needs additional study.

Table 18.--Number and percentage of seals identified in 1979 that were resighted in 1980 on Laysan Island.

	1979	1980	%
Juvenile males	15	14	93
females	14	9	64
Subadult males	15	13	87
females	15	13	87
Adult males	61	53	87
females	53	45	85

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Appendix Table A.--Itinerary. Arrival and departure dates, Laysan Island, 1977-80.

Year	Arrive Laysan	Depart Laysan
1977	27 February	3 September
1978	27 February	18 June
	28 June	1 October
	12 October	13 October
	12 December	18 December
1979	12 March	17 August
1980	14 March	18 September

Appendix B.--Biases affecting sex ratio data.

It is rarely possible to determine the sex of all seals ashore on a census. If the probability of sexing males and females is equal, then the sex ratio of unsexed animals should be the same as the ratio of sexed animals. Unfortunately, several potential biases exist which can alter the relative probability of sexing males and females. On censuses in which a large percentage of the animals are unsexed, these biases can significantly alter the calculated sex ratio.

Female-With-Pup Bias

The clearest example of a bias which affects sex ratio data occurs during the pupping season. All adults accompanied by black pups are routinely recorded as female, without the prerequisite ventral examination required for sexing other animals. The effect of this bias can be seen by looking at a hypothetical adult population made up of 50 males and 50 females, 25 of which are accompanied by black pups. Two counts are made. On the first count all animals are sexed, resulting in a 1:1 sex ratio. On the second survey, conditions are such that the probability of sexing each individual seal is only 20%, except that all adults accompanied by pups are sexed as female. The results of these counts show that the second count, including the unsexed animals, will be strongly biased toward females.

	Males	Females			Unknowns	Male:Female Sex Ratio
		Alone	with Pup	Total		
Count 1	50	(25)	(25)	50	0	1:1
Count 2	10	(5)	(25)	30	60	1:3

In theory, this bias can be corrected by estimating how many of the mothers would have been sexed as female by the normal method of sexing animals, based on the ratio of sexed adults to total adults.

$$A/B = X/M \quad \text{or} \quad \hat{X} = (MA/B)$$

where:

- A = total adults sexed (excluding mothers)
- B = total adults (excluding mothers)
- M = females with pups (mothers)
- X = estimate of mothers which would have been classed as female without presence of pup.

In the above population, where 20% of the nonmothers were sexed, $X = (25)(15)/75 = 5$, indicating that of the 25 mothers, only 5 would have been sexed using the normal sexing techniques. Added to the 5 females sexed using the normal methods, a total of 10 females results. When compared to the 10 seals sexed as males, the corrected sex ratio becomes 1:1.

In practice, this correction factor will not eliminate all problems, as other biases in both ageing and sexing animals may exist. However, it should reduce the problem during the pupping season, especially at atolls like French Frigate Shoals where a large percentage of animals are generally not sexed.

Other Biases

Several other biases may exist which could affect sex ratio data; but the relative magnitude of these biases is difficult to predict and probably varies from study to study. Some of these are listed below.

Identified Animals.--In the Laysan study, and others where a significant number of seals are individually recognizable, the sex of "marked" animals seen on censuses is not generally reconfirmed. On Laysan, research priorities resulted in proportionally more adult females being identified than males. On censuses in which a large number of seals were unsexed, this would bias the sex ratio in favor of females. (Other studies, such as those involving tagging, could also be affected by this bias. Data from Laysan indicate that adult males spend less time ashore than other age/sex classes, and would tend to be underrepresented in random marking efforts.) If a good population estimate is available, it may be possible to correct for the identified animal bias, based on the ratio of identified animals to total population for each age/sex class. Unfortunately, this analysis is complicated by such factors as differences between observers (in the number of animals they can identify) and the variability in the conspicuousness of markings (the identifying marks on some animals are inconspicuous and may occur only on the ventral area). These factors make it difficult to calculate a correction for identified animals in the Laysan study, but they should present less of a problem in tagging studies.

Male Vocalizations.--There is a characteristic adult male vocalization (the "rolling bellow") given in threat and courtship displays which, when it occurred during a census, was often used to sex the animal as male without ventral examination. If a sufficient number of males were sexed in this way it would result in a count biased in favor of males. However, the general response of seals in the presence of a displaying adult male was to shift to a position exposing the ventral surface to the approaching male, thereby often allowing the observer to sex the other animal as well.

Visibility Bias.--It is possible that males were, in general, easier to sex than females. This was because males were sexed by the presence of the penile opening and the penile ridge (a line extending from the penile opening to the anus), while females were sexed primarily by the absence of these features. On censuses where many animals were unsexed this would result in a bias favoring males. But this bias, if it exists, is likely to vary with viewing conditions and between observers.

Incomplete Count Bias.--Data from Laysan, French Frigate Shoals, and elsewhere indicate various haul-out areas within an atoll are used disproportionately by one sex. Differences in sex ratio are likely when comparing complete atoll counts with partial atoll counts. The specific direction of the bias depends on which areas are excluded during partial counts. This bias would be particularly significant at atolls such as French Frigate Shoals,

where weather conditions and time constraints often make it impossible to visit all haul-out areas available to the seals.

This bias does not affect data collected during the Laysan study because the entire island was covered on all censuses. But it could affect comparisons with future studies on Laysan if those studies exclude animals in the water or hauled out on offshore rocks, both groups being disproportionately male.

Testing for Sex Ratio Bias

Excluding the Female-with-pup bias, the total effect of the above biases (if any) on sex ratio data is difficult to predict and may vary from study to study. Studies involving a series of censuses can be used to test for any overall bias by comparing counts in which a high proportion of the animals are sexed (minimizing bias) with counts in which large numbers of seals are unsexed (when the effect of any bias would be greatest).

During 1977, an average of 43% of the seals were not sexed on censuses, increasing the probability of a sexing bias having a significant effect on the calculation of sex ratio. The adult counts made during the 1977 pupping season (March through June) clearly show the problem. A Pearson Product-Moment Correlation indicates there is a significant correlation between the percentage of sexed adults classed as female and the percent of adults which were unsexed ($r = 0.666$, $t = 4.462$, $df = 25$, $p < 0.001$). This suggests a bias in favor of females. But when the same statistic is run comparing the percentage of adults sexed as female when a correction has been made for the Female-with-pup bias, the results are nonsignificant ($r = -0.154$, $t = -0.782$, $df = 25$, $p > 0.10$). Thus, when the Female-with-pup bias is taken into account and a correction factor applied to the counts, the resulting adult sex ratio data appear unbiased.

Count Verses Population Sex Ratio

Although sex ratio data obtained from ground counts can be useful when comparing counts in different months or years within an atoll, or between atolls, it should not be considered a direct measure of the population sex ratio. Data from Laysan indicate that adult males tend to spend less time ashore than other age/sex classes; thus would be underrepresented in sex ratios based on ground counts. Further, data indicate the sex ratio of seals ashore changes from month to month, a result of different haul-out patterns for the various age/sex classes (e.g., different molting seasons). As the data in Appendix C show, the sex ratio obtained on ground counts does vary considerably from month to month.

Appendix C.--Laysan Island count data.

Appendix Tables C-1 through C-4 present the count data for all censuses conducted during the study, from 1977 through 1980. Two of the counts (10 March 1977 and 27 February 1978) included animals which were not classified by age; therefore, no age/sex data are included for those dates. The following is a brief description of the headings found on each table.

DATE: Date of count
 TIME: Time count began
 ADM: Number of adult males counted
 ADF: Number of adult females counted
 AD?: Number of unsexed adults
 SAM: Number of subadult males
 SAF: Number of subadult females
 SA?: Number of unsexed subadults
 JM: Number of juvenile males
 JF: Number of juvenile females
 J?: Number of unsexed juveniles
 YM: Number of yearling males (or yearling size male seals in 1977)
 YF: Number of yearling females (or yearling size female seals in 1977)
 Y?: Number of unsexed yearling size seals, used only in 1977
 WP: Number of weaned pups
 MP: Number of pups still attended by a female (i.e., nursing)
 TOT: Total of all seals counted
 STOT: Total excluding WP and MP counts
 %UNK: Percentage of STOT counts that were not sexed
 AM/C: Corrected adult male count corrected for female-with-pup bias (Appendix B) and with a sex assigned to the unsexed adults based on the resulting sex ratio
 AF/C: Corrected adult female count (same as AM/C)
 IM/C: Corrected immature male count (includes subadult, juvenile, and yearling males) with sexes assigned to unsexed animals on the basis of sex ratio of sexed immatures
 IF/C: Corrected immature female count (same as IM/C)
 %AD: Percentage of STOT that were classified as adults
 %FEM: Percentage of STOT that were sexed as female (based on the AF/C and IF/C totals)

A summary table is provided at the end of the census data for each year. The table includes a total mean for all counts conducted during the year, and separate means for each month.

