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Dynamics of Abundance and Distribution for Pacific Harbor Seal, *Phoca vitulina richardsi*, on the Coast of California

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in Biology

by

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ABSTRACT OF THE DISSERTATION

DYNAMICS OF ABUNDANCE AND DISTRIBUTION FOR PACIFIC HARBOR SEAL, *Phoca vitulina richardsi*, ON THE COAST OF CALIFORNIA

by

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Doctor of Philosophy in Biology

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Pacific harbor seals, *Phoca vitulina richardsi*, are important members of the California near-shore community. Because the seal population is increasing and has been doing so since at least 1940, it is exerting a growing influence on the near-shore ecosystem and has been the subject of numerous research investigations. These investigations have been limited to individual hauling sites, islands, or one- to three-year statewide surveys during which harbor seals were incidentally included while focusing on other species. Studies presented here were designed to

examine harbor seals along the entire California coast over an extended time period, 1982-1995.

For these studies, I tested the hypothesis that changes in population structure are related to long term perturbations (i.e., decimation and recovery of a marine mammal species) as well as short-term perturbations (inter-annual variation of environmental factors). To further investigate these concepts, I examined differential colonization related to regional nearshore factors including intraspecific and interspecific relationships. Previous harbor seal investigations had not focused on these aspects of population growth because data were not available in sufficient detail on a state-wide, long-term basis.

I studied harbor seal population dynamics by examining number of seals hauled out and number of hauling sites utilized. Data were stratified by time and area with emphasis on most recent data which I collected with particular attention to improving count accuracy. Given current protection and on-going population recovery, I have tested hypotheses about population fluctuation as it approaches carrying capacity.

CHAPTER 1

CENSUSES AND VARIANCE ESTIMATION

INTRODUCTION

Pacific harbor seals, *Phoca vitulina richardsi* (Shaughnessy and Fay 1977), were first censused in California during 1927 statewide pinniped surveys (Bonnot 1928). Since then, harbor seals have been censused many times (Bureau of Marine Fisheries 1947; Bonnot 1951; Bartholomew and Boolootian 1960; Odell 1971; Carlisle and Aplin 1966; Frey and Aplin 1970, Carlisle and Aplin 1971; Le Boeuf et al. 1976; Mate 1977; Bonnell et al. 1981; and Bonnell et al. 1983; see Table 1).

Harbor seals haul out (crawl or move from the ocean) onto beaches, rocks, and other substrates to rest, whelp, and molt. They are not territorial, although when hauled out, they tend to line up at water's edge and keep other seals at least a flipper's length away. At hauling sites, counts of harbor seals range from one to one thousand and average about fifty seals (Hanan and Beeson 1994). They may haul out near other pinniped species but usually do not. For these reasons and because harbor seal hauling sites are located along California's entire coast and in embayments aerial photographic surveys are used for census.

Miller's 1981-1982 (Miller et al. 1983) and my 1983-1994 surveys (Hanan 1990, Hanan and Beeson 1994, Beeson and Hanan 1994, and Hanan et al. 1985, 1986a, 1986b, 1987, 1988, 1989, 1991, 1992, and 1993) were designed to systematically count Pacific harbor seals during their molting period, a period of peak abundance on shore (Miller et al. 1983, Allen et al. 1989). Herein, I also present and utilize for analyses results of the 1995 California Department of Fish and Game (CDFG) aerial harbor seal survey (Figure 1). Beeson and Hanan (1994) and Hanan and Beeson (1994) update and revise harbor seal counts surveys of 1982-1994. In addition to these statewide surveys, others were conducted at specific locations and islands within California waters (e.g., Bartholomew 1949, 1967; Antonelis and Fiscus 1980; Slater and Markowitz 1983; Stewart and Yochem 1984a, 1984b, 1994; Stewart et al. 1988; Allen et al. 1988, 1989).

California surveys for pinnipeds have been conducted from aircraft, including airplanes, blimps, and helicopters. Many surveys included counts from observers on ships or on shore. Until late 1970, harbor seal counts were made as part of censuses for California sea lions and northern sea lions. Because those surveys were specifically designed to count sea lions, they likely under-represented harbor seals.

An important issue addressed by my research relates to changes in number of seals hauled out over time. Miller et al (1983) and Stewart (1984) showed that number of seals hauled out increased during an afternoon falling tide as more haul-out substrate became available. Allen et al. (1989) showed that number of seals hauled out is subject to human disturbance.

The major objective of this study was to design a survey appropriate for producing an index of abundance for harbor seals. It was understood that neither all seals nor all pups were ashore during any relatively short time period, as with elephant seals or sea lions (see Boveng 1988a, Lowry et al. 1992); therefore, annual surveys were conducted year to year with consistent methodology (e.g., aerial survey during molt period, mid-day falling tide cycle, 70 millimeter film, hand-held cameras, and counts directly from developed film). Counts were then comparable year to year when considering time of census and census technique, and changes in total seals counted accurately paralleled on a statewide basis, population growth rates as an index of true abundance. With proper treatment the index could reveal population trends (See Chapter 3). I refined and parameterized this index by estimating seal proportion hauled out (from radio tagging studies) and applied this correction factor to survey results (see Chapter 2, Proportion Hauled).

Had aerial photographic surveys been repeated by a second airplane or repeated by a second pass another time during surveys, I could have estimated survey variance directly from paired photographic counts. Although some hauling sites were repeated on the following day, survey costs precluded duplicate flights and there was no systematic method for variance estimates within surveys. Surveys were flown and counts recorded as a one time pass over all hauling sites. Therefore, no standard or practicable method of estimating variance within surveys was available. I further parameterized the abundance index by developing and applying a method of estimating daily haul out variance from shore-based counts.

METHODS

Survey and Census Techniques:

Aerial photographic censuses were flown in high-wing aircraft at an altitude of approximately 600 feet (183 meters). Each aircraft was equipped with a floor mounted photographic port which facilitates unobstructed downward viewing of hauled-out seals well before passing over them and allows nearly vertical photographs of seals. Vertical photographs contribute less counting bias to aerial surveys than oblique pictures taken through side windows (Miller et al. 1983).

The survey team consisted of a pilot, data recorder, and photographer using motor-driven Hasselblad cameras (models: 500ELM and 2000FCW), 100 mm lens, and large capacity (70 frames) film magazines. Area covered in pictures with these cameras and lens' at 600 foot altitude was approximately 100 meters by 100 meters (Miller et al. 1983). A Soligor II spotmeter was used to assess lighting conditions and set camera F stops; all film (either Kodak 64 or 200 ASA 70 millimeter Ektachrome film) was exposed at 1/500th seconds. The data recorder kept track of position, time, frames exposed, estimated number of seals, and substrate utilized in a flight book of coastal charts.

Because cameras occasionally malfunctioned and the problem could not be detected until after film was developed and because photographs occasionally missed or did not include seals at edges of photographs, some site counts were based wholly or partially on photographer's estimates, which were recorded routinely as each site was photographed. Hanan et al. (1991) compared photographer's estimates for 1986-1990 to the film counts and showed the estimates to be, on average, lower counts than film counts. Thus, photographer's estimates were conservative estimates of actual seal numbers.

Mainland surveys were flown (weather permitting) sequentially northward because tidal cycle changed in a northward progression and because tidal change moved northward faster than survey progress, only a discrete coastal section was surveyed each day during the low tide 'window'. To assure continuity, each survey day started at the previous day's last photographed site approximately one hour before local low tide and continued northward until approximately one and one half hours after local low tide.

I was usually able to survey southern California's mainland coast to Monterey on survey day one, to the Russian River on day two, to Humbolt Bay on day three, and to Oregon and California's border on day four. The Channel Islands were surveyed between 1000 and 1430 hours on two or three consecutive days several weeks prior to surveying the mainland. In contrast to exposed coastal sites, major bays and estuaries were surveyed one hour before to an hour and a half after local high tide, because seals haul out on mud flats or above them, during high tide in these areas. Surveys were also planned to coincide with time periods when fewest people were utilizing beaches.

To view, identify, and count seals from developed photographic film, dissecting microscopes were used and pin pricks were made over each seal on a thin plastic sheet laid over developed photographic film. Because harbor seal pups grow within a month to nearly yearling size and because females whelp successfully as early as February or as late as August, all harbor seals were counted except those in the water. Film counters recorded by site, number of frames exposed, substrate, photographer's count estimate, and number of seals counted.

There may have been some bias in counts from film but it was minimized or negligible because several people counted, counts were compared frequently, and recounted several times. To count seals from developed film, Miller et al. (1983) tested two methods of projecting images from film and a third method of viewing film through a dissecting microscope. The third method gave least variance; I used it and further reduced counting variance by methods mentioned. All developed film was retained for future site comparison and identification.

In addition to aerial surveys, observers counted seals from shore (ground counts) at selected mainland hauling sites during 1981-93 aerial surveys. Their counts were conducted during one to four days, every half hour or, if numbers were large, as frequently as conditions permitted. They used binoculars or spotting scopes and counted from approximately one hour before low tide to one and one half hours after local low tide.

Estimates of Survey Variance:

To estimate between-year statistical variance from annual film counts, I developed a procedure for estimating variance within aerial surveys based on variance from multiple shore counts of observers. This technique allows investigation and greater understanding of apparent localized changes in harbor seal abundance.

Previous radio tagging studies indicated that 50 to 70 percent of tagged seals haul out daily (Boveng 1988b). Results of my radio tagging study presented in Chapter 2 indicate that percentage hauled out during census periods was much higher. Therefore, I assume that seals not hauled out at one site were very likely to be at a nearby site and would be included in counts. Mainland California was surveyed in approximately one week thus achieving essentially an instantaneous count of all seals hauled out. Because survey time duration was short, there was little or no possibility of seals moving between sites; therefore, seals were not likely to be counted twice or missed entirely except at the starting point of each day's survey.

Harbor seal site fidelity was high and surveys showed that seals habitually use the same hauling sites every year. With this *a priori* knowledge, the survey team was not likely to miss seals or haul out sites during aerial surveys. For these reasons, I assume there was little variance in the survey teams ability to reliably detect harbor seals when they were hauled out. I further assume that sightings were independent and identifying or observing seals at one site is not dependent on observing them at another site. Additionally, seals hauled out at one site were not dependent on seals hauled out at other sites.

Day-to-day variance of total seals hauled out, including variance within and among days, were determined from shore-based ground counts. Variance from shore-based counts were pooled utilizing a technique derived from coefficients of variation. Estimated variance was then applied to counts from aerial census.

Aerial surveys for this study were conducted during harbor seal molting season, when maximum numbers of seals were assumed to be ashore (Loughlin 1978, Sullivan 1979, Stewart 1981, Bonnell et al. 1983, Miller et al. 1983), but number of seals ashore changes by time of day, tides, weather conditions, as well as other factors mentioned above. To standardize counts and develop an index of abundance for rate of growth calculations, surveys were flown during presumed peak daily abundance (one hour before to one and one half hours after local low tide).

I developed a method to estimate variance in daily maximum seals ashore from direct counts. During 1981 through 1993, observers (ground counters) counted seals at assigned hauling sites every fifteen minutes, or less frequently if seal numbers were large or counting took a relatively long time. Ground counters were also instructed to count seals from one hour before to 1.5 hours after local low tide. Time periods were determined based on published NOAA tide tables and adjusted to local haul out location. Ground counters used binoculars or spotting scopes to improve accuracy of counts and positioned themselves at strategic locations above or near hauling sites.

I estimate total survey variance as a sum of between-day variances from the ground counter's daily maximum counts over all sites during years 1981-1993. Because counts tended to increase each day towards a daily peak and I was interested in variance between days, I did not evaluate within-day variance. Between-day coefficients of variation from maximum ground-count data were pooled and a geometric mean regression fit to natural logarithms of means and standard deviations. I make a series of assumptions based on prior knowledge of seal behavior and survey technique. I then assume that pooled ground count variance can be applied to aerial survey results.

First, I assume that there was little or no variance in survey crew's ability to detect seals during flight. Because harbor seals were extremely habitual, they hauled out at the same locations repeatedly, even using the same position on the same rock or beach from day to day and year to year as demonstrated by the fifteen-year photographic aerial record. During surveys, data recorders continually referred to coastal topographic charts to ascertain airplane location and record observed seal locations. They informed pilots and photographers of approaching known seal hauling sites. Simultaneously, pilots, recorders, and photographers maintained constant vigil to detect seals hauled out at new sites. Thus, I assumed that all seals hauled out were photographed. Some seals were observed in the water but were not photographed or counted because of high detection variability.

Second, I assume that no seals were counted twice, because surveys progressed rapidly during one or two days at offshore Channel Islands and four to six days over mainland sites. Airplane ground speed (approximately 90 knots) and the speed at which the survey was completed precluded seal movement between sites during surveys. There may have been some movement between hauling sites during ground counts contributing to expected daily variance along with other factors affecting number of seals ashore (e.g., tides, disturbance, feeding episodes, etc.). As long as there is no net shift in abundance because of this factor, it should not impact results.

Third, I assume that most seals haul out during their molting period when my surveys were conducted. I assume that sites and sightings were independent and, since there was a strong likelihood for seals not present at one hauling site to have been at a nearby site, they were not missed by aerial surveys. This assumption was confirmed by radio tagging studies (see Chapter 2) which show that over 80 percent of harbor seals haul out during the molt. Those studies also showed that seals tended to haul out for long periods of time, further increasing detection probability and eliminating the need to adjust counts to a daily hauling peak.

Fourth, I assume all seals were photographed during daily abundance peaks, so daily peak numbers corresponded to maximum daily ground count. Radio tag results confirmed this assumption (see Chapter 2).

All film and ground count information were entered by year into computer database files using the database management program, DBASE IV, as individual records for each hauling site. Records contained descriptive information about each site in addition to seal counts. Means and standard deviations of daily maximums were calculated for sites counted on multiple days. A geometric mean regression was then fit to log-transformed means and standard deviations to estimate slope. This slope (b_{GM} = 0.99, SE = 0.037) approached unity, indicating independence of sites and sightings. I develop this method based on Snedecor and Cochran (1967) using exact sums of variances:

(Equation 1)

$$s^2_{(y_1+y_2)} = s_1^2 + s_2^2 + 2\, r_{12}\, s_1\, s_2$$

where s^2 is variance of samples y_i , s is standard deviation and r is coefficient of correlation. Because radio tagging studies confirm that seals not at one site have a strong likelihood of being at a nearby site and there is little or no correlation between hauling out at one site or another, r in this formula is zero or negative. Thus pooled estimates of variance are high estimates of variance for maximum number of seals hauled daily.

