Exxon Valdez Oil Spill
Restoration Project Final Report

1993 Trial Aerial Survey of Sea Otters in Prince William Sound, Alaska

Restoration Project 93043-2

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Study History: Restoration Project 93043, *Sea Otter Population Demographics in Areas Affected by the Exxon Valdez Oil Spill*, was initiated in 1993. The aerial survey reported herein was one of three components. The other two components of Project 93043 were a population model (reported separately, *A Population Model for Sea Otters in Western Prince William Sound*, by M. Udevitz, B. Ballachey, and D. Bruden) and 1993 mortality patterns (reported separately, in NRDA MM6 Report, *Age Distributions of Sea Otters Found Dead in Prince William Sound, Alaska, Following the Exxon Valdez Oil spill*, by D. Monson and B. Ballachey).

Abstract: We developed an aerial survey method for sea otters, using a strip transect design where otters observed in a strip along one side of the aircraft are counted. Two strata are sampled, one lies close to shore and/or in shallow. The other strata lies offshore and over deeper water. We estimate the proportion of otters not seen by the observer by conducting intensive searches of units (ISU's) within strips when otters are observed. Two studies were conducted in 1993 to improve methods of estimating the abundance of sea otters in Prince William Sound. The first study found no significant differences in sea otter detection probabilities between ISU's initiated by the sighting of an otter group compared to systematically located ISU's. The second study consisted of a trial survey of all of Prince William Sound, excluding Orca Inlet. The survey area consisted of 5,017 km^2 of water between the shore line and an offshore boundary based on shoreline physiography, the 100 m depth contour or a distance of 2 km from the shore. From 5-13 August 1993, two observers surveyed 1,023 linear km of high density sea otter habitat and 355 linear km of low density habitat. Our adjusted estimate of abundance is 16,814 sea otters with a proportional standard error of 0.38.

Key Words: *Enhydra lutris*, *Exxon Valdez*, oil spill, sea otter.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

EXECUTIVE SUMMARY

We have developed an aerial survey methodology for sea otters consisting of a strip transect design where all otters observed along one side of the aircraft are counted. Two strata are sampled proportional to expected sea otter abundance. One strata lies close to shore and/or in water less than 40 m deep. The other strata lies offshore and over water greater than 40 m deep. We estimate the proportion of otters not seen by the observer by conducting intensive searches of units (ISU's) within strips when otters are observed. The strip counts within ISU areas, divided by the ISU counts, provide estimates of detection probability for strip counts. Intensive searches consist of 3 repetitive passes around the perimeter of a 400 m diameter circle defined by the inner and outer boundaries of the strip.

Survey design research and development have been ongoing for three years. Methods and results from 1991 and 1992 are summarized following the introduction to provide the background necessary to evaluate the 1993 work. Two studies were conducted in 1993 as part of the continued development of an improved method of estimating the abundance of sea otters in Prince William Sound.

The first study found no significant differences in sea otter detection probabilities between ISU's initiated by the sighting of an otter group compared to systematically located ISU's. This allows increased efficiency in design by permitting ISU's to be initiated by the presence of a group of sea otters rather than through systematic selection.

The second study consisted of a trial survey of all of Prince William Sound, excluding Orca Inlet. The survey area consisted of 5,017 km^2 of water between the shore line and an offshore boundary based on shoreline physiography, the 100 m depth contour or a distance of 2 km from the shore. From 5-13 August 1993, two observers surveyed 1,023 linear km of high density sea otter habitat and 355 linear km of low density habitat. Our adjusted estimate of abundance is 16,814 sea otters with a proportional standard error of 0.38. Significant differences in detection probabilities between observers and high variance in the low density stratum contributed to the lack of precision in our trial survey point estimate. This variance can likely be reduced through increased ISU sampling effort, redefinition of the low density stratum and observer training designed to reduce variability in detection probabilities.

INTRODUCTION

Surveys of sea otter populations in the North Pacific have been conducted over the past several decades (Ebert 1968, Kenyon 1969, Estes 1971, Pitcher 1975, Schneider 1975, Estes 1977, Estes and Jameson 1983, Jameson et al. 1986, Simon-Jackson 1986, Johnson 1987, Irons et al. 1988, Pitcher 1989, Douglas et al. 1990, Burn 1994). The primary objective has been to describe changes that may have occurred in the abundance and distribution of the species over time or to provide baselines against which future surveys may be compared. Previous methods were based on counts from the ground (Estes and Jameson 1988), small or large vessels (Jameson et al. 1982, Johnson 1987), fixed (Ebert 1968, Simon-Jackson et al. 1986) or rotary wing aircraft (Pitcher 1975, Douglas et al. 1990), or a combination of two or more platforms (Jameson et al. 1986).

Two factors have generally led to difficulty in interpreting survey data. First, with the exceptions of Estes and Jameson (1988) and Udevitz et al. (1995), methods have not been rigorously tested to determine the proportion of the animals actually observed and the effects of activity and environmental conditions on detection probabilities. Second, excepting Estes and Jameson (1988), Jameson et al. (1986), and Burn (1994), survey methodologies have not been standardized, creating difficulty in comparing estimates generated by different methods.

Counts of sea otters from the ground have been generally recognized as providing the most accurate estimates of near shore sea otter abundance (Schneider 1971). Estes and Jameson (1988) estimated the probability of sighting sea otters was 94.5% for standardized shore side counts, using two experienced observers, high-resolution 10X binoculars and 50X Questar telescopes (New Hope, PA). This was the first study to rigorously evaluate the effect of activity, group size and distance from observer on sighting probability of sea otters. Their results provide a baseline against which other methods might be evaluated. However, due to limited access and transportation along most coastlines, ground counts can not be used over the large geographic areas occupied by most sea otter populations.

Initial damages to the sea otter population resulting from the *Exxon Valdez* oil spill included lethal and sub-lethal levels of direct exposure. One method used to estimate the total immediate loss to the sea otter population in Prince William Sound (PWS) was a comparison of estimates of sea otter abundance based on boat surveys conducted before and after the spill (Garrott et al. 1993). Boat surveys were used after the spill to estimate sea otter density (Burn 1994) in order to be consistent with the method used before the spill. This consistency was necessary for assessing the immediate loss of otters, but it became widely recognized that boat survey methodology, as conducted, would not provide population estimates with accuracy necessary for management purposes, primarily due to detection bias and sea otter avoidance behavior (Burn 1990, Udevitz et al. 1994, Burn 1994).

The long term objective of this study was to develop and implement a standardized survey methodology that will provide improved accuracy and precision in estimates of sea otter abundance and that will be applicable throughout the species' range. Our objectives in this report are to: 1) provide a summary of the methods and results of the survey platform evaluation conducted in 1991 and the trial survey conducted in western PWS in 1992, 2) present results of the 1993 survey methodology research and the 1993 PWS sea otter survey, and 3) to recommend changes in survey design and methodology that could potentially increase precision and efficiency.

Summary of 1991 and 1992 Research Results

Due to otter diving behavior it is not possible to use standard line or strip transect techniques in sea otter surveys. These methods rely on the assumption that all of the animals in some region (e.g., on the line or in the strip) are seen. To obtain unbiased density estimates, we need to develop estimates of the actual probability of detecting animals with the survey protocol. Our approach is based on the assumption that the probability of detecting otters in a strip transect survey can be reliably estimated based on intensive searches over subsamples of the strips (intensive search units or ISU's). Detection probability is estimated by comparing the number of otters detected in ISU's with the strip transect protocol to the number determined to be actually present with the intensive search protocol. Strip transect counts can then be adjusted by the estimated detection probability.

Aircraft Evaluation

The first phase of this work consisted of trials conducted in April and July, 1991 to evaluate the suitability of a float-equipped Piper PA-18 Super-Cub as the platform for this type of sea otter survey. The Super-Cub has been selected repeatedly for wildlife survey work based on its slow stall speed and high degree of maneuverability (Erickson and Siniff 1964, LeResche and Rausch 1974, Gasaway et al. 1986). It seats one pilot and one passenger in tandem, an arrangement recommended by Erickson and Siniff (1964) as allowing navigation and observation to occur from the same spatial orientation in the plane.

The overall objective of the trials was to evaluate the validity of the assumption that all of the otters present in subsamples of strip transects could be detected with intensive searches. Specific trails were designed to evaluate the accuracy with which strip boundaries could be delineated by an observer in the aircraft, to provide a general idea of the detectability of sea otters as a function of distance from the aircraft, and to evaluate the effects of altitude, search pattern and search duration on the proportion of otters detected during intensive searches. Assuming that the aircraft proved suitable, the information generated by the trials was expected to provide guidance for developing a survey protocol.

1. Strip delineation

By aligning a mark on the struts with the outer margin of the floats an observer can assure consistent viewing orientation and define an inner margin of the strip (Fig. 1). By sighting, from the predetermined orientation, through marks placed further out on the struts, boundaries of strips of various widths can be identified. We used a clinometer to calibrate strut marks corresponding to strip widths extending in 50 m increments from 50 to 550 m with the aircraft at an altitude of 92 m.

We used radar and a small boat to evaluate the accuracy with which an observer, using the clinometer calibrated strut marks, could estimate perpendicular distances. The boat was placed at radar measured distances from shore while the aircraft flew along the shoreline at the specified altitude and the aerial observer estimated the distance to the boat using the strut marks. Distances were estimated to the nearest 25 m by interpolating between the strut marks. Distances estimated by the aerial observer were quite consistent but were slightly less than distances measured with radar (e.g., at a radar measured distance of 400 m the aerial observer consistently estimated a distance of about 350 m, Fig. 2).

This suggested that distance estimates based on strut marks could be sufficiently accurate if field trials were used for final calibration of the marks. Final calibration of clinometer established strut marks requires reference points, at the appropriate distances apart, on the surface that can be viewed from the aircraft at the specified altitude during level flight. For all subsequent work we used a radar equipped boat placed at measured distances off a straight shoreline to accomplish the final calibration.

2. Detection function

A series of randomly located line transects in western Prince William Sound were surveyed using standard line transect methodology (Buckland et al. 1993) in order to obtain a general idea of the pattern of detectability of sea otters from the aircraft. Transects were surveyed at a speed of 27 m/s and an altitude of 92 m. Observation was only on 1 side of the aircraft. The observer recorded the number of individuals and the perpendicular distance to each group of otters detected. Distances were recorded in 50 m distance categories based on strut marks calibrated as discussed above. A total of 135 groups of sea otters ranging in size from 1 to 6 individuals were detected (Fig. 3). The region of highest detectability appeared to be from about 150 to 300 m from the inner strip boundary. Eighty six percent of the detected groups were detected at distances less than 400 m. There was no apparent relation between group size and detectability over the rather limited range of group sizes that were observed (Fig. 4). In subsequent work, all strips were of finite width and observers made explicit efforts to focus their effort uniformly within the strip in order to increase detectability of groups at distances less than 200 m.

3. Intensive searches

Two series of trials were conducted to determine the proportion of the sea otters that could be detected by intensive searches. Both sets of trials used ground based observers to quantify the proportion of animals detected from the air. The first series of trials was conducted in April 1991 to assess the effect of altitude (altitude evaluation) on sea otter detectability. The second series of trials was conducted in July 1991 to assess the effect of search pattern (pattern evaluation) on sea otter detectability.

Trials were conducted on areas of ocean (survey units) that did not contain canopy forming kelp, were large enough to contain a full search pattern, allowed unrestricted observation from an adjacent vantage point, and contained 1 or more otters immediately prior to arrival of the aircraft. Survey units were selected by ground crews based on previous reconnaissance and observation of the area immediately before ground crew deployment. All survey units for the altitude evaluation were located in Eastern Prince William Sound. Survey units for the pattern evaluation were distributed throughout Prince William Sound, though most were in the west.

Ground crews approached each selected survey unit by skiff after a thorough study of the area from offshore, taking care to minimize disturbance to sea otters. Following deployment at the vantage point, the ground crew defined the boundaries of the unit, established an orientation for the aerial search pattern and determined the position and activity of each otter within the unit. The ground crew then contacted the aircraft by VHF radio to begin the trial. Ground observations followed methods established by Estes and Jameson (1988). Immediately prior to arrival of the aircraft, the ground crew recorded the location, group size, number of dependent pups and activity of each otter or group of otters.

Activity categories included swimming (changing location), resting (stationary on water surface) and diving (stationary and temporarily submerging). The ground crew also recorded the location and behavior of all otters observed outside the boundaries of the unit, observations regarding changes in sea otter activity associated with the approach of the aircraft, and the time the aircraft entered and departed the unit. Following the departure of the aircraft, the ground crew was transported by boat to the next survey unit.

Altitude evaluation trials were conducted at 46 m, 92 m and 137 m above sea level. Trials were conducted in sets of 3, with one trial at each altitude, in random order, within each set. All altitude evaluation trials were conducted using a 750 m circle intensive search pattern. In this pattern, the aircraft was piloted along the circumference of a 750 m diameter circle while the aerial observer viewed the circumscribed area. The aircraft pilot was unable to assist in visual observation due to the technical aspect of the survey procedures. Aircraft speed was maintained as close as possible to 27 m/sec (60 mph). The pilot used a stopwatch, airspeed and minute of turn to define the 750 m diameter circle (128 seconds to complete, 32 seconds through each quadrant). The location and orientation of the circle was indicated by markers positioned at the vantage point by the ground crew. The aerial observer recorded the time, location, group size, number of pups and activity of each new sea otter or group of sea otters observed. Circling was continued until 5 minutes had elapsed without any new otters being observed.

Pattern evaluation trials were conducted using 3 different intensive search patterns in conjunction with a strip count. The same aircraft, but different pilots, were used for the altitude and pattern evaluations. All pattern evaluation trials were conducted at an altitude of 92 m above sea level and at a speed of 27 m/s. Each trial began with a strip count in which the plane flew along one edge of a strip transect while the aerial observer recorded the location, group size, number of pups and activity of each sea otter or group of sea otters observed in the strip. Width of the strip was determined by the aerial observer using distance indicators marked on the wing struts and was either 400 m or 750 m, depending on the subsequent search pattern. The length of the strip was either 400 m, 750 m or 800 m, depending on the subsequent search pattern. Immediately following the strip count, the plane began one of three search patterns over the strip that had just been counted. The aircraft was piloted along the circumference of either a 400 m diameter circle, a 750 m diameter circle, or a 400 m x 800 m oval while the aerial observer viewed the circumscribed area. Selection of the search pattern was made by the ground crew according to the distribution of sea otters and the physiography of the coastline, while attempting to obtain an equal number of trials for each pattern. Ground crews indicated the location and orientation of each strip, circle and oval with markers at the vantage point. The pilot used techniques analogous to those developed for the 750 m circle to maintain each of the other 2 search patterns. The aerial observer recorded the circle or oval number, location, group size, number of pups and activity of each new sea otter or group of sea otters observed during the search. Intensive search patterns were continued until 5 minutes had elapsed without any new otters being observed.

At the end of each day, ground and aerial crews compared the mapped locations of all observed otters (for both altitude and pattern evaluations). For the otters present in trial i, $i=1, \cdots, r$, when the aircraft arrived, the number observed by both crews (b_i), the number observed only by the ground crew (g_i), and the number observed only by the aerial observer (a_i) in the observation circle or strip were determined. The number of otters in the circle or strip before any response to the approaching aircraft was determined based on ground crew observations prior to the arrival of the aircraft.

Sea otter detection probabilities (detectabilities) for the aerial observer were estimated as

$$\hat{P}_d = \frac{\sum_{i=1}^{r} b_i}{\sum_{i=1}^{r} (b_i + g_i)} \quad , \tag{1}$$

where r is the number of trials. Detectabilities were also estimated separately for each trial as

$$\hat{P}_{di} = \frac{b_i}{b_i + g_i} \quad . \tag{2}$$

Kruskal-Wallis tests were used to evaluate differences in detection probabilities among altitudes and patterns. Fisher's exact test for contingency tables was used to evaluate the effect of altitude and pattern on the proportion of trials in which all otters were detected and the proportion of trials in which otters exhibited disturbance behavior. All statistical tests were conducted at the 0.05 significance level.

We conducted a total of 98 trials, with observations of 329 groups of sea otters (741 individuals), in our evaluation of altitude and search pattern. Intensive searches resulted in detectability estimates greater than or equal to 0.90 for all altitudes and patterns investigated (Tables 1 and 2). All otters were detected in over half of the samples (Tables 1 and 2). The type of avoidance behavior observed in boat surveys (Udevitz et al. 1995), in which otters leave the search area before the survey platform arrives, was not observed in response to the aircraft. However, on some occasions it was apparent that otters were disturbed and began diving, swimming out of the area, or swimming erratically within the search area in response to the aircraft after it arrived. However, due to the approach speed of the aircraft, otters were unable to leave the survey area prior to the aircraft arrival.

We could not detect any differences in detection probability between trials conducted at 46, 92, or 137 m altitude (P = 0.72, Table 1). We would expect detectability to decrease substantially at altitudes much greater than those we considered. In general, safety is expected to increase with altitude (for altitudes up to at least 164 m). We considered forty-six meters as the minimum altitude safe enough for conducting this type of survey work. However, at the 46 meter altitude, disturbance to sea otters within the survey area occurred on 0.23 of our trials, compared to 0.08 at 92 and 137 meters altitude (difference not significant, P = 0.84, Table 1). We selected an altitude of 92 m for conducting subsequent work because it provides an added margin of safety above 46 meters, and minimized disturbance without appreciably decreasing detectability.

We also found no differences among the 3 intensive search patterns evaluated (P = 0.64, Table 2). However, with the 400 m circle, the entire ISU remained within the observer's view at all times, making it easier to keep track of which otters and groups had already been detected. With both of the other two patterns, the portion of the ISU furthest from the plane was always out of view (although all portions of the ISU were eventially seen each time the plane circled around). Detection probability estimates for initial strip counts ranged from 0.52 to 0.72 (Fig. 5). Detection probabilities increased sharply with the first 3 circles or ovals after the strip count (range 0.88 - 0.93) and continued to increase slightly for the next 3 to 4 circles or ovals (Fig. 5). No new otters were ever detected after the 7th circle or oval. In the absence of strong differences in detection probabilities, selection of a search pattern could be based on the probability of encountering otters in each search. We hypothesize that this probability decreases with decreasing the size of the search pattern, thus increasing the number of ISU's necessary to obtain a detection probability estimate with a given level of precision. However, because of decreasing detection probabilities with distance from observer (Fig. 3), and the need to keep track of otters within ISU's, the 400 m diameter ISU and the corresponding 400 m strip width were selected for further evaluation.

The data suggest that the most efficient search intensity consisted of 3 circles or ovals after an initial strip count (Fig. 5). Even with intensive searches, however, not all of the otters were detected. Population size estimates based on correction factors derived from these types of intensive counts can be expected to be negatively biased on the order of 0.05-0.10. This amount of bias represents a substantial improvement over some previously used methods, such as uncorrected boat and aircraft surveys.

Trial Survey

In 1992 we designed and implemented a trial survey in western Prince William Sound, using the results of our 1991 studies as a foundation. The design consisted of a series of parallel strip transects, 400 m wide and 1.2 km apart, overlaying the study area (Fig. 6). Electrical tape on wing struts indicated the viewing angle and the 400 m strip width when the aircraft wings were level at 92 m and the inside boundary was in-line with the outside edge of the airplane floats (Fig. 1). Each transect was identified by its intersection with the shoreline and an offshore boundary based on shoreline physiography (bays and inlets < 6 km wide were included in the study area regardless of depth), and the 100 m depth contour or a distance of 2 km from the shore, whichever was greater. The criteria we used to define the sample area was based on maximum known sea otter dive depths (approx. 100 m) and the otter's requirement for frequent access to foraging habitat. A GPS in the aircraft was used to locate the endpoints and navigate along each transect. Endpoint coordinates were downloaded from an external source via a memory card to the aircraft GPS. The study area contained 2,404 km^2, between shore and the seaward boundary. Transects were flown at an airspeed of 27 m/s and an altitude of 92 m. The observer searched the 400 m region between the float and the strut marks, scanning as far forward as conditions allowed. The location and size of each otter group were recorded on a transect map. A group was defined as 1 or more otters spaced less than 3 otter lengths apart. Groups of more than 30 otters were circled until a complete count was made. A camera with a 70-210 mm telephoto lens was available to photograph any groups too large and concentrated to count accurately. The number of pups (determined by size, coloration and association with a larger animal), in a group was noted behind a slash (e.g., 6/4 = 6 adults and 4 pups). Activity was recorded for each group as either diving or non-diving. If any individual(s) in a group were diving, the whole group was classified as diving. Diving otters included any individuals that swam below the surface and out of view, whether traveling or foraging. Non-diving otters were animals seen resting, interacting, swimming (but not diving), or hauled-out on land. Observation conditions were noted for each transect (wind, seas, swell, cloud cover, and glare). The pilot did not assist in sighting sea otters. A list of equipment used in the survey and a protocol for methods and survey design is provided in Appendix 1. Strip transect data forms and ISU data forms with keys to data collection are provided in Appendices 2 and 3, respectively.