The "corrected" (e.g., estimated) counts for the four age/sex classes can be misleading for censuses where large numbers of seals were not sexed (such as the count on 17 April 1977). These data are best used when the corrected counts are based on the mean of several counts (e.g., semimonthly or monthly means).

Although only whole numbers are presented in the tables, all summary calculations for the last seven columns (%UNK to %FEM) are based on numbers carried out to several decimal places. As a result, the summary calculations may differ slightly from the sum of the columns.

Appendix Table C1.--Counts from 1977 on Laysan Island (age/sex breakdown not available for all seals seen on 10 March).

DATE	TIME	ADM	ADF	AD?	SAM	SAP	SA?	JM	JF	J?	YM	YF	Y?	WP	MP	TOT	STOT	ZUNK	AM/C	AF/C	IM/C	IF/C	%AD	%FEM
2/27	1145	37	24	16	10	5	19	21	13	24	6	1	5	1	5	187	181	35	48	29	69	35	43	36
3/06	1200	25	25	42	10	8	29	9	13	22	5	1	3	1	5	198	192	50	48	44	52	48	48	48
3/10	1230	--	--	--	--	--	--	--	--	--	--	--	--	0	7	117	110	--	--	--	--	--	--	--
3/15	930	20	14	65	4	1	13	7	6	18	1	1	2	0	7	159	152	64	68	31	32	21	65	34
3/20	1510	25	14	51	1	0	24	4	5	21	2	0	2	1	8	158	149	66	66	24	34	25	60	33
3/24	1430	21	17	40	3	3	17	7	5	26	0	0	5	4	11	159	144	61	52	26	37	29	54	38
3/28	1430	40	18	22	13	3	14	12	6	12	5	1	6	5	10	167	152	36	58	22	54	18	53	26
4/01	1530	29	19	33	4	3	28	5	4	30	3	0	8	5	11	182	166	60	55	26	54	31	49	35
4/05	1415	34	22	46	5	4	22	8	1	26	0	2	5	6	14	195	175	57	71	31	47	26	58	32
4/09	1445	33	23	37	9	7	18	7	3	15	3	0	3	5	16	179	158	46	64	29	43	22	59	33
4/13	1230	43	25	24	8	6	22	6	2	11	2	0	5	4	17	175	154	40	63	29	41	21	60	32
4/17	1430	14	22	50	0	1	21	0	0	23	0	0	8	5	18	162	139	73	53	33	0	53	62	62
4/21	1415	36	29	47	3	8	21	5	2	20	0	0	2	8	17	198	173	52	71	41	27	34	65	43
4/25	1410	46	24	26	8	5	13	8	4	17	3	2	2	10	16	184	158	37	68	28	39	23	61	32
4/29	1400	34	24	26	5	3	16	4	4	17	2	1	2	10	15	163	138	44	55	29	31	23	61	38
5/03	1350	42	24	22	5	3	23	8	1	25	0	2	0	12	13	180	155	45	59	29	46	21	57	32
5/07	1400	25	17	30	6	6	20	7	3	14	2	0	3	13	11	157	133	50	49	23	38	23	54	34
5/11	1430	46	23	30	7	4	9	7	3	21	1	1	6	14	12	184	158	42	70	29	38	21	63	31
5/15	1420	28	22	32	4	10	14	4	4	9	3	0	2	17	9	159	132	43	50	32	22	28	62	45
5/19	1445	34	23	35	7	4	26	5	2	32	2	0	2	17	9	198	172	55	59	33	56	24	53	33
5/23	1430	31	22	19	1	6	17	3	2	19	0	0	3	19	10	152	123	47	45	27	17	34	59	50
5/27	1430	40	25	17	5	7	19	9	5	11	3	1	5	20	9	176	147	35	52	30	37	28	56	39
5/31	1410	25	22	25	5	4	25	2	2	19	2	0	4	20	8	163	135	54	41	31	38	25	53	42
6/04	1345	31	23	26	9	10	20	4	2	25	2	1	3	21	7	184	156	47	48	32	41	35	51	43
6/08	1410	35	24	28	9	7	17	6	4	13	2	0	2	22	8	177	147	41	54	33	36	24	59	38
6/16	1430	25	22	31	5	4	20	5	1	13	1	0	3	18	8	156	130	52	45	33	36	16	60	38
6/20	1430	29	21	29	6	5	26	8	1	11	1	1	5	21	7	171	143	50	49	30	44	20	55	36
6/24	1425	39	22	13	12	19	16	9	7	8	2	1	5	24	5	182	153	27	48	26	36	43	48	45
6/28	1400	31	18	16	17	11	19	6	1	19	2	1	2	27	4	174	143	39	42	23	51	27	45	35
7/02	1430	29	14	17	18	17	13	9	8	8	1	1	3	25	2	165	138	30	41	19	40	38	43	41
7/06	1445	28	20	22	21	7	21	10	10	18	4	1	3	18	2	185	165	39	41	29	63	32	42	37
7/10	1335	28	24	14	23	12	15	20	20	9	3	2	3	23	2	198	173	24	36	30	62	45	38	44
7/14	1445	22	13	18	13	17	25	16	11	25	5	1	7	25	1	199	173	43	34	19	65	55	31	43
7/18	1430	26	13	13	13	14	25	14	11	19	3	1	2	22	1	177	154	38	35	17	55	47	34	42
7/22	1430	34	16	18	17	10	22	14	9	25	6	1	3	24	1	200	175	39	46	22	69	38	39	34
7/24	1430	30	18	22	18	8	23	18	10	26	7	2	2	26	1	211	184	40	44	26	78	36	38	34
7/26	1425	32	18	10	25	13	18	21	14	18	3	3	3	22	1	201	178	28	39	21	73	45	34	37
7/28	1310	34	19	4	18	10	22	18	11	22	6	4	5	21	1	195	173	31	37	20	73	43	33	37
7/30	1430	25	16	17	19	8	18	12	10	33	3	3	4	20	1	189	168	43	36	22	68	42	35	38
8/03	1345	37	22	13	17	6	20	16	14	19	7	2	6	23	2	204	179	32	45	27	69	38	40	36
8/07	1430	25	21	15	23	8	14	20	17	19	6	1	3	23	2	197	172	30	34	27	73	38	35	38
8/11	1430	25	9	33	12	8	17	11	12	21	4	1	5	23	1	182	158	48	50	17	51	40	42	36
8/13	1400	22	14	17	10	6	21	8	6	17	8	3	6	17	1	162	144	44	33	20	53	38	37	41
8/15	1330	29	13	16	7	6	26	11	11	22	8	3	6	16	1	175	158	44	40	18	57	43	37	39
8/17	1445	31	12	11	15	5	19	10	9	16	2	4	0	15	1	150	134	34	39	15	48	32	40	35
8/19	1330	36	13	8	15	7	15	15	14	18	4	2	5	17	1	170	152	30	42	15	57	38	38	35
8/21	1400	27	14	18	14	7	16	17	13	14	7	4	3	20	1	175	154	33	39	20	58	37	38	37
8/23	1415	40	10	20	18	4	19	11	6	18	6	4	0	16	2	174	156	37	57	13	61	25	45	24
8/25	1415	41	12	18	14	7	11	16	13	17	3	3	4	17	2	178	159	31	55	16	52	36	45	32
8/27	1345	40	12	18	15	2	17	22	11	10	4	4	3	20	2	180	158	30	54	16	62	26	44	26
8/31	1415	57	12	14	13	5	17	13	11	28	4	2	4	22	1	203	180	35	69	14	61	36	46	28
9/02	1500	46	12	41	8	2	10	9	10	19	4	3	4	20	1	189	168	44	79	20	40	29	59	29

Appendix Table C1.--Continued.