I develop this concept further to a working formula using the relationship for coefficient of variation:

(Equations 2-4)

$$cv = \frac{s_{\bar{y}}}{\bar{y}} \;;\; s_{\bar{y}} = \bar{y} * cv \;;$$
$$(s_{\bar{y}})^2 = (\bar{y} * cv)^2$$

where

cv = *coefficients of variation,*
$\bar{y}$ = *means of ground counts,*
$s_{\bar{y}}$ = *standard errors of mean,*

using exact sums of variance (Equation 1) from above, squaring, and rearranging :

(Equation 5)
$$s^2_{\Sigma\bar{y}} = \Sigma s^2_{\bar{y}} = \Sigma(\bar{y} * cv)^2 = cv^2 \Sigma \bar{y}^2$$

and taking the square root:

(Equation 6)
$$s_{\Sigma\bar{y}} = cv_{\Sigma\bar{y}} \sqrt{\Sigma(\bar{y}^2)}$$

I fit a geometric mean regression line (Ricker 1973) to log transformed means and standard deviations and obtain:

(Equation 7)
$$\ln \bar{s} = a + b_{GM} \ln \bar{y}$$

If b_{GM} is within 2 standard errors of $b_{GM} = 1$ and therefore not detectably different from one, the formula can be rearranged and solved for the intercept:

(Equation 8)
$$a = \ln \bar{s} - \ln \bar{y}$$

and the antilogarithm of this intercept represents a pooled cv for daily maximum ground counts:

(Equation 9)

$$e^{a} = \frac{\bar{s}}{\bar{y}} = cv$$

and applying a correction factor to the geometric mean for exponential fit (Beauchamp and Olson 1973) gives:

(Equation 10)

$$cv = e^{a + \frac{s^{2}_{\bar{s}\bar{y}}}{2}}$$

Practical Application of Variance Technique:

To apply this procedure to ground count data, I regressed natural logarithm of mean daily peak counts against natural logarithm of mean standard errors over all years and calculated slope for geometric mean of the linear regression (b_{GM}).

Pooled coefficient of variation was equal to antilogarithm of quantity: mean of all logged standard errors of mean, minus mean of all logged peak counts per site by survey, plus the correction factor (Equation 10).

Returning to Equation 6 with the calculated value for pooled coefficient of variation and assuming that y bar represents each individual site count, I obtain an estimate for standard error of the estimate for each California survey by utilizing the derived estimate of cv and sums of squared site counts. This standard error of the estimate for each survey total count was then multiplied times the Student's *t* value (1.96) to obtain the 95 percent confidence intervals for each survey (see Table 2).

RESULTS

Censuses:

Results from 13 peak abundance aerial surveys are presented in Table 3, which documents a mean annual count of 18,654 seals (SE = 863). Harbor seals utilized sites year after year, even occupying the same portions of beaches and rocks each time they hauled out. They were observed in each of California's coastal counties and on each of the Channel Islands, Año Nuevo Island, and Gulf of the Farallon Islands. Each year, a majority of the seals counted were occupying sites in the northern portion of the state (Table 3).

Film counters recounted film from previous years (including Miller et al. 1983) and found very little discrepancy or bias in the time series of harbor seal counts.

I identified eight different substrate types on which harbor seals hauled out (Table 4). They primarily hauled out on sandy beaches (27%), rocks near shore (26%), reefs (21%), harbors and estuaries (18%), and shoreline rocky substrate (7%). Average seals per site by substrate type showed no change over time (Figure 2).

I documented a continual population increase and a concurrent increase in occupied hauling sites, as well as increases in new sites not previously utilized (428 mainland sites in 1983; 877 in 1995; Table 5; Figure 2). I also observed a constant increase in average seals per site (Figure 3) and documented an average increase of 38 (SE = 19.4) new mainland hauling sites per year and 25 (SE = 16) new Channel Island hauling sites per year for 1982 through 1995.

Survey Variance Estimates:

Observers from shore made 10,188 counts of seals present at individual hauling sites during aerial surveys, from which 1,260 maximum daily counts (peak hauling) were identified for all surveys from 1981 through 1993, including counts made during Miller's 1981 and 1982 aerial surveys (Miller et al. 1983). A total of 431 mean counts and standard errors of mean were calculated per ground count site from maximum daily counts.

I calculated $b_{GM} = 0.990$ (SE = 0.037), which was within 2 standard errors of $b_{GM} = 1.000$, and therefore was not detectably different from $b_{GM} = 1.000$, allowing utilization of my derived procedure for pooled sums of variance. Mean of logged standard error of means was 2.114 and mean of all logged peak counts per site by survey was 3.859 with an additive correction factor of 0.419.

Utilizing the variance formulae developed above and applying the technique to ground count data, I calculated a pooled cv of 26.5 percent which was used with annual abundance estimates to estimate annual variance in aerial surveys. This estimate was used in Equation 6 to calculate standard error of the estimate and 95 percent confidence intervals for each year's survey (Table 2).

DISCUSSION

These surveys were important for development of survey techniques providing census continuity and ensuring consistency of results. They also were successful in controlling for a number of variables that likely could have increased variance to unacceptable levels. Therefore, data collected were suitable as an index of abundance for Pacific harbor seals in California.

By choosing to survey in late June or early July during the molting season, I was able to census when seals spent more time out of water, were more tolerant of disturbance, and were more likely to haul out again shortly after disturbance (Hazard 1977). Although onset of molt might have been clinal progressing south to north, completion of molt takes about five weeks for each seal (Scheffer and Slipp 1944), and all seals may complete molt in two months (Stutz 1967). My surveys were accomplished when a majority of seals in southern California were well into the molt, and a majority of seals in northern California were molting but closer to molt onset. These observations were apparent in photographs but not quantified. Results of radio tagging studies (Chapter 2) indicated that these surveys were conducted at optimal time of day for survey; they were centered on early afternoon during lower tides of a slack tide cycle.

Human disturbance was an important variable affecting number of seals hauled out and I controlled for it by surveying on weekdays during slack tides too high for clamming. Even so, there was some disturbance as noted in flight notes and data reports, but statewide, observed disturbance was minimal as shown for in my pooled variance estimation technique.

During 13 aerial surveys from 1983 through 1995 (Table 3), I confirmed harbor seal utilization of hauling sites as identified by Miller et al. (1983) and documented new sites as seal population increased for analysis of density dependant effects (see MacCall 1983, 1990; chapter 3). Harbor seal abundance continued to increase overall and although rate of increase slowed (see Chapter 3), it is still increasing.

CONCLUSIONS

Calculated variance is relatively low compared to abundance estimation techniques utilized for other species and even other marine mammal species. Eberhardt (1978) reviewed population indices for ten different populations and showed that variation in estimates, expressed as coefficients of variation ranged from 40 percent to 250 percent. He further stated that "regardless of any theoretical justification, the coefficient of variation of many kinds of index data seems sufficiently constant in practice to supply an approximate guide for planning purposes." His review and my estimate of pooled variance illustrate the constant nature of harbor seal hauling behavior and low variance in abundance estimates relative to other populations.

Pooled variance technique, as developed above, was an important step towards verifying validity of aerial survey techniques for harbor seal abundance estimation. With development of this variance technique, I was able to answer a recurring question of how to estimate survey variance with no survey repetition. I believe that this technique and relatively low calculated coefficients of variation is further verification that these survey methods, including timing by molt, slack tides, and mid-day counts, were appropriate.

Obvious advantages for biologists counting harbor seals is that they do not hide behind cover, they are relatively easy to see at water's edge, they do not lie on top of each other, and they are spaced far enough apart that they are not missed in photographic counts. There was an unknown but probable disturbance component to total counts that I did not address: harbor seals are quite likely to startle and flee into the water with very little provocation. If seals at a particular site were disturbed and had fled to the water prior to the airplane passing over, they were missed. However, I assume that daily variance estimates from ground counts account for this component. I also assume that seals missed because of disturbance were not a significant portion of the whole population, especially when comparing counts on a statewide basis and on a year to year basis. This component should contribute an analogous portion of total count for an index of abundance, thus it will not affect relationships for growth rate or optimum sustainable population (OSP) determination.

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Table 1. Counts and estimates of harbor seals in California for 1927 to 1981 with source or reference (YEAR = Year of count, MNLD = Mainland count/estimate, ISDS = islands of the Southern California Bight, TOT = sum of MNLD and ISLAND when both available)

YEAR	MNLD	ISDS	TOT	SOURCES
1927	287	33	320	Bonnot '28
1928	320	30	350	Bonnot '28
1946			550	Bureau Marine Fish (CFG) '47
1951			500	Bonnot '51
1958		65		Bartholomew & Boolootian '60
1959		100		Bartholomew & Boolootian '60
1964		645		Odell '71
1965	852	210	1062	Carlisle & Aplin '66
1967		500		Bartholomew '67
1969	1605	534	2139	Frey & Aplin '70
1970	1664	11	1675	Carlisle & Aplin '71
1975	3500	1192	4692	Mate '77; Bonnell '81; Le Boeuf '76
1976			1714	Bonnell et al. '81
1977			1656	Le Boeuf et al. '76; Bonnell et al. '81
1978			3000	Bonnell '81 (speculation)
1979			6100	SOS WORKSHOP '80
1980	6776			Bonnell et al. '83
1981	7562			Bonnell et al. '83

Table 1. (Continued) Counts and estimates of harbor seals in California for 1927 to 1981 with source or reference (YEAR = Year of count, MNLD = Mainland count/estimate, ISDS = islands of the Southern California Bight, TOT = sum of MNLD and ISLAND when both available)

YEAR	MNLD	ISDS	TOT	SOURCES
1982	12776	3892	16668	Miller et al. '83; Stewart &Yochem '84
1983	10945	3472	14417	Hanan et al. '92
1984	10946	3218	14164	Hanan et al. '92
1985	12598	2280	14878	Hanan et al. '92
1986	13831	1801	15632	Hanan et al. '92
1987	15124	4322	19446	Hanan et al. '92
1988	14095	3947	18042	Hanan et al. '92
1989	16034	4279	20313	Hanan et al. '92
1990	15675	2808	18483	Hanan et al. '92
1991	18346	4743	23089	Hanan et al. '92
1992	18700	4433	23133	Hanan et al. '93
1993	14933	3166	18099	Hanan & Beeson '94
1994	17162	4300	21462	Beeson & Hanan '94
1995	20297	3005	23302	This Dissertation

Table 2. Annual aerial counts with standard error of the estimate and 95 percent confidence interval from pooled coefficient of variation technique.

YEAR	COUNT	SE	95% CI
1982	16668	421	825
1983	14584	400	784
1984	14173	479	939
1985	14903	423	828
1986	15585	431	845
1987	19447	555	1089
1988	18051	538	1054
1989	20347	518	1016
1990	18507	493	966
1991	22893	652	1278
1992	23124	555	1087
1993	18109	414	812
1994	21461	532	1043
1995	23302	636	1247

Table 3. Pacific harbor seal counts by year 1982-1995 for the California mainland, number of sites, percentage of sites occupied, Channel Islands, and three California mainland regions (northern California, central California, and southern California; divided at latitudes 37°50' and 35°00').

Year	Mainld	sites	%	Island	NCal	CCal	SCal	Total
1982	12,776	427	56	3,892	7,325	4,794	4,549	16,668
1983	10,945	488	38	3,472	6,611	3,031	4,942	14,417
1984	10,946	524	41	3,218	7,282	2,932	3,959	14,164
1985	12,598	580	47	2,280	8,005	3,315	3,583	14,878
1986	13,831	646	49	1,801	8,240	4,239	3,106	15,632
1987	15,124	678	46	4,322	9,263	4,631	5,553	19,446
1988	14,095	696	40	3,947	8,227	4,622	5,202	18,042
1989	16,034	711	40	4,279	8,587	5,950	5,810	20,313
1990	15,675	737	40	2,808	8,260	5,832	4,415	18,483
1991	18,346	764	40	4,743	10,658	6,195	6,040	23,089
1992	18,700	824	49	4,433	10,441	6,334	6,349	23,133
1993	14,933	848	39	3,166	7,549	6,042	4,518	18,099
1994	17,162	859	41	4,300	8,879	6,815	5,767	21,462
1995	20,297	877	43	3,005	13,038	6,059	4,205	23,302

Table 4. Substrate types and percentage of seals utilizing substrate all years combined and total sites by substrate (1994).

SUBSTRATE	%	#SITES (1994)
Extended Reef	20.6	226
Offshore Rock	25.8	566
Onshore Rock & Ledges	7.4	218
Estuary	17.7	29
Sandy Beach	26.5	114
River Logs	0.1	3
Floats	0.0	1
Night	0.1	3
Rocky Beach	1.8	32

Table 5. Total California sites and total sites occupied during aerial surveys.

YEAR	OCCUPIED	NEW
1983	*	51
1984	315	36
1985	363	56
1986	369	66
1987	417	32
1988	373	18
1989	354	15
1990	378	26
1991	410	27
1992	523	60
1993	426	24
1994	481	11
1995	499	18

*no data for Channel Islands

Figure 1. Pacific harbor seal counts from aerial surveys along California's entire coastline and offshore islands, 1982 through 1995.

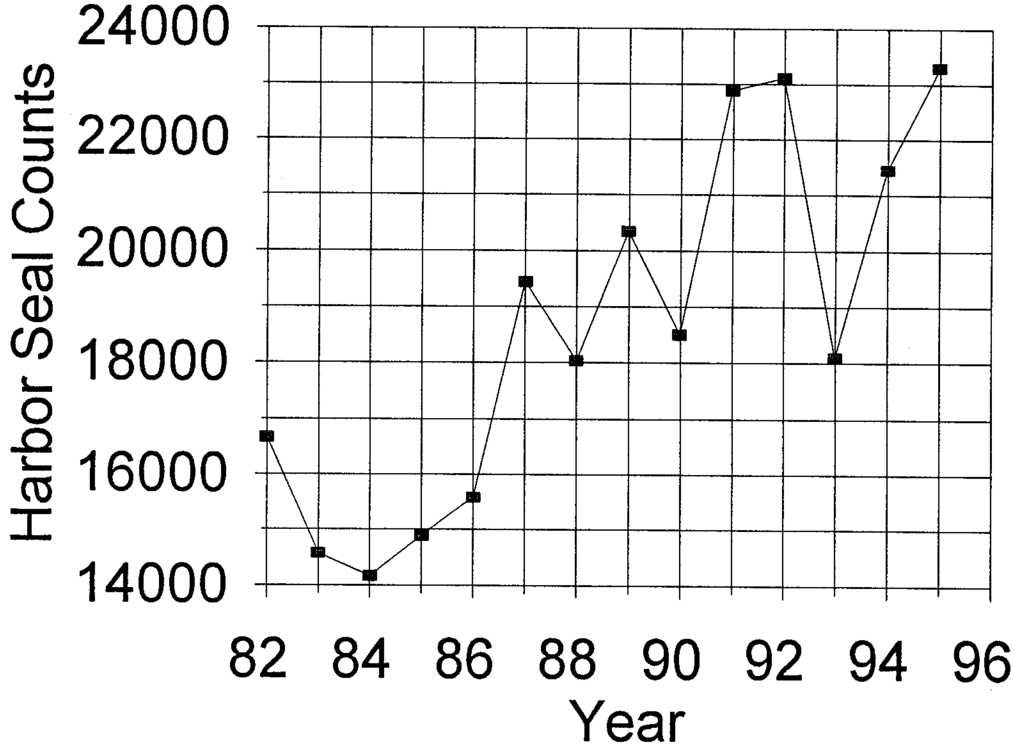

24000
22000
20000
18000
16000
14000
Harbor Seal Counts
82 84 86 88 90 92 94 96
Year

Figure 2. Pacific harbor seal counts by substrate type for all years combined, 1982 through 1995.