The intensive search method of estimating detectability developed here is expected to only be useful for relatively small groups of otters. We assume that groups of 30 or more otters within a 400 m strip will be detected with certainty. Thus we conceptually divide the population (as it exists during a given survey) into two portions and derive separate estimates for the portion that occurred in groups of 30 or less (small groups) and the portion that occurred in groups of more than 30 (large groups). Complete counts, aided by photography, are made of all detected large groups. These counts are expanded directly based on the proportion of the total area sampled, without any adjustment for detectability (i.e., detectability is assumed to be 1 for this portion of the population). The estimate for the portion of the population occurring in small groups is also expanded based on the portion of the total area sampled but is then adjusted based on the estimated detectability of otters in these groups. The overall estimate of the population size is obtained by summing the estimates for these two components of the population.

In general, more than 1 observer may participate in a survey and the study area may be stratified based on various habitat characteristics. A separate estimate of small group detectability is required for each observer. Each estimate should be based only on intensive searches conducted by that observer. For notational convenience, consider each portion of a stratum surveyed by a different observer to be a separate stratum. The unadjusted population size for stratum j can be estimated as:

$$\hat{Y}_{(un)j} = \frac{\sum_{i=1}^{n_j} y_{ij}}{\sum_{i=1}^{n_j} a_{ij}} A_j$$

$$var(\hat{Y}_{(un)j}) = \frac{A_j^2\,(1-f_j)\,n_j}{\left(\sum_{i=1}^{n_j} a_{ij}\right)^2 (n_j-1)} \sum_{i=1}^{n_j} \left(y_{ij} - \frac{a_{ij}\sum_{i=1}^{n_j} y_{ij}}{\sum_{i=1}^{n_j} a_{ij}} \right)^2 \qquad \textbf{(3)}$$

where

A_j = total area of stratum j,
n_j = number of surveyed transects in stratum j,
y_{ij} = number of otters detected in strip count on transect i in stratum j, $i=1,\cdots,n_j$,
a_{ij} = area of transect i in stratum j, and
f_j = the sampling fraction, approximated by

$$f_j = \frac{1}{A_j} \sum_{i=1}^{n_j} a_{ij} \; . \tag{4}$$

The correction factor for observer k can be estimated as:

$$\hat{p}_k = \frac{\sum_{i=1}^{t_k} c_i}{\sum_{i=1}^{t_k} s_i}$$

$$var(\hat{p}_k) = \frac{t_k \sum_{i=1}^{t_k} (c_i - \hat{p}_k s_i)^2}{(t_k - 1) \left(\sum_{i=1}^{t_k} s_i \right)^2} \tag{5}$$

where

s_i = number of otters detected in strip count of ISU i, $i=1,\cdots,t_k$, and
c_i = total number of otters detected after intensive search of ISU i.

The adjusted population size for stratum j (surveyed by observer k) can then be estimated as:

$$\hat{Y}_j = \hat{p}_k \, \hat{Y}_{(un)j}$$

$$var(\hat{Y}_j) = \hat{Y}^2_{(un)j} \, var(\hat{p}_j) + \hat{p}_j^{\,2} \, var(\hat{Y}_{(un)j}) - var(\hat{p}_j) \, var(\hat{Y}_{(un)j}) \; . \tag{6}$$

For the portion of the population in large groups, population size estimates for each stratum can be obtained as in (3) with no adjustment for detectability. The overall estimates of population size and variance for each stratum can then be obtained by summing the respective estimates for otters in small and large groups. Combined estimates of population size and variance for any (or all) of the strata can be obtained by summing the respective overall stratum estimates.

In the 1992 trial survey, a single observer surveyed 1,936 linear km of transects (744.4 km^2). There was no stratification and no large groups (more than 30 individuals) were detected. Intensive search units were systematically located by time along the transects, each consisting of three concentric circles over a 400 m diameter circle within the width of the survey strip. Otters were observed in 18 of the intensive search units. Estimates based on the 1992 trial survey in western PWS are presented in Table 3. The distribution of otters encountered in the 1992 survey suggested that about 85% of the otters were in 32% of the survey area, in water depths less than 40 m (Fig. 7).

Results of the 1992 trial survey suggested that precision in the estimate of abundance could be improved by: 1)increasing our sample size of ISU's, used to estimate detection probabilities and 2) by stratifying the survey area into high and low density strata and allocating sampling effort proportional to expected densities (Fig. 7). Our research efforts in 1993 were aimed at investigating and implementing these strategies, as outlined in the following sections.

METHODS AND MATERIALS

ISU Studies - 1993

The precision of ISU detection probabilities is limited by the number of intensive search units in which otters are observed. In the trial survey of 1992, otters were observed in only a small proportion of the systematically located ISU's. Systematically located ISU's are usable for estimating detection probability only when they contain one or more otters. The objective of the July 1993 research was to investigate methods for increasing the proportion of usable ISU's. If the probability of detecting each group of otters is independent, then detection probabilities could be estimated for ISU's initiated upon detection of a group, with the estimate only based upon any additional groups that might be present in the ISU. Group initiated ISU's would be usable only if they contained additional groups. Because otter groups tend to occur in clusters, this could result in a higher proportion of usable ISU's. The July 1993 research focused on comparing detection probabilities and proportions of usable ISU's obtained from systematically located and group-initiated searches.

Systematic ISU's were located at two minute intervals along 400 m wide strip transects within high and low density strata (see PWS Trial Survey below) in eastern Prince William Sound. Group-initiated ISU's were located at each otter group separated by more than 800 meters (30 seconds) along 400 m wide strip transects, also in high and low density strata in eastern Prince William Sound. Most of the transects (and associated ISU's) were surveyed by a new observer (designated GE), but a number of the transects were surveyed by the observer who had participated in the 1991 trials (designated JB). For each group of sea otters, observers recorded the activity and number of otters observed (independents and dependents) on the strip count and the number observed during the intensive search. Size and activity of the initiating group were recorded separately when the ISU was group-initiated. Detection probabilities were estimated based on all detected otters in each systematically located ISU that contained otters. For group-initiated ISU's, detection probabilities were based on all otters except the initial group in ISU's that contained additional groups. Detection probabilities were estimated according to equation (2) for both types of ISU. Differences between detection probabilities by type of ISU, observer, and stratum were compared with Kruskal-Wallis tests at a significance level of 0.05. The overall test was followed by pairwise contrasts (Conover 1980:231) if $P \leq 0.05$. The same testing procedure was used to compare differences between the proportion of diving groups by observer and stratum. Power ($1-\beta$) of selected tests was estimated using a bootstrap technique patterned after the approach of Collins and Hamilton (1988).

PWS Trial Survey - 1993

We designed and implemented a trial survey throughout all of Prince William Sound, excluding Orca Inlet, in August of 1993, using the results of 1991, 1992, and 1993 research. The survey was conducted using the same methodology as in 1992 with the following exceptions: 1) two strata, a high and low density, were sampled proportional to expected abundances, 2) two observers conducted the survey, and 3) the sampling intensity per unit area was lower (a larger area was sampled with similar effort) in 1993.

Using the spatial distribution data obtained in the 1992 trial survey, we identified two strata. Sea otter habitat was sampled by strip transect counts in each of these strata, high density and low density, distinguished by distance from shore and/or depth contour (Fig. 9). The high density stratum extended 400 m seaward from shore or to the 40 m depth contour, whichever was further from shore. The low density stratum extended from the offshore high density boundary to an offshore boundary based on shoreline physiography, and the 100 m depth contour or a distance of 2 km from shore, whichever was greater. Bays and inlets less than 6 km wide were included in the high density stratum, regardless of depth. Parallel strip transects were spaced systematically within each stratum. Survey effort was allocated in proportion to expected otter abundance (Fig. 7), with approximately 0.20 of the high density stratum sampled (every 5th strip) and 0.05 of the low density stratum sampled (every 20th strip).

Based on the results (see below) of 1993 ISU studies, ISU's were initiated by the sighting of the first group observed within each 15 minute period of an hour (0-15, 15-30 ...) in the high density stratum and by each group sighted in the low density stratum on a strip transect. All successive ISU's were separated by a minimum distance of 800 m (30 seconds). The initiating group sighting was followed by 3 concentric circles flown over the 400 m strip. The ISU began at a point on the transect line that was perpendicular to a line from the transect to the group that initiated the ISU. The pilot used a stopwatch to time the minimum 30 second spacing between consecutive ISU's and to navigate the circumference of each circle. ISU locations were drawn on the transect map and group size and activity recorded on a separate data sheet for each ISU. For each group, we recorded the number of otters observed (independents and dependents) on the strip count and the number observed during the intensive search. Sizes of initiating groups were recorded separately. Otters that swam into an ISU post factum were not included. Population size for Prince William Sound, excluding Orca Inlet, was estimated according to equations (3) - (6).

RESULTS

ISU Studies - 1993

In July 1993, we conducted searches in 101 systematically located ISU's and 99 group initiated ISU's (Table 4). Systematically located ISU's could only be used for estimating detection probabilities if they contained at least one sea otter. Twenty-one of 101 (0.208) systematic ISU's met this criteria. Group initiated ISU's could be used for estimating detection probabilities only if they contained more than one group of sea otters. Forty-one of 99 (0.414) group initiated ISU's met this criteria. Kruskal-Wallis tests indicated that detection probabilities did not depend on the method for locating ISU's (P = 0.27 for GE, P = 0.86 for JB)., though the power of these tests were quite low ($1-\beta$ = 0.28 for GE, $1-\beta$ = 0.16 for JB). Differences between observer were significant for both methods (P = 0.02 for group-initiated, P = 0.01 for systematic). Differences in detection probabilities between strata were not significant for either observer (P = 0.23 for GE, P = 0.63 for JB). Differences in the proportion of diving groups were not significant for observer or strata (P = 0.07). Based on these data we used group-initiated ISU's in the 1993 trial survey.

PWS Trial Survey - 1993

In August 1993, we conducted a trial survey of the entire Prince William Sound, excluding Orca Inlet. The survey area consisted of 5,017 km^2 (Fig. 8) and was partitioned into two stratum (high and low) as defined above. We sampled 1,023 linear km of high stratum transects (approximately 0.20 of total) and 355 linear km of low stratum transects (approximately 0.05 of total) using two observers (Table 5). A total of 934 otters were detected in small groups in the surveyed transects. Forty ISU's with more than one group of otters were searched, resulting in correction factors of 1.23 for JB and 3.27 for GE (Table 5). In addition to the small groups, 52 otters were detected in a single large group (size > 30). This expanded to a population size estimate of 277 otters (SE = 249) occurring in large groups. Combining the adjusted stratum estimates for small groups (Table 5) and the estimate for large groups gave an estimate of 16,814 sea otters (SE = 5,741) in Prince William Sound, excluding Orca Inlet. Flight time required to complete the survey was 79.9 hours, including transit.

DISCUSSION

Previous researchers have recognized that some proportion of sea otters in the area surveyed are not observed, regardless of the method employed. The result is a bias in the estimate of abundance. This bias can be reduced by estimating the proportion of animals not observed, and using the reciprocal of this proportion as a correction factor. Correction factors may be affected by differences in observers and by survey conditions. Thus, any survey method should incorporate techniques for estimating a correction factor specific for the observers and conditions associated with each application of the method.

An evaluation of the PA-18 Super-Cub as a survey platform indicated that detection probabilities in strip counts were low (0.52 - 0.72), but that intensive searches over selected portions of the strip could provide correction factors to compensate for most of the detectability bias. Use of this approach in a trial survey suggested that precision could be improved by optimizing sampling effort among strata and increasing the usable sample of ISU's. Research conducted in 1993 indicated that for a given number of ISU's, the number of usable ISU's could be approximately doubled by initiating searches only when groups were detected. Detection probability estimates based on group initiated ISU's will not be more biased than estimates based on systematically located ISU's if the initiating group is not included in the estimate and if the detection of groups is independent. The assumption of independence of group detection is common in line transect theory (e.g., Burnham et al. 1980, Quang and Lanctot 1991, Buckland et al. 1993). Though the power of the tests was low, the fact that we did not find differences in estimated detection probabilities between the two methods for locating ISU's is also consistent with this assumption.

The potential for relations between size and detectability of animal groups is well known (Buckland et al. 1993) and the relation has been demonstrated for sea otters in certain cases (Estes and Jameson 1988, Drummer et al. 1990). Our line transect data did not indicate any effect of group size on detectability, but the range of observed group sizes was quite small. Other studies have found that group size effects were not evident for sea otters when there was little variation in group size or observation distances were relatively short (Udevitz et al. 1995, Drummer et al. 1990). Buckland et al. (1993) suggested that group size effects can usually be eliminated by truncating observation distances. We only apply the ISU technique for estimating detection probabilities of groups with less than 30 individuals and observation distances are truncated at 400 m. Thus, it is unlikely that there would be any strong group size effects on detectability in these surveys. In any case, if detections of groups are independent, the size of the initially detected group (or its detection probability) will not affect the estimated detection probabilities in group-initiated ISU's.

Our experience with the 1993 ISU study and trial survey indicates that differences in detectability between observers may be large. A difference in detectability between observers will not increase the bias of the adjusted population estimate as long as the correction factor for each observer is estimated separately. This can be done, as long as each observer can achieve the minimum acceptable detectability (i.e., 90%) in the intensive searches. The precision of the estimated correction factors will depend on the number of usable ISU's for each observer. The 1993 data also suggest that correction factor estimates may be more variable for less experienced observers. It may be possible to reduce this variability with additional experience or more rigorous training. In order to achieve an acceptable level of precision for the adjusted population size estimates, it will be necessary to either limit the number of observers or increase the sampling intensity so that a sufficient number of usable ISU's are obtained for each observer.

We were able to improve our allocation of sampling effort in the 1993 survey by stratifying sampling in proportion to expected densities within each stratum, but proportional standard errors for the total estimated population size were larger in the 1993 survey than in the 1992 trial survey. Several factors apparently contributed to the reduced overall precision. First, our sampling effort was slightly less in 1993 compared to 1992, while the survey area more than doubled, resulting in high variances in counts, particularly among low density transects. Also, a second observer participated in the 1993 survey. Because of inter-observer differences in detection probabilities (Table 4) we had to estimate separate correction factors for each observer. Splitting the ISU's among observers resulted in small sample sizes with high standard errors. The higher variability associated with the larger area surveyed and the large standard errors associated with estimating two correction factors led to a decrease in the precision of the population estimate between 1992 and 1993. It should be noted that the smallest sample size of ISU's (13/40) was available for estimating the detection probability of the observer with the most variation in detection probabilities (GE). If only one observer had conducted the survey so that all ISU's could be used to estimate a single correction factor, or if more of the ISU effort had been allocated to the observer with the greater variability, the precision of the overall estimate could have been substantially improved.

Future efforts to improve precision and efficiency should include a training regime to decrease variability in detection probabilities and assure that all observers detect at least 90% of the otters within ISU's. Additionally, the survey should be designed so that each observer obtains 40 usable ISU's. We did not detect differences in detectability or diving behavior (that would be expected to affect detectability) between strata. This suggests that focusing ISU's in the high density stratum where ISU's can be located most efficiently may not increase the bias of detectability estimates. Further improvements in precision may be achieved by analyzing separately the two components of detection: 1) the probability of detecting a group, and 2) the proportion of the otters detected in a group, given that the group is detected. This separation would allow the use of all ISU's in estimating the second component of the detection probability. Greater overall sampling effort would also increase precision of the population estimate.

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Table 1. Detection probabilities (estimated by comparing air to ground observations) at three altitudes in a 750 m diameter search pattern continued for 5 minutes following the last otter sighting.

	Altitude		
	46M	92M	137M
Number of trials	13	12	12
Number of groups	58	43	44
Number of otters	133	104	106
Detection probability	0.92	0.91	0.90
Detection = 1.0[a]	0.62	0.50	0.50
Disturbance [b]	0.23	0.08	0.08

[a] Proportion of samples in which all otters were detected.

[b] Proportion of samples in which disturbance by aircraft was detected by ground.

Table 2. Detection probabilities (estimated by comparing air to ground observations) for three search patterns at 92 m continued for 5 minutes following the last otter sighting.

	Search pattern		
	400M Circle	750M Circle	800M Oval
Number of trials	20	19	22
Number of groups	58	40	86
Number of otters	113	72	213
Detection probability	0.96	0.93	0.90
Detection = 1.0[a]	0.80	0.79	0.68
Disturbance [b]	0.15	0.26	0.19

[a] Proportion of samples in which all otters were detected.

[b] Proportion of samples which disturbance by aircraft was detected by ground.

Table 3. Estimates from the 1992 trial sea otter survey in western Prince William Sound, Alaska.

	Estimate	SE
Unadjusted N	1,973	391
Correction factor	1.77	0.33
Adjusted N	3,493	937

Table 4. Comparison of detection probabilities obtained from systematic and group initiated intensive search units (ISU's), by observer, stratum (high and low) and otter behavior (diving or non-diving). Sample sizes are in parentheses.

	Observer[a]	
	JB	GE
Method		
Systematic	0.95 (7)	0.68 (14)
Group Initiated	0.75 (12)	0.56 (29)
Stratum		
High	0.84 (17)	0.80 (2)
Low	0.59 (37)	0.50 (6)
Proportion of Groups Diving		
High Stratum	0.57 (17)	1.00 (2)
Low Stratum	0.30 (37)	0.57 (6)

[a] Differences between observers significant for both methods ($P < 0.05$, Kruskal-Wallis test).

Table 5. Otter counts, unadjusted population size estimates, correction factors and adjusted population size estimates for small groups in the 1993 trial sea otter survey, Prince William Sound, Alaska.

Counts and Unadjusted Estimates

Observer	Stratum	Count[a]	Area[b]	Estimate	SE
JB	High	358	204	1,906	299
	Low	53	81	1,059	468
GE	High	444	206	2,363	339
	Low	79	61	1,578	1,293

Correction Factors

Observer	ISU's[c]	Factor	SE
JB	27	1.23	0.12
GE	13	3.27	1.45

Adjusted Estimates

Observer	Area[d]	Estimate	SE
JB	2,704	3,637	729
GE	2,313	12,900	5,689
Total	5,017	16,537	5,735

[a] Number of otters observed on transects.

[b] Area of surveyed transects (km^2).

[c] Number of usable ISU's.

[d] Size of study area (km^2).

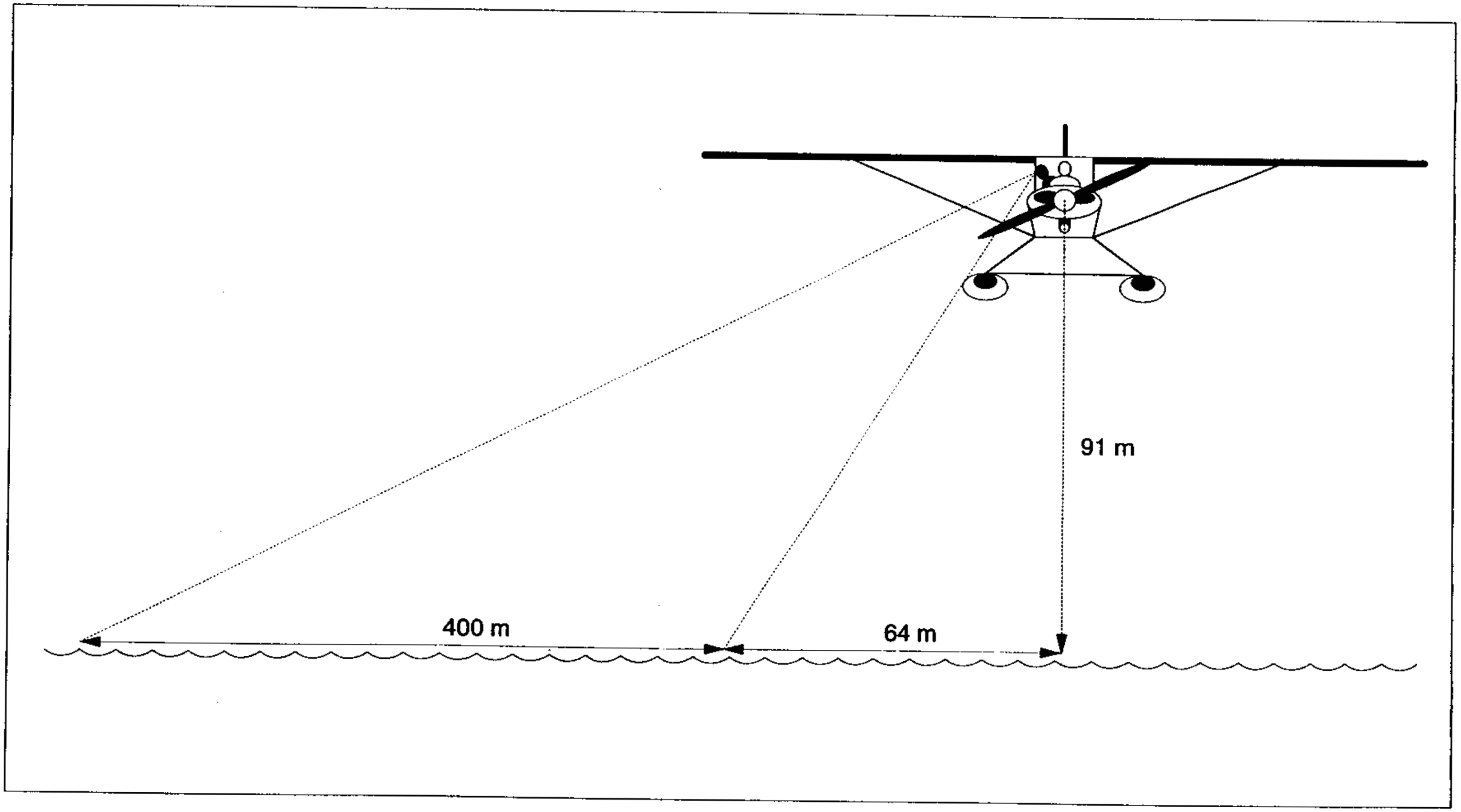


Figure 1. Illustration of delineation of 400 m wide transect from the float equipped PA-18 aircraft in sea otter survey design.