		Summary of mean monthly counts, 1977																							
		ADM	ADF	AD?	SAM	SAF	SA?	JM	JF	J?	YM	YF	Y?	WP	MP	TOT	STOT	%UNK	AM/C	AM/F	IM/C	IF/C	ZAD	ZFEM	
MEAN		32	19	25	11	7	19	10	7	19	3	1	4	15	6	178	156	43	50	26	49	32	49	37	
FEB*		37	24	16	10	5	19	21	13	24	6	1	5	1	5	187	181	35	48	29	69	35	43	36	
MAR		26	18	44	6	3	19	8	7	20	3	1	4	2	8	160	150	55	58	29	42	28	59	36	
APR		34	24	36	5	5	20	5	3	20	2	1	4	7	16	180	158	51	63	30	35	29	59	38	
MAY		34	22	26	5	6	19	6	3	19	2	1	3	17	10	171	144	47	53	29	37	25	57	38	
JUN		32	22	24	10	9	20	6	3	15	2	1	3	22	7	174	145	43	48	29	41	27	53	39	
JUL		29	17	16	19	12	20	15	11	20	4	2	4	23	1	192	168	35	39	23	65	42	37	39	
AUG		34	14	17	14	6	18	14	11	18	5	3	4	19	1	179	159	36	46	18	58	36	41	34	
SEP*		46	12	41	8	2	10	9	10	19	4	3	4	20	1	189	168	44	79	20	40	29	59	29	

*The February and September "means" are based on single counts.

Appendix Table C2.---Counts from 1978 on Laysan Island (age/sex breakdown not available for all seals seen on 27 February).

DATE TIME	ADM	ADF	AD?	SAM	SAF	SA?	JM	JF	J?	YM	YF	WP	MP	TOT	STOT	ZUNK	AM/C	AF/C	IM/C	IF/C	ZAD	ZFEM	
2/27 1600	--	--	--	--	--	--	--	--	--	--	--	0	2	121	119	--	--	--	--	--	--	--	
3/06 1430	31	20	22	8	3	5	7	10	15	7	8	0	2	138	136	31	45	28	32	31	54	43	
3/10 1330	46	13	27	3	6	5	6	5	12	7	4	0	2	136	134	33	68	18	25	23	64	31	
3/14 1430	54	18	7	8	2	5	3	5	6	4	2	0	3	117	114	16	59	20	22	13	69	29	
3/18 1430	48	18	9	8	3	12	12	6	6	4	6	2	4	139	134	17	55	20	31	28	56	36	
3/20 1445	26	10	19	4	3	13	8	6	11	4	5	2	4	115	109	39	41	14	29	25	50	36	
3/22 1410	46	16	11	9	5	6	7	10	9	5	4	2	4	134	128	20	55	18	29	26	57	35	
3/26 1400	34	20	11	2	7	6	7	11	11	2	5	2	4	122	116	24	41	24	17	35	56	50	
3/28 1400	39	22	7	10	1	5	7	9	4	7	3	2	6	122	114	14	44	24	30	16	60	35	
3/30 1400	43	21	4	9	6	3	9	11	5	3	3	2	6	125	117	10	46	22	25	24	58	39	
4/01 1430	51	20	8	8	2	4	9	9	5	5	5	2	7	135	126	13	57	22	27	20	63	33	
4/03 1415	51	20	2	12	7	7	10	10	5	6	6	2	8	146	136	10	53	20	35	28	54	36	
4/07 1300	45	22	9	7	7	6	8	6	3	4	3	2	10	132	120	15	52	24	24	20	63	37	
4/09 1400	46	23	10	7	5	3	6	11	6	4	3	2	10	136	124	15	54	25	21	24	64	39	
4/11 1400	40	21	12	4	4	10	9	2	7	4	5	2	11	131	118	25	50	23	27	18	62	35	
4/15 1430	45	22	8	5	4	7	6	7	8	3	5	2	13	135	120	19	52	23	21	24	63	39	
4/17 1350	27	26	7	8	4	7	5	8	3	2	3	2	13	115	100	17	32	28	20	20	60	48	
4/21 1530	41	25	11	3	2	10	3	7	11	2	5	4	15	139	120	27	50	27	16	27	64	45	
4/23 1415	43	25	4	9	5	6	7	5	6	4	4	4	15	137	118	14	46	26	27	19	61	38	
4/27 1500	42	22	6	4	7	5	7	4	4	5	2	6	13	128	109	14	47	23	18	21	64	40	
4/29 1200	57	24	0	9	3	1	11	6	3	3	5	2	5	141	122	3	57	24	25	16	66	32	
5/01 1530	21	15	19	2	1	6	3	3	2	2	2	5	13	94	76	36	38	17	11	10	72	35	
5/05 1330	30	19	20	3	2	6	4	3	15	3	0	8	13	126	105	39	47	22	24	12	66	33	
5/06 1145	26	24	26	0	3	10	4	3	14	2	2	7	13	134	114	44	44	32	16	22	67	47	
5/07 1200	26	19	22	3	0	9	6	4	10	2	2	1	6	131	102	40	44	23	24	11	66	33	
5/09 1430	36	26	9	7	5	6	4	4	7	1	1	7	13	126	106	21	43	28	19	16	67	42	
5/13 1500	42	26	13	5	2	6	12	7	9	3	1	11	11	148	126	22	52	29	30	15	64	35	
5/17 930	25	24	12	4	1	5	3	4	7	2	3	14	9	113	90	27	32	28	15	14	68	47	
5/19 1600	41	24	6	5	2	4	5	5	10	2	1	15	8	128	105	19	45	26	20	14	68	37	
5/21 1430	30	23	12	3	1	5	4	4	9	4	4	14	7	120	99	26	38	27	19	15	66	43	
5/23 1250	45	22	5	2	3	3	3	4	2	2	4	16	7	118	95	11	49	23	9	14	76	39	
5/27 1415	46	22	5	4	9	1	7	4	2	2	3	18	7	130	105	8	50	23	14	18	70	39	
5/29 1415	32	20	7	6	4	5	9	5	2	1	4	18	4	117	95	15	37	22	20	16	62	40	
6/02 1545	24	22	10	4	3	13	3	7	3	4	2	17	7	119	95	27	30	26	19	20	59	49	
6/04 645	16	24	10	6	6	3	2	2	3	2	0	10	7	91	74	22	21	29	13	11	68	54	
6/04 1200	30	29	3	8	7	3	6	6	2	2	0	16	7	119	96	8	32	30	19	15	65	47	
6/04 1730	25	31	4	6	9	1	6	6	3	2	0	17	7	117	93	9	27	33	16	17	65	54	
6/06 1415	35	27	4	4	4	2	7	5	4	3	0	18	7	120	95	11	38	28	18	11	69	42	
6/10 1400	39	23	2	10	7	3	5	3	2	2	1	17	7	121	97	7	40	24	20	13	66	38	
6/12 1430	36	26	5	6	4	2	8	2	1	4	0	18	6	118	94	9	39	28	20	7	71	37	
6/16 1500	39	22	3	8	6	2	6	3	2	2	0	17	6	116	93	8	41	23	19	10	69	36	
6/28 1040	16	22	15	4	6	9	6	3	1	1	1	20	4	108	84	30	23	30	16	15	63	53	
6/30 1500	36	23	5	7	9	9	5	6	5	2	0	23	4	134	107	18	39	25	21	22	60	44	
7/04 1530	24	23	6	5	12	4	5	3	3	3	1	0	19	3	108	86	15	27	26	14	19	62	52
7/06 1545	30	21	1	4	8	6	7	6	6	1	0	20	3	113	90	14	31	21	18	20	58	46	
7/08 1345	36	14	6	12	9	8	6	3	3	0	0	17	2	116	97	18	41	15	25	16	58	33	
7/12 1515	30	20	8	10	12	4	7	4	5	2	0	21	1	124	102	17	35	23	24	20	57	42	
7/14 700	21	21	2	11	15	4	3	5	4	0	0	15	1	102	86	12	22	22	17	25	51	54	
7/14 1230	33	23	1	13	14	4	8	7	4	1	0	21	1	130	108	8	34	23	26	25	53	45	
7/14 1800	26	19	2	12	10	1	4	7	2	2	0	19	1	105	85	6	27	20	20	18	55	45	
7/16 1545	28	27	0	10	10	3	7	4	4	4	0	22	1	120	97	7	28	27	25	17	57	45	
7/18 1100	27	10	17	9	10	7	2	2	8	1	0	13	1	107	93	34	40	14	20	20	58	36	

Appendix Table C2.--Continued.