Legend

1 = extended reef
2 = off shore rock
3 = rock ledges
4 = estuary
5 = sandy beach
9 = rocky beach

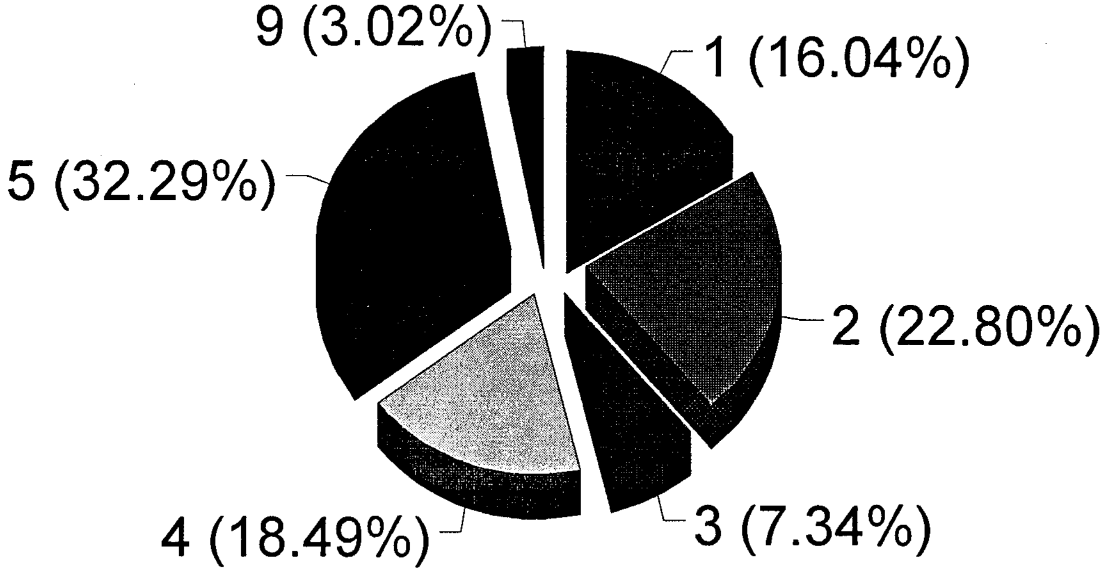

9 (3.02%)
1 (16.04%)
5 (32.29%)
2 (22.80%)
4 (18.49%)
3 (7.34%)

Figure 3. Occupied sites determined by aerial surveys, all years combined 1982 through 1995.

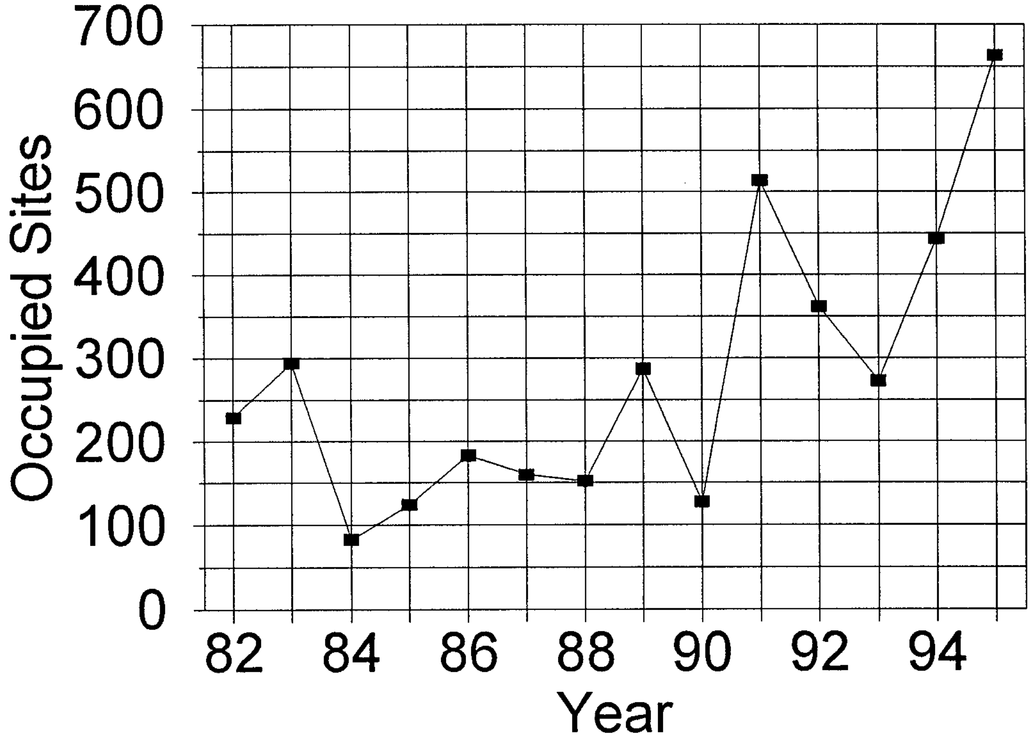
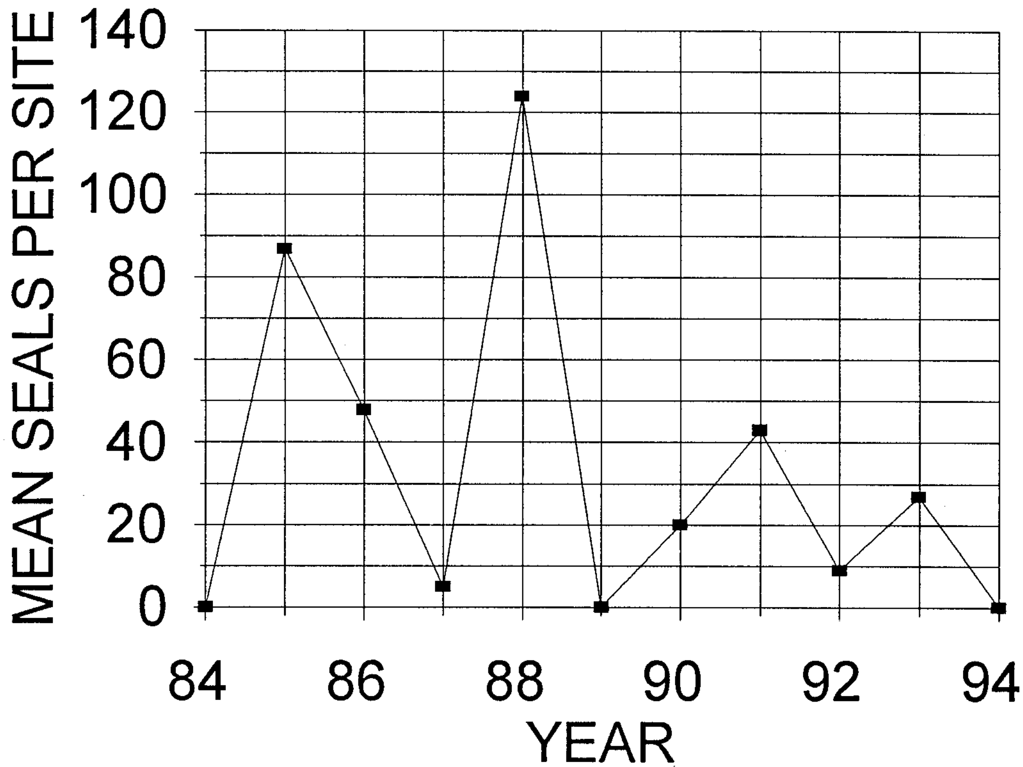

700
600
500
400
300
200
100
0
Occupied Sites
82
84
86
88
90
92
94
Year

Figure 4. Mean harbor seal counts per site, all years combined 1982 through 1995.


MEAN SEALS PER SITE
140
120
100
80
60
40
20
0
84
86
88
90
92
94
YEAR

CHAPTER 2

TAGGING STUDIES AND ESTIMATION OF PROPORTION OF SEALS ASHORE

INTRODUCTION

A question of major significance when utilizing aerial counts of pinnipeds is what portion of the population is actually observed during the survey (Eberhardt et al. 1979). Because some of the population is always at sea, a method of determining proportion hauled out during surveys was radio tagging a subset of the population and monitoring for proportion of tagged seals hauled out. It is assumed that the tagged seals behave the same as the whole population and that the portion of tagged seals ashore is representative of hauling patterns for the whole population.

Boveng (1988) reviewed tagging studies addressing questions related to harbor seal proportion hauled out by time and season. He discussed difficulties of applying results of those radio tagging studies to surveys performed during the molt because those radio tags were glued to seal pelage and therefore shed with pelage during molt. He estimated, based on available radio tagging results, that proportion counted during a molting period census would be 50 to 70 percent of total population. He evaluated a range of population correction factors from 1.0 to 2.0 times total seals counted but suggested 1.4 as an optimal correction factor based on results from proportion hauled out studies. Huber et al. (1993) recommended a correction factor of 1.61 for harbor seals in Oregon and Washington.

To obtain an estimate of harbor seals hauled out during molt (when recent aerial surveys were flown), I developed and employed a new method of gluing VHF radio tags to cattle ear tags and then attaching the tag to seals through hind flipper webbing, not glued to pelage as in previous studies (Yochem et al. 1987, Herder 1986, Pitcher and McAllister 1981). This method gives more accurate estimates over longer time periods because light-weight radio tags remained on seals and transmitted signals through molting. When a seal was hauled out, its radio tags emitted unique frequencies that were detected by land based scanning receivers as a set number of pulses per minute. The frequencies were recorded in data logging computers with julian day, time, and number of pulses detected within a ten second scanning period.

I analyzed these data to determine harbor seal hauling patterns by time and location. The major objective of this study was to determine proportion of individuals hauled out by day during the molt. Analyses provided estimates of proportion of individuals hauled by day during molting season. I determined proportion of days that seals hauled out for a three month period, centered on annual molt (May-July) for 1989 through 1993. I calculated a correction factor for each annual count as inverse of proportion hauled out and applied each estimate to counts of Pacific harbor seals in California by year. In addition, I assessed preferred time of day for hauling and also examined differences in haul-out patterns by sex and age of individuals.

Site Descriptions:

Six semi-permanent radio tracking stations were established at four mainland harbor seal haul-out sites where seals were captured and radio tagged (Figure 1). These sites were located in Santa Barbara County, California: Ellwood (near Golleta), Point Conception (2 stations), Rocky Point (near Point Arguello); and Otter Harbor and Crooke Point (San Miguel Island, SMI). Monitored sites were selected based on harbor seal site usage and site fidelity determined from previous aerial surveys and observations.

The southern-most receiver station, Ellwood was located approximately 27 kilometers west of Santa Barbara. This haul-out site was a narrow sandy beach below 10-15 meters steep cliffs and was awash during high tides when seals could be seen occupying near shore reef and kelp bed habitat. Beach access was achieved by climbing a rocky trail, visible to seals. Other access not visible to seals was through a small canyon, overrun with poison oak about 100 meters east. I observed seals from bluffs above with binoculars and spotting scopes. The receiver station was camouflaged by chaparral and located about 500 meters west on an opposing hillside.

A hauling site near Carpinteria State Beach, 40 kilometers southeast of Ellwood, was used to capture and radio tag three seals. Capture and tagging was discontinued at this site because of local residents participating in a docent program for seal protection and public education. I occasionally monitored for radio tagged seals and counted seals at this site but did not establish a receiver station because of the high degree of human presence and disturbance.

Study sites at Point Conception, included multiple hauling sites and different substrates: sand, cobble, and rock reef. Of six monitored hauling sites, Pt. Conception consistently accounted for more seals than any other mainland site in southern California. Access required permission to drive several kilometers over a private one lane road to the unmanned Coast Guard station.

The southern-most Pt. Conception site was a long low rocky reef, "Blind Reef", extending from shore. Seals were protected at this site because one could not approach them without being seen. Typically, seals hauled out at Blind Reef until high tide washed them off and they moved to surf protected sites. On-shore from Blind Reef was a site named "Blind Beach", a sandy beach used for hauling out by males and females during early study years, but later used only by females during pupping. There was a wooden shield or "blind" on the bluff above Blind reef and Blind beach. About 800 meters west of Blind Beach was "Little Cove" a small rock and cobble beach site rarely used except during pupping and molting. "Satellite Beach", a sand and rock beach, bordered by a rocky reef was free of most disturbances including coyote predation and was used by seals during high tide when other sites were awash. This was a preferred site and was highly utilized until a rock slide covered portions of it in 1992. "Big Cove" was a bottle-neck protected deep-water entrance cove, surrounded by 100-meter high bluffs and was most utilized haul-out site at Pt. Conception. Seals did not haul out at Big Cove until 1987; currently it is used year-round by harbor seals, elephant seals, and on rare occurrence by California sea lions.

Blind Beach, Little Cove, and Satellite Beach were approached inconspicuously by climbing a rope east of blind beach and sneaking among boulders and rock ledges. At Big Cove and outlying rock ledges, there was no concealed access and entrance was by swimming or climbing along rocky walls completely visible to seals. Seals could be inconspicuously viewed with binoculars and spotting scopes from multiple sites on cliffs high above each haul out site.

Two receiver stations were set up at Point Conception: one on a hill adjacent to a coast guard lighthouse above Big cove (referred to as "lighthouse" station), and a second on a cliff above Blind reef (referred to as "blind" station). The lighthouse receiver was protected behind cement walkways and walls while blind receiver was protected behind a wooden wall. Therefore, both receivers and researchers were not detectable to seals below.

Northern-most of study sites and last to be established was a location at a series of haul out sites near Rocky Point on Vandenberg Air Force Base south of Point Arguello. Primary among these hauling sites was a long secluded sandy beach and adjacent rocky reefs stretching northward. Beach access required climbing a steep ravine, crawling through a watery cave (passable only at low tide) and sneaking about 50 meters through large boulders. This approach could not be seen by seals except those on offshore rocks.

Seals were viewed at close distance from a bluff directly above the southern end of a sand and cobble beach, where I also installed a receiver station, as well as from many other locations along the bluffs.