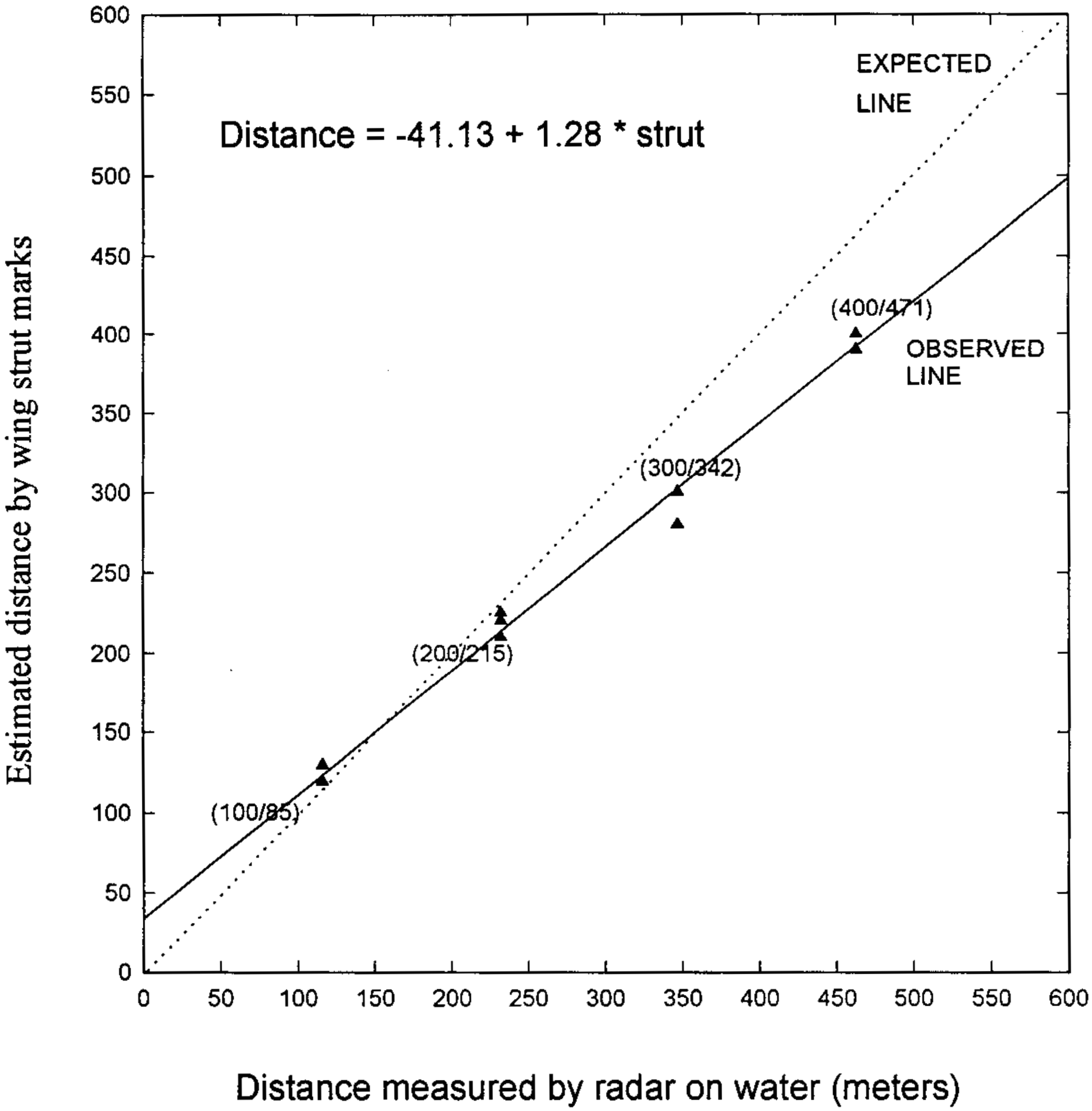


Figure 2. Estimated distances from inner strip line to radar measured distances on the water using wing strut markers and assuming no radar error. Radar measured / mean estimated distances are in parentheses.

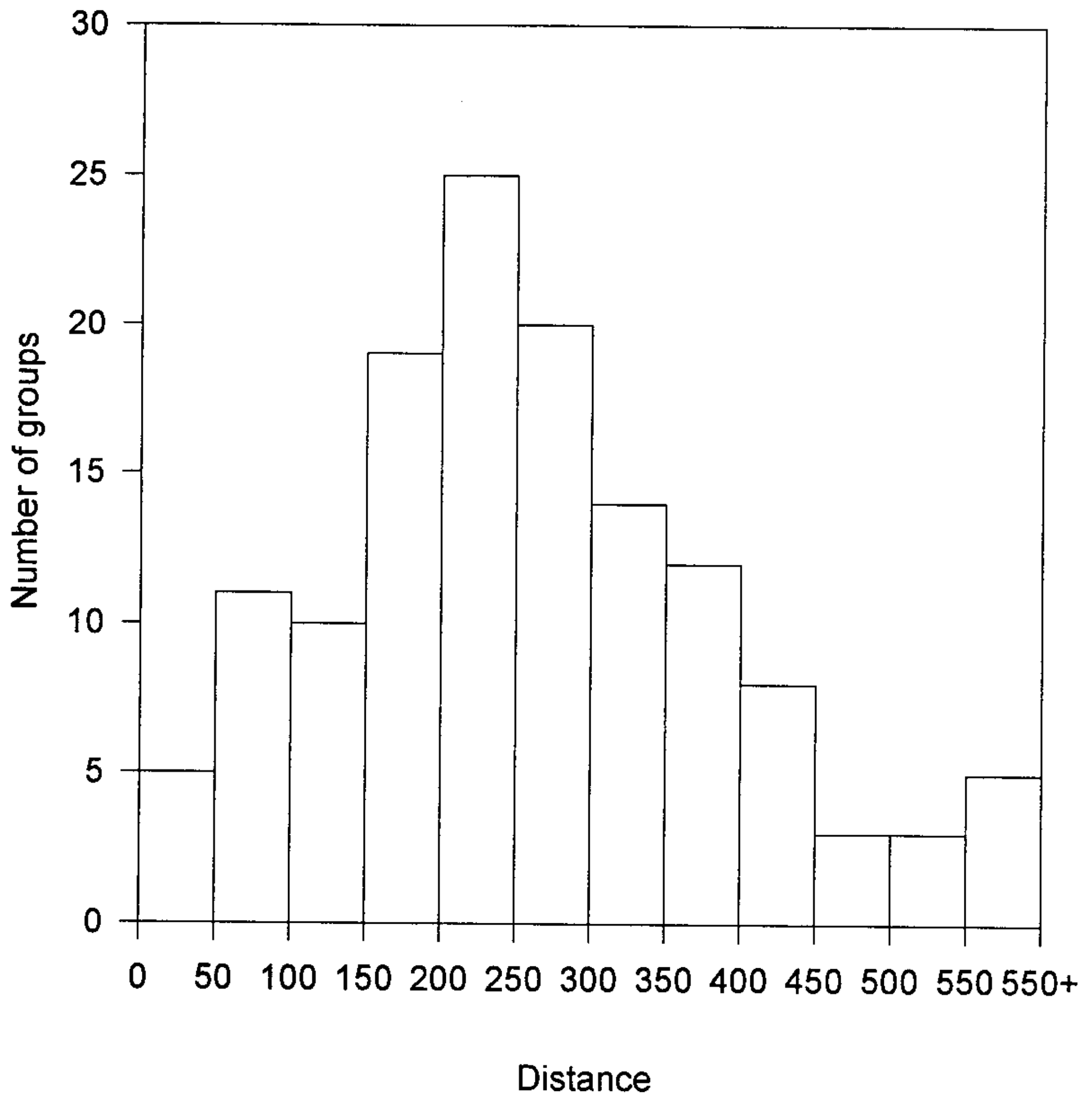


Figure 3. Number of sea otter groups observed in each distance category from the flight line with a standard line transect survey protocol.

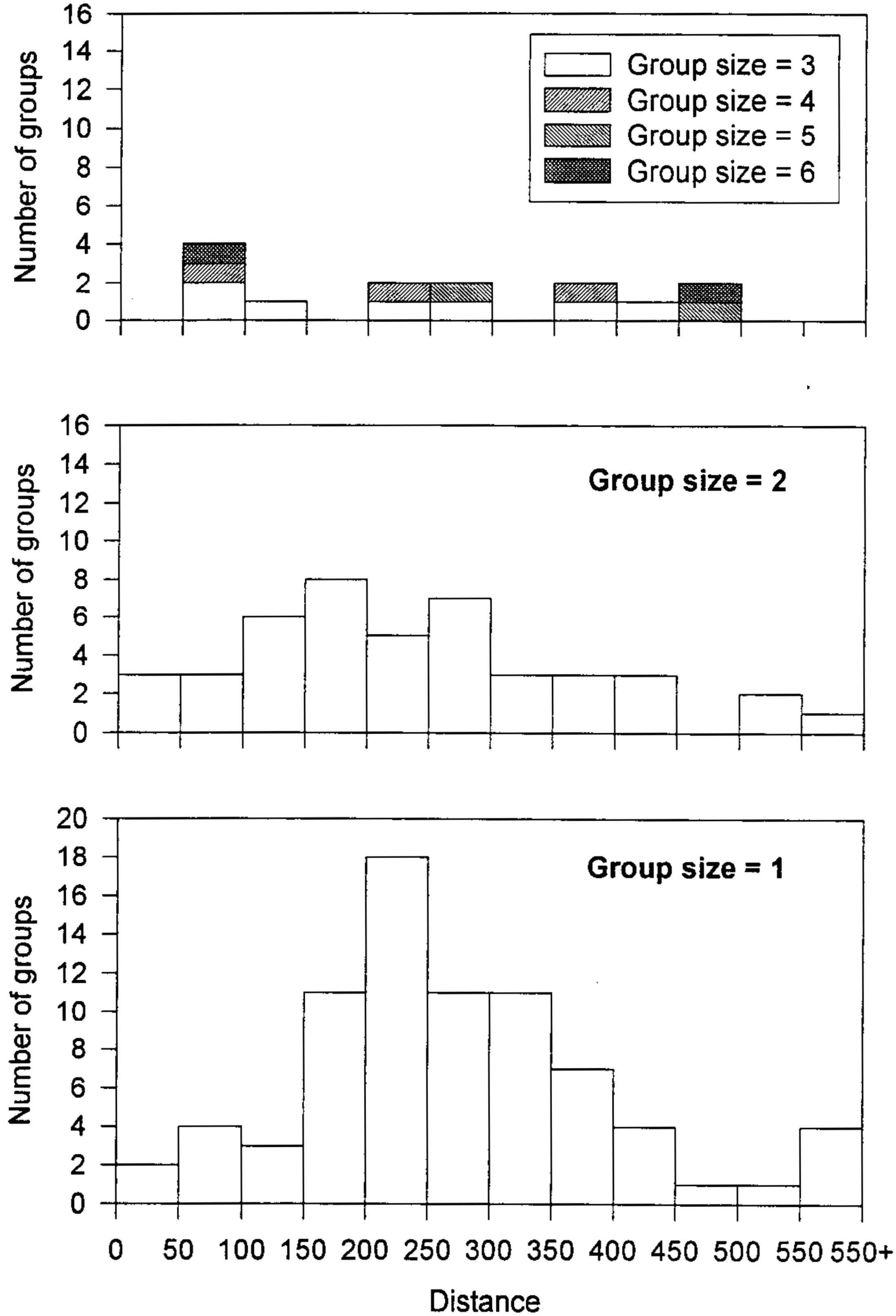


Figure 4. Number of sea otter groups of various sizes observed in each distance category from the flight line with a standard line transect survey protocol.

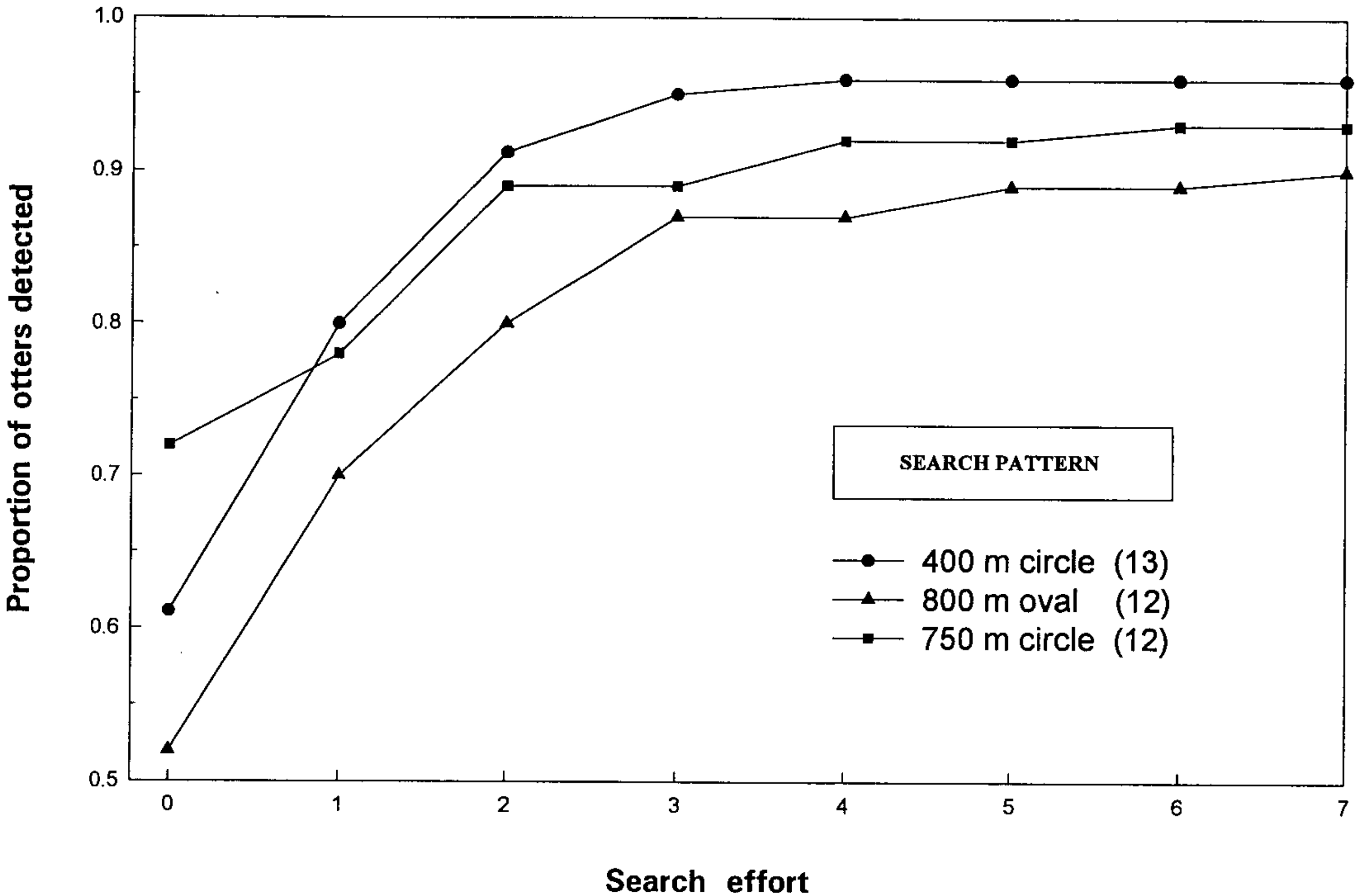


Figure 5. Mean detection probability as a function of search effort, as indicated by the number of concentric flight paths, for three different search patterns, for one observer in 1991. Sample sizes are in parentheses.

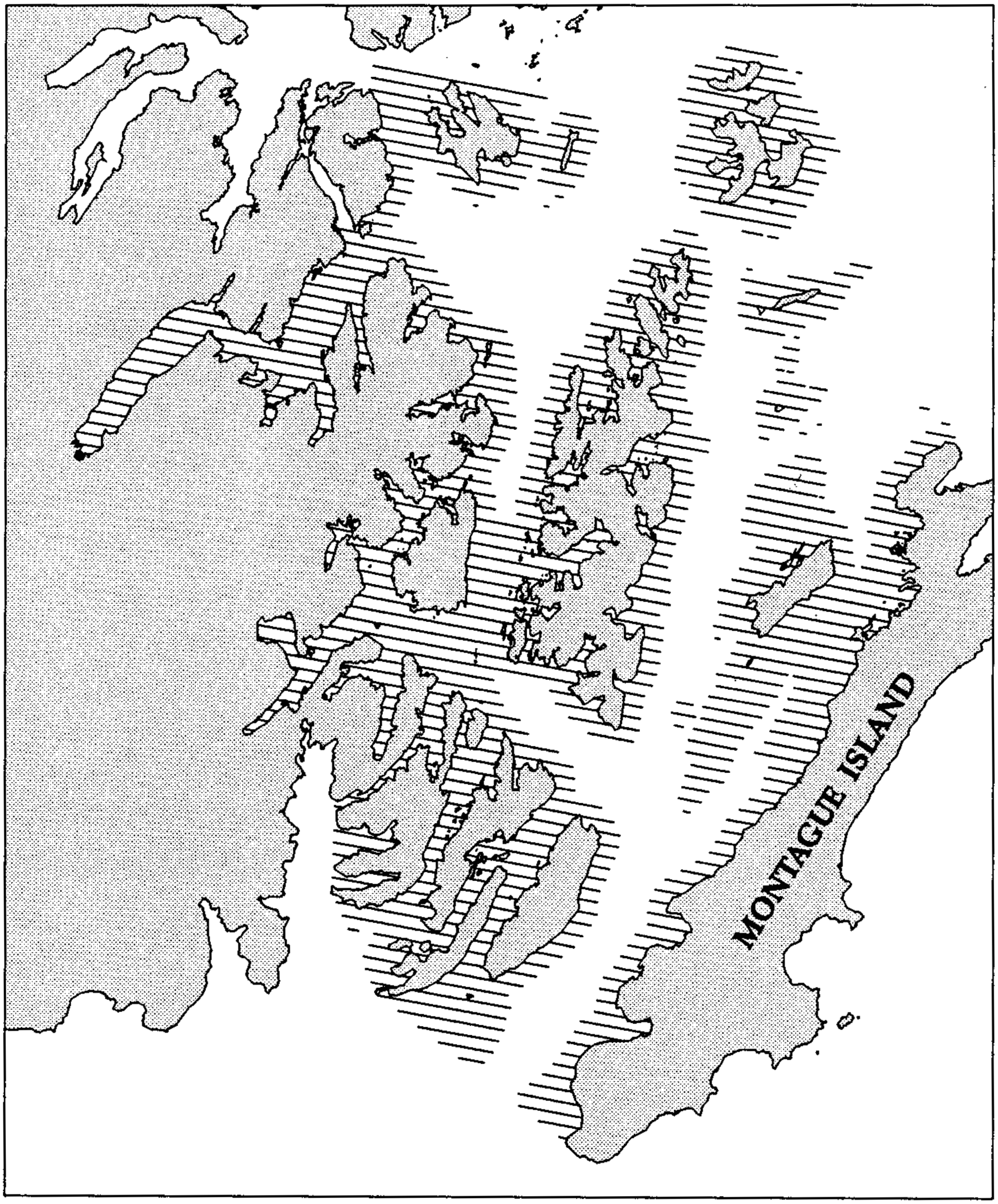


Figure 6. Survey area and location of transects surveyed in 1992 trial survey of Western Prince William Sound, Alaska.