DATE TIME	ADM	ADF	AD?	SAM	SAF	SA?	JM	JF	J?	JM	JF	J?	JM	JF	J?	YM	YF	WP	MP	TOT STOT	ZUNK	AM/C	AF/C	IM/C	IF/C	ZAD	ZFEM
7/20 1500	33	17	5	10	9	8	9	6	11	3	0	20	1	132	111	22	36	19	33	23	50	37					
7/22 1445	25	26	7	8	4	10	9	5	8	2	0	13	1	119	105	25	29	29	32	15	55	42					
7/26 1610	38	24	5	11	7	10	9	6	8	3	0	19	1	141	121	19	41	26	35	20	55	38					
7/28 1515	28	22	4	12	9	6	12	5	4	1	0	16	1	120	103	14	30	24	31	18	52	40					
8/01 1430	33	20	5	13	7	5	17	9	2	1	0	13	0	125	112	11	36	22	36	18	52	36					
8/05 1530	27	22	3	18	4	4	11	5	4	2	1	17	0	118	101	11	29	23	37	12	51	35					
8/07 1430	26	19	7	12	7	5	14	8	5	3	0	13	0	119	106	16	30	22	36	18	49	38					
8/09 1530	28	19	6	17	9	7	16	6	5	3	0	15	0	131	116	16	32	21	44	19	46	34					
8/13 1500	37	16	5	16	10	9	9	8	4	3	1	14	0	132	118	15	40	18	36	24	49	35					
8/17 1430	36	17	5	12	6	5	11	10	8	2	1	14	0	127	113	16	39	19	33	22	51	36					
8/21 1530	25	16	8	9	3	10	12	6	13	3	1	14	0	120	106	29	30	19	40	17	46	34					
8/25 1415	34	12	1	16	4	4	13	10	4	3	2	14	0	117	103	9	35	12	37	19	46	30					
8/27 1400	39	14	7	12	3	5	13	3	3	2	0	13	0	114	101	15	44	16	34	7	59	23					
8/29 1045	44	13	2	17	4	2	11	6	0	2	0	14	0	115	101	4	46	13	32	11	58	24					
8/29 1530	39	13	1	16	5	1	16	5	0	3	0	12	0	111	99	2	40	13	36	10	54	24					
9/02 1500	38	12	6	11	1	5	9	5	7	1	0	13	0	108	95	19	43	13	30	9	59	23					
9/04 1445	42	13	10	12	5	3	6	8	7	2	1	8	0	117	109	18	50	15	26	18	60	31					
9/06 1445	45	11	20	8	6	6	5	4	6	1	0	14	0	126	112	29	61	15	21	15	68	27					
9/10 1530	45	10	14	11	3	5	6	6	3	0	0	10	0	113	103	21	56	13	22	12	67	24					
9/12 1330	64	9	6	10	5	7	12	4	1	0	0	11	0	129	118	12	69	10	28	11	67	18					
9/14 1130	77	9	3	14	4	4	10	8	0	2	1	10	0	142	132	5	80	9	29	14	67	18					
9/18 1130	85	12	3	11	7	7	7	7	3	2	0	10	0	154	144	9	88	12	26	18	69	21					
9/20 1345	65	11	19	10	3	6	8	5	1	0	0	11	0	139	128	20	81	14	23	10	74	19					
9/22 1400	76	12	11	8	4	4	7	2	4	2	0	10	0	140	130	15	86	14	23	8	76	17					
9/24 1400	67	13	23	3	6	4	7	8	5	0	0	12	0	145	133	23	86	17	14	16	77	24					
9/26 1430	84	7	16	8	7	5	4	5	8	3	0	10	0	157	147	20	99	8	22	18	73	18					
9/28 1300	60	7	35	5	6	10	5	4	4	2	1	10	0	149	139	35	91	11	19	18	73	20					
9/30 1415	78	3	10	5	1	5	6	3	8	2	2	9	0	132	123	19	88	3	22	10	74	11					
10/12 1645	34	6	30	5	1	14	6	1	6	4	0	10	0	117	107	47	60	11	33	4	65	14					
10/13 1115	68	6	11	6	5	3	8	5	3	1	1	13	0	130	117	15	78	7	18	14	73	17					
12/13 1230	30	11	27	4	5	5	0	3	3	2	0	5	0	95	90	39	50	18	9	13	76	34					
12/14 1145	30	13	20	2	7	5	2	3	0	0	2	11	0	95	84	30	44	19	5	16	75	41					
12/15 1245	38	14	19	4	5	2	6	4	5	1	0	12	0	110	98	27	52	19	15	12	72	32					

Summary of mean monthly counts, 1978

ADM	ADF	AD?	SAM	SAF	SA?	JM	JF	J?	JM	JF	J?	YM	YF	WP	MP	TOT STOT	ZUNK	AM/C	AF/C	IM/C	IF/C	ZAD	ZFEM
MEAN	40	18	10	8	5	6	7	6	5	2	2	11	4	124	109	19	47	21	24	17	62	35	
FEB*	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
MAR	41	18	13	7	4	6	7	9	9	5	4	0	2	121	119	23	51	21	27	25	58	37	
APR	44	23	7	7	5	6	7	7	6	4	4	3	12	134	119	16	50	24	24	21	62	38	
MAY	33	22	13	4	3	6	5	4	7	2	2	12	10	123	102	26	43	25	19	15	67	39	
JUN	30	25	6	6	6	5	5	4	3	2	0	17	6	116	93	14	33	28	18	14	65	45	
JUL	29	21	5	10	10	6	7	5	5	2	0	18	1	118	99	16	32	22	25	20	55	42	
AUG	33	16	5	14	6	5	13	7	4	2	1	14	0	121	107	13	36	18	36	16	51	32	
SEP	64	10	14	9	4	6	7	5	4	1	0	11	0	135	124	19	75	12	23	14	70	21	
OCT	51	6	21	6	3	9	7	3	5	3	1	12	0	124	112	30	69	9	26	9	69	16	
DEC	33	13	22	3	6	4	3	3	3	1	9	0	109	91	32	49	19	10	13	74	36		

*The February "mean" is based on a single count.

Appendix Table C3.--Counts from 1979 on Laysan Island.