Two additional haul out sites were monitored at San Miguel Island: Otter Harbor and Crooke Point. SMI, western-most of Channel Islands, is about 65 kilometers offshore of Point Conception. Otter Harbor, a protected sandy cove on SMI's north side, was utilized by elephant seals and occasionally sea lions in addition to harbor seals. During peak abundance for elephant seals and during harbor seal pupping, they competed for space (see Chapter 3). A twin engine CDFG airplane was flown to SMI and landed on a restricted, short, dirt runway in Larsen dry lake bed, approximately 1.5 kilometers from Otter Harbor. Seals were observed from sandy bluffs above the cove and the receiver station was placed on a hill about 50 meters south.

The second island site, Crooke Point, consisted of low relief, sandy beaches on SMI's west side. Harbor seals hauled out on a beach just east of Crooke Pt. The receiver station was placed on a high hill about 1 kilometer inland of Crooke Pt. Depending on weather conditions, access was gained by CDFG airplanes that landed either at Larsen dry lake bed or at another dirt runway, located at SMI's east end near a park ranger station. Use of either landing strip required an hour hike over hilly terrain to reach Crooke Point and another one hour hike between receiver stations.

Disturbance to Seals:

Of six observed haul out sites, Ellwood was subject to more human disturbance than all other sites because it was a popular site for surfers and joggers. Although joggers were present only during low tide cycles (when seals tended to haul out), dogs, coyotes, humans, and even automobiles were common on this beach.

Occasional human disturbance at Point Conception hauling sites was limited to a few fishermen because beach access required permission from Coho Ranch staff. On several occasions I observed commercial and recreational boats nearby but they rarely caused disturbance. I observed some low-flying aircraft including military helicopters over haul out sites causing disturbance to seals. Human and coyote prints were observed on this beach and ranch security even reported a mountain lion on this beach. Potential disturbances were occasional fishermen, boats, rock slides, deer, and cattle who routinely appeared walking along cliff edges. Once a gray whale spouted as it passed close-by Satellite Beach and caused all harbor seals to charge into the water.

At Rocky Point, human disturbance was infrequent. However, base visitors and other researchers periodically caused disturbance by viewing seals or showing their silhouette over cliff's edge. This entire area was located within a special wildlife protection area on Vandenberg Air Force Base and was patrolled by military police. Other observed disturbances were deer, cattle, rock slides, and low flying military helicopters.

SMI Island is quite remote and aside from a few researchers and National Park Service personnel there is little human disturbance. There are, however, local commercial fisheries for abalones, sea urchins, and finfish, in addition to sport divers, sport fishermen, and kayakers. Any of these activities could, and occasionally did, cause disturbance to these seals.

Receiver Station Design:

Radio signals were monitored continuously from six shore-based receiving stations. At each station, a data log computer was programmed to control frequencies scanned by a radio receiver and record pulse rate and time of detection. Each receiver station included a scanning radio receiver, data log computer, directional antennae, and batteries. I used scanning radio receivers manufactured by two companies: Telonics Incorporated of Tucson, Arizona and Advanced Telemetry Systems (ATS) of Cedar Creek, Minnesota. Telonics receivers had data loggers attached. These data loggers were developed and built by Dr. Jay Barlow (National over the cliff's edge so it could not be reached by free roaming bulls that had knocked it over during winter, 1993. San Miguel Island receiver stations were set up in May 1990, including solar panels. ATS receivers were used at first; however, I switched to Telonics receivers in July 1991, because they had much lower power requirements.

Description of Tags:

VHF radio tags were incased in water and pressure resistant resin housing and fitted with either an internal coiled antenna or external six-to-eight inch woven stainless steel antenna. Each radio housing was glued to a plastic cattle ear tag (Temple livestock identification tag supplied by Nasco, Modesto, California). Different colored cattle ear tags were used for each tagging season (1989 and 1990 dark green, 1991 red or white, 1992 light green, 1993 light blue). Radio tags cost $160 to $180 each, and each transmitted a unique radio frequency, ranging from 164.000 to 165.986 kilohertz (Khz). Each tag emitted radio signals that were detected and interpreted by the scanner as a set number of pulses per minute. Tags with external antennas transmitted over a greater range with a stronger signal than internal coiled antennas but were more likely to get tangled and/or broken off. I observed several tags with external antennas broken off but still transmitting a detectable radio signal.

METHODS

Capture Techniques:

Harbor seals were captured individually at hauling sites onshore using hand-held nets. These nets were made of nylon attached to a high impact plastic hoop bolted to a titanium shaft. Similar techniques were used by Yochem et al. (1987) and Stewart and Yochem (1994) at SMI. A rocket net was tried once during May, 1989, at Ellwood. It employed a large net (30 meters by 10 meters) which was fired up and over an area by four gun-powder propelled rockets. Because most seals were not directly in front when the net was deployed, only one seal was captured. This technique was labor intensive, not very successful, and was not used again during my study. To catch seals, one to four people crawled and slithered (nets in hand) along beaches, hiding behind rocks and other objects until close enough to jump up and catch seals before they escaped. Each person ran towards a single seal and swung a net over its head and body. Capture of one seal often took from one to three hours depending on capture site. Harbor seals have exceptionally good hearing and they responded to any sudden or unusual sound. At other times, when they did haul out, they were frightened away by an unexpected sound or unfamiliar sight.

On several occasions, a passive capture technique of hiding behind natural cover and waiting for seals to haul-out was successfully used to capture seals. However, on many occasions, would be seal taggers remained concealed for hours and no seals hauled out to be caught. At SMI, where there was little human disturbance, seals were less wary and could be approached and captured more easily. At Otter Harbor researchers used dozing elephant seals for cover and crawled close to harbor seals prior to capture.

Once captured, seals were pulled away from water's edge, tagged, and usually photographed. Distinguishing marks, scars and wounds were recorded in addition to sex, age category, length, and girth. Adult seals were left in nets and restrained during tagging. Pups and juveniles were usually restrained during tagging without a net. A hole punch was used to pierce a hole through hind flipper webbing between second and third digits. Tissue removed was saved and preserved for future DNA studies. Tags were pried open, inserted through the pierced webbing hole, and screwed together with a brass screw to reduce tag loss. I applied two tags each to 67 seals, one in each hind flipper and, because of seal size or tagging conditions, only one tag was applied to eleven seals. Each seal was restrained an average of five minutes.

Data Collection:

Radio signals detected at receiver stations were stored in data log computers, transferred (downloaded) on a monthly basis to portable laptop computers, and stored on computer diskettes. Each downloaded file was treated separately and named by location and date retrieved. In addition to semi-permanent receiver stations, portable hand held receivers and department aircraft with radio receivers and antennas secured to wing struts were used to confirm receiver data and provide additional information. This information verified presence or absence of signals stored by data loggers at receiver stations. Re-sight effort consisted of monthly field trips and aerial monitoring, to observe, monitor for radio tags and download data stored by data log computers.

Radio scanners were programmed to monitor for each frequency approximately ten seconds and number of frequencies monitored varied from 6 to 72 depending year on number of tags used and battery life of previous year's tags; total time scanned for all frequencies varied from 60 to 720 seconds. Several battery types were tested and expected battery life ranged from 90 days to two years. During an hour all frequencies would have been scanned a minimum of five, ten-second passes. Data logging computers were programmed in basic language to scan radio frequencies of tagged seals. When a frequency representing a tagged seal was detected, data loggers stored julian day, time, frequency, and number of pulses detected within a ten second scanning period.

Data Analyses:

I combined computer files by seal and year for May, June, and July. Files were edited to remove obvious radio noise; in some cases noise was manifest as too many pulses at particular frequencies during period scanned or too few records during an hour or adjoining hours. Because scanners monitored each frequency every ten seconds, in one hour all frequencies would have been scanned a minimum of five ten-second passes. Therefore, I assumed seals to be present if one or both tags were detected at least twice during an hour. When a seal was deemed present, it was considered present for the day.

Four tagged seals were not detected after tagging at my radio receiver stations or by hand held receivers and therefore they were not included in my analyses for proportion hauled out or hauling by time of day.

Proportion of days hauled out was totaled for each seal as sum of "days" during which one or both radio tags were detected. Total days hauled out was divided by total possible days during which a seal could have been detected. To assess preferred time of day for hauling, all records for each year were combined. Duplicate records by seal and hour were removed and histograms of total seals hauled by hour were created.

I calculated a correction factor for each annual count as the inverse of proportion hauled out and applied each factor to estimates of Pacific harbor seal abundance in California by year (Table 1). For future reference and general use with Pacific harbor seals in California, I suggest a best estimated correction factor as inverse of my five year mean proportion hauled out by day. This mean includes an El Niño event which might be considered an important inclusion given frequencies of these events in recent years (Hayward et al. 1994). Because I applied a constant to indices of abundance, further analyses of stock status (Chapter 3) are not affected except in absolute numbers.

RESULTS

I tagged 75 harbor seals with 141 radio tags during 1989 through 1993 and report presence of tagged seals monitored at six locations during April, May, June of those years. There were no observed seal mortalities as a result of capture or tagging. I tagged five seals at Carpinteria, seven at Ellwood, 37 at Pt. Conception, 21 at Rocky Point, two near Crooke Point, and three at Otter Harbor. Distribution of tagged seals by sex was: 35 female and 40 male; by age class 16 pups, four juvenile/yearlings, and 55 adults (Table 2).

Table 3 presents results for proportion of days hauled out by year, age, and sex. There was no difference by sex, and proportion of pups hauling out was lower than other age classes. For all seals during 1989 through 1993, proportion of days hauled out was 83.3 percent (SE = 13.9) and annual mean proportion hauled out ranged from 72.5 to 89.2 percent (Table 4). These results give an overall (1989 to 1993) population correction factor of 1.2 (range of 1.12 to 1.38 by year) for the five year study period. The mean proportion hauled out for 1993 was lower than other years and also reduced the five-year mean. Table 4 presents counts and estimates of abundance utilizing this overall California correction factor for seals counted during annual aerial surveys.

Analyses of recorded data confirmed daily hauling peaks in early afternoon and a tendency for seals to be away from hauling sites shortly after midnight (Figures 2-6). I also detected a trend for some adults to make daily trips away from hauling sites, and also on approximately a monthly basis to make longer trips of about one week absence away from receiver stations. There was movement between mainland sites and SMI. Sixteen of seventeen seals tagged on the mainland were recorded at San Miguel Island at least once, and four of the five seals tagged at San Miguel Island were recorded at mainland sites at least once.

DISCUSSION

Opportunity to conduct a five-year tagging program was unique and valuable because this long time scale allowed interannual comparison in addition to usual within-year comparisons. Capture technique in this study was different from other recent studies where large numbers of harbor seals were obtained by beach seine and radio tagged in rivers, estuaries, or embayments (e.g., Allen 1988, Herder 1986, Harvey 1987, Kopec and Harvey 1995, Jeffries et al. 1993). Because my study sites were all open, rocky coast, where beach seine capture techniques were ineffective, I employed hand-held nets and captured individual seals. This technique was time consuming yet effective, but it caused repeat disturbances at hauling sites in order to obtain adequate sample sizes.

My sample of tagged seals was representative of the whole population with nearly equal numbers of seals tagged by sex, as well as being representative of the whole population by age group. This distribution of tagged seals was important for determining proportion of the whole population hauled out because all seals were counted in aerial surveys and the correction factor was applied to all seals counted.

There was little difference by sex in proportion hauled out during the three-month study period. This result might be expected because both sexes molt at the same time and there is little size differential between male and female harbor seals. The tendency for older seals to haul out more than pups might be explained by molt and energy requirements. Pups do not molt until their second summer; consequently, there was no need for extended haul out periods and energy needs probably dictated need for more time feeding than hauling out.

Results from monitoring 71 harbor seals tagged with 135 radio tags indicate that, on average, adult harbor seals leave haul-outs daily, and additionally, on a monthly basis, they make approximately week-long excursions away from hauling sites. Activity patterns observed in this radio tagging study are similar to those reported in previous studies (Brown and Mate 1983) and especially those reported by Stewart and Yochem (1994). I speculate that daily absences most likely were related to shallow water feeding while longer absences may have been due to deeper water feeding or possibly movement to and from other hauling sites. Additional studies using time-depth recorders and satellite tags would clarify these questions.

Disturbance:

Human disturbance did not confound this analysis because tag analysis was performed for a three month period, including molt, when seals more likely to haul out or return after disturbance (Hazard 1977). My own personal observations at Ellwood confirm, on numerous occasions, that seals haul out soon after disturbance. In fact, they often will linger in the surf zone or nearshore kelp until perceived disturbances leave, then haul out, usually in the same location; therefore I built blinds at Ellwood and Pt. Conception from which multiple captures were made during the same day and at the same site.

At some locations seals modified preferred time of day used for hauling in response to previous harassment. At Carpinteria, seals hauled out mostly at night; however, after a docent program substantially reduced day-time human disturbance, seals started hauling out in large numbers during daylight hours. I addressed potential human disturbance effects on detection of daily proportion hauled out by using semi-permanent receiver stations which recorded seal presence day and night.

Correction Factor:

Because I monitored harbor seals during their molting period, I obtained higher estimates of proportion hauled out than previous studies. These higher estimates were consistent during my five-year study except during 1993, when there was an El Niño event. This indicated that harbor seals spent more time at sea during El Niño events possibly feeding or searching for adequate prey.

The correction factor for population estimates that I obtained is lower than that recommended by Boveng (1988) or Huber (1993) because those studies were conducted at times other than molt or with radio tags that dropped off during molt. My correction factor of 1.2 indicates that population estimates from aerial surveys, conducted during harbor seal molting, are much closer to total population abundance than previously accepted. This finding also confirms my choice of the molting period as best for estimates of total abundance.

ACKNOWLEDGEMENTS

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Table 1. Correction factor and pooled variance estimates of abundance by year, film count, film count times mean correction factor (1.2), film count times best correction factor (based on mean correction factor, correction factor calculated from that year's data, or correction factor from the 1993 El Niño year applied to an El Niño year).

YEAR	COUNT	SE	95 CI	TOT*1.2	BEST	BEST%
1982	16668	421	825	20002	20002	1.2
1983	14584	400	784	17501	20111	1.38
1984	14173	479	939	17008	17008	1.2
1985	14903	423	828	17884	17884	1.2
1986	15585	431	845	18702	18702	1.2
1987	19447	555	1089	23336	23336	1.2
1988	18051	538	1054	21661	24892	1.38
1989	20347	518	1016	24416	24254	1.19
1990	18507	493	966	22208	20889	1.13
1991	22893	652	1278	27472	25665	1.12
1992	23124	555	1087	27749	28130	1.22
1993	18109	414	812	21731	24972	1.38
1994	21461	532	1043	25753	25753	1.2
1995	23302	636	1247	27962	27962	1.2

Table 2. Percentage of days hauled out during months May, June, and July by harbor seals tagged with VHF radio tags, 1989 - 1993 sorted by age and sex.