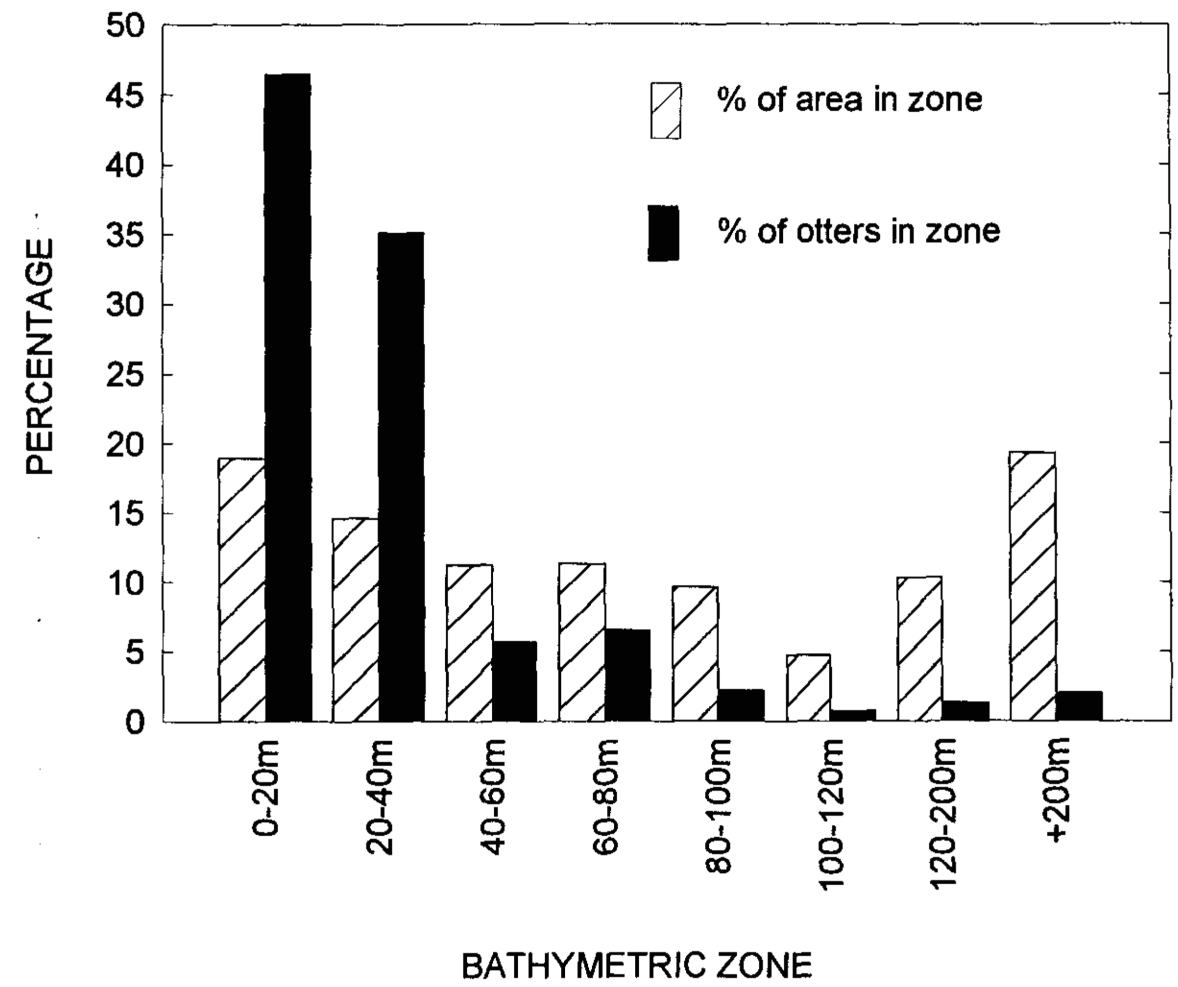


Figure 7. Percentage of otters observed in eight bathymetric zones and the percentage of total survey area represented by those zones in 1992 trial survey of Western Prince William Sound, Alaska.

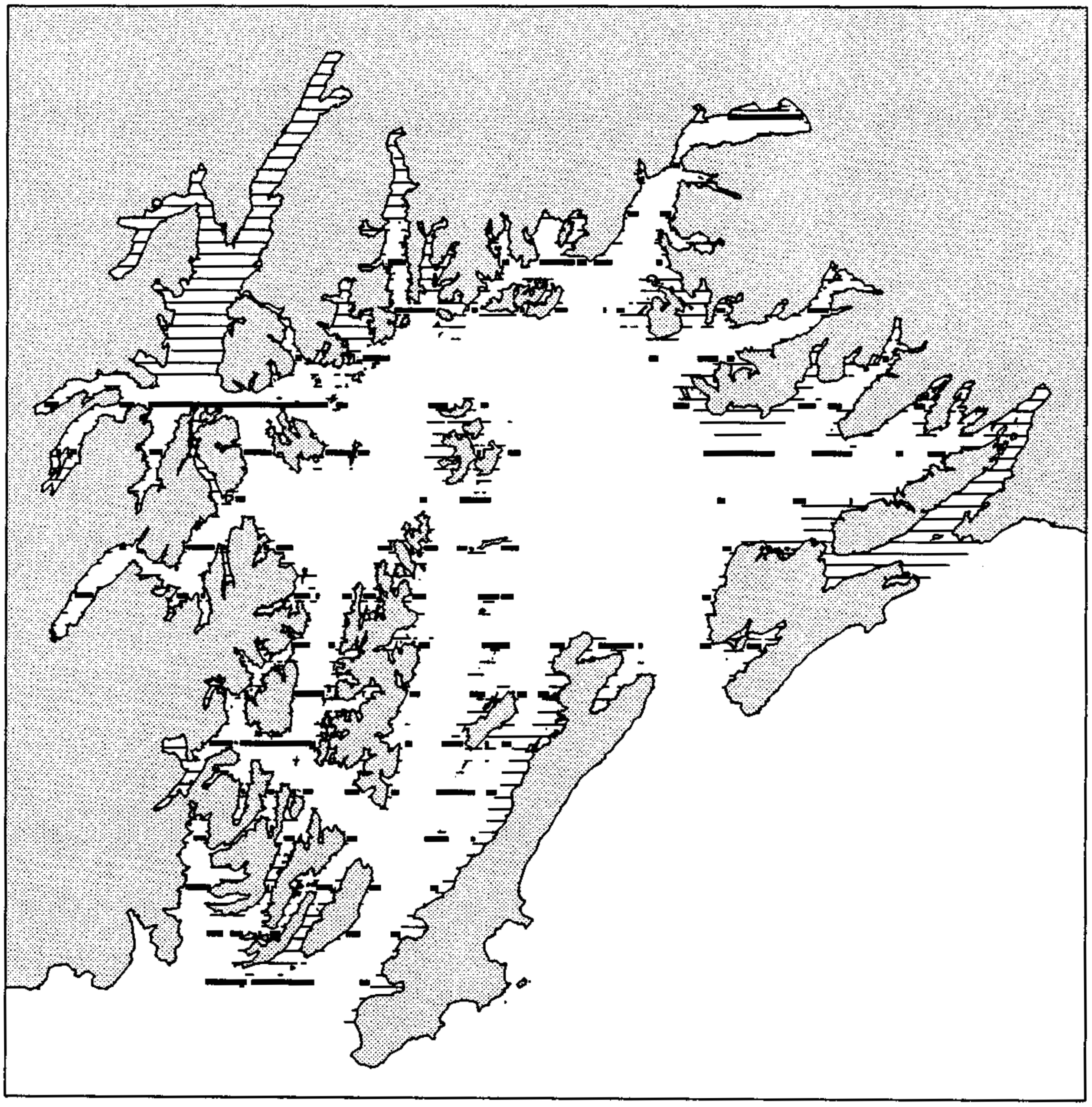


Figure 8. Survey area and location of transects surveyed in 1993 trial survey of Prince William Sound, Alaska.

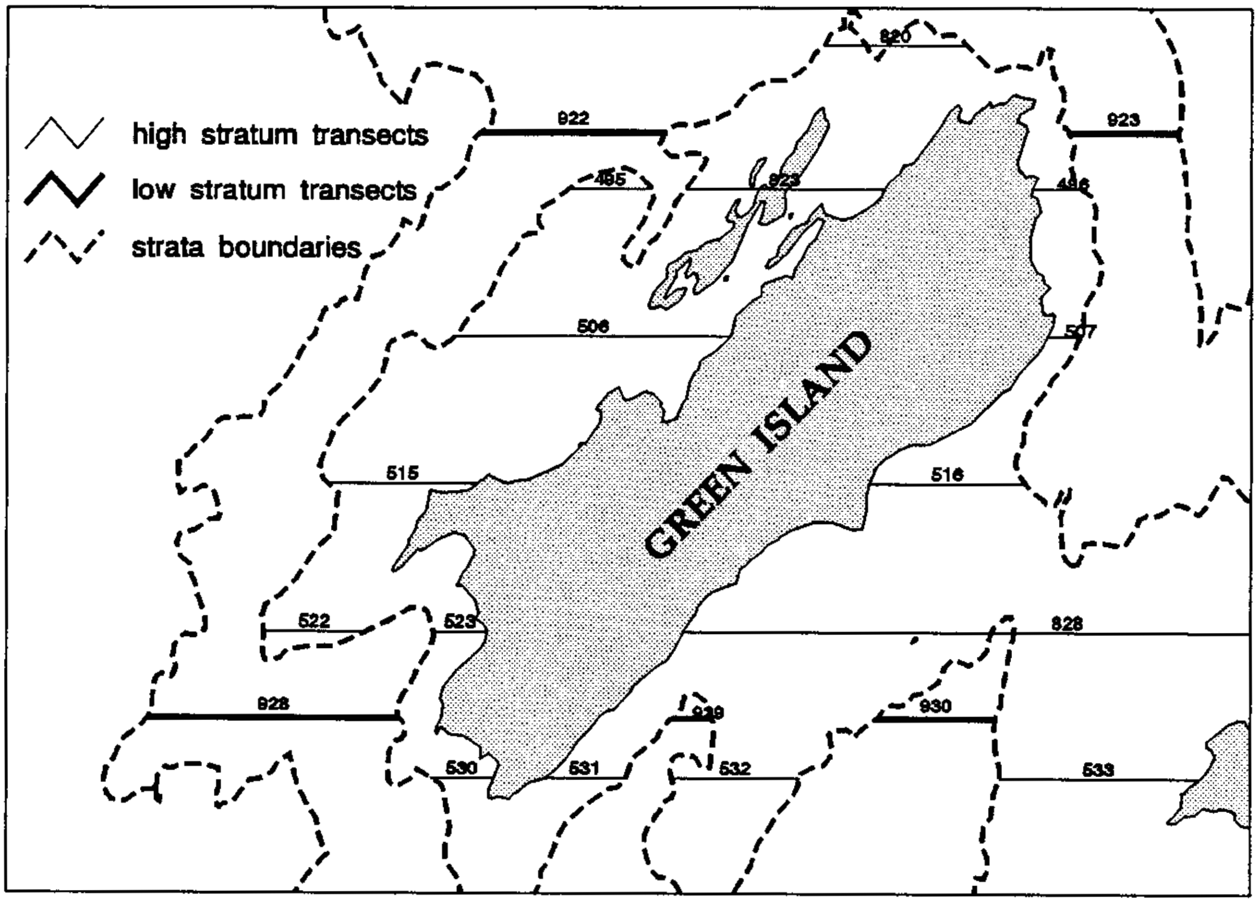


Figure 9. Example of distinction between high and low stratum transects and relative sampling intensity.

APPENDIX 1: Sampling Protocol for Sea Otter Aerial Surveys

Overview of survey design

The survey design consists of 2 components: 1) strip transect counts, and 2) intensive search units.

1) Strip Transect Counts

Sea otter habitat is sampled in two strata, high density and low density, distinguished by distance from shore and depth contour. The high density stratum extends from shore to 400 m seaward or to the 40 m depth contour, whichever is greater. The low density stratum extends from the high density line to a line 2 km offshore or to the 100 m depth contour, whichever is greater. Bays and inlets less than 6 km wide are sampled entirely, regardless of depth. Transects are spaced systematically within each stratum. Survey effort is allocated proportional to expected otter abundance in the respective strata.

Prior to surveying a geographic area (e.g., College Fjord), the observer will determine which side of the transect lines (N, S, E, or W) has less glare. The side with less glare will be surveyed by a single observer in a fixed-wing aircraft. Transects with a 400 meter strip width are flown at an airspeed of 60 mph (27 m/s) and an altitude of 300 feet (92 m). The observer searches forward as far as conditions allow and out 400 m, indicated by marks on the aircraft struts, and records otter group size and location on a transect map. A group is defined as 1 or more otters spaced less than 3 otter lengths apart. Any group greater than 30 otters is circled until a complete count is made. A camera should be used to photograph any groups too large and concentrated to count accurately. The number of pups in a group is noted behind a slash (e.g., 6/4 = 6 adults and 4 pups). Observation conditions are noted for each transect and the pilot does not assist in sighting sea otters.

2) Intensive Search Units

Intensive search units (ISU's) are flown at intervals dependent on sampling intensity*, throughout the survey period. An ISU is initiated by the sighting of a group and is followed by 3 concentric circles flown within the 400 m strip perpendicular to the group which initiated the ISU. The pilot uses a stopwatch to time the minimum 1 minute spacing between consecutive ISU's and guide the circumference of each circle. With a circle circumference of 1,256 m and an airspeed of 60 mph (27 m/s), it takes 48 seconds to complete a circle (e.g., 12 seconds/quarter turn). With 3 circles, each ISU takes about 2.4 minutes to complete. ISU circle locations are drawn on the transect map and group size and behavior is recorded on a separate form for each ISU. For each group, record number observed on the strip count and number observed during the circle counts. Otters that swim into an ISU post factum are not included and groups greater than 30 otters cannot initiate an ISU.

Behavior is defined as "whatever the otter was doing before the plane got there" and recorded for each group as either diving (d) or nondiving (n). Diving otters include any individuals that swim below the surface and out of view, whether traveling or foraging. If any individuals(s) in a group are diving, the whole group is classified as diving. Nondiving otters are animals seen resting, interacting, swimming (but not diving), or hauled-out on land or ice.

* The targeted number of ISU's per hour should be adjusted according to sea otter density. For example, we have an area that is estimated to take 25 hours to survey and the goal is to have each observer fly 40 "usable" ISU's; an ISU must have more than one group to be considered usable. Because previous data show that only 40 to 55% of the ISU's end up being usable, surveyors should average at least 4 ISU's per hour. Considering the fact that one does now always get 4 opportunities per hour - especially at lower sea otter densities, this actually means taking something like the first 6 opportunities per hour. However, two circumstances may justify deviation from the 6 ISU's per hour plan:

1) If the survey is not progressing rapidly enough because flying ISU's is too time intensive, *reduce* the minimum number of ISU's per hour slightly.

2) If a running tally begins to show that, on average, less than 4 ISU's per hour are being flown, *increase* the targeted minimum number of ISU's per hour accordingly.

The bottom line is this: each observer needs to obtain a preset number of ISU's for adequate statistical precision in calculation of the correction factor. To arrive at this goal in an unbiased manner, observers must pace themselves so ISU's are evenly distributed throughout the survey area.

Preflight

Survey equipment:
- stopwatches (2)
- low power, wide angle binoculars (e.g., 4 x 12)
- clipboards (2)
- transect maps
- transect data forms
- ISU data forms
- list of transects waypoints
- Global Positioning System (GPS)
- memory cards with waypoints
- 35 mm camera with 70-210 mm zoom lens
- high-speed film

Airplane windows must be cleaned each day prior to surveying.

Global Positioning System (GPS) coordinates used to locate transect starting and end points, must be entered as waypoints by hand or downloaded from an esxternal source via a memory card.

Electrical tape markings on wing struts indicate the viewing angle and 400 m strip width when the aircraft wings are <u>level</u> at 300 feet (92 m) and the inside boundary is in-line with the outside edge of the airplane floats.

The following informatiion is recorded at the top of each transect data form:

Date - Recorded in the DDMMMYY format.
Observer - First initial and up to 7 letters of last name.
Start time - Military format.
Aircraft - Should always be a tandem seat fixed wing which can safely survey at 60 mph.
Pilot - First initial and up to 7 letters of last name.
Area - General area being surveyed.

Observation conditions

Factors affecting observation conditions include wind velocity, seas, swell, cloud cover, glare, and precipitation. Wind strong enough to form whitecaps creates unacceptable observation conditions. Occasionally, when there is a short fetch, the water may be calm, but the wind is too strong to allow the pilot to fly concentric circles. Swell is only a problem when it is coupled with choppy seas. Cloud cover is desirable because it inhibits extreme sun-glare. glare is a problem that can usually be moderated by observing from the side of the aircraft opposite the sun. Precipitation is usually not a problem unless it is extremely heavy.

Chop (C) and glare (G) are probably the most common and important factors effecting observation conditions. Chop is defined as any deviation from flat calm water up to whitecaps. Glare is defined as any amount of reflected light which may interfere with sightability. After each transect is surveyed, presence is noted as C, G, or C/G and modified by a quartile (e.g., if 25% of the transect had chop and 100% had glare, observation conditions would be recorded as 1C/4G). Nothing is recorded in the conditions category if seas are flat calm and with no glare.

Observer fatigue

To ensure survey integrity, landing the plane and taking a break after every 1 to 2 hours of survey time is essential for both observer and pilot. Survey quality will be compromosed unless both are given a chance to exercise their legs, eat, go to the bathroom, and give their eyes a break so they can remain alert.

Vessel activity

Areas with fishing or recreational vessel activity should still be surveyed.

Unique habitat features

Local knowledge of unique habitat features may warrant modification of survey protocol:

1. **Extensive shoaling or shallow water** (i.e., mud flats) may present the opportunity for extremely high sea otter densities with groups much too large to count with the same precision attainable in other survey areas. Photograph only otters within the strip or conduct complete counts, typically made in groups of five or ten otters at a time. Remember, groups > 30 cannot initiate an ISU.

   Example: Orca Inlet, PWS. Bring a camera, a good lens, and plenty of film. Timing is important when surveying Orca Inlet; the survey period should center around a positive high tide - plan on a morning high tide due to the high probability of afternoon winds and heavy glare. Survey the entire area from Hawkin's cutoff to Nelson Bay on the same high tide because sea otter distribution can shift dramatically with tidal ebb and flow in this region.

2. **Cliffs** - How transects near cliffs are flown depends on the pilot's capabilities and prevailing weather conditions. For transects which intersect with cliff areas, including tidewater glaciers, discuss the following options with the pilot prior to surveying.

   In some circumstances, simply increasing airspeed for turning power near cliffs may be acceptable. However, in steep/cliff-walled narrow passages and inlets, it may be deemed too dangerous to fly perpendicular to the shoreline. In this case, as with large groups of sea otters, obtain complete counts of the area when possible.

   In larger steep-walled bays, where it is too difficult or costly to obtain a complete count, first survey the entire bay shoreline 400 m out. Then survey the offshore transect sections, using the 400 m shoreline strip just surveyed as an approach. Because this is a survey design modification, these data will be analyzed separately.

   Example: Herring Bay, PWS. Several cliff areas border this area.
   Example: Barry Glacier, PWS. Winds coming off this and other tidewater glaciers may create a downdraft across the face. The pilot should be aware of such unsafe flying conditions and abort a transect if necessary.

3. **Seabird colonies** - Transects which intersect with seabird colonies shoud be shortened accordingly. These areas can be buffered for a certain distance in ARC dependant on factors such as colony size, species composition, and breeding status.

   Example: Kodiak Island. Colonies located within 500 m of a transect AND Black-legged Kittiwakes > 100 OR total murres > 100 OR total birds > 1,000 were selected from the seabird colony catalog as being important to avoid.

4. **Drifters** - During calm seas, for whatever reason - possibly a combination of ocean current patterns and geography - large numbers of sea otters can be found resting relatively far offshore, over extremely deep water, miles (up to 4 miles is not uncommon) from the nearest possible foraging area.

   Example: Port Wells, PWS. Hundreds of sea otters were found scattered throughout this area with flat calm seas on 2 consecutive survey years. As a result, Port Wells was reclassified as high density stratum.

5. **Glacial moraine** - Similar to the drifter situation, sea otters may be found over deep water on either side of this glaciel feature.

   Example: Unakwik, PWS. Like Port Wells, Upper Unakwik was reclassified as high density stratum.

Planning an aerial survey

Several key points should be considered when planning an aerial survey:

1. Unless current sea otter distribution is already well known, it is well worth the effort to do some reconnaissance. This well help define the survey area and determine the number of observers needed, spacing of ISU's, etc.

2. Plan on using 1 observer per 5,000 otters.

3. Having an experienced technical pilot is extremely important. Low level flying is, by nature, a hazardous proposition with little room for error; many biologists are killed this way. While safety is the formost consideration, a pilot must also be skilled at highly technical flying. Survey methodology not only involves low-level flying, but also require intimate familiarity with a GPS and the ability to fly in a straight line at a fixed heading with a fixed altitude, fixed speed, level wings, from and to fixed points in the sky. Consider the added challenge of flying concentric 400 meter circles, spotting other air traffic, managing fuel, dealing with wind and glare, traveling around fog banks, listening to radio traffic, looking at a survey map, and other distractions as well. Choose the best pilot available.