DATE	TIME	ADH	ADF	AD?	SAM	SAF	SA?	JM	JF	J?	YM	YF	WP	MP	TOT	STOT	ZUNK	AM/C	AF/C	IN/C	IF/C	ZAD	ZFEM
3/17	1530	37	14	22	4	6	6	4	7	3	4	7	0	7	121	114	27	55	17	15	26	64	38
3/21	1400	34	17	4	3	2	7	1	2	3	2	3	0	9	87	78	18	37	18	11	12	71	38
3/23	1200	40	17	7	8	9	0	8	4	1	0	4	0	9	107	98	8	46	18	17	17	65	36
3/25	1430	34	14	10	3	2	6	4	6	2	2	2	0	9	94	85	21	43	15	13	14	68	34
3/27	1700	35	18	13	4	8	3	4	3	2	1	4	0	9	104	95	19	45	21	11	18	69	41
3/29	1430	41	20	5	7	4	5	2	6	2	1	1	1	8	103	94	13	45	21	14	14	70	38
3/31	1415	36	19	4	3	4	7	2	3	7	4	1	1	9	100	90	20	39	20	15	16	66	40
4/02	1500	29	19	7	4	3	1	3	6	2	1	2	1	9	87	77	13	34	21	9	13	71	44
4/04	1315	40	19	1	6	3	3	4	2	1	3	3	1	9	95	85	6	41	19	16	9	71	34
4/06	1530	36	20	7	9	3	2	3	1	3	1	4	3	8	100	89	13	41	22	17	9	71	35
4/08	1415	41	22	5	8	5	5	7	7	0	4	5	3	8	120	109	9	45	23	22	19	62	39
4/10	1430	46	17	3	11	4	5	5	5	5	4	4	4	8	120	109	12	49	17	26	17	61	31
4/12	1600	44	15	8	10	5	3	12	9	1	1	4	4	7	123	112	11	51	16	26	19	60	32
4/14	1315	47	19	6	9	9	4	8	6	1	3	4	4	9	129	116	9	52	20	23	21	62	36
4/18	1530	36	21	14	3	6	6	4	4	4	2	2	4	10	116	102	24	47	24	13	18	70	41
4/20	1300	51	23	4	8	4	2	5	3	3	1	3	4	11	122	107	8	54	24	17	12	73	33
4/22	1300	43	22	8	9	4	5	1	5	2	2	2	6	9	118	103	15	49	24	16	14	71	37
4/26	1300	41	19	4	10	4	3	4	2	1	2	3	8	9	110	93	9	44	20	19	10	69	32
4/28	1600	26	18	3	9	4	3	3	2	2	3	2	7	9	91	75	11	28	19	18	10	63	38
4/30	1345	41	22	0	7	3	3	3	3	0	1	2	8	10	103	85	4	41	22	13	9	74	36
5/02	1515	31	18	1	6	2	1	6	5	0	2	3	8	13	96	75	3	32	18	15	10	67	38
5/03	730	16	19	1	7	4	3	4	4	0	2	2	7	13	82	62	6	17	19	15	11	58	49
5/03	1200	33	19	3	8	4	3	8	4	0	1	4	8	13	108	87	7	36	19	19	13	63	37
5/03	1715	17	17	1	7	2	3	6	2	1	0	4	8	13	81	60	8	18	17	16	9	58	44
5/04	1430	29	19	3	7	2	5	3	4	3	2	1	7	13	98	78	14	31	20	17	10	65	38
5/08	1600	26	26	7	6	2	5	5	1	1	2	4	8	13	106	85	15	31	28	18	8	69	43
5/12	1145	45	22	3	5	2	2	12	4	2	3	5	10	12	127	105	7	47	23	23	12	67	33
5/16	1045	31	17	7	11	5	2	6	1	1	2	2	11	11	107	85	12	37	18	21	9	65	32
5/18	1330	34	24	3	5	3	6	8	6	2	1	3	11	10	116	95	12	36	25	19	15	64	42
5/20	1500	25	21	3	9	5	0	10	5	2	1	7	11	12	111	88	6	27	22	21	18	56	45
5/24	1400	25	22	4	9	6	1	4	3	3	3	3	13	11	104	80	10	28	23	16	13	64	45
5/26	1330	28	16	3	5	10	6	7	4	3	3	3	3	10	109	88	14	30	17	19	22	53	44
5/28	1530	32	18	3	8	1	3	4	0	3	1	15	8	104	81	5	34	19	15	14	65	40	
5/29	1500	28	16	6	7	6	5	4	3	2	2	14	8	103	81	16	33	17	17	14	62	39	
5/30	1500	40	17	2	6	7	1	4	7	1	1	4	15	8	113	90	4	42	17	12	19	66	41
6/01	1230	32	19	2	8	11	0	5	7	2	4	1	15	8	114	91	4	33	20	18	20	58	44
6/03	1445	25	15	3	5	10	5	11	5	2	3	3	19	5	111	87	11	27	16	22	22	49	43
6/05	1630	18	13	2	3	9	2	8	5	1	5	5	16	5	92	71	7	19	14	17	21	46	49
6/07	1345	21	17	6	7	9	2	10	7	1	3	5	19	6	113	88	10	25	19	21	23	50	47
6/09	1400	29	17	5	9	13	1	14	5	2	3	6	18	6	128	104	8	33	18	28	25	49	42
6/11	1600	21	16	1	5	10	2	8	4	1	1	3	16	5	93	72	6	22	16	15	19	53	49
6/12	1115	32	14	3	9	9	4	11	9	1	2	3	18	5	120	97	8	34	15	25	23	51	39
6/13	1530	32	18	3	4	12	3	11	5	0	4	3	18	6	119	95	6	34	19	20	22	56	43
6/15	1400	28	19	3	8	13	1	12	5	1	4	5	20	6	125	99	5	30	20	25	24	51	44
6/17	1345	32	27	4	10	12	1	10	9	0	2	3	18	6	134	110	5	34	29	22	25	48	44
6/21	1230	30	23	8	7	14	2	14	3	0	2	2	20	5	130	105	10	35	26	24	20	58	44
6/22	1745	14	19	4	7	14	8	11	7	2	4	3	19	5	117	93	15	16	21	26	30	40	55
6/24	1030	29	20	1	9	16	3	13	7	1	4	3	20	4	130	106	5	30	20	28	28	47	46
6/24	1530	26	19	1	9	15	1	19	8	1	4	3	19	4	129	106	3	27	19	33	27	43	44

Appendix Table C3.--Continued.

DATE TIME	ADM	ADF	AD?	SAM	SAF	SA?	JM	JF	J?	JM	JF	J?	YM	YF	WP	MP	TOT STOT	ZUNK	AM/C	AF/C	IM/C	IF/C	ZAD	ZFEM
6/25 1400	36	21	1	14	12	1	17	10	0	2	5	21	4	144	119	2	37	21	34	27	49	41		
6/26 1630	23	20	6	10	16	1	13	5	1	3	2	19	4	123	100	8	27	22	27	24	49	46		
6/27 1345	34	21	1	15	18	2	12	7	0	3	2	18	4	137	115	3	35	21	31	28	49	43		
6/28 1730	19	20	6	9	14	1	11	5	2	4	2	17	4	114	93	10	22	23	26	22	48	48		
6/29 1545	32	20	2	12	15	0	14	5	0	3	4	21	3	131	107	2	33	21	29	24	50	42		
6/30 1300	31	22	4	12	17	0	12	6	1	4	4	17	3	133	113	4	33	24	29	27	50	45		
7/02 1500	23	19	5	14	16	1	14	5	1	3	2	19	3	125	103	7	26	21	32	24	46	44		
7/03 1530	24	17	4	10	12	3	15	6	0	4	4	17	3	120	100	7	27	18	30	25	45	43		
7/04 830	23	20	5	19	10	3	8	9	1	4	4	15	3	124	106	8	26	22	33	25	45	44		
7/05 1615	25	20	0	14	11	5	12	6	2	4	3	19	3	124	102	7	25	20	34	23	44	42		
7/06 1645	17	20	1	14	5	5	13	7	1	5	7	19	3	117	95	7	18	20	36	21	40	43		
7/07 1400	23	20	0	15	15	0	13	4	2	4	4	20	3	123	100	2	23	20	34	23	43	43		
7/09 1315	30	26	6	15	13	5	10	4	4	5	2	19	3	142	120	13	33	29	36	22	52	43		
7/11 1400	28	19	3	13	17	2	14	10	2	4	3	15	3	133	115	6	30	20	33	32	43	45		
7/13 745	29	20	6	13	15	1	13	5	1	4	3	16	3	129	110	7	33	22	31	24	50	42		
7/15 1530	20	21	4	8	12	5	10	9	3	3	3	14	3	115	98	12	22	23	25	28	46	52		
7/17 1045	31	21	1	11	14	5	15	4	5	3	2	18	3	133	112	10	32	21	35	24	47	40		
7/19 1130	28	16	1	14	12	7	8	6	2	4	4	17	3	122	102	10	29	16	31	26	44	42		
7/21 1700	19	7	1	16	5	2	5	9	1	5	2	16	2	90	72	6	20	7	28	17	38	34		
7/23 1445	29	18	2	14	10	3	16	9	1	6	3	14	2	127	111	5	30	19	38	24	44	38		
7/25 1630	22	14	6	13	7	3	6	9	2	3	4	13	2	104	89	12	26	16	25	22	47	43		
7/27 1530	23	21	6	16	13	0	6	6	4	4	1	16	2	118	100	10	26	24	28	22	50	46		
7/29 845	24	17	5	17	11	3	8	4	4	5	3	15	2	118	101	12	27	19	34	21	46	39		
7/31 1545	19	12	2	15	10	4	10	2	1	5	2	16	1	99	82	9	20	13	33	16	40	35		
8/02 730	19	15	3	12	4	0	8	6	3	4	1	12	1	88	75	8	21	16	26	12	49	38		
8/04 1330	31	14	2	17	10	1	13	7	2	4	2	17	1	121	103	5	32	15	36	20	46	34		
8/06 1645	16	11	9	15	6	1	4	4	4	5	2	15	1	91	75	16	22	14	26	13	48	37		
8/08 1415	26	13	2	18	8	3	14	4	3	3	2	14	1	111	96	8	27	14	39	16	43	30		
8/10 1600	14	10	7	12	4	3	9	2	6	1	1	13	1	83	69	23	18	13	29	9	45	31		
8/12 1145	31	14	3	21	12	2	5	1	0	5	2	16	1	113	96	5	33	15	32	16	50	32		
8/14 1345	28	10	0	18	7	3	9	4	1	5	2	14	0	101	87	5	28	10	35	14	44	28		
8/16 1315	31	12	6	19	10	4	8	3	1	4	3	15	0	116	101	11	35	14	34	18	49	31		