SEX	MEAN	SD	RANGE	N
MALE	82.7	15.4	30-99	36
FEMALE	84.0	14.0	39-100	35

AGE	MEAN	SD	RANGE	N
PUP	77.5	20.8	30-100	15
JUVENILE	89.4	8.8	79-100	4
ADULT	84.5	11.5	44-99	52

Table 3. Tagged seal information including seal number; age (1 = pup, 2 = juvenile, 3 = adult); sex (1 =male, 2 = female); PRES = sum of days hauled out; TOT = total days possible for hauling out; % = percentage of days hauled out; START = julian day tagged; and END = last julian day monitored.

SEAL	AGE	SEX	PRES	TOT	%	START	END
1	3	2	28	33	85	152	184
2	3	1	25	33	76	152	184
3	3	1	29	32	91	153	184
4	3	2	25	32	78	153	184
5	3	1	24	31	77	154	184
6	1	1	29	30	97	155	184
7	1	2	51	56	91	157	212
8	1	2	60	76	79	137	212
9	1	2	58	63	92	150	212
10	3	2	64	69	93	144	212
11	1	1	60	63	95	150	212
12	3	2	61	70	87	144	212
13	3	2	47	63	75	150	212
14	2	2	44	56	79	157	212
15	3	2	72	76	95	137	212
16	3	2	54	63	86	150	212
17	3	1	53	56	95	157	212
18	3	2	55	56	98	157	212
19	3	1	53	55	96	157	212
20	3	1	51	62	82	151	212
21	3	1	55	68	81	157	212
22	1	1	74	79	94	127	212
23	1	2	76	76	100	137	212
24	3	1	52	63	83	150	212
25	3	2	69	77	90	136	212

Table 3. (continued). Tagged seal information including seal number; age (1 = pup, 2 = juvenile, 3 = adult); sex (1 =male, 2 = female); PRES = sum of days hauled out; TOT = total days possible for hauling out; % = percentage of days hauled out; START = julian day tagged; and END = last julian day monitored.

SEAL	AGE	SEX	PRES	TOT	%	START	END
26	3	1	57	63	90	150	212
27	3	1	85	90	94	121	212
28	3	2	85	90	94	121	212
29	3	2	74	87	85	126	212
30	3	2	57	76	75	137	212
31	3	1	89	90	99	123	212
32	1	1	68	90	76	121	212
33	2	2	76	76	100	137	212
34	3	1	85	90	94	121	212
35	3	1	86	89	97	122	212
36	2	2	39	43	91	135	212
37	1	2	60	90	67	121	212
38	3	1	77	87	89	126	212
39	3	2	75	77	97	138	213
40	3	2	79	88	90	122	213
41	3	1	73	88	83	122	213
42	1	1	45	72	63	127	213
43	3	1	45	85	53	129	213
44	3	1	70	80	88	134	213
45	3	1	72	73	99	142	213
46	3	1	59	79	75	135	213
47	1	1	59	79	75	135	213
48	1	2	59	74	80	135	213
49	3	2	83	85	98	129	213

Table 3. (continued). Tagged seal information including seal number; age (1 = pup, 2 = juvenile, 3 = adult); sex (1 =male, 2 = female); PRES = sum of days hauled out; TOT = total days possible for hauling out; % = percentage of days hauled out; START = julian day tagged; and END = last julian day monitored.

SEAL	AGE	SEX	PRES	TOT	%	START	END
50	3	2	61	85	72	129	213
51	3	1	69	70	99	141	213
52	3	1	60	72	83	142	213
53	3	1	58	72	81	142	213
54	3	2	48	53	91	142	211
55	3	2	63	71	89	142	213
56	3	1	56	72	78	121	212
57	3	1	64	72	89	121	212
58	1	1	63	72	88	121	212
59	3	2	46	72	64	121	212
60	3	2	33	44	75	148	212
61	3	2	59	72	82	121	212
62	3	1	27	61	44	132	212
63	3	1	51	72	71	121	212
64	3	2	59	72	82	121	212
65	1	2	28	72	39	121	212
66	3	1	61	72	85	121	212
67	1	1	21	70	30	123	212
69	2	2	60	68	88	125	212
70	3	2	43	66	65	123	212
71	3	1	62	68	91	125	212
72	3	2	53	59	90	134	212

Table 4. Percentage of days hauled out during months May, June, and July by harbor seals tagged with VHF radio tags for years 1989 - 1993.

YEAR	MEAN	SD	N	RANGE
1989	83.9	8.4	6	76-97
1990	88.6	7.7	12	75-98
1991	89.2	9.2	21	67-100
1992	82.2	12.8	16	63-98
1993	72.5	19.4	20	30-91
All Years	83.3	13.9	75	30-100

Figure 1. Map of Southern California with study site locations: Rocky Point, Lighthouse and Blind, Ellwood, Otter Harbor, and Crook Point.

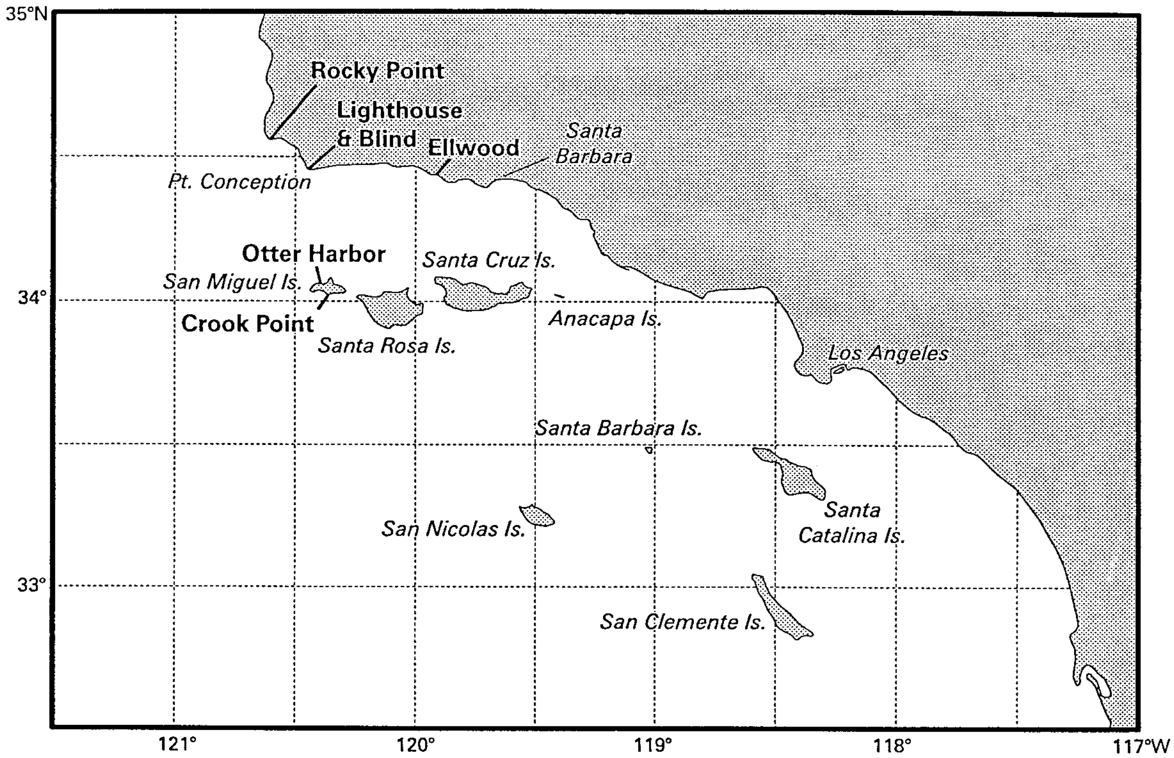

35°N
Rocky Point
Lighthouse
& Blind
Ellwood
Santa
Barbara
Pt. Conception
Otter Harbor
Santa Cruz Is.
San Miguel Is.
34°
Crook Point
Anacapa Is.
Santa Rosa Is.
Los Angeles
Santa Barbara Is.
Santa
Catalina Is.
San Nicolas Is.
33°
San Clemente Is.
121°
120°
119°
118°
117°W

Figure 2. Haul-out profile by time of day for all seals, 1989.

1989 ALL SEALS COMBINED

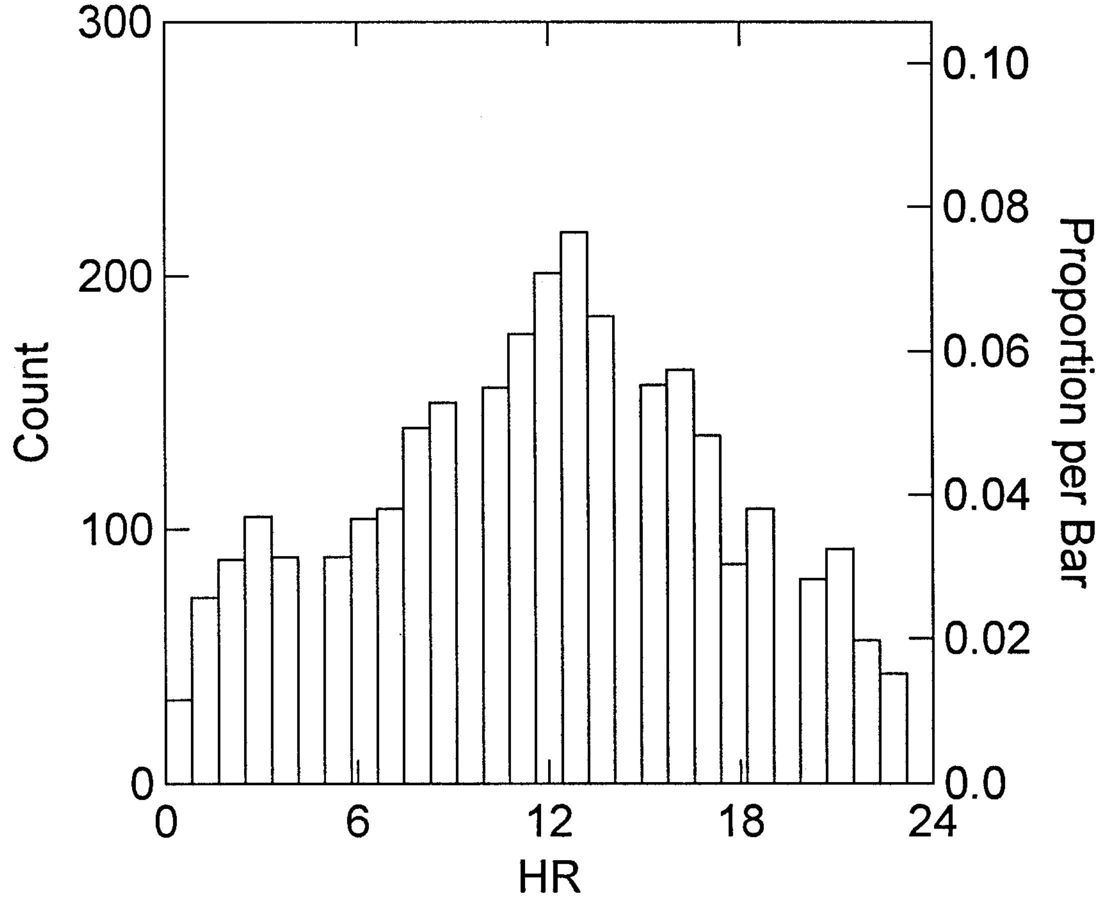


Figure 3.Haul-out profile by time of day for all seals, 1990.

1990 ALL SEALS COMBINED

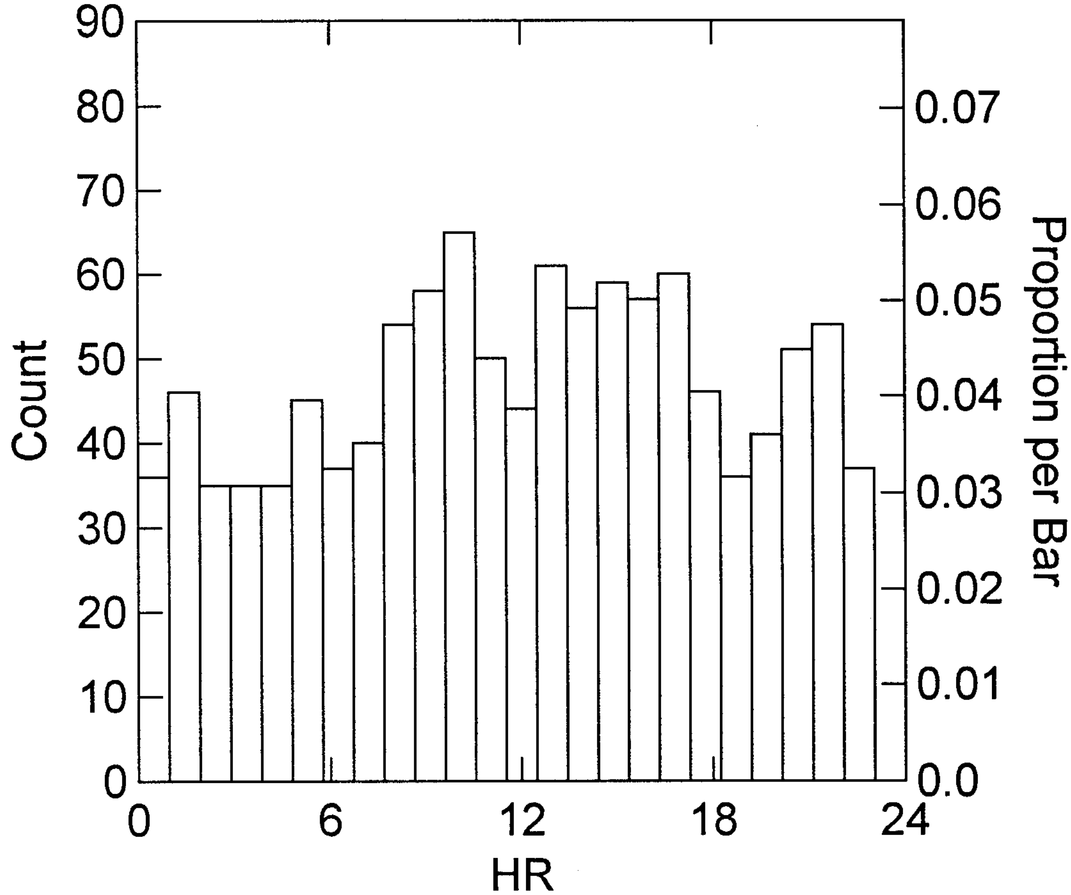


Figure 4. Haul-out profile by time of day for all seals, 1991.