APPENDIX 2: Strip Transect Data Form

AERIAL SEA OTTER SURVEY DATA SUMMARY FORM

Date____________ Observer____________________ Time begin_________________

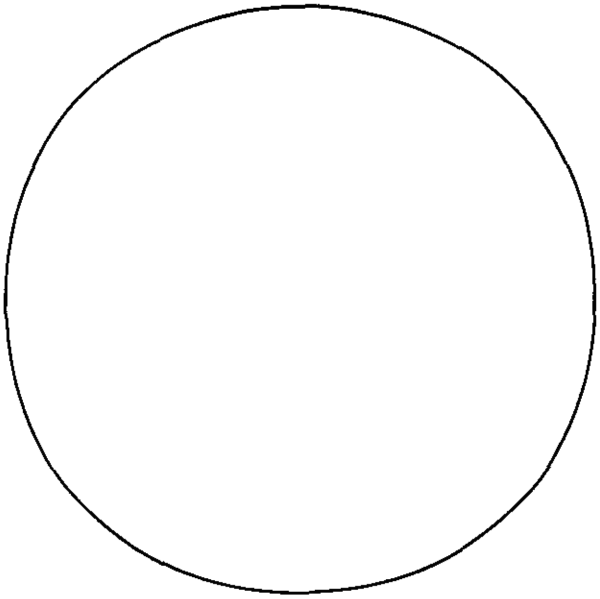
Aircraft__________ Pilot____________________ Area___________________________

Conditions (1-10)-______ Wind (kts)______ Seas (ft)______ Cloud cover (%)_________

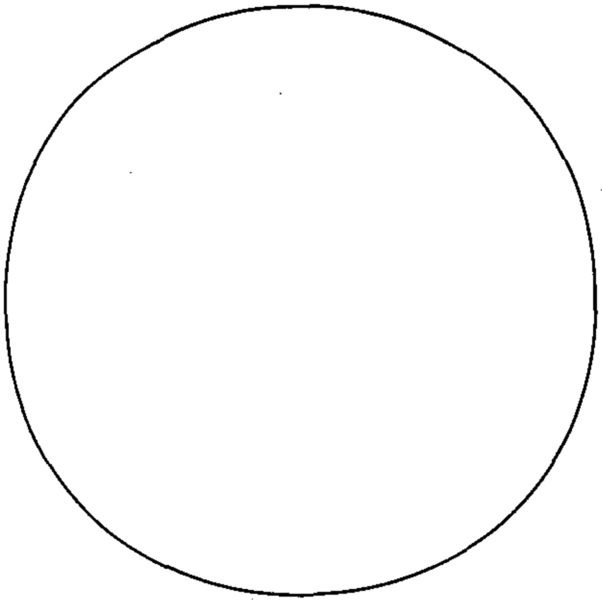
Glare (None, Lt, Mod, Heavy)______ Remarks____________________________________

Transect Number	Conds	ID Number	Strip Count	ISU Number	Circle Count

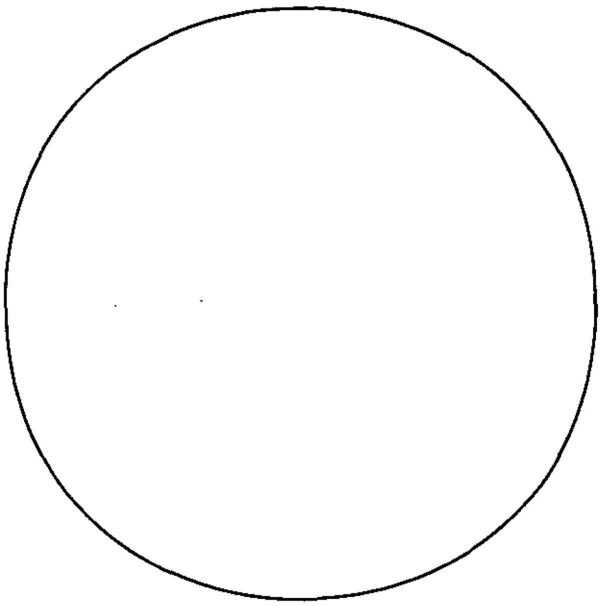
APPENDIX 3: ISU Data Form



Transect #	Random / Nonrandom	
Group #	Strip count	Circle count
*1		
2		
3		
4		
5		



Transect #	Random / Nonrandom	
Group #	Strip count	Circle count
*1		
2		
3		
4		
5		



Transect #	Random / Nonrandom	
Group #	Strip count	Circle count
*1		
2		
3		
4		
5		

Exxon Valdez Oil Spill
Restoration Project Final Report

A Population Model for Sea Otters in Western Prince William Sound

Restoration Project 93043-3
Sea Otter Demographics

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May 1996

A Population Model for Sea Otters in Western Prince William Sound

Restoration Project 93043-3
Final Report

Study History: Restoration Project 93043, *Sea Otter Population Demographics in Areas Affected by the Exxon Valdez Oil Spill*, was initiated in 1993. The population model reported herein was one of three components. The other two components were aerial surveys (reported separately, *1993 Trial Aerial Survey of Sea Otters in Prince William Sound, Alaska*, by J. Bodkin and M. Udevitz) and mortality patterns (reported separately, as part of NRDA MM6 Report, *Age Distributions of Sea Otters Found Dead in Prince William Sound, Alaska, Following the Exxon Valdez Oil spill*, by D. Monson and B. Ballachey).

Abstract: A large portion of the western Prince William Sound (PWS) sea otter population was killed by the *Exxon Valdez* oil spill in March 1989, but little is known about the dynamics of this population before the spill or the rate at which the population can be expected to recover. We estimated age-specific reproductive and survival rates for the western PWS population before the spill based on examinations of reproductive tracts and the age structure of carcasses collected in 1989. We developed a new technique for estimating survival rates that uses age-structure and age-at-death data, and does not require the assumption of a stable age structure. A Leslie 2-sex projection matrix was used to integrate these estimates with other available information on the western PWS sea otter population and to project its potential recovery. Because of the lack of data for estimating juvenile survival rates, we considered a series of 4 potential scenarios. The population was projected to decrease slightly during the first year under all of the scenarios and then begin increasing, achieving maximum rates of increase ranging from 10% to 14% per year and recovering to its estimated 1985 population size in 10 to 23 years. Projected population sizes during the first few years after the spill are in broad agreement with estimates based on boat surveys in 1990, 1991 and 1993. Although it probably is not possible to fully quantify the uncertainty associated with the projected population trajectories, we recognize that the amount of uncertainty is likely to be large. This uncertainty is reflected to some extent by the disparity between the projected recovery times under the various scenarios.

Key Words: age structure, *Enhydra lutris*, *Exxon Valdez*, oil spill, population model, reproduction, sea otter, survival.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

EXECUTIVE SUMMARY

A large portion of the western Prince William Sound (PWS) sea otter population was killed by the *Exxon Valdez* oil spill in March 1989, but little is known about the dynamics of this population before the spill or the rate at which the population can be expected to recover. We estimated age-specific reproductive and survival rates for the western PWS population before the spill based on examinations of reproductive tracts and the age structure of carcasses collected in 1989. We developed a new technique for estimating survival rates that uses age-structure and age-at-death data, and does not require the assumption of a stable age structure. A Leslie 2-sex projection matrix was used to integrate these estimates with other available information on the western PWS sea otter population and to project its potential recovery. Because of the lack of data for estimating juvenile survival rates, we considered a series of 4 potential scenarios. The population was projected to decrease slightly during the first year under all of the scenarios and then begin increasing, achieving maximum rates of increase ranging from 10% to 14% per year and recovering to its estimated 1985 population size in 10 to 23 years. Projected population sizes during the first few years after the spill are in broad agreement with estimates based on boat surveys in 1990, 1991 and 1993. Although it probably is not possible to fully quantify the uncertainty associated with the projected population trajectories, we recognize that the amount of uncertainty is likely to be large. This uncertainty is reflected to some extent by the disparity between the projected recovery times under the various scenarios.

INTRODUCTION

The *Exxon Valdez* oil spill in March 1989 resulted in lethal and sublethal exposure of sea otters to oil. The most severe effects on sea otters were in western Prince William Sound (PWS), where an estimated 2,650 otters were killed (Garrott et al. 1993). An unknown additional number of otters received sublethal exposures that may have reduced their subsequent survivorships or reproductive rates (Ballachey et al. 1994). Current research and management is directed at restoration of resources damaged by the oil spill, but the rate at which the western PWS sea otter population can be expected to recover is unknown.

Little is known about the dynamics of the western PWS sea otter population before the spill. A small population in south-western PWS was one of the few remnant populations that survived following the extensive eighteenth and nineteenth century fur harvests (Lensink 1962). This population began increasing in the early part of this century and then began expanding rapidly to the north and east beginning about 1950, with the last areas of favorable habitat in eastern PWS being occupied by about 1980 (Garshelis et al. 1984). The western portion of PWS is generally considered to have been occupied at or near carrying capacity for some years preceding the oil spill, with the population size either constant (Johnson 1987) or growing very slowly (Garrott et al. 1993). There is some evidence to suggest that the western PWS population structure was relatively stable from at least 1976 through 1989 (Monson and Ballachey 1995). There is a very limited amount of information about survival rates of pups (Garshelis and Garshelis 1987) and weanlings (Monnett 1988) from before the oil spill. There are no published estimates of adult survival rates from that period. Jameson and Johnson (1993) have suggested that reproductive rates were probably comparable to estimated rates in the Aleutian Islands and in California.

A number of studies were initiated after the spill to assess damages and monitor recovery of the western PWS sea otter population (Ballachey et al. 1994). There were extensive collections of beach cast carcasses (DeGange and Lensink 1990, Doroff et al. 1993) that provided data for estimating reproductive rates (Bodkin et al. 1993) and age structures (Monson and Ballachey 1995). Telemetry-based studies provided direct estimates of survival and reproductive rates for certain components of the population (Rotterman and Monnett 1991, Monnett and Rotterman 1992, NBS unpubl. data). Boat-based surveys were used to estimate the size of the population in 1989, 1990, 1991, and 1993 (Burn 1994, Agler et al. 1994).

OBJECTIVES

This report presents the modeling component of Restoration Project #93043, Sea Otter Demographics and Habitat Use. The objectives of this component were to 1) estimate age specific reproductive and survival rates for the western PWS sea otter population based on the beach cast carcass collections in 1989, and 2) develop a model to integrate these estimates with other available information and project recovery of the western PWS sea otter population.

METHODS

Data Collection

Sea otter carcasses were collected throughout the oil spill zone as part of the oil spill response effort (DeGange and Lensink 1990, Doroff et al. 1993). Five hundred and eight sea otter carcasses were collected in western Prince William Sound between 30 March and 30 August 1989 (Figure 1). Personnel at the collection centers attempted to record, among other things, location and date of collection, sex, lactational status, and extent of decomposition for each carcass. Female reproductive tracts were removed and examined to determine reproductive status. Teeth (premolar, when available) were extracted for age determination.

Time of death (before or after the oil spill) was estimated for each carcass based on the extent of decomposition and the degree to which skeletal remains were dried or bleached. Evidence of lactation or the presence of a fetus, embryo, or corpus luteum in the reproductive tract was used to identify females that could have produced a pup between 1 October 1988 and 30 September 1989 (Bodkin et al. 1993).

Ages at the time of death were estimated from decalcified, longitudinal tooth sections (Garshelis 1984, Pietz et al. 1988). Up to 4 sections were prepared from each tooth and examined by Matson's Laboratories (Box 308, Milltown, MT). Age determination was based on the assumption that a cementum annulus was deposited each winter after an otter had its permanent teeth. Otters with deciduous teeth were assumed to be less than 6 months old. Otters were grouped into age classes with age class 0 corresponding to ages less than 6 months (no permanent teeth), age class 1 corresponding to ages ranging from 6 to 18 months (permanent teeth, no annulus), age class 2 corresponding to ages ranging from 18 to 30 months (permanent teeth, 1 annulus), and so on.

Reproductive Rates

Estimation of reproductive rates was based on the 148 carcasses examined by Bodkin et al. (1993) that came from western Prince William Sound. Of these, 143 were a subset of the known-age females used for estimating the age and sex structure of the population (see below). The other 5 carcasses were known-age females that died at a rehabilitation center. Bodkin et al. (1993) reported results for these and an additional 28 carcasses that came from outside Prince William Sound.

Age specific reproductive rates were estimated as the proportions of pregnant or lactating females in each age class (ages 2 - 16). These estimates were then smoothed by fitting the observed proportions to the proportional hazards model used by Eberhardt and Siniff (1988). The form of this model was

$$m_x = m(A,B)m(D,E),$$

where m_x is the reproductive rate (including male and female offspring) for age class x,

$$m(A,B) = A(1-\exp[-B(x-2)])$$

is a function that describes the rate at which reproductive rates increase with age for young otters,

$$m(D,E)=\exp[-D(\exp[Ex]-1)]$$

is a function that describes the rate at which reproductive rates decrease with age for old otters, and A, B, D, and E are parameters to be estimated (Eberhardt and Siniff 1988). Parameters were estimated by the method of least squares.

Structure of Ages-at-death

We used all carcasses classified as dying before the spill with known sex and age > 1 (n = 29) to estimate the structure of natural mortality that occurred during the year preceding the oil spill. Carcasses in age classes 0 and 1 were not considered because smaller beach cast carcasses tend to persist for shorter periods of time and are therefore less likely to be recovered (Bodkin and Jameson 1991). The proportion of deaths in each age and sex class of the population was estimated by its respective proportion in the carcass sample.

Population Age Structure

We used all carcasses classified as dying after the oil spill with known sex and age > 0 (n = 344) to estimate the structure of the population just before the spill. We included age class 1 carcasses because collections began almost immediately after the spill so it was not likely that any size related differences in carcass persistence would have had time to affect recovery probabilities. This assumption was tested based on a comparison of recoveries of lactating females and dependent pups (see below).

The proportion of age class 0 otters in the age structure could not be estimated from the recovered age class 0 carcasses because this class was defined to include otters that were not yet born (actual ages between -6 and +6 months). Therefore, the number of age class 0 otters corresponding to the collected carcasses was estimated as

$$N_0 = \sum_{x=1}^{25} N_x m_x ,$$

where N_x is the number of recovered carcasses of females in age class x and m_x is the estimated reproductive rate for age class x. We assumed a 1:1 sex ratio for age class 0 otters based on the observed sex ratio of sea otters born in rehabilitation centers during the summer of 1989 (8 males, 9 females, USFWS unpublished data). The proportion of otters in each age and sex class of the population was estimated by its respective proportion in the carcass sample, with the estimated numbers of age class 0 otters substituted for the observed numbers.

Relative Recovery Rates

An approximate test of the hypothesis that carcass size did not affect carcass recovery rate of otters that died after the spill was based on a comparison of the proportions of recovered dependent pups and lactating females. We assumed that if either member of a mother-pup pair was killed by the spill, then both were likely to have been killed. Under this assumption, if recovery rates did not depend on carcass size, then the proportion of dependent pups should approximately equal the proportion of lactating females in the recovered carcass sample. The proportion of dependent pups could be obtained directly as the proportion of recovered carcasses in age class 0. The proportion of lactating females had to be estimated because some carcasses had unknown sex or lactational status.

In order to construct an approximate statistical test, we further assumed that for the sample of $N_1 = 407$ recovered carcasses,

$$(f,m,d) \sim \text{multinomial } (N_1, P_f, P_m, P_d),$$

where f = the number of independent females, m = the number of independent males, and d = the number of dependent pups. The number of independent otters with unknown sex is N_1-f-m-d. We assumed that for the sample of $N_2 = 148$ females examined to determine reproductive status,

$$l \sim \text{binomial } (N_2, P_l),$$

where l = the number of females that were lactating. Finally, we assumed that distributions of (f,m,d) and l were approximately independent. The assumption of independence is not strictly valid because most of the N_2 examined females were a subset of the N_1 recovered carcasses. However, we do not expect that this form of dependence would greatly affect the test. Under these distributional assumptions the joint likelihood for (f,m,d,l) is proportional to

$$P_f^f \, P_m^m \, P_d^d (1-P_f-P_m-P_d)^{N_1-f-m-d} \, P_l^l (1-P_l)^{N_2-l} \, . \tag{1}$$

The proportion of lactating females out of the N_1 carcasses is

$$P_l^* = P_l \left(P_f + \frac{P_f(1-P_f-P_m-P_d)}{P_f+P_m} \right) .$$

Under the assumption that carcass size did not affect recovery probability, the proportions of lactating females and dependent pups out of the N_1 recovered carcasses will be the same, so that

$$P_l = \frac{P_d}{P_f + \dfrac{P_f(1-P_f-P_m-P_d)}{P_f+P_m}} \, . \tag{2}$$

We obtained maximum likelihood estimates of P_f, P_m, P_d, P_l, and P_l^* based on the likelihood (1) with and without the constraint (2) and used the likelihood ratio to test the assumption represented by that constraint.

Survival Rates

Basic relations.-- The relations between survival rates, age structure, and structure of ages-at-death are well known for populations with stable age structures (e.g., Tanner 1978). The standard expressions for these relations in birth pulse populations are

$$s_x = \frac{c_{x+1}\lambda}{c_x}, \quad x=0,\cdots,m, \tag{3}$$

and

$$s_x = 1 - \frac{d_x\lambda^x}{\sum_{i=x}^{m} d_i\lambda^i}, \quad x=0,\cdots,m, \tag{4}$$

where

s_x = the annual survival rate for individuals in age class x,
λ = the finite rate of increase for the population,
c_x = the proportion of live individuals in age class x at the time of a birth pulse,
d_x = the proportion of annual deaths in age class x, and
m = the maximum attainable age.

Equations (3) and (4) rely on the assumption of a stable age structure and the resulting constancy of the parameters over time. If the population growth rate is known and an unbiased estimate of the age structure is available, then equation (3) can be used to obtain unbiased estimates of the survival rates. Likewise, if the population growth rate is known and an unbiased estimate of the structure of ages-at-death is available, then equation (4) can be used to obtain unbiased estimates of the survival rates. Age specific survival rate estimates obtained from (3) or (4) will usually require some form of smoothing (Tanner 1978).

We are not aware of any previously developed techniques for estimating survival rates from age structure and age-at-death data in cases where age structures are not stable. To develop the necessary relations we allow all of the parameters to depend on time. Let t index the annual birth pulses,

$N_x(t)$ = the number of live individuals in age class x at time t,
$c_x(t)$ = the proportion of live individuals in age class x at time t,
$s_x(t)$ = the proportion of live individuals in age class x at time t that survive to time t+1 (when they will be in age class x+1),
$F_x(t+1)$ = the number of live individuals in age class x at time t that die before time t+1,
$d_x(t+1)$ = the proportion of individuals dying between times t and t+1 that were in age class x, and

$\lambda(t)$ = the finite rate of increase for the population between times t and t+1.

Finally, let

$$N(t) = \sum_{i=0}^{m} N_i(t)$$

be the total number of live individuals at time t and let

$$F(t+1) = \sum_{i=0}^{m} F_i(t+1)$$

be the total number of live individuals at time t that died before time t+1. We consider ages $x=0,\cdots,m$, where m is the maximum attainable age so that $s_m=0$ and $c_{m+1}=0$.

Now, by definition we have

$$c_x(t)N(t)s_x(t) = c_{x+1}(t+1)N(t+1), \quad x=0,\cdots,m$$

and

$$N(t+1) = \lambda(t)N(t)$$

so that

$$s_x(t) = \frac{c_{x+1}(t+1)\lambda(t)}{c_x(t)}, \quad x=0,\cdots,m. \tag{5}$$

Also by definition, we have

$$F_x(t+1) = c_x(t)N(t)[1-s_x(t)], \quad x=0,\cdots,m,$$

so that

$$\begin{aligned} d_x(t+1) &= \frac{F_x(t+1)}{F(t+1)} \\ &= \frac{c_x(t)[1-s_x(t)]}{\sum_{i=0}^{m}\left(c_i(t)[1-s_i(t)]\right)}, \quad x=0,\cdots,m. \end{aligned} \tag{6}$$

If the age structure is stable, then $c_x(t+1)=c_x(t)$ and this identity can be used to derive equations (3) and (4) from equations (5) and (6). However, equations (5) and (6) can also be solved directly for $s_x(t)$ and $c_x(t)$ without any assumptions about stability to give

$$c_x(t) = c_{x+1}(t+1)\lambda(t) + d_x(t+1)\left(1 - \lambda(t)[1 - c_0(t+1)]\right)$$

and

$$s_x(t) = \frac{c_{x+1}(t+1)\lambda(t)}{c_{x+1}(t+1)\lambda(t) + d_x(t+1)\{1 - \lambda(t)[1 - c_0(t+1)]\}}, \quad x = 0,\cdots,m. \tag{7}$$

If the population growth rate is known and unbiased estimates of the age structure and the structure of ages-at-death are available, then equation (7) can be used to obtain unbiased estimates of the survival rates. Because the age structure is not assumed to be stable, the survival rates are not assumed to be constant. The estimated survival rates apply only to the period between t and t+1.

If data for age classes less than or equal to some value z are not available or not reliable (as in our case, where z=1 for the structure of ages-at-death data), then the proportions can be based on only age classes > z with

$$c_x(t) = \frac{N_x(t)}{\sum_{i=z+1}^{m} N_i(t)},$$

$$d_x(t) = \frac{F_x(t)}{\sum_{i=z+1}^{m} F_i(t)}, \quad x=z+1,\cdots,m,$$

and all of the relations discussed in this section will still hold. In this case, however, $\lambda(t)$ represents the finite growth rate only for age classes > z rather than for the whole population. If the age structure is stable, the finite growth rates for the population and any subsets of age classes will be the same.

Estimation.-- We obtained 3 separate sets of survival rate estimates based on 3 different combinations of the age-structure and age-at-death data sets and associated assumptions. The first set of estimates was based only on the estimated age structure at the time of the spill (age classes 0 - 25) and the following assumptions:

1. Reproduction could be approximated as an annual birth pulse occurring at the time of the spill.
2. The population was not increasing or decreasing (λ = 1).
3. The population had a stable age structure.