Summary of mean monthly counts, 1979

ADM	ADF	AD?	SAM	SAF	SA?	JM	JF	J?	YM	YF	WP	MP	TOT STOT	ZUNK	AM/C	AF/C	IM/C	IF/C	ZAD	ZFEM		
MEAN	30	18	4	10	8	3	8	5	2	3	3	12	6	113	94	10	33	19	24	19	55	40
MAR	37	17	9	5	5	4	4	4	3	2	3	0	9	102	93	18	44	19	14	17	67	38
APR	40	20	5	8	4	3	5	4	2	2	3	4	9	110	97	11	44	21	18	14	67	36
MAY	29	19	3	7	5	3	6	4	1	2	3	10	11	104	83	9	32	20	17	13	63	40
JUN	27	19	3	9	13	2	12	6	1	3	3	18	5	122	99	7	29	20	25	24	50	45
JUL	24	18	3	14	12	3	11	6	2	4	3	17	3	120	101	8	26	19	32	23	45	42
AUG	25	12	4	17	8	2	9	4	2	4	2	15	1	103	88	10	27	14	32	15	47	32

Appendix Table C4.--Counts from 1980 on Laysan Island.

DATE TIME	ADM	ADF	AD?	SAM	SAP	SA?	JM	JF	J?	YM	YF	WP	MP	TOT	STOT	ZUNK	AM/C	AF/C	IM/C	IF/C	ZAD	ZPEM
3/16 1545	39	15	23	7	3	3	1	4	8	8	3	1	6	121	114	30	58	19	20	17	68	32
3/20 1330	37	12	7	8	3	1	3	2	5	8	3	1	7	97	89	15	43	13	23	10	63	26
3/22 1145	20	12	20	5	2	2	4	4	6	6	2	0	6	89	83	34	35	17	19	12	63	34
3/24 1215	39	13	9	10	5	5	7	5	4	9	4	1	6	117	110	16	47	14	32	17	55	29
3/28 1345	47	18	3	11	9	6	6	1	4	7	4	1	7	121	113	9	49	19	28	17	60	31
4/01 1300	41	21	8	6	5	2	5	2	3	10	5	1	7	116	108	12	47	23	24	14	65	34
4/05 1230	38	21	6	7	4	2	4	7	1	9	4	1	10	114	103	9	43	22	22	16	63	38
4/13 1415	47	24	6	16	9	2	6	4	1	11	5	4	12	151	135	7	52	25	35	23	57	36
4/15 1530	38	20	9	9	6	2	6	4	0	5	7	4	12	122	106	10	45	22	21	18	63	37
4/17 1530	40	23	10	10	7	4	6	4	1	5	2	3	13	128	112	13	48	25	24	15	65	36
4/21 1545	24	19	12	10	1	7	1	2	3	5	4	4	12	104	88	25	33	22	23	10	63	36
4/24 1230	36	17	17	7	2	4	4	5	4	6	5	5	11	123	107	23	51	19	22	15	65	32
4/25 1400	43	18	5	12	2	2	4	5	1	9	6	7	9	123	107	7	47	19	27	14	62	31
4/29 1445	29	12	16	4	4	6	6	3	3	6	2	7	8	106	91	27	43	14	21	13	63	30
5/03 1315	48	18	6	11	4	5	3	2	1	10	4	7	8	127	112	11	53	19	28	12	64	27
5/10 1600	34	21	6	5	6	1	3	5	1	8	5	10	6	111	95	8	38	23	17	17	64	42
5/11 1515	34	16	5	9	6	3	4	4	1	6	5	10	7	110	93	10	38	17	21	17	59	36
5/13 1015	34	17	7	7	8	3	2	1	1	7	1	10	8	106	88	13	40	18	18	12	66	35
5/15 1445	36	22	7	7	8	0	3	1	0	3	6	8	8	109	93	8	41	24	13	15	70	42
5/19 1500	27	18	6	9	8	0	2	3	0	2	4	11	6	96	79	8	31	20	13	15	65	44
5/23 1345	31	17	7	10	6	3	1	3	0	7	1	11	4	101	86	12	36	19	20	11	64	35
5/27 1345	30	13	2	14	9	0	2	7	0	4	6	14	4	105	87	2	32	13	20	22	52	41
5/31 1600	27	18	3	10	11	0	2	3	1	7	4	15	4	105	86	5	29	19	19	23	56	44
6/04 1430	30	20	3	14	13	1	1	5	1	3	4	14	7	116	95	5	32	21	19	19	56	47
6/08 1230	25	20	2	17	18	0	3	5	1	4	2	15	8	120	97	3	26	21	24	26	48	48
6/10 1645	16	20	2	6	12	2	6	5	0	4	9	15	8	105	82	5	17	21	17	27	46	59
6/12 1345	25	23	4	8	15	1	4	3	0	5	1	14	8	114	92	9	27	24	19	21	57	49
6/14 1445	29	20	2	13	14	1	6	6	0	6	7	14	8	126	104	3	30	21	25	28	49	46
6/16 1600	25	20	4	13	12	0	5	6	1	4	6	13	7	116	96	5	28	21	22	25	51	48
6/17 1445	25	21	4	11	13	0	7	9	0	6	2	15	7	120	98	4	28	22	24	24	51	47
6/18 1530	26	21	1	11	9	1	5	6	2	3	1	14	6	106	86	5	27	21	20	18	56	45
6/19 1230	24	18	2	13	10	0	8	5	2	4	3	17	6	110	87	2	25	19	25	18	51	42
6/20 1430	36	15	2	13	16	0	6	9	0	3	4	15	6	125	104	2	38	15	22	29	51	43
6/21 1700	14	18	4	7	9	1	5	6	1	2	3	15	6	91	70	9	16	20	15	19	51	56
6/24 1515	27	15	2	17	11	0	4	5	0	3	4	18	6	112	88	2	29	15	24	20	50	40
6/25 1245	24	16	5	16	9	0	6	7	0	4	2	17	6	112	89	6	28	17	26	18	51	40
6/26 1145	32	18	5	12	10	3	5	9	0	5	3	17	6	125	102	8	36	19	24	23	54	42
6/27 845	27	17	17	11	12	5	6	5	2	4	5	11	7	129	111	22	39	22	24	26	55	42
6/28 1515	18	15	2	14	8	1	4	7	0	6	4	15	7	101	79	4	19	16	25	19	44	44
6/30 1200	33	17	7	17	13	2	6	6	3	4	6	14	7	135	114	11	38	19	30	27	50	40
7/02 1115	39	17	0	18	12	0	6	8	0	7	3	14	7	131	110	0	39	17	31	23	51	36
7/03 1230	42	17	1	17	10	0	8	8	0	7	6	15	7	138	116	1	43	17	32	24	52	36
7/04 800	12	18	6	17	9	3	4	8	1	7	1	13	7	106	86	12	15	21	30	20	42	47
7/06 1415	27	16	2	19	8	0	7	6	0	6	5	18	5	119	96	2	28	17	32	19	47	37
7/08 1730	17	15	1	16	3	2	5	7	1	5	2	17	4	95	74	5	18	15	28	13	45	38
7/09 1415	22	13	3	17	6	0	4	6	0	6	3	19	4	103	80	4	24	14	27	15	48	36
7/10 1500	13	13	2	15	10	1	5	4	0	7	5	16	4	95	75	4	14	14	28	19	37	44
7/11 1515	23	15	1	15	6	1	4	4	0	6	4	18	4	101	79	3	24	15	26	14	49	37
7/12 1345	27	18	6	19	11	0	6	4	0	5	4	17	4	121	100	6	31	20	30	19	51	39
7/14 1630	23	14	3	13	6	1	3	4	1	4	6	14	3	95	78	6	25	15	21	17	51	41
7/16 1445	26	14	6	19	5	2	2	6	1	7	6	10	3	107	94	10	30	16	30	18	49	36
7/18 1445	29	14	1	16	3	1	5	7	1	7	2	16	3	105	86	3	30	14	29	13	51	31
7/19 1530	19	16	5	16	3	2	9	6	0	9	6	16	3	110	91	8	22	18	36	15	44	37
7/20 1400	27	17	1	24	7	0	4	5	0	8	7	20	3	123	100	1	28	17	36	19	45	36