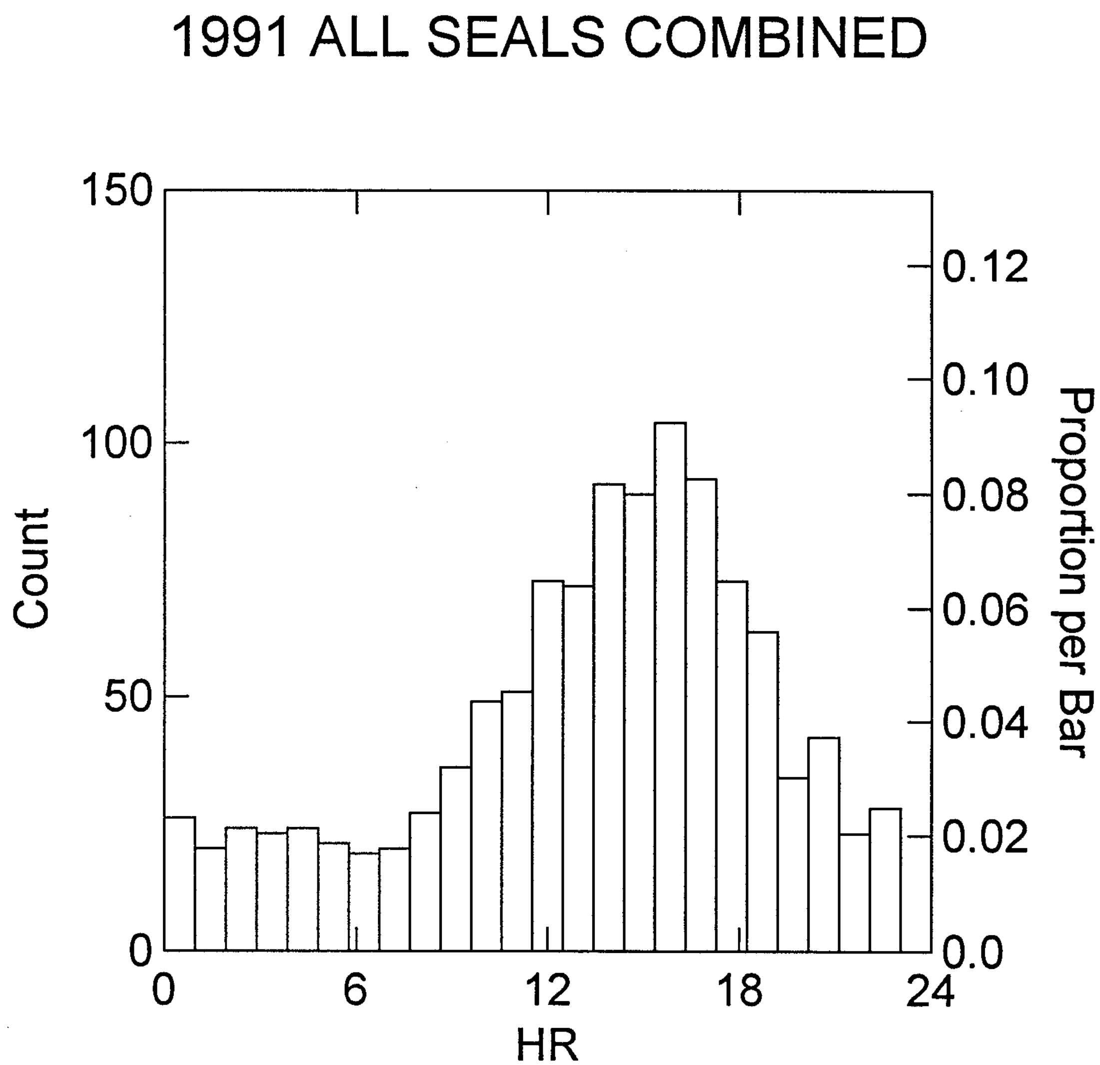

1991 ALL SEALS COMBINED
150
100
50
0
Count
0.12
0.10
0.08
0.06
0.04
0.02
0.0
Proportion per Bar
0
6
12
18
24
HR

Figure 5. Haul-out profile by time of day for all seals, 1992.

1992 ALL SEALS COMBINED

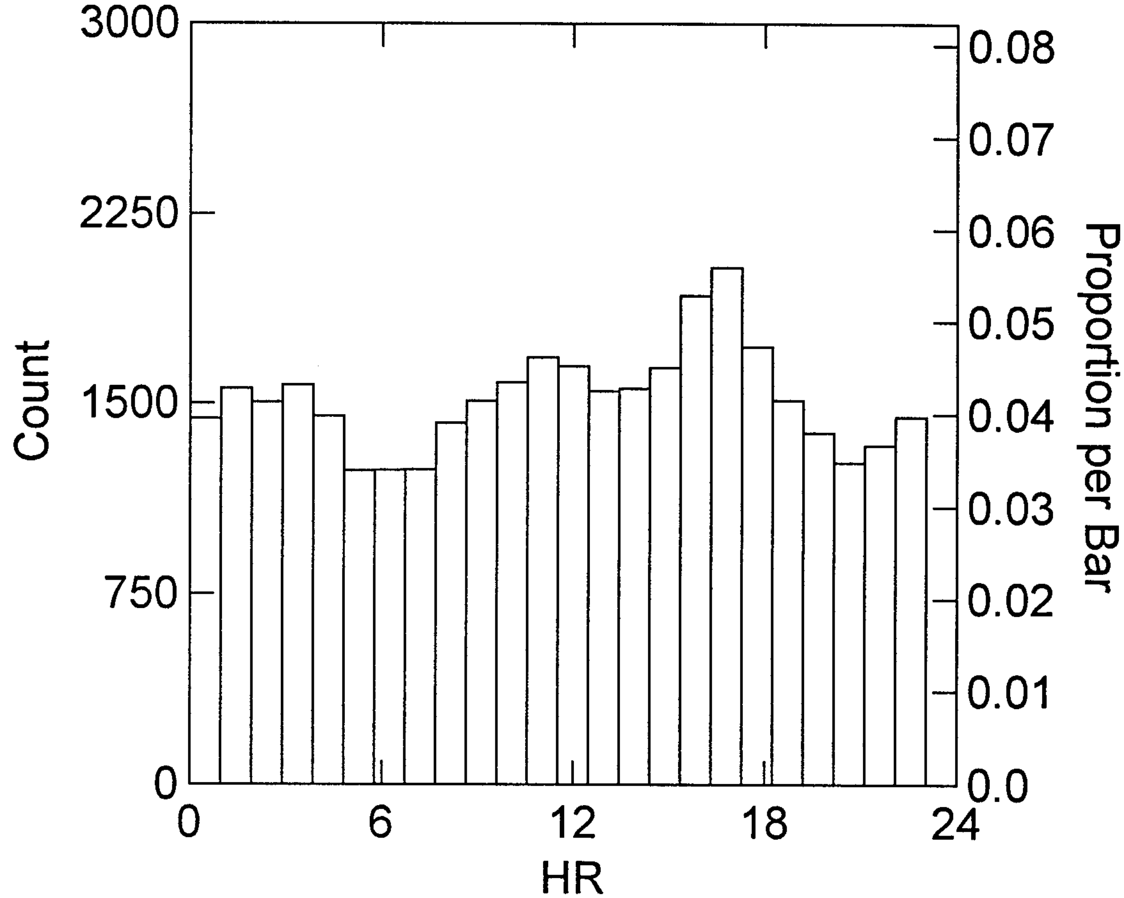
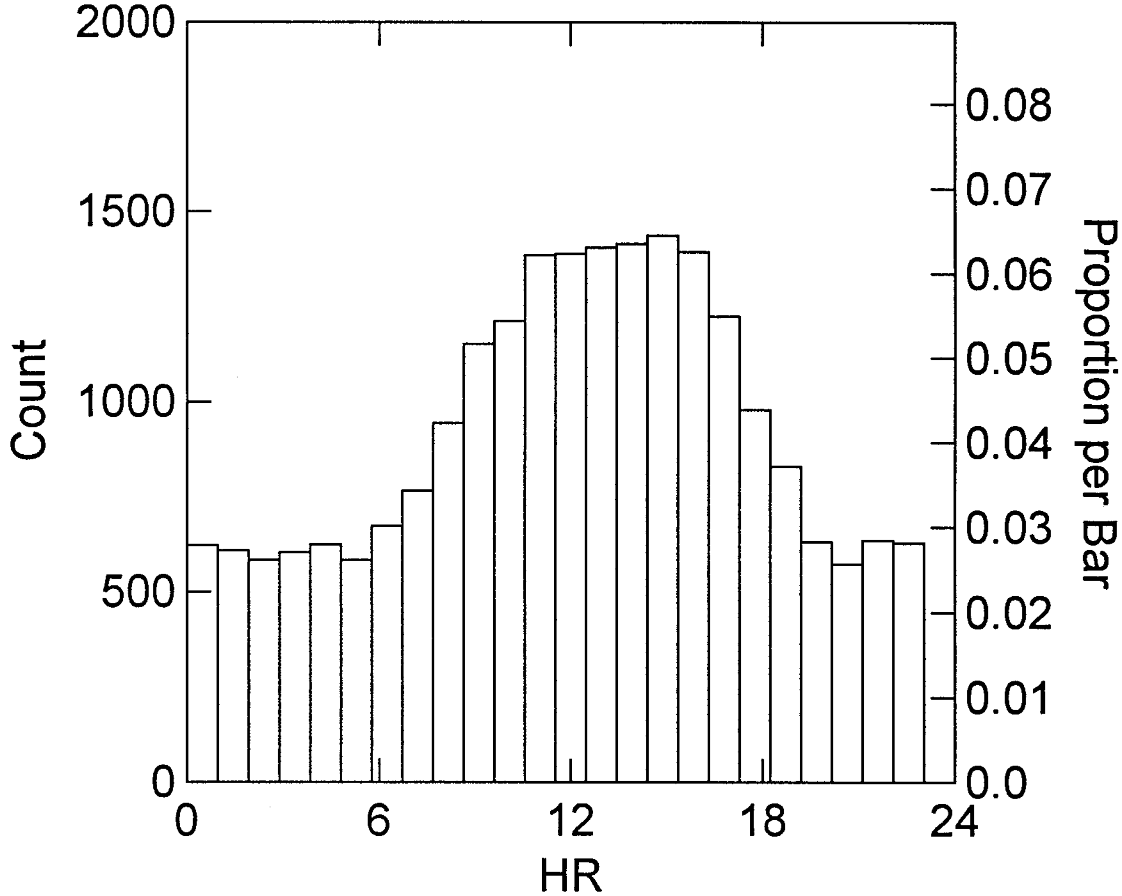


Figure 6. Haul-out profile by time of day for all seals, 1993.

1993 ALL SEALS COMBINED



CHAPTER 3

STATUS OF PACIFIC HARBOR SEAL STOCK IN CALIFORNIA

INTRODUCTION

During the late nineteenth and early twentieth centuries, north American pinniped populations were greatly reduced by commercial and bounty hunting (Bonnot 1928, 1951; Bartholomew and Boolootian 1960, Bartholomew and Hubbs 1960). Pacific harbor seals, *Phoca vitulina richardsi,* numbered only a few hundred individuals in a few isolated areas along California's coast (Bonnot 1928). Two species of pinnipeds, northern elephant seal, *Mirounga angustirostris*, and Guadalupe fur seal, *Arctocephalus townsendi*, were essentially eliminated from California waters.

The State of California first protected pinnipeds from uncontrolled hunting in 1938. At the federal level, provisions of the 1972 Marine Mammal Protection Act (MMPA) and subsequent amendments, prohibited harassment or killing of all marine mammals except under special permit issued by National Marine Fisheries Service (NMFS). Federal MMPA permits were issued for research, display, or incidental catch during commercial fishing. Harassment or killing of marine mammals was defined as a "take" and number of takes allowed was limited based on stock status relative to optimum sustainable population (OSP). OSP was defined by NMFS to be a range between maximum net productivity level (MNPL) and environmental carrying capacity (Federal Register, 21 December 1976, 41FR55536). MMPA further specified that permitted take could not be so great as to reduce a stock below OSP.

Pacific harbor seal, California sea lion, *Zalophus californianus*, and northern elephant seal populations increased significantly in the last half of this century (Barlow et al. 1993, 1995). Northern elephant seal population growth was described as passing through an abundance bottleneck to expand at high annual growth rates, filling previous habitat, and even expanding to occupy habitat not historically utilized (Bodkin et al. 1985, Lehman et al. 1992). Expansion into new habitat and hauling sites, specifically mainland shore sites, was likely prevented during historical times by large predators (grizzly bear and mountain lion) or Native Americans.

During the last decade, epizootic outbreaks of a morbilli virus (phocine distemper) were observed in two stocks of Atlantic harbor seals (Dietz et al. 1989). Approximately 60 percent of eastern north Atlantic harbor seals, *P. v. vitulina*, died (Härkönen and Heide-Jørgensen 1990). A significant decline in Gulf of Alaska harbor seals at Tugidak Island was documented by Pitcher (1990), however, no cause was identified and no epizootic occurrences have been reported for Pacific harbor seal stocks.

Incidental Take:

In California, Pacific harbor seals were killed incidentally in several gill net fisheries (Barlow et al. 1994, Diamond and Hanan 1986, Herrick and Hanan 1988, Hanan and Diamond 1989, Hanan et al. 1988a, 1993a, Perkins et al. 1992, 1994; Julian 1993, 1994; Lennert et al. 1994). To determine extent of intentional and accidental kills in various fisheries, observers were placed aboard fishing vessels. Their observations along with calculations of fishing effort were used to estimate total numbers of marine mammals killed during fishing operations. In California waters, it was estimated that between 800 and 2,000 Pacific harbor seals were killed annually during 1983 through 1987 period (Hanan and Diamond 1989, Hanan et al. 1988a), and 500 to 1,100 were killed annually during 1988 through 1993 (Julian 1993, 1994; Perkins et al. 1992, 1994; and Lennert et al. 1994).

Mortality of harbor seals in gill nets may have been as high as 5-10 percent in California. A kill this large would have strong influences on population growth rates and may artificially depress growth rates. However, more seals were killed in the southern half of the state (Hanan and Diamond 1989, Hanan et al. 1988) while seal abundance was greater in the northern half of the state (Hanan et al. 1992). This differential kill rate by geographic area had not been investigated; however, it may have been an important factor in apparent slowing of growth rates especially in southern California. Set gill nets have not been allowed within state waters (5 kilometers of shore) south of Point Arguello because of a 1990 voter-approved California state initiative (Proposition 132). There has been little or no incidental kill south of Point Arguello since implementation of this state constitutional amendment, January 1, 1994 (Barlow 1995). There have been similar closures in central and northern California throughout the 1980's.