Survival rates were estimated separately for males and females according to equation (3) with λ = 1. The second set of estimates was based on the same set of assumptions, but using only the estimated structure of ages-at-death during the year preceding the spill (age classes 2 - 25). Survival rates were estimated separately for males and females according to equation (4) with λ = 1. For the final set of estimates, we relaxed the assumption of a stable age structure and used both the estimated age structure and the estimated structure of ages-at-death. Survival rates were estimated separately for males and females according to equation (7) with $\lambda = 1$.

Smoothing.-- Eberhardt and Siniff (1988) used a proportional hazards model (Eberhardt 1985, Siler 1979) to smooth survivorship estimates based on age structure data. We adapted their basic approach to provide a consistent method for smoothing survival rate estimates obtained according to any of the above methods. Our approach consisted of transforming survival rate estimates into l_x values that are formally equivalent to survivorship rates, smoothing these by fitting to the proportional hazards model used by Eberhardt and Siniff (1988), and then back-transforming the smoothed l_x values to obtain smoothed survival rate estimates.

Survival rate estimates obtained from (3), (4), or (7) were transformed according to

$$l_0 = 1 ,$$
$$l_x = \prod_{i=0}^{x-1} s_i(t) , \quad x=1,\cdots,26. \tag{8}$$

When the survival rates in (8) are based on equation (3) or (4) under the assumption of a stable age structure, then the l_x values can be interpreted in the conventional sense as survivorship rates. Survivorship rates cannot be expressed as a function of the $s_x(t)$ at a single time t when survival rates are not constant over time. Thus, when the survival rates in (8) are based on equation (7), the l_x values will not generally be equivalent to survivorships. However, equation (8) still defines a one-to-one transformation of the s_x, $x=0,\cdots,k$ if $s_x > 0$ for all $x \leq k$. The resulting l_x values form a nonincreasing function of x that can be smoothed by fitting to the proportional hazards model used by Eberhardt and Siniff (1988).

The form of the proportional hazards model was

$$l_x = l(A,B)l(G)l(D,E),$$

where

$$l(A,B) = A(1\text{-}\exp[\text{-}Bx])$$

is a function describing the initial rapid decrease in survivorship with age for juvenile otters,

$$l(G) = \exp[-Gx]$$

is a function describing the constant decrease in survivorship with age for prime-aged adults,

$$l(D,E) = \exp[-D(\exp[Ex]-1)]$$

is a function describing the accelerated decrease in survivorship with age for senescent otters, and A, B, G, D, and E are parameters to be estimated (Eberhardt and Siniff 1988).

Parameters were estimated by the method of least squares. In cases where survival rates were not estimated for the youngest age classes, we set l(A, B) = 1 and did not attempt to fit the initial phase of the survivorship model. Otherwise, if the least squares estimate of B was greater than 10, the value of B was set to 10 and B was no longer treated as an unknown parameter. Values of B ≥ 10 result in l(A, B) being essentially constant for x > 0. Finally, if we were unable to obtain convergence and a nonsingular jacobian, then we set l(D, E) = 1 and attempted to fit the reduced model that did not include a senescence effect.

Predicted non-zero survivorships from the fitted model were then back transformed to obtain the smoothed survival rate estimates

$$s_x = \frac{l_{x+1}}{l_x}, \quad x=0,\cdots,25.$$

RESULTS

Reproductive Rates

Positive reproductive rates estimates were obtained for age classes 3 through 16, with estimates of 0.6 or greater for ages greater than 3 (Figure 2). Least square estimates of the parameters in the smoothing function were

A = 0.907955
B = 0.544397
T = 16.056893
S = 0.064483

where D=exp[-T/S] and E=1/S. This gave smoothed reproductive rate estimates that increased from 0 at age 2 up to a high of 0.91 at age 15 and then decreased back to 0 by age 17 (Figure 2).

Structure of Ages-at-death

Female sea otters accounted for an estimated 79% (23/29) of the natural mortality in age classes ≥ 2 during the year preceding the oil spill (Figure 3). An estimated 70% (19/23) of the female mortality and 83% (5/6) of the male mortality was in age classes 8 - 16. 13% (3/23) of the female mortality occurred in age classes 19 and above, with 2 of the female carcasses (9%) in age class 21. No male carcasses were recovered in age classes greater than 15 (Figure 3).

Population Age Structure

The estimated population structure at the time of the oil spill consisted of 26% (120/464) age class 0 otters and 35% (164/464) age class 1 - 3 otters, with the remaining 39% in age classes 4 - 17 (Figure 4). We estimated that 57% (265/464) of the population was female (Figure 4).

Relative Recovery Rates

Without assuming equal recovery rates, we estimated that 5.4% of the 407 recovered carcasses of otters that died after the spill were dependent pups and 5.7% were lactating females (Table 1). The difference in these proportions was not significant (likelihood ratio test, $\chi^2 = 0.03$, df=1, P=0.86). Under the assumption that the proportions of dependent pups and lactating females were equal, we estimated that each of these subclasses comprised 5.6% of the recoverable population (Table 1). These results suggest that, of the otters that died after the spill and were recovered, most were probably recovered before any size related differences in persistence could affect recovery rates.

Survival Rates

Survival rates estimated from age structure data were quite variable, with 7 of the female and 6 of the male age classes having estimated rates greater than 1 (Figures 5A and 6A). An estimate greater than 1 results whenever the proportion of individuals in an age class is greater than the proportion in the next youngest age class. The fitted smoothing functions indicated sharp initial increases in survival rates from age 0 to 1 followed by nearly constant rates of about 0.93 for females and 0.79 for males up to at least age 10 (Table 2, Figures 5A and 6A). Smoothed survival rate estimates then decreased to 0 by age 18 for females. We were not able to fit a term for a senescent phase to the male data (Table 2).

Survival rates estimated from ages-at-death data were somewhat less variable (Figures 5B and 6B). This was due, at least in part, to the fact that these estimates cannot exceed 1. However, survival rate estimates will equal 1 for each age class with no recovered carcasses if there is an older age class for which some carcasses were recovered. In many cases, the absence of any carcasses in an age class probably only resulted from the small total number of carcasses recovered. There were 12 female age classes with recovered carcasses that provided survival rate estimates less than 1. There were only 6 male age classes with any recovered carcasses and each of these had just 1 carcass. We did not attempt to fit the initial phase of the smoothing function to these data because we only considered age classes 2 and above. We were able to fit the constant as well as the senescent phase of the function to both male and female ages-at-death (Table 2). Smoothed survival rates for age class 2 (0.98 for females and 0.97 for males) were higher than the corresponding smoothed estimates based on age structure data. Smoothed female rates remained above 0.95 through age 6 and then declined to 0.20 by age 25 (Figure 5B). Smoothed male rates remained above 0.95 through age 4 and then declined relatively rapidly to below 0.10 by age 19 (Figure 6B).

As might be expected, survival rates estimated from both the age structure and ages-at-death data were somewhat in between the estimates obtained from either data set by itself (Figures 5C and 6C). Age classes that had survival rate estimates equal to 1 when based on only ages-at-death data also had estimates equal to 1 when based on both data sets. This reduced some of the variability in the estimated rates, but also nullified any information the age structure data could have provided for those age classes. Once again, we did not attempt to fit the initial phase of the smoothing function to these data because we only considered age classes 2 and above. We were able to fit both remaining phases of the function to the female data (Table 2), resulting in smoothed survival rate estimates starting at 0.95 for age class 2 and decreasing to less than 0.10 by age 18 (Table 3, Figure 5C). Smoothed survival rate estimates for males were a constant 0.86 for age classes 2 and above (Table 3, Figure 6C). We were not able to fit the senescent phase of the smoothing function to the male data (Table 2).

DISCUSSION

Reproductive Rates

Our estimates of age-specific reproductive rates assumed that mortality of otters and recovery and selection of carcasses for examination were independent of reproductive status within each age class, and that there was no bias in determining the age class or reproductive status of each examined carcass. These are the same assumptions used by Bodkin et al. (1993), who considered them to be reasonable based on the extent of the oil spill and evaluations of the selection, aging and examination techniques. Our unsmoothed estimates are similar to those obtained by Bodkin et al. (1993), but are more variable because we did not combine any age classes. We note that our age class i corresponds to age class i+1, $i=0,\cdots,25$ as defined by Bodkin et al. (1993).

The smoothing function fit the observed reproductive rates quite well (Figure 2). However, the onset and form of senescence were entirely determined by the observed rate for age 16 (0.60, based on only 5 examined otters) and the lack of any data for older age classes. Lack of data for these older age classes was a result of their apparent rarity in the population. Assuming a reproductive rate of 0 for age classes > 16 will not have much effect on overall population dynamics if the number of females in those age classes is negligible.

Jameson and Johnson (1993) estimated a minimum annual reproductive rate of 0.64 for mature females based on observations of 49 tagged otters near Green Island during 1975-84. They considered this estimate to be a minimum because the otters were observed infrequently and they suggested that the true rate may have been close to the value of 0.88 obtained from examination of reproductive tracts of mature females collected by Kenyon (1969) at Amchitka Island. Based on comparisons from the Aleutian Islands, Prince William Sound, and California, Jameson and Johnson (1993) concluded that annual reproductive rates of 0.85 to 0.90 were typical for mature females (age > 4) regardless of population status. Weighting our smoothed reproductive rate estimates by the estimated proportions in age classes > 4 gives an overall reproductive rate estimate of 0.85 for mature females, which is consistent with the conclusions of Jameson and Johnson (1993). This estimate is higher than estimates obtained after the oil spill by Monnett and Rotterman (1992). Their telemetry-based estimates of reproductive rates for mature females in western PWS were 0.58 (21/36) during 1990 and 0.78 (29/37) during 1991. These estimates may be lower than ours, at least in part, because Monnett and Rotterman (1992) did not instrument otters that were in advanced stages of pregnancy when captured and they may not have detected pups that died within the first few days after birth. Also, our estimates are partly based on detected pregnancies, some of which may not have resulted in live births.

Structure of Ages-at-death

Our estimate of the structure of natural mortality that occurred during the year preceding the oil spill assumed that 1) there was no age or sex related bias in recovery of carcasses of otters that died during the year preceding the spill, 2) there was no age or sex related bias in determining time of death for recovered carcasses, and 3) there was no bias in determining sex or age class for recovered carcasses. The most likely bias that could have affected recovery of carcasses is related to carcass size (Bodkin and Jameson 1991). We reduced the potential for this bias by not considering the 2 age classes with the smallest carcasses. Almost all adult sea otter mortality in PWS occurs during the winter (Johnson 1987, Monnett 1988), so that the adult carcasses on beaches in early spring should be representative of total annual adult carcass deposition. The potential for violations of assumptions (2) and (3) was reduced by not including any carcasses without clear determinations of time of death, sex and tooth-based age.

Our estimated structure of ages-at-death is broadly consistent with patterns observed previously for this region (Johnson 1987). Monson and Ballachey (1995) were not able to detect significant differences among age distributions from annual collections of beach-cast carcasses in western PWS during 1976 through 1984 and during the oil spill response in 1989 (carcasses classified as dying before the spill). This result is consistent with the assumption of a stable population structure during this period, but annual sample sizes and, therefore, the power to detect differences were quite low.

Population Age Structure

Our estimate of the population structure at the time of the spill assumed that 1) there was no age or sex related bias in mortality due to the oil spill, 2) there was no age or sex related bias in determining time of death for recovered carcasses, 3) there was no age or sex related bias in recovery of carcasses of otters that died after the spill, 4) otters classified as dying after the oil spill died as a result of the oil spill, 5) our smoothed estimates of age-specific reproductive rates were unbiased, and 6) the sex ratio of age class 0 was 1:1 at the birth pulse.

It is not known whether there was any age or sex related bias in oil spill mortality. All age and sex classes (ages < 14) were represented in the recovered carcass sample. Oil related mortality is not likely to be biased with respect to fitness of individuals in the path of an oil spill (Piatt et al. 1990). However, age and sex related differences in behavior and spatial distribution (Garshelis et al. 1984, Riedman and Estes 1990) may have resulted in an age or sex related bias in exposure and subsequent mortality of sea otters. Oiled areas in western PWS were primarily breeding areas, occupied by territorial males and adult females. Geographic information system plots of recovery locations gave no indication of any age or sex related segregation within the oil spill area.

Assumptions (2) and (3) were also required for estimating the structure of ages-at-death and were discussed above. In this case, however, we were able to test the assumption of no size related bias in carcass recovery and found it to be valid even for age class 0 otters. Assumption (4) was not likely to be seriously violated because the vast majority of the carcasses were recovered shortly after the spill and almost all natural adult mortality occurs during the winter.

Assumptions (5) and (6) were required for estimating the proportion of age class 0 otters in the population. The smoothed reproductive rate estimates appear reasonable, as discussed above. Our assumed 1:1 sex ratio for age class 0 is consistent with the observed ratios for pups born at rehabilitation centers (9 female : 8 male), recovered dependent pups with known sex that died after the oil spill (9 female : 10 male), and dependent pups captured with tangle nets and dip nets in 1992 (17 female : 18 male, NBS unpubl. data). Other efforts to capture dependent pups in western Prince William Sound have resulted in lower proportions of females (15 female : 20 male, Monnett 1988; 14 female : 25 male, Rotterman and Monnett 1991). The proportion of females in the sample of recovered fetal sea otters was higher than our assumed value for age class 0 (32 female : 17 male, Bodkin et al. 1993). It may be that sea otter sex ratios generally favor females at conception (Bodkin et. al 1993), but males have higher survival rates than females in utero, and perhaps as neonates (Monnett 1988), so that sex ratios of dependent pups tend to favor males. Our assumption of a 1:1 sex ratio was probably reasonable because we approximated reproduction with birth-pulse dynamics and estimated numbers in age class 0 based on pregnant and lactating females at the time of the pulse.

The estimated age structures for both sexes included a large number of age classes with higher proportions of individuals than the next youngest age classes. This suggests either very poor precision in estimating the age structure, violation of one or more of the assumptions about age bias, or that the population structure was not stable. Because of the relatively large sample size for estimating age structure and the other considerations discussed above, it seems most likely that the age structure was not stable at the time of the spill.

Survival Rates

Our estimates of age-specific survival rates were based on some or all of the following assumptions.

1) The estimated structure of ages-at-death was unbiased.
2) The estimated population age structure was unbiased.
3) The annual growth rate for either the whole population or for age classes >1 was $\lambda=1$ during the year preceding the oil spill.
4) The population age structure was stable at the time of the spill.

Assumptions (1) and (2) were discussed above. There are no data for directly assessing assumption (3). If the population was actually growing during the year preceding the spill, then our estimated survival rates would be negatively biased. We expect that any such bias would be small because it is widely believed that if the population was growing, its growth rate was small (Garrott et al. 1993). As discussed above, the assumption of a stable age structure was not likely to have been true.

The traditional survival rate estimates based on equations (3) and (4) rely on the assumption of age structure stability. The estimates based on equation (7) are the only ones that do not rely on the assumption of age structure stability and therefore are probably the most appropriate for this case. The estimates based on equation (7) do rely on assumptions (1), (2), and (3). We were not able to obtain estimates of survival rates for age classes 0 and 1 based on equation (7) because of the possible size bias in recovery of otters that died before the spill. The quality of the estimates was also limited by the small overall sample size of ages-at-death data. This was particularly true for males (n=6). Lack of age structure data for age classes > 16 for females and 17 for males may have prevented the fitting of a realistic form for senescence in the smoothing function. The actual form of senescence may not be important to overall population dynamics, however, if the older age classes are a negligible portion of the population.

There are no published estimates of survival rates for PWS sea otters in age classes > 1 from before the spill. Garshelis and Garshelis (1987) observed survival rates of 0.60 (n=5) for female and 0.33 (n=3) for male pups that were tagged near Green Island while dependent and then followed approximately 1 month after independence. This pup category may correspond most closely with the last 3 to 6 months of our age class 0, but the weanings were considered atypical (Garshelis and Garshelis 1987). Monnett (1988) estimated annual survival rates of 0.34 for female and 0.21 for male weanling sea otters based on telemetry data from eastern and western PWS during 1984-87, under the assumption that otters died on the day their carcasses were found and that missing otters were dead. This weanling category may approximately correspond to our age class 1.

Rotterman and Monnett (1991), Monnett and Rotterman (1992) and NBS (unpubl. data) provided telemetry-based estimates of survival rates for certain segments of the western PWS population during time periods after the oil spill. Monnett and Rotterman (1992) estimated a 10 month survival rate of 0.96 for adult females during 1990-91 based on the assumption that missing otters were dead. Weighting our smoothed survival rate estimates from equation (7) by the estimated proportions in each age class gives an overall estimate of 0.86 for females in age classes ≥ 2. The overall survival rate estimated by Monnett and Rotterman (1992) may have been greater than ours because their sample of otters may have included a higher proportion in the prime age classes. We estimated survival rates of 0.95 for female age classes 2 through 4 and rates > 0.90 for age classes 2 through 9.

All of the other estimates of survival rates in western PWS after the spill are for otters in age classes ≤ 1. Monnett and Rotterman (1992) estimated 2 month survival rates for dependent pups, both sexes combined, to be 0.76 in 1990 and 0.97 in 1991. This dependent pup category corresponds approximately to months 7 and 8 of our age class 0. Rotterman and Monnett (1991) estimated 8 month survival rates of 0.08 for male and 0.21 for female weanling sea otters during 1991 based on the assumption that missing otters were dead. These rates appear to be extremely low and may be a result of chronic oil effects (Rotterman and Monnett 1991). This weanling category approximately corresponds to the first 8 months of our age class 1. NBS (unpubl. data) estimated 15 month survival rates of 0.59 for females and 0.47 for males monitored from 3 months of age during 1992-93, based on the assumption that missing otters were dead. This 1.5 year weanling category most closely corresponds to our age class 1.

MODEL

We used a Leslie-type 2-sex projection matrix (Caswell 1989) to integrate the available information on western PWS sea otter population dynamics and to project its potential recovery following the oil spill. We assumed that there was no emigration from or immigration to western PWS, which is largely consistent with telemetry data from after the spill (Monnett and Rotterman 1992b, NBS unpubl. data). The model approximated the reproductive cycle with an annual birth pulse occurring at the anniversary of the oil spill. This date is close to when most pups are born in this population (Garshelis et al. 1984). Parameter values used with the model are given in Tables 3 and 4. Fecundity values were obtained from our smoothed reproductive rate estimates (Figure 2) and the assumption of a 1:1 sex ratio for age class 0. Based on the conclusions of Jameson and Johnson (1993), we assumed that reproductive rates remained constant and were not affected by the oil spill or the status of the population. Survival rates for age classes 2 - 20 for females and 2 - 17 for males were the smoothed estimates from equation (7) (Figures 5C and 6C). We set survival rates for males in age classes 18 - 20 equal to 0, because no carcasses in age classes greater than 17 were recovered and there were insufficient data for fitting the senescent phase of the smoothing function. Based on the relatively high survival rate for adult females observed by Monnett and Rotterman (1992a) during 1990-91, we assumed that adult survival rates also remained constant and were not affected by the oil spill or the status of the population.

Following Eberhardt and Siniff (1988), we assumed that the most likely parameters to be affected by the oil spill or population status would be survival rates for the youngest age classes. Telemetry data suggest that there may have been an initial depression in survival rates for age class 1 (Rotterman and Monnett 1991), followed by increases in survival rates for age classes 0 and 1 in the first few years after the spill (Monnett and Rotterman 1992a, Rotterman and Monnett 1991, NBS unpubl. data). We allowed survival rates for age classes 0 and 1 to vary over time, and used telemetry-based estimates of those rates in the years for which they were available.

We assumed that if survival rates were perturbed from equilibrium levels, then density dependent processes would eventually cause them to return toward equilibrium levels. Density dependence was modeled separately for males and females with a generalized logistic function (Taylor and DeMaster 1993). The general form of this function is

$$s_N = s_c + (s_m - s_c)\left(1 - \left(\frac{N}{N_c}\right)^{\theta}\right)$$

where s_N is the survival rate when the population is size N, N_c is the population size at equilibrium, s_c is the survival rate at equilibrium, and s_m is the maximum survival rate (the theoretical rate when $N=0$). Here, we set $N_c=5808$, which was the estimated population size in 1985 (Garrott et al. 1993). The parameter θ controls the shape of the function. Following Eberhardt and Siniff (1988), we used a relatively large value of θ ($\theta=9$) so the effect of density dependence would not be evident until the population came close to its equilibrium size (Figure 7). Nine was the largest value for θ that consistently resulted in stationary trajectories rather than limit cycles in our model projections.

Because of the lack of data for estimating survival rates of age class 0 and 1 otters in most years, we considered a series of 4 potential scenarios (Table 4). In all of the scenarios, we used the telemetry-based estimates of survival rates for age class 1 otters in 1990-91 (Rotterman and Monnett 1991) and 1992-93 (NBS unpubl. data). We used the mean of the 1990-91 and 1992-93 estimates for age class 1 otters in 1991-92. Based on the extremely low survival rate observed for age class 1 otters in 1990-91 (Rotterman and Monnett 1991), we assumed that there was no survival of age class 0 or 1 otters in 1989-90.