Appendix Table C4.--Continued.

DATE TIME	ADM	ADF	AD?	SAM	SAF	SA?	JM	JF	J?	YM	YF	WP	MP	TOT STOT	ΣUNK	AM/C	AF/C	IM/C	IF/C	ΣAD	ΣFEM	
7/21 1610	18	15	1	20	5	2	5	4	0	6	6	18	3	103	82	4	19	15	33	15	41	38
7/22 1600	19	20	4	20	8	1	4	4	0	10	8	14	3	115	98	5	21	22	35	20	44	43
7/24 1600	19	18	2	20	6	0	7	3	0	11	6	16	3	111	92	2	20	19	38	15	42	37
7/26 1415	16	19	1	23	5	0	3	8	2	12	6	19	3	117	95	3	17	19	39	20	38	42
7/27 900	23	16	4	21	4	1	4	7	1	11	5	17	3	117	97	6	26	17	37	17	44	35
7/28 1730	10	10	0	14	7	2	1	1	2	9	3	12	3	74	59	7	10	10	26	13	34	38
7/29 1600	16	9	3	15	3	1	4	8	1	9	3	13	2	87	72	7	18	10	29	15	39	34
7/30 1315	34	18	5	23	6	0	6	6	0	14	6	18	2	138	118	4	37	20	43	18	48	32
8/01 1300	33	9	3	22	4	0	9	7	0	12	4	18	1	122	103	3	35	10	43	15	44	24
8/03 1300	30	11	2	20	5	0	6	5	0	13	7	20	1	120	99	2	32	17	39	17	43	29
8/04 1615	20	9	14	17	8	2	4	5	0	11	6	16	1	113	96	17	30	13	33	20	45	34
8/05 1415	28	13	3	15	6	3	2	5	1	7	5	14	1	103	88	8	30	14	26	18	50	36
8/07 1330	35	10	1	22	5	0	8	4	0	11	5	15	1	117	101	1	36	10	41	14	46	24
8/09 1545	33	9	3	17	6	1	3	4	1	12	5	15	1	110	94	5	35	10	33	16	48	27
8/11 1515	35	8	2	16	5	1	4	6	0	10	5	16	0	108	92	3	37	8	31	16	49	27
8/12 1330	26	12	4	21	4	3	4	7	0	9	5	16	0	111	95	7	29	13	37	16	44	31
8/13 1115	36	12	1	20	6	0	7	5	0	10	6	14	0	117	103	1	37	12	37	17	48	28
8/14 1745	21	10	6	14	3	1	3	5	1	10	5	7	0	86	79	10	25	12	28	14	47	33
8/15 1115	34	9	0	22	2	0	6	6	1	12	6	17	0	115	98	1	34	9	41	15	44	24
8/17 1600	32	14	5	18	6	0	7	6	2	9	6	16	0	121	105	7	35	16	35	19	49	33
8/19 1230	44	11	1	28	6	1	4	7	0	12	5	18	0	137	119	2	45	11	45	18	47	25
8/20 1545	50	7	1	20	8	0	6	4	0	11	6	22	0	135	113	1	51	7	37	18	51	22
8/21 1515	49	7	3	24	7	0	6	7	0	10	4	18	0	135	117	3	52	7	40	18	50	22
8/22 1245	55	8	1	21	5	0	4	8	0	9	8	22	0	141	119	1	56	8	34	21	54	24
8/23 1500	49	9	5	19	3	0	5	5	1	10	4	19	0	129	110	5	53	10	35	13	57	20
8/25 1530	51	8	4	9	2	1	6	6	0	8	8	16	0	119	103	5	54	9	24	16	61	24
8/27 1530	50	14	9	16	1	0	5	6	0	8	7	19	0	135	116	8	57	16	29	14	63	26
8/28 1600	53	10	5	13	3	1	5	4	2	9	6	11	0	122	111	7	57	11	29	14	61	22
8/29 945	57	11	2	23	4	0	6	4	0	8	5	18	0	138	120	2	59	11	37	13	58	20
8/31 1700	43	12	14	16	2	1	4	2	1	8	7	13	0	123	110	15	54	15	30	11	63	24
9/02 1415	64	8	2	20	4	2	9	7	1	11	4	20	0	152	132	4	66	8	42	16	56	18
9/04 1430	62	9	8	16	1	3	3	5	0	12	7	21	0	147	126	9	69	10	34	13	63	18
9/05 1445	78	9	0	9	0	0	4	3	2	8	4	17	0	134	117	2	78	9	22	8	74	14
9/06 1615	64	8	11	12	3	0	7	2	0	6	3	15	0	131	116	9	74	9	25	8	72	15
9/08 1600	58	10	8	6	5	5	1	2	4	8	2	13	0	122	109	16	65	11	19	14	70	23
9/10 1115	68	11	5	16	2	1	4	3	2	8	6	17	0	143	126	6	72	12	30	12	67	19
9/13 1145	70	11	10	14	4	2	6	5	1	11	3	16	0	153	137	9	79	12	33	13	66	18
9/15 1215	50	8	30	12	5	2	5	6	2	5	3	17	0	145	128	27	76	12	24	16	69	22
9/17 1315	81	7	2	13	2	1	4	6	1	6	3	16	0	142	126	3	83	7	24	12	71	15

Summary of mean monthly counts, 1980

ADM	ADF	AD?	SAM	SAF	SA?	JM	JF	J?	YM	YF	WP	MP	TOT STOT	ΣUNK	AM/C	AF/C	IM/C	IF/C	ΣAD	ΣFEM		
MEAN	35	15	5	14	6	1	5	5	1	7	5	13	4	117	100	8	39	16	28	17	55	33
MAR	36	14	12	8	4	3	4	3	5	8	3	1	6	109	102	20	47	16	25	14	62	30
APR	37	19	10	9	4	3	5	4	2	7	4	4	10	121	106	14	45	21	24	15	63	35
MAY	33	18	5	9	7	2	2	3	1	6	4	11	6	108	91	8	37	19	19	16	62	38
JUN	26	18	4	13	12	1	5	6	1	4	4	15	7	115	94	6	28	20	23	23	51	46
JUL	23	16	3	18	7	1	5	6	1	8	5	16	4	110	90	4	25	16	32	17	46	38
AUG	39	10	4	19	5	1	5	5	0	10	6	16	0	121	104	5	43	11	35	16	51	26
SEP	66	9	8	13	3	2	5	4	1	8	4	17	0	141	124	9	74	10	28	12	67	18

Appendix Table D.--Tag numbers read on Laysan Island. Sighting records of tagged seals seen on Laysan Island from 1977 through 1980.