Population Growth Rates:

Examination of census data (1927-1995) reveals a growth curve with a typical pattern of exponential growth for Pacific harbor seals in California during the first half of this century (Figure 1). I did not utilize counts nor estimate rates of growth for those early years because of differences in survey techniques. Pacific harbor seal total counts have been increasing at least since 1960. Rates of increase have changed over time and although the population was still increasing, rates of increase appeared to slow during 1984-1995, indicating that harbor seal population may have been approaching environmental carrying capacity. Barlow and Hanan (1995) describe a regional stock designation for harbor porpoise, *Phocoena phocoena*, a concept that I examined for OSP analysis of harbor seals distributed along three regions of California's coast and at California's Channel Islands. Such small stock designations are appropriate for harbor seals as genetic studies show limited interchange of individuals over relatively small distances (Lamont et al. 1996).

Interspecific Competition:

Ecologists have shown that interactions of plants or animals within any community influence survival or propagation of conspecifics (intraspecific competition) as well as other species, genera, or higher taxa (interspecific competition). The body of literature is replete with examples of interspecific competition and a few are: plants competing for nutrients, water, sun light, or space (Goldberg and Barton 1992); barnacles competing for substrate (Connell 1961); fish competing for forage and space (Donaldson 1995, Hearn 1987, Robertson 1996); birds competing for nesting space and food (Diamond 1975, Lack 1971, Wallace et al. 1992); fish and seabirds competing for forage fish (Fiedler et al. 1986); lizards competing for space (Case and Bolger 1991); and insects and rodents competing for seeds (Brown and Davidson 1987).

There is a paucity of data describing interspecific competition in marine mammals: fur seals displaced seabirds from nesting sites (Crawford et al. 1989) and fur seals competed aggressively with sea lions for space (Guerra C. and Portflitt K. 1991, Stewart et al. 1987, Vaz-Ferreira and Bianco 1987).

Because harbor seal population growth rates appeared to vary between individual Channel Islands and personal observations suggested that northern elephant seals were increasing at formerly exclusive harbor seal hauling sites while harbor seal numbers were decreasing, I investigated possible occurrences of interspecific competition for harbor seals at island sites where elephant seals may have excluded harbor seals. I also investigated mainland sites where interspecific competition may have occurred.

Density Dependent Habitat Selection:

As MacCall (1983, 1990) explained in his basin model theory, Fretwell-Lucas' density dependent habitat selection (DDHS) predicts that individuals in an ideal free distribution will expand into and utilize marginal habitat as a population grows and availability of suitable unoccupied habitat declines (Fretwell and Lucas 1970). Bodkin et al. (1985) explored this concept of expanding population and expansion to new hauling sites by northern elephant seals, but no studies have examined this aspect of harbor seal population dynamics. My goal was to refine understanding of this complex pattern by which a recovering population occupies former range and habitat following catastrophic events (i.e., El Niño). Harbor seal census data were appropriate for this type of analysis because this species exhibits strong site fidelity, is widely distributed along North America's west coast, and does not make a large annual migrations.

Preliminary investigation of Pacific harbor seals suggested that distribution was clustered among California coastal hauling sites. Some areas and hauling sites have many more seals than other areas and clustering patterns were unevenly distributed. Because harbor seals were not evenly distributed and because of population expansion (increasing numbers of seals and increasing number of hauling sites), assessment of this population and available data appeared to be appropriate for DDHS studies.

Environmental Perturbations:

Short term, large scale perturbations such as El Niño events often caused devastating effects on many marine communities by raising water temperatures and indirectly initiating catastrophic storms (Dayton and Tegner 1984). Benthic invertebrates as well higher trophic level species such as fish and birds are also impacted by these climatic changes (Arntz et al. 1988, Clark et al. 1990, Gibbs and Grant 1987, Fiedler et al. 1986, Schreiber and Schreiber 1989).

Pinniped population responses to the 1982-83 El Niño are presented in Trillmich and Ono (1991). They state that "The effect of the 1982-83 El Niño on pinnipeds appeared to have decreased with distance from the center of the anomaly." However, several papers in Trillmich and Ono show that El Niño events impact pinniped populations off California. They further discuss the importance of understanding "abundance and distribution of food" and state that "too little was known about this aspect of marine life". Because harbor seals feed in part on nearshore benthic prey (Olesiuk 1993, Hanson 1993), they might be affected indirectly by changes in distribution of prey items reacting to El Niño conditions. Such short term environmental perturbations are likely to influence harbor seal population growth and habitat utilization. Those effects are also likely to confound OSP determinations.

OSP Assessment:

Dynamic response analysis was first developed by DeMaster et al. (1982) to determine population status relative to carrying capacity of the environment and determine OSP status. The technique was further refined by Gerrodette (1988), Goodman (1988), and Eberhardt (1992). Dynamic response tests the trajectory of a population growth curve as it relates to maximum net productivity level (MNPL); the trajectory of populations below MNPL will be curved upward and the trajectory of populations above MNPL will be curved downward (DeMaster et al. 1982).

Gerrodette (1988) reported that it may be difficult to determine status of a population when that population is very close to MNPL. Fowler (1981) predicted that marine mammal populations near MNPL may also be quite close to carrying capacity. If Fowler's hypothesis holds for Pacific harbor seals, confirmation of OSP status may be confounded because Hanan (1993) predicted harbor seals to be near OSP in California. Human impacts on growth rates (specifically mortality in coastal set nets) may have further confounded this analysis. Therefore, additional models (e. g., Boveng et al. 1988, Gerrodette and DeMaster 1990) were considered.

Boveng (1988) assessed OSP for Pacific harbor seals based on simplified dynamic response analysis (DeMaster et al. 1982) applied to mainland counts for years prior to the 1983-84 El Niño event. He stated that available data were indicative of a population below MNPL, however, he concluded that a significance level of $P < 0.10$ did not allow a "definitive statement" that the population was below MNPL. He explained that there were too few data beyond 1982 to determine whether harbor seal population status had changed prior to 1982.

Because this study included harbor seal censuses through 1995, adding thirteen data points beyond the 1983 data with which Boveng (1988) concluded his study, I have explored OSP utilizing dynamic response. I have done so for comparative purposes and recognize two significant deviations from requisite assumptions with this type of analysis: 1) there was a significant (although incidental) harvest of harbor seals through 1993 mainly in coastal and island set net fisheries for California halibut, angel shark, and white seabass (Herrick and Hanan 1988; Hanan and Diamond 1989; Hanan et al. 1988a; Julian 1993, 1994; Perkins et al. 1992, 1994; and Lennert et al. 1994); and 2) data collected for census and data calculated for estimated gill net mortality are not synchronous (census is a point estimate at time of seal molting, while total mortality is an estimate for an entire year) and these two estimates should not be combined as total population for dynamic response analysis.

METHODS

Population Growth Rates:

To assess current status of Pacific harbor seals, I compared growth rates between northern, central, and southern California regions during 1982 through 1995 (Figure 3). I chose latitudes 37°50' and 35°00' as dividing points for regions (Table 1). To obtain growth rates, I used linear regression of natural logarithms of aerial counts versus years. Mean annual finite growth rate was calculated as antilogarithm of regression slope minus one (Olesiuk et al. 1990).

Because most seals in southern California inhabit the Channel Islands rather than mainland sites, I examined population growth rates for individual islands. As with regional and island comparisons, I used Student's *t* to test for significant differences between slopes of logistic growth curves.

Interspecific Competition:

To examine whether interspecific competition was manifest between harbor seals and elephant seals and affecting harbor seal population growth rates, I tested slopes of harbor seal logistic growth curves at sites where interspecific competition might be occurring. I selected sites based on personal observations of elephant seals present at or very near former harbor seal hauling sites as observed during aerial surveys and field trips to sites. Slopes of logistic growth curves for harbor seals were tested against slopes of logistic growth curves for harbor seals at all other island sites combined using Student's *t* to detect significant differences.

For Channel Island investigations, I regressed natural logarithms of San Miguel Island harbor seal counts versus years for 1983 through 1995 (Table 3) and compared the slope of that regression to regressions for harbor seals at all other Channel Islands combined.

To examine possible combined Channel Islands effect of interspecific competition, I summed San Miguel Island harbor seal counts with one site on Santa Rosa Island (southwest of Sand Point) and with three sites on San Nicolas Island (south side) where both harbor seals and elephant seals haul out. I tested slopes of regressions for harbor seal growth rates during 1984 through 1995, the years for which I had individual site counts.

For mainland investigations, I performed tests on slopes of harbor seal logistic growth curves for mainland sites where harbor seals and elephant seals were potentially exhibiting interspecific competition. Those slopes were compared to slopes of logistic growth curves for sums of counts at all other sites in that region and tested using Student's t to detect significant differences.

Density Dependent Habitat Selection:

I regressed total counts versus total sites occupied to test for correlation. I used Student's t tests for regression slopes of total seal counts versus total sites occupied. If slopes did not deviate significantly, I assumed close relationship of annual growth rates and sites occupied for confirmation of DDHS. Further testing of DDHS was accomplished by examination of habitat type and was accomplished by examination of annual seal counts by substrate type (Figure 2).

Environmental Perturbations:

There were too few data to perform meaningful tests for potential effects of El Niño events on Pacific harbor seals; however plots of aerial and shore based counts were evaluated with particular attention to El Niño periods (Figure 4).

OSP Assessments:

To test OSP relationships in harbor seal data, I used methods described in

Gerrodette (1988) and Eberhardt (1992). For these analyses, I did not add estimated seal mortalities in fisheries to abundance estimates because units of measurement were not comparable as previously described. Using harbor seal aerial counts, if slope of linear regression was negative or not significantly different from zero, I assumed the population to be above MNPL. If slope was positive, I fit a second order regression to the data and to determine sign of slope. If positive, I assumed the population was below MNPL.

I utilized Eberhardt's combined dynamic response method (Eberhardt 1992). I first tested growth rate for curvilinearity (Snedecor and Cochran 1967: 455) relative to MNPL using linear regressions and second order polynomial multiple regressions on an arithmetic scale. If results were not statistically significant at 5 percent level, I performed the test for curvilinearity on linear regressions and second order polynomial multiple regressions of the log-transformed data.

An additional method (Boveng et al. 1988) using moving intervals to determine optimal number of data points for dynamic response testing was used for further clarification of OSP status. Second-order polynomials were fit to a series of intervals of data: first a four-data-point moving interval, then a five-point, and continuing until reaching total number of data points. The successively increasing number of data-point moving intervals were regressed against time. Because sign of second-order coefficients changes from positive to negative at the inflection point (MNPL), a plot of second-order coefficients for a series of data including MNPL will pass through the abscissa from positive to negative as the growth curve changes from concave upwards to concave downwards. Boveng et al. (1988) suggested that optimal number of data points for OSP definition occurs when a plot of second-order coefficients passes through the abscissa only once.

RESULTS

Population Growth Rates:

Harbor seal mean annual growth rate for all sites and regions in California combined was 3.5 percent (SE = 0.007) during 1982 through 1995 (Table 1). Although not significant, there were differences between regions. Southern California had relatively lower rates of growth. Of three regions (northern, central, and southern), central California had highest growth rate (5.8 %, SE = 0.011), southern California had lowest (1.9%, SE = 0.013), and northern California (3.1%, SE = 0.009) was close to the overall rate (Figure 4).

Annual growth rates increased at all Channel Islands (Table 2) except San Miguel Island (− 1.1%, SE = 0.024) and Santa Barbara Island (− 0.97%, SE = 0.114). Santa Cruz Island was the highest annual growth rate (5.8%, SE = 0.045) which was nearly identical to central California during this same time period. Student's *t* tests for significant differences between slopes of logistic growth curves are presented in Table 3. Differences between northern, central, and southern regions, although relatively large, were not statistically significant.

Interspecific Competition:

When comparing regression slopes for San Miguel Island against all other Channel Islands combined, I calculated a Student's *t* value of 1.349 (df = 22, P< 0.190). Total San Miguel Island counts combined by year with appropriate harbor seal counts from Santa Rosa Island and San Nicolas Island (sites with both harbor seals and elephant seals) and tested against annual harbor seal counts from all other island sites combined (Table 3). I obtained a Student's *t* value of 1.696 (df = 20, P <0.110) for this relationship. Using this same test comparing slopes of log-transformed counts from San Miguel Island to log-transformed counts from islands with higher growth rates (Table 3) revealed a significant differences with each island: Santa Cruz Island (*t* = 2.104, df = 22, P = 0.048), San Clemente Island (*t* = 4.182, df = 22, P< <0.001), Santa Catalina Island (*t* = 4.044, df = 22,

$P << 0.001$).

Of six mainland sites where elephant seals hauled out near or adjacent to harbor seals (Point Conception, Piedras Blancas Point, Año Nuevo Island, South Farallon Islands, and Castle Rock), harbor seal numbers declined significantly at two sites: Año Nuevo Island (near Monterey Bay) and Castle Rock (near Crescent City), compared to regression slope of all other sites totaled by year in the nearest region (Figures 7 and 8). I confirmed this relationship using Student's *t* (Table 3), comparing regression slopes of logged counts to regression slopes of appropriate regions for Año Nuevo Island ($t = 6.214$, df = 24, $P < 0.0001$) and Castle Rock ($t = 2.190$, df = 22, $P < 0.05$).

Density Dependent Habitat Selection:

Linear regression for natural logarithm of number of sites versus year revealed a slope of +0.035 (SE = 0.007, $R^2 = .70$) and linear regression for natural logarithm of number of sites versus natural logarithm of total counts estimated a slope of +0.708 (SE = 0.169, $R^2 = .63$). I obtained Student's *t* value for significant differences between linear regression slopes of number of sites versus year compared to natural logarithm of total counts versus year ($t = 0.01$, df = 22, $P > 0.50$).

Environmental Perturbations:

Inspection of annual harbor seal counts plotted by year (Figure 4) reveal a consistent pattern: harbor seal counts declined during and immediately following El Niño events. The largest harbor seal decline was observed during and following the 1982-83 event which was the most extreme El Niño event yet recorded (Dayton and Tegner 1984). There were subsequent declines in harbor seal counts with the El Niño events of 1987-88 and 1992-93 (Table 5). Radio tagging data also confirmed a substantial change in percentage of harbor seals ashore during and following the El Niño event of 1993 (see Chapter 2, Table 4).

OSP Assessments:

Considering harbor seals on a statewide basis during the period 1982 through 1995 (Table 4), slope of linear regression was +639.288 (SE = 125.080) and was significantly different from zero ($F = 26.12$; df = 1, 12; $P = 0.0003$). Slope of second order polynomial multiple regression was −3.308 (SE = 36.502) and was significant ($F = 11.98$; df = 2, 11; $P = 0.002$). Slope of linear regression of log-transformed data was +0.035 (SE = 0.007) and was significant ($F = 26.57$; df = 1, 12; $P = 0.0002$). Slope of the quadratic equation fit to log-transformed data was −0.0005 (SE = 0.002) and was significant ($F = 12.28$; df =

2, 11; P = 0.002). Eberhardt's combined test for curvilinearity (Eberhardt 1992) on arithmetic scale was not significant (F <1.0, P> 0.5) and for log-transformed data, the test also documented non-significant curvilinearity (F < 1.0, P> 0.5).