In scenarios 3 and 4, we used the telemetry-based estimates for age class 0 otters in 1990-91 and 1991-92 reported by Monnett and Rotterman (1992a). These values are likely to be overestimates of the actual survival rates because they account for mortality only during the first 2 months after the neonatal period. The rate of 0.97 for 1991-92 (Monnett and Rotterman 1992a) is higher than rates observed for any other populations in Alaska (Monnett and Rotterman 1992a; Monson 1995; Monson and DeGange 1995) or California (Loughlin 1981; Siniff and Ralls 1991; Jameson and Johnson 1993; Riedman et al. 1994). We assumed that in 1992-93, survival rates for age class 0 otters began a density dependent decrease to equilibrium values, and survival rates for age class 1 otters increased to our estimated rate for prime age adults and then began a density dependent decrease to equilibrium values (Table 4, Figure 7). It is unlikely that survival rates for age class 1 otters could actually be as high as those of prime-aged adults. The assumed survival rates for age classes 0 and 1 in these scenarios probably can be best viewed as upper limits for the actual rates that potentially could occur in this population. The differences between scenarios 3 and 4 are the assumed values for the equilibrium survival rates (see below).

In scenarios 1 and 2, we again assumed that survival rates for age class 0 increased to their maximum level in 1991-92 and then began a density dependent decrease to their equilibrium values (Table 4, Figure 7). However, we used a lower, telemetry-based estimate of the age class 0 survival rate from Kodiak (0.83; Monson and DeGange 1995) for the maximum rate. Kodiak provides an example of an increasing sea otter population in recently occupied, prime habitat (Monson and DeGange 1995) with survival rates that are probably close to the maximum for the species. The rate reported by Monson and DeGange (1995) accounts for mortality during the first 5 months after the neonatal period. We obtained a survival rate of 0.65 for age class 0 in 1990-91 by assuming the same proportional reduction from the 1990-91 rate reported by Monnett and Rotterman (1992a) as effectively assumed for the 1991-92 rate (i.e., 0.65/0.76=0.83/0.97). We assumed that survival rates for age class 1 were at their equilibrium values in 1993-94 and that they remained at that level throughout the recovery period (Table 4, Figure 7). Given the other parameters in the model, this is the most conservative assumption that can be made about age class 1 survival rates that will still allow the population to eventually recover. The differences between scenarios 1 and 2 are in the assumed values for the equilibrium survival rates.

There were no data for directly estimating equilibrium survival rates in the western PWS population. However, given values for the other parameters in the model and an assumed equilibrium value for the survival rate of either age class 0 or age class 1 females, the equilibrium value of the other female survival rate can be derived numerically. We used this approach to derive equilibrium survival rates based on two different sets of assumptions. In the first set (equilibrium assumption A), we assumed that the observed age class 1 survival rates of 0.59 for females and 0.47 for males in 1992-93 (NBS unpubl. data) were the equilibrium survival rates for this population. This results in an equilibrium survival rate of

0.56 for age class 0 females. We assumed that the survival rate for age class 0 males was the same as for age class 0 females. Scenarios 1 and 3 were based on equilibrium assumption A (Table 4, Figure 7).

The second set of assumptions (equilibrium assumption B) is based on the observed survival rate of 0.47 for age class 0 sea otters at Amchitka, Alaska (Monson et al. In prep.). The Amchitka population is the only other Alaskan sea otter population which is thought to be at equilibrium and for which we have pre-weaning survival data. The telemetry-based estimate from Amchitka (Monson et al. In prep.) is similar to the estimate of 0.46 (Siniff and Ralls 1991), but somewhat lower than the estimate of 0.60 (Riedman et al. 1994) for the California population, which also appears to be close to equilibrium. However, dynamics of California and Alaska populations may not be generally comparable (Bodkin et al. 1995; Estes et al. 1995). Given the other parameters in our model, an equilibrium survival rate of 0.47 for age class 0 females results in an equilibrium rate of 0.70 for age class 1 females. As in equilibrium assumption A, we assumed that age class 0 survival rates were the same for males and females. We obtained the equilibrium survival rate of 0.56 for age class 1 males by assuming the same proportional increase from the observed 1992-93 male rate (NBS unpubl. data) as effectively assumed for females (i.e., 0.56/0.47=0.70/0.59). Scenarios 2 and 4 were based on equilibrium assumption B (Table 4, Figure 7).

We used the model to project a separate population recovery trajectory based on each of the 4 scenarios. For each scenario, the model was initiated with our estimate of the population structure at the time of the spill (Figure 4) and the total population size of 3,898 otters estimated to remain after the spill by Garrott et al. (1993). We then incremented the population annually at the anniversary of the spill with a projection matrix parameterized according to Table 3 and the appropriate column of Table 4. In all of the scenarios, there was a projected decrease to a population size of 3,234 otters after the first year (Figure 8). The initial decrease was due to the assumption of no survival for juvenile otters in the first year. The population was projected to begin increasing after the first year in all of the scenarios, with maximum rates of increase of 10% per year in scenarios 1 and 2 and 14% per year in scenarios 3 and 4. The projected times required to recover to the estimated 1985 population size of 5808 otters (Garrott et al. 1993) were 23 years in scenario 1, 16 years in scenario 2, and 10 years in scenarios 3 and 4 (Figure 8). Projected recovery times were more sensitive to assumptions about maximum survival rates than assumptions about equilibrium survival rates over the range of scenarios we considered.

The equilibrium survival rates are the rates required for the population to maintain a constant size. We assume that annual survival and reproductive rates fluctuated around their equilibrium values in the years preceding the spill (i.e., mean annual survival rates were the equilibrium values) because the population was maintaining its size during that period. If none of the survival or reproductive rates increased above their equilibrium values following the spill, then the population would not recover to its previous size. Recovery, in our model, is driven by the possibility that survival rates for age classes 0 and 1 can exceed their equilibrium values. All of the scenarios we considered assume that survival rates for age class 0 exceeded their equilibrium values by 1990-91 and that survival rates for age class 1 reached or exceeded their equilibrium values by 1993-94. Once all of the survival rates reach or exceed their equilibrium values, the population will continue to increase as long as the survival rate for at least one age class remains above its equilibrium value.

Scenarios 3 and 4 are highly optimistic with respect to survival rates for both age classes 0 and 1. The rate of recovery under these scenarios probably represents the maximum that could occur considering the available data. Scenarios 1 and 2 are more conservative but probably still somewhat optimistic with respect to survival rates for age class 0. This is because these rates still do not include fetal or neonatal mortality. Also, it is not known whether the western PWS habitat could have recovered to the point where it could support survival rates equivalent to those at Kodiak so quickly. However, other factors such as predation rates may also differ between the two areas. On the other hand, scenarios 1 and 2 are quite conservative with respect to survival rates for age class 1. Because they combine somewhat optimistic assumptions for age class 0 with conservative assumptions for age class 1, the projected recovery rates for scenarios 1 and 2 are probably more realistic than those for scenarios 3 and 4.

The assumption that adult survival rates were not affected by the spill may also be somewhat optimistic. This assumption was used in all 4 scenarios and is consistent with the available telemetry data (Monnett and Rotterman 1992a). However, age distributions of beach-cast carcasses collected in 1990 and 1991 suggest that adult mortality may have been relatively high in those years (Monson and Ballachey 1995). Given the pathologies observed in oiled otters dying in 1989 (Lipscomb et al. 1994) and patterns generally observed in laboratory studies of toxic effects, it is possible that sub-lethal effects of oil exposure could have reduced survival of adult sea otters for some period of time after the spill.

All of the scenarios we considered indicated that the population would decrease during the first year after the spill and then begin a relatively steady increase to its equilibrium size. Agler et al. (1994) were not able to detect any trend in the western PWS sea otter population size based on their analysis of the boat-based surveys conducted from 1989 through 1993. This may be due, at least in part, to the large amount of variability associated with each of the survey estimates (Table 5). The model projections under all of the scenarios are well within the 95% confidence intervals of the population estimates from all of the boat-based surveys conducted after the spill if they are adjusted for detectability following Garrott et al. (1993) (Table 5).

We believe that the model presented here provides a reasonable structure for approximating the dynamics of the western PWS sea otter population. However, we want to stress that there is considerable uncertainty associated with the various assumptions used to estimate parameters and with the estimation of the parameters, given the assumptions. It might be possible to use bootstrap (Efron 1982) or Bayesian (Raftery et al. 1995) approaches to quantify some of this uncertainty. Of most concern, though, is that beyond 1993, there are no data for estimating the model parameters and their values must be based purely on assumptions about how future values are likely to relate to past estimates. In addition to assuming a particular form for this relationship, all the scenarios assume that the relationship will remain unperturbed throughout the recovery period. The uncertainty associated with these assumptions is partially evident in the disparity between projected recovery times under the various scenarios. These projections might best be viewed as benchmarks, indicating how the population is likely to recover, given the available data and selected sets of assumptions. The potential for recovery under alternative sets of assumptions could be roughly evaluated by comparison to the sets of assumptions we have considered. Continued monitoring would be required to determine how the population vital rates actually change after 1993. Updated (or improved) estimates of survival rates, reproductive rates and population size should be incorporated into the model as they become available.

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Table 1. Maximum likelihood estimates of proportions of otters in sample subclasses.

Sample subclass	Proportions of lactating females and dependent pups assumed equal	
	No	Yes
Of 407 recovered carcasses		
Independent females	0.523	0.522
Independent males	0.354	0.354
Independent unknown sex	0.069	0.068
Dependent pups	0.054	0.056
Independent lactating females[a]	0.057	0.056
Of 143 examined independent females		
Lactating	0.101	0.099
Non-lactating	0.899	0.901
-2 ln(L)[b]	950.448	950.478

a These include the proportion of known females estimated to be lactating and the portion of unknown sex estimated to be lactating females.

b $L = (P_f)^f(P_m)^m(P_d)^d(1-P_f-P_m-P_d)^{1-f-m-d}(P_l)^l(1-P_l)^{1-l}$. See text for symbol definitions. Difference in proportions of lactating females and dependent pups not significant (likelihood ratio test, $\chi^2 = 0.03$, df=1, P=0.86).

Table 2. Least squares estimates of parameters in smoothing functions for survival rates.

Source of survival rate estimates	Parameter[a]				
	A	B	exp(-G)	T	S
Female					
Age structure	0.94	10[b]	0.92	16.38	0.87
Ages-at-death	-c-	-c-	1	11.45	5.54
Age structure & Ages-at-death	-c-	-c-	0.95	12.31	2.18
Male					
Age structure	0.39	10[b]	0.79	-d-	-d-
Ages-at-death	-c-	-c-	0.98	10.03	3.25
Age structure & Ages-at-death	-c-	-c-	0.86	-d-	-d-

a $D = \exp(-T/S)$, $E = 1/S$.

b Least squares estimate of B was greater than 10, so B was set equal to 10 and no longer treated as a parameter.

c Parameters for initial phase of smoothing function not estimated because only age classes 2 and above were considered.

d Parameters for senescent phase of smoothing function not estimated because unable to obtain convergence and nonsingular jacobian.

Table 3. Parameter values used for projecting recovery of the western PWS sea otter population following the *Exxon Valdez* oil spill in March 1989.

	Parameters		
Age class	Fecundity	Female Survival	Male Survival
0	0.00	*	*
1	0.00	*	*
2	0.00	0.95	0.86
3	0.38	0.95	0.86
4	0.60	0.95	0.86
5	0.73	0.94	0.86
6	0.81	0.94	0.86
7	0.85	0.93	0.86
8	0.87	0.92	0.86
9	0.89	0.90	0.86
10	0.90	0.88	0.86
11	0.90	0.84	0.86
12	0.90	0.78	0.86
13	0.91	0.69	0.86
14	0.91	0.57	0.86
15	0.91	0.43	0.86
16	0.60	0.27	0.86
17	0.00	0.13	0.86
18	0.00	0.04	0.00
19	0.00	0.01	0.00
20	0.00	0.00	0.00

* See Table 4 for survival rates of age class 0 and 1 otters.

Table 4. Survival rates used for age classes 0 and 1 in projecting recovery of the western PWS sea otter population under 4 potential scenarios following the *Exxon Valdez* oil spill in March 1989.

		Scenario			
Age	Year	1	2	3	4
0	1989-90	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
	1990-91	0.65/0.65	0.65/0.65	0.76/0.76	0.76/0.76
	1991-92	0.83/0.83	0.83/0.83	0.97/0.97	0.97/0.97
	equilib.[a]	0.56/0.56	0.47/0.47	0.56/0.56	0.47/0.47
1	1989-90	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
	1990-91	0.21/0.08	0.21/0.08	0.21/0.08	0.21/0.08
	1991-92	0.40/0.28	0.40/0.28	0.40/0.28	0.40/0.28
	1992-93	0.59/0.47	0.59/0.47	0.59/0.47	0.59/0.47
	1993-94	0.59/0.47	0.70/0.56	0.95/0.86	0.95/0.86
	equilib.[b]	0.59/0.47	0.70/0.56	0.59/0.47	0.70/0.56

a Survival rates assumed to begin density dependent decrease to equilibrium values after 1991-92 in all scenarios.

b Survival rates assumed to remain constant after reaching equilibrium values in 1992-93 (scenario 1) or 1993-94 (scenario 2). Survival rates assumed to begin density dependent decrease to equilibrium values after 1993-94 in scenarios 3 and 4.

Table 5. Estimates of the western PWS sea otter population size derived from boat-based surveys and from model-based projections.

	Boat-based survey estimates		Model-based projections			
Year	Unadjusted ±95% C.I.	Adjusted[e] ±95% C.I.	Scenario 1	Scenario 2	Scenario 3	Scenario 4
1989	2709±884[a]	3898±1272	3898	3898	3898	3898
1990	1991±606[b]	2865±871	3234	3234	3234	3234
1991	2149±976[c]	3092±1404	3560	3560	3671	3671
1993	1525±1560[d]	2194±2245	3486	3644	3883	3883

a Based on June, July, and August surveys (Garrott et al. 1993).

b Based on June, July, and August surveys (Burn 1994).

c Based on July survey (Burn 1994).

d Based on July survey (Agler et al. 1994).

e Adjusted for detectability following Garrott et al. (1993). Approximate variance obtained by multiplying the unadjusted variance by the square of the correction factor. This results in an underestimate of the variance (and the confidence interval) because it does not account for the error in estimating the correction factor.

Total Carcasses	Time of death	Age	Sex
508	407 After spill	385 Known	214 Female
			149 Male
			22 Unknown
		22 Unknown	8 Female
			5 Male
			9 Unknown
	73 Before spill	57 Known	33 Female
			15 Male
			9 Unknown
		16 Unknown	10 Female
			0 Male
			6 Unknown
	28 Unknown	19 Known	2 Female
			3 Male
			14 Unknown
		9 Unknown	1 Female
			1 Male
			7 Unknown

Figure 1. Sea otter carcasses collected in Prince William Sound between 30 March and 15 September 1989. Carcasses with unknown ages are all in age classes >0.

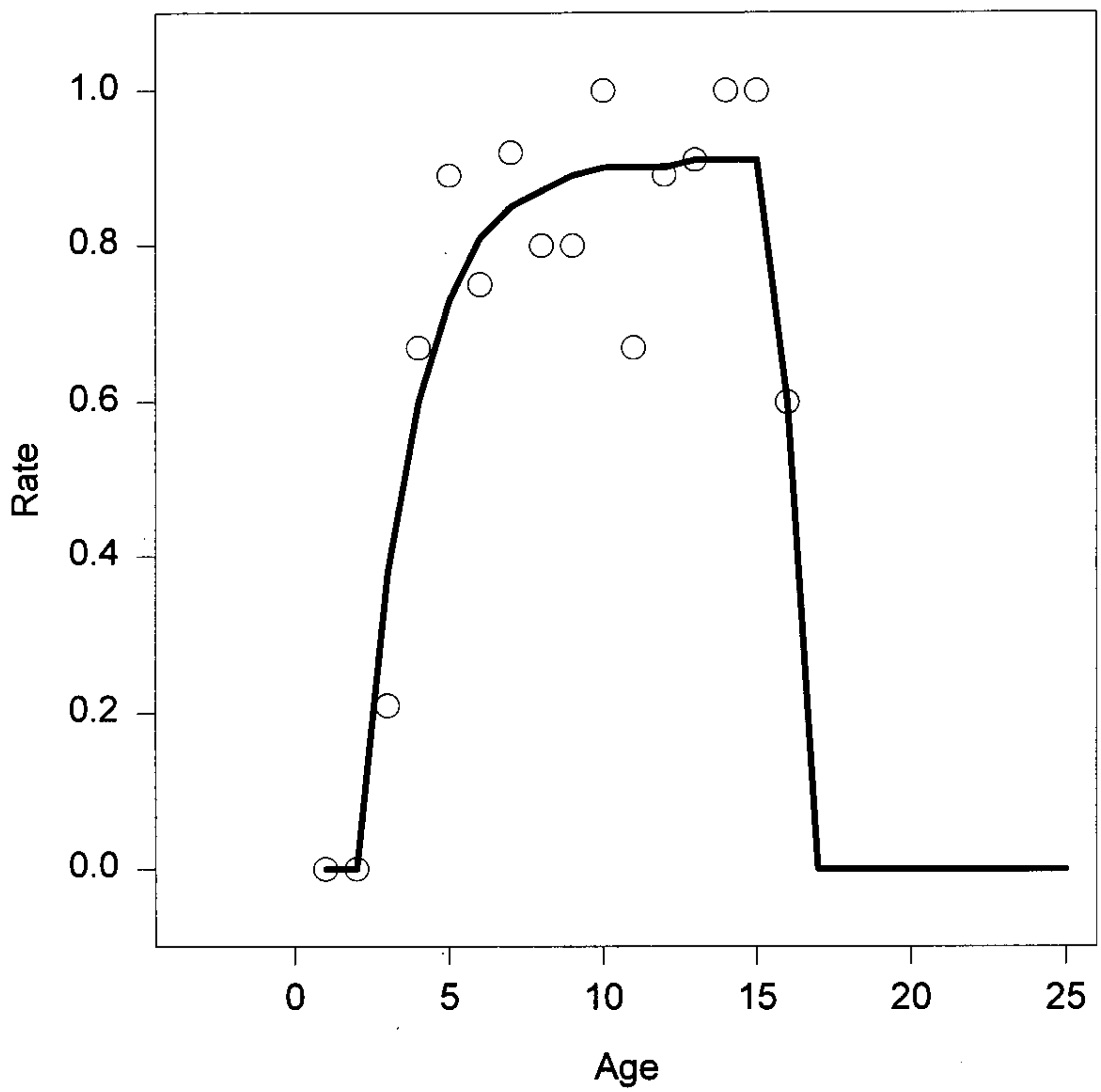

Figure 2. Observed and smoothed reproductive rate estimates for female sea otters at the time of the spill.

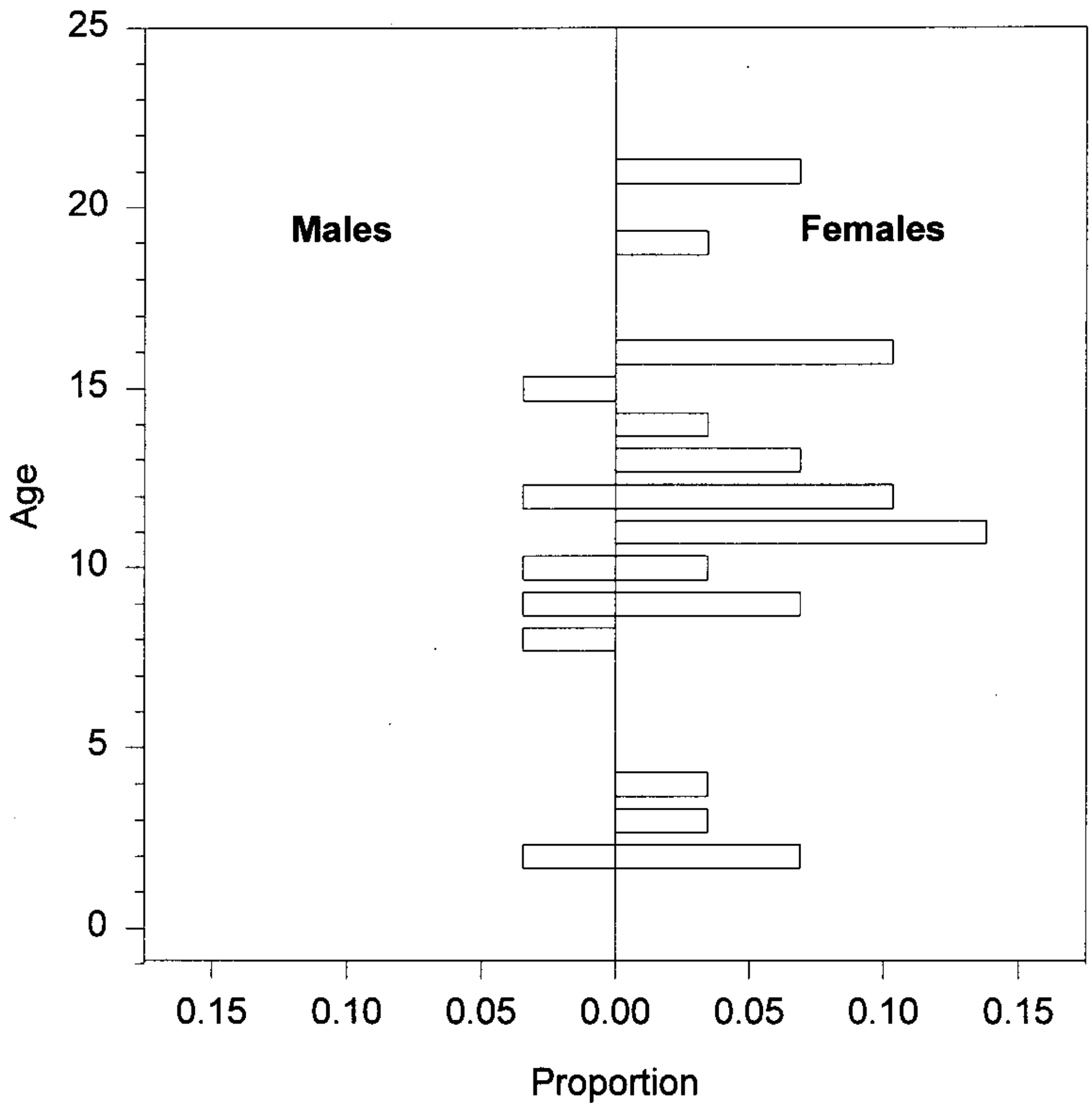

Figure 3. Estimated structure of natural mortality for age classes 2 and above during the year preceeding the spill. Numbers in each age and sex class are expressed as proportions of the total number of deaths in age classes 2 and above.