Tag	Sex	Originally Tagged			Years Seen			
		Date	Age	Atoll	1977	1978	1979	1980
A5	F	3/12/67	Year	FFS	x	x	x	x
A43	F	3/19/67	P	Laysan	x	x		
A59	F	3/19/67	P	Laysan	x	x	x	
A389	F	9/05/68	P	Laysan	x	x	x	x
707	F	6/02/69	P	Laysan	x	x	x	x
708	M	6/02/69	P	Laysan	x	x		
764	M	7/ /70	P	FFS	x	x	x	
818	F	3/26/69	Year	Laysan	x	x	?	
931	F	8/17/70	P	Laysan	x			
944	F	8/17/70	P	Laysan	x	x	x	x
945	M	8/17/70	P	Laysan	x			
1018	M	9/07/71	P	Laysan	x	x	x	x
1072	M	9/10/72	P	Laysan	x	x		
1073	F	9/10/72	P	Laysan	x			
1074	M	9/10/72	P	Laysan	x	x	x	x
1092	F	5/ /72	P	FFS	x	x	x	

Appendix Table E.--Reproductive patterns of mature females. Yearly reproductive status of females classified as adult and seen in 3 or more years on Laysan Island (P = parturient, N = nonparturient, S = subadult size, - = not seen).

Female	1977	1978	1979	1980	
01	P	P	P	P	Tag number 389.
02	P	P	P	P	
03	P	P	P	P	Also pupped in 1976.
04	P	P	P	P	
05	P	P	P	P	
06	P	P	P	P	
07	P	P	P	P	
08	P	N	P	N	
09	P	N	P	N	
10	P	N	P	N	
11	P	N	P	N	
12	P	P	N	P	
13	P	P	P	?	Seen early in 1980 only.
14	P	N	N	P	Tag number 707.
15	P	N	N	P	
16	P	N	N	P	
17	P	N	P	P	
18	P	N	P	P	
19	P	N	P	P	
20	P	N	P	-	Also pupped in 1976.
21	P	N	N	P	
22	P	P	P	-	
23	S	P	P	P	
24	N	P	P	P	
25	-	P	P	P	
26	N	P	N	P	Tag number A5.
27	N	P	N	P	
28	N	P	N	P	
29	N	P	N	N	
30	-	P	N	P	
31	N	P	P	?	Seen early in 1980 only.
32	N	P	P	?	Seen early in 1980 only.
33	N	P	P	-	
34	-	P	N	P	
35	N	N	P	P	
36	P	P	P	-	
37	N	N	P	N	
38	S	N	N	P	
39	N	N	N	P	
40	N	N	P	-	Tag number A59.
41	N	N	P	-	
42	N	P	P	-	
43	N	N	N	P	Tag number 944.
44	N	N	N	N	

Appendix Table F1.--Survival data. Data used to calculate Figure 30 including age (in days), the number of pups which could have been seen at that age (N), and the number of pups known to be alive at that age (OBS).

Age	1977		1978		1979		1980		Total
	N	OBS	N	OBS	N	OBS	N	OBS	% Alive
Birth	42	41	29	28	32	31	33	32	97
10	42	40	29	28	32	29	33	28	92
20	41	39	29	28	32	29	33	27	91
30	41	37	29	28	32	29	33	27	90
40	40	36	29	28	31	27	33	27	89
50	40	36	29	28	31	27	33	27	89
60	39	35	29	28	30	26	33	27	89
70	39	34	29	28	29	25	33	27	88
80	39	34	29	28	28	24	32	26	88
90	37	32	29	26	27	24	30	24	86
100	36	29	28	25	23	20	30	24	84
110	34	27	28	25	18	16	26	20	83
120	31	24	28	24	15	14	24	18	82
130	29	23	24	21	11	10	23	17	82
140	25	19	22	19	9	8	22	16	80
150	21	17	20	17	7	6	21	16	81
160	16	13	19	16	5	4	18	13	79

Appendix Table F2.--Data used to calculate Figure 31. Laysan data are from Appendix Table F1; Midway data from Rice (1960); and Kure data from Wirtz (1968).

Age (days)	N	Laysan		Midway (N = 17)		Kure (N = 56)	
		OBS	% Alive	OBS	% Alive	OBS	% Alive
10	136	126	92	12	71	50	89
20	135	123	91	11	65	46	82
30	135	121	90	9	53	36	64
40	133	118	89	8	47	15	27
50	133	118	89	7	41	3	5
60	131	116	89	6	35	2	4
70	130	114	88	6	35	2	4

Appendix Table F3.--Data used to calculate Figure 32. N = number of pups which would have been at least "age" days old at the end of their yearling field season. OBS = the number of those pups which had not died or disappeared by that age.

Age (days)	1978		1979		Total
	N	OBS	N	OBS	% Alive
Birth	29	28	32	31	97
52	29	28	32	28	92
104	29	26	32	27	87
157	29	25	32	27	85
209	29	24	32	27	84
261	29	21	32	27	79
313	29	19	32	27	75
365	29	17	32	26	71
417	29	17	32	26	71
470	20	10	29	22	65

Appendix Table F4.--Data used in Appendix Table F3. First year survival for pups born on Laysan in 1978 and 1979. Pups are numbered in order of birth for each year. Column headings are: Age last seen = age (in days) of a pup when last seen (if the seal was seen within 2 weeks of its "max. pos. age" it was listed as surviving to that age); Max. pos. age = the number of days between birth of a pup and the end of the field season the following year (the maximum number of days an animal could have been seen); Status: S = survived through the yearling field season, D = disappeared (migrated or died) prior to the end of the yearling field season, or M = known mortality; Assigned M/D age - estimated disappearance age (seals which disappeared during a field season were given an M/D age 1 day after their last sighting, and seals which disappeared between field seasons were given an M/D age halfway between their last sighting and the start of the next field season).

1978 pups	Age last seen	Max. pos. age	Status	Assigned M/D age	Notes
1	559	559	S	--	
2	551	551	S	--	
3	521	521	S	--	
4	454	519	D	455	M/D during 1979 season.
5	211	519	D	286	M/D between October 1978 and the 1979 season.
6	270	515	D	314	M/D between December 1978 and the 1979 season.
7	508	508	S	--	
8	265	508	D	308	M/D between December 1978 and the 1979 season.
9	117	504	D	118	M/D during 1978 season.
10	162	501	D	163	M/D during 1978 season.
11	500	500	S	--	
12	89	498	D	90	M/D during 1978 season.
13	493	493	S	--	
14	450	491	D	451	M/D during 1979 season.
15	489	489	S	--	
16	442	483	D	443	M/D during 1979 season.
17	482	482	S	--	
18	482	482	S	--	
19	83	482	D	84	M/D during 1979 season.
20	473	473	S	--	
21	469	469	S	--	
22	354	462	D	355	M/D during 1979 season.
23	213	459	D	257	M/D between December 1978 and the 1979 season.
24	459	459	S	--	
25	338	448	D	339	M/D during 1979 season.
26	0	443	M	0	Born dead.
27	442	442	S	--	
28	442	442	S	--	
29	176	418	D	218	M/D between December 1978 and the 1979 season.

Appendix Table F4.--Continued.

1979 pups	Age last seen	Max. pos. age	Status	Assigned M/D age	Notes
1	576	576	S	--	
2	576	576	S	--	
3	574	574	S	--	
4	562	562	S	--	
5	33	559	D	34	M/D during 1979 season.
6	554	554	S	--	
7	553	553	S	--	
8	548	548	S	--	
9	547	547	S	--	
10	442	538	D	443	M/D during 1980 season.
11	535	535	S	--	
12	527	527	S	--	
13	525	525	S	--	
14	524	524	S	--	
15	523	523	S	--	
16	518	518	S	--	
17	490	515	D	491	M/D during 1980 season.
18	101	513	D	102	M/D during 1979 season.
19	338	508	M	338	Died during 1980 season.
20	3	507	M	3	Died during 1979 season.
21	8	506	M	8	Died during 1979 season.
22	506	506	S	--	
23	503	503	S	--	
24	497	497	S	--	
25	480	496	D	481	M/D during 1980 season.
26	490	490	S	--	
27	489	489	S	--	
28	0	485	M	0	Born dead.
29	471	471	S	--	
30	465	465	S	--	
31	457	457	S	--	
32	434	434	S	--	

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