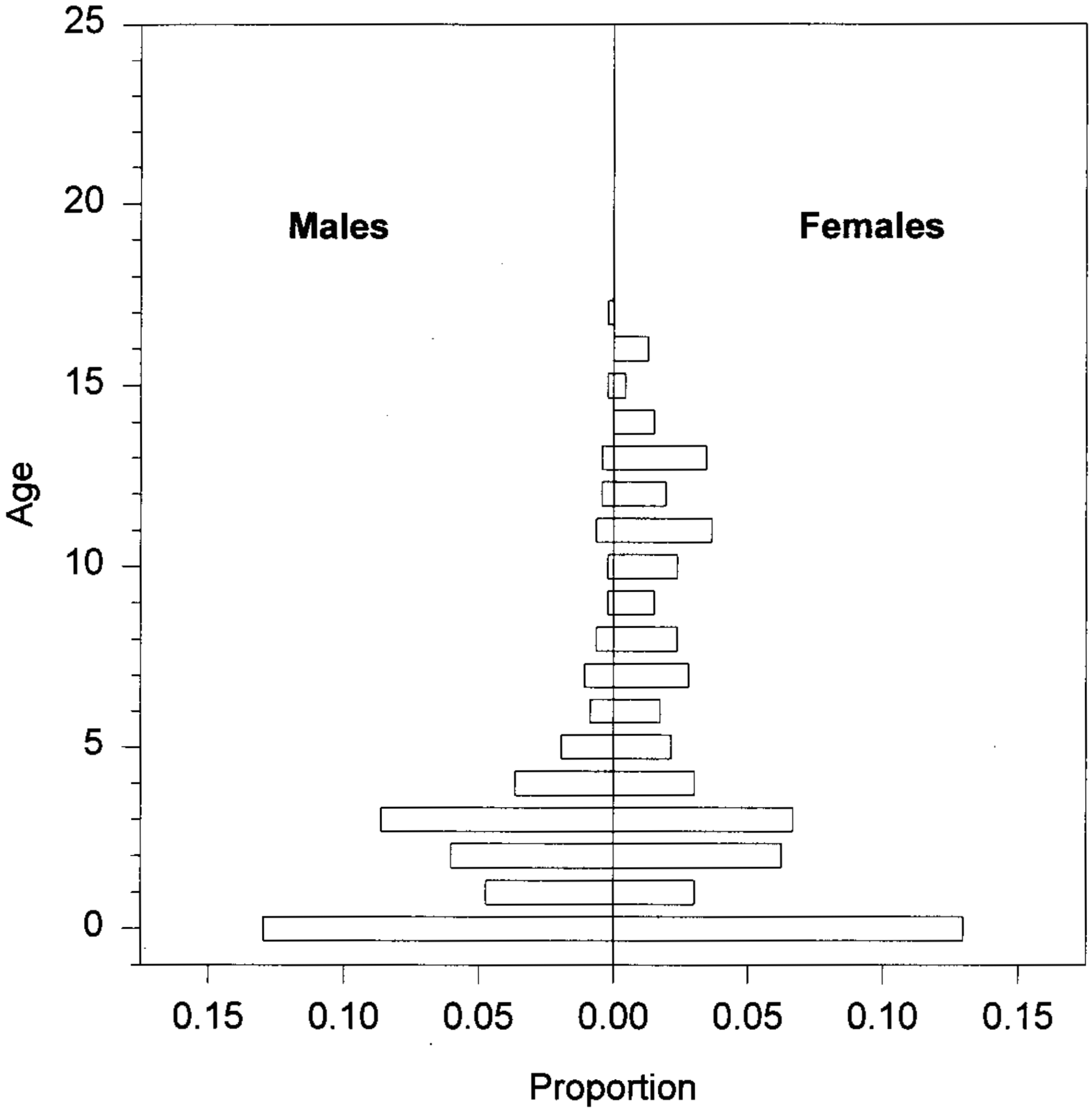

Figure 4. Estimated population structure at the time of the spill. Numbers in each age and sex class are expressed as proportions of the total population size.

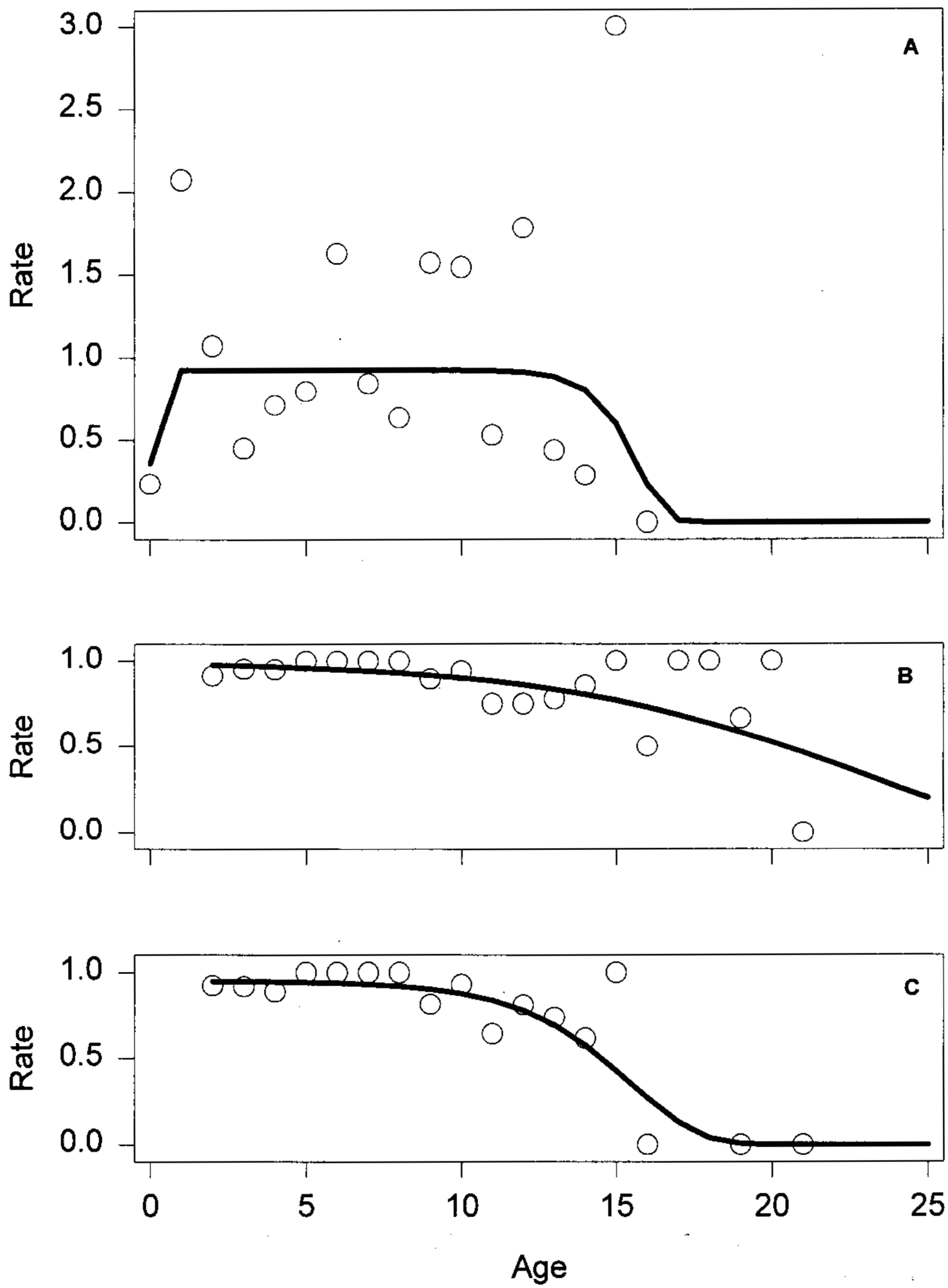

Figure 5. Estimated and smoothed survival rates for female sea otters: A) based on age structure data, B) based on ages-at-death data, C) based on age structure and ages-at death data.

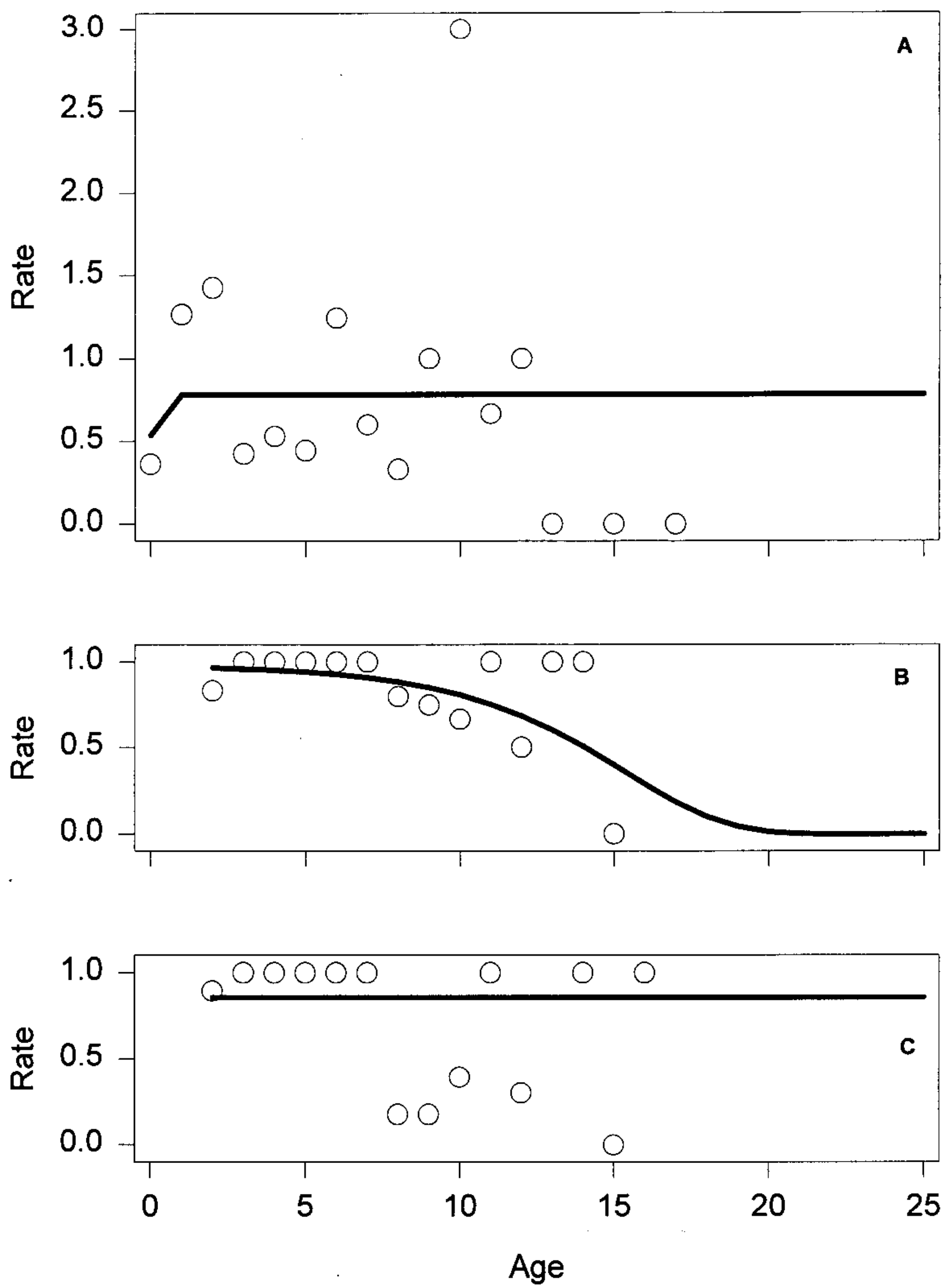

Figure 6. Estimated and smoothed survival rates for male sea otters: A) based on age structure data, B) based on ages-at-death data, C) based on age structure and ages-at death data.

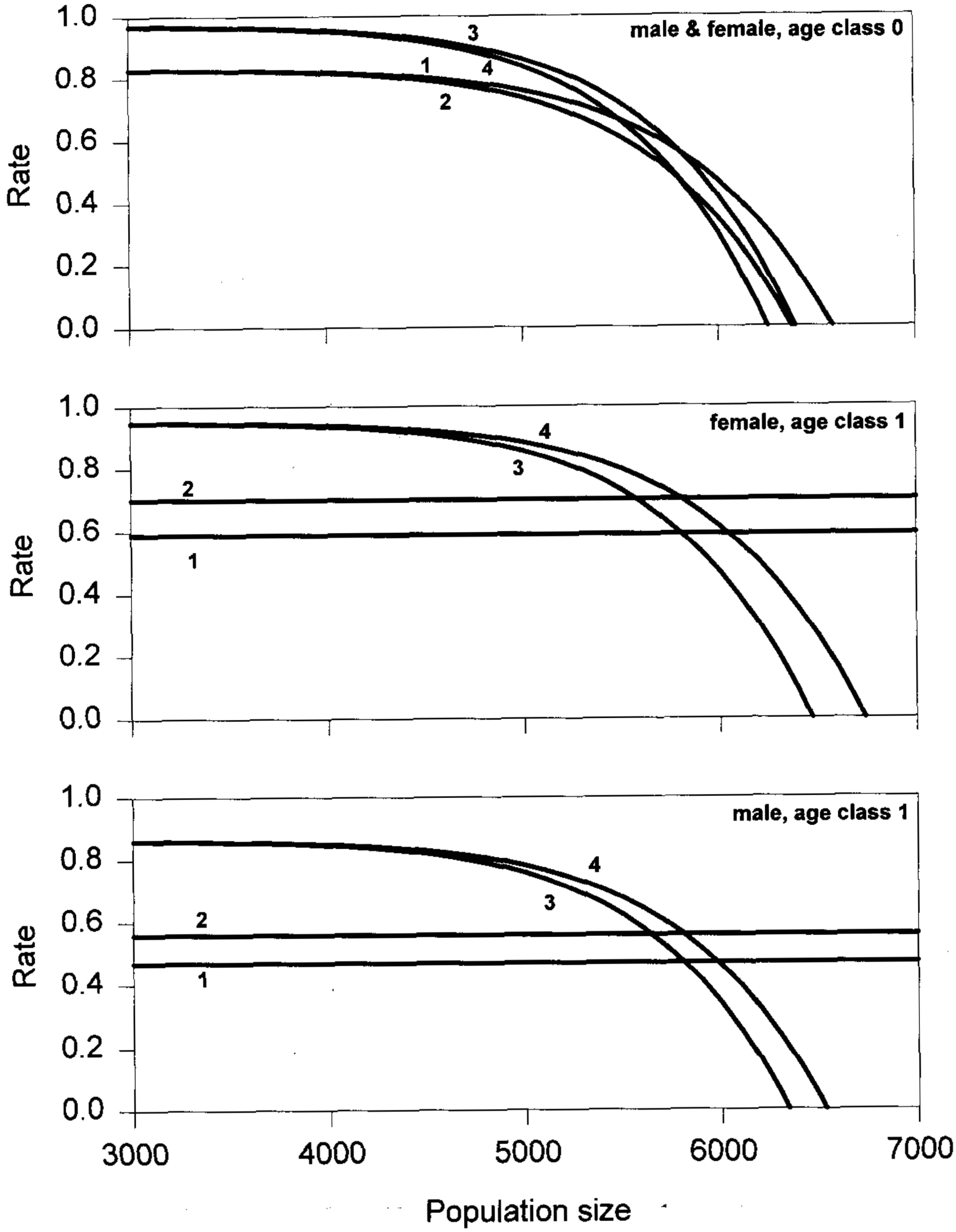

Figure 7. Relation of juvenile sea otter survival rates to population size under 4 different model scenarios.

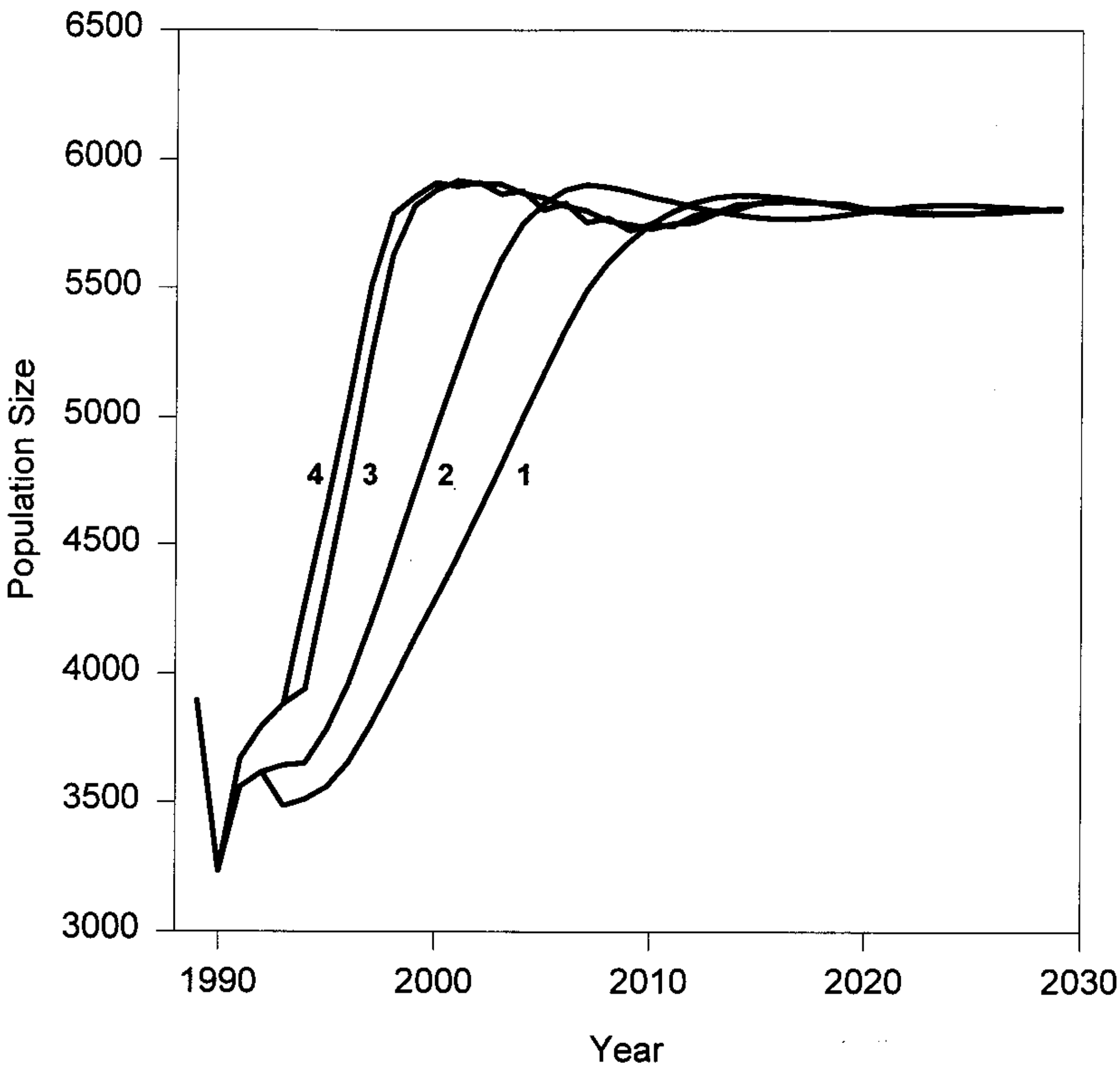

Figure 8. Four scenarios for projected recovery of the western Prince William Sound sea otter population following the *Exxon Valdez* oil spill in March 1989.