Using a moving interval method (Boveng et al. 1988) to determine optimal number of data points for dynamic response testing revealed 10 harbor seal counts to be optimal (Figure 5 and 6). When using ten counts from 1986 through 1995, slope of linear regression was +585.200 (SE = 221.453) which was significantly different from zero (F = 6.98; df = 1, 8; P = 0.03). Slope of the second order polynomial multiple regression was − 64.527 (SE = 90.347) and was not significant (F = 3.53; df = 2, 7; P = 0.087). Slope of linear regression of log-transformed data was +0.030 (SE = 0.011) and was significant (F = 7.01; df = 1, 8; P = 0.029). Slope of the quadratic equation fit to log-transformed data was − 0.004 (SE = 0.005) and was not significant (F = 3.74; df = 2, 7; P = 0.079).

Eberhardt's combined test for curvilinearity (Eberhardt 1992) on the arithmetic scale was not significant (F <1.0, P> 0.5). For log-transformed data, this test on ten data points also revealed non-significant curvilinearity (F <1.0, P> 0.5). As Table 4 shows, none of the regional OSP results depicted populations above MNPL.

DISCUSSION

Population Growth Rates:

Pacific harbor seal abundance has increased in eastern North Pacific habitats since sporadic counts began in 1928 (Bonnet 1928). Improvement in census technique might be hypothesized to explain apparent population increases, however most recent data, collected in a systematic manner with attention to consistency and accuracy, also show increasing numbers. Similar findings were reported in Oregon by Harvey et al. (1990) with a growth rate of 8.1 percent for 1975-1983 and 12.5 percent in British Columbia during 1977-87 (Olesiuk et al. 1990).

Studies at individual sites have shown harbor seal growth rates that are much higher than rates statewide and regionally for 1982 through 1995. Stewart et al. (1988) described a rate of growth for San Miguel Island (22%) during an earlier time period, 1958-1976. Allen et al. (1989) found annual growth rates at 7.6 percent at Double Point (outside San Francisco Bay) from 1976 through 1987 and 17 percent at the Gulf of the Farallon Islands from 1974 through 1986.

Interspecific Competition:

Overall growth rate of Pacific harbor seals during 1982 through 1995 was shown to be slowing statewide. In some localized areas, where interspecific competition for space with elephant seals may be a limiting factor, annual counts were declining and may indicate an approach towards carrying capacity at those individual sites or regions. Peak abundance for elephant seals (McGinnis and Schusterman 1990) occurred during harbor seal pupping; however, elephant seal presence was also conspicuous during harbor seal molting when I conducted aerial surveys. Therefore, declining seal counts and declining rates of population growth at these sites probably did not indicate actual decline in population growth rates.

Regional and statewide growth rates, although slowing, were not declining and localized declines in abundance were more likely the result of space competition and displacement of harbor seals to other sites. This was exemplified by a decrease in harbor seals at San Miguel Island while at nearby Santa Cruz Island (where there were no elephant seals hauling out) there was a significant increase in abundance and there was a significant difference between growth rates of the two islands (Table 2). There was also significant differences with two other Channel Islands that had much higher annual growth rates: Santa Catalina (no elephant seals) and San Clemente (elephant seals at one site).

In addition, two mainland sites, Año Nuevo and Castle Rock, showed significant decreases in harbor seal abundance (Figures 7 and 8). Elephant seals were abundant and increasing at Año Nuevo Island (Barlow et al. 1992). It was likely that declining harbor seal abundance was the result of competition with elephant seals for haul out space. California sea lions were also abundant at this Island; during July 1995, Beeson and Hanan (1996) counted over 6700 individuals. It was possible that sea lions also contributed to harbor seal decline at this site. At Castle Rock, I observed elephant seals and seal lions on and near harbor seal hauling sites. Again there was a significant decline of harbor seal abundance at this site.

These results were a surprise. I had concentrated on intraspecific competition in harbor seals, but the data suggest interspecific competition with elephant seals and possibly sea lions. Increased presence of elephant seals at these sites suggests harbor seal abundance on shore might be limited by available haul out space.

Density Dependent Habitat Selection:

At MNPL, a population may begin to exhibit evidence of density dependence in population factors such as DDHS (MacCall 1983, 1990). As total counts and apparent abundance increased statewide, harbor seals began to colonize previously unoccupied portions of established hauling sites. As numbers continued to increase, seals started to occupy new additional hauling sites nearby, which resulted in increased numbers of hauling sites (see Table 5). These observations were confirmed by photographic records summarized in reports of surveys (Miller et al. 1983, Hanan 1990, Hanan and Beeson 1994, Beeson and Hanan 1994, and Hanan et al. 1985, 1986a, 1986b, 1987, 1988b, 1989, 1991, 1992, and 1993b). Those reports recorded counts by site, summarize counts by year, and especially, document year a hauling site was first occupied by harbor seals. These data showed that as the population grew, seals expanded to occupy more hauling sites within their existing range, thereby occupying more space for hauling out, and not necessarily by expanding occupied range. Those results suggested that MacCall's basin model (1983, 1990) was valid for harbor seals: if harbor seals occupied the best or most suitable habitat within their range first and as population increased, seals began to occupy less desirable or possibly less suitable habitat within their range.

During this time period, as total number of hauling sites increased annually, percentage of sites occupied remained about the same level of 60 percent and percentage of maximum seals observed at a site also remained at approximately 50 percent (Table 5). If harbor seal growth rate is space limited, percentage of sites occupied and percentage of maximum observed should increase as the population approaches carrying capacity. Because this was not shown in my data, it is an indicator that harbor seals are not yet at OSP.

Environmental Perturbations:

Each of three recent El Niño events (1982-83, 1987-88, 1992-93) was followed by a decline in number of seals counted. Results of radio tagging studies (see Chapter 2) for proportion of seals ashore following the 1992-93 El Niño event were a minimum of 10 percentage points lower than other years (Chapter 2, Table 4).

OSP Assessments:

Use of Gerrodette's (1988) dynamic response model indicated that Pacific harbor seals in California were above MNPL and at OSP (slope of linear regression of counts significantly positive and second-degree polynomial regression coefficient significantly negative); however, using Eberhardt's (1992) test for curvilinearity, the population would not have been above MNPL and not at OSP.

Using Boveng et al. (1988) to choose the last ten year period as optimal for

OSP determination removes the important 1983-84 El Niño effect from data analysis, as well as, the high but real 1982 count (Table 4). Following Gerrodette (1988), this ten-year data set indicated that harbor seals were not at OSP, but very close (slope of linear regression of counts significantly positive and second-degree polynomial regression coefficient not significantly negative at $P = 0.087$). Additionally, testing these data with Eberhardt's (1992) test indicated no significant curvilinearity.

CONCLUSIONS

Population Growth Rates:

Clearly the Pacific harbor seal population continues to grow in California although rate of growth has slowed and especially in certain regions. Incidental mortality in fisheries may have been a confounding factor with differential slowing of the growth rate in central and southern California regions compared to the northern region, where there was no nearshore gill net fishing. In some specific areas, declining rates of growth can be attributed to interspecific competition (e.g. San Miguel Island and Año Nuevo Island) but this was not likely a factor for slower rates of growth in central or southern regions.

Interspecific Competition:

I have not observed violent interactions between elephant seals and harbor seals as reported between fur seals and sea lions in South America. Harbor seals occasionally hauled out among elephant seals, but this was not the general pattern. I speculate that the mere presence of large numbers of elephant seals and the resultant lack of hauling space for harbor seals may have precluded harbor seals. Thus harbor seals may have moved to other sites, and possibly occupied new sites.

Density Dependent Habitat Selection:

As the number of harbor seals has increased, so has the number of identified hauling sites. Harbor seals are expanding within their range to occupy new sites. It is assumed that those new sites were less desirable or available at lower population levels or they would have been utilized according to the concept of ideal free distribution.

Environmental Perturbations:

Because harbor seal numbers recovered to levels documented prior to El Niño events, I speculate that El Niño events did not result in actual loss of seals from the population or reduced production. Instead, as radio tagging studies showed, there was most likely a change in hauling patterns such that fewer seals were hauled out during censuses.

OSP Assessments:

Hanan (1993) reported that as of 1991 Pacific harbor seals were near, but not at OSP. Results presented herein indicated that although rates of population growth appear to be slowing, as of 1995, Pacific harbor seals off California were not above MNPL. Thus they were not at OSP in California, although they appeared to be very close to MNPL.

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Table 1. Pacific harbor seal population growth rates and standard error by region.

REGION	ANNUAL %	SE
Statewide	3.5	0.007
Northern	3.1	0.009
Central	5.8	0.011
Southern	1.9	0.013

Table 2. Pacific harbor seal population growth rates and standard errors for the Channel Islands.

ISLAND	ANNUAL %	SE
San Miguel Island	− 1.15	0.024
Santa Rosa Island	0.02	0.021
Santa Cruz Island	5.72	0.045
Anacapa Island	0.05	0.052
Santa Catalina Island	11.23	0.039
Santa Barbara Island	− 0.97	0.114
San Nicolas Island	0.02	0.036
San Clemente Island	11.11	0.035

Table 3. Student's t test results for comparisons of slopes of linear regressions for rates of Pacific harbor seal population growth at selected haul out sites.

REGION	*t* value	df	P
Northern vs Central	0.648	24	>0.50
Northern vs Southern	0.288	24	>0.50
Central vs Southern	0.968	24	<0.50
Año Nuevo vs Central	6.214	24	<<0.0001
Castle Rock vs Northern	2.190	22	<0.05
SMI vs Rest of CIs	1.349	22	= 0.19
SMI+ vs Rest of CI Sites	1.696	20	= 0.11

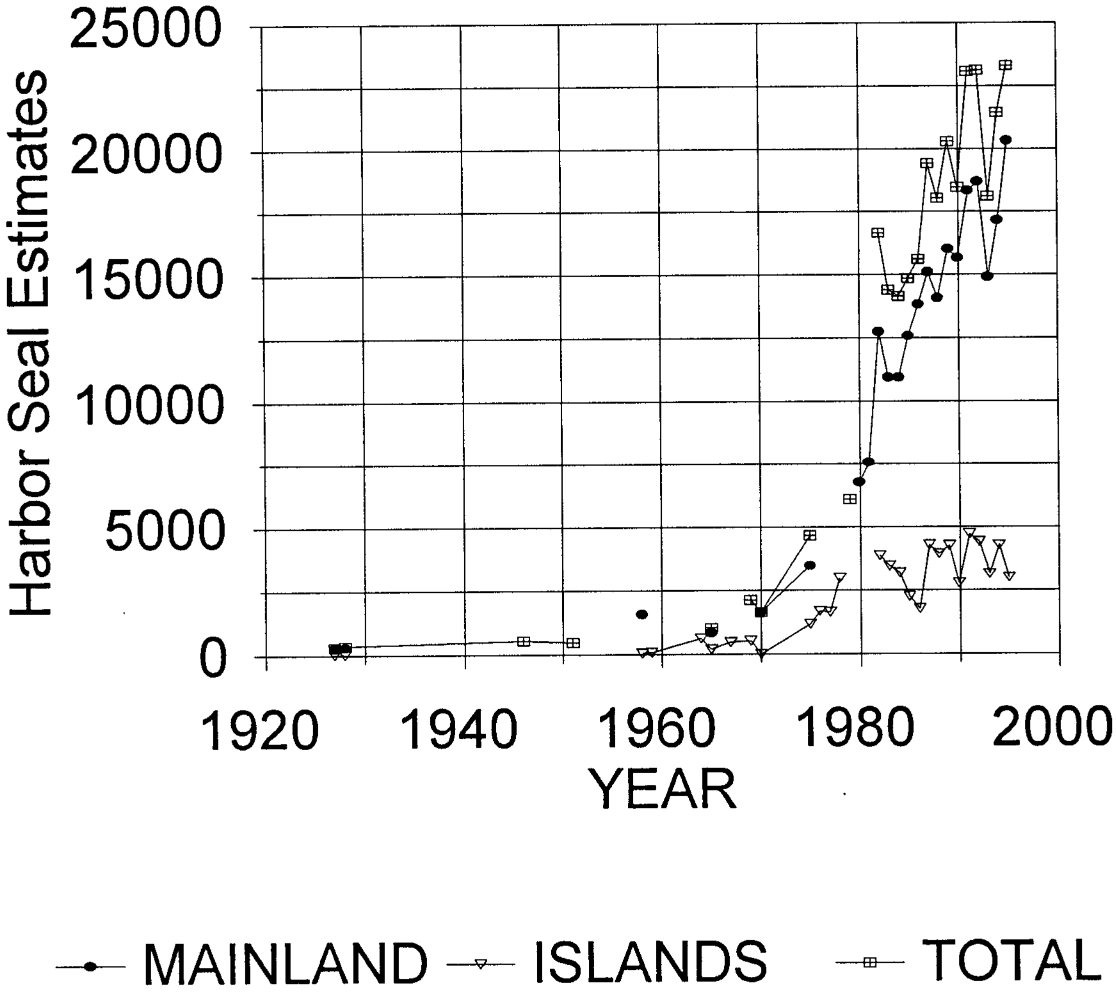
Table 4. Results of tests for detecting optimum sustainable population (OSP) relative to maximum net productivity level (MNPL) of Pacific harbor seal in California. California mainland regions (northern California, central California, and southern California; divided at latitudes 37°50' and 35°00').

REGION	SLOPE	SE	P
All Years (linear)	+639.288	125.080	0.003
All Years (quadratic)	−3.308	36.502	0.002
Ln All Years (linear)	0.035	0.007	0.0002
Ln All Years (quadratic)	−0.00005	0.002	0.002
10 Years (linear)	+585.200	221.453	0.030
10 Years (quadratic)	− 64.527	90.347	0.087
Ln 10 Years (linear)	+0.030	0.011	0.029
Ln 10 Years (quadratic)	− 0.004	0.005	0.079
N Cal (linear)	+281.567	82.737	0.005
N Cal (quadratic)	+9.791	23.972	0.022
Ln N Cal (linear)	+0.031	0.009	0.004
Ln N Cal (quadratic)	+0.001	0.003	0.019
C Cal (linear)	+267.919	46.182	0.0001
C Cal (quadratic)	− 0.911	13.479	0.001
Ln C Cal (linear)	+0.057	0.011	0.0002
Ln C Cal (quadratic)	− 0.001	0.003	0.002
S Cal (linear)	+89.802	61.910	0.173
S Cal (quadratic)	− 12.189	17.696	0.326
Ln S Cal (linear)	+0.019	0.013	0.183
Ln S Cal (quadratic)	− 0.002	0.004	0.373

Table 5. Pacific harbor seal counts by year 1983-1995 for the California mainland, number of sites, percentage of sites occupied, Channel Islands, and three California mainland regions (northern California, central California, and southern California; divided at latitudes 37°50' and 35°00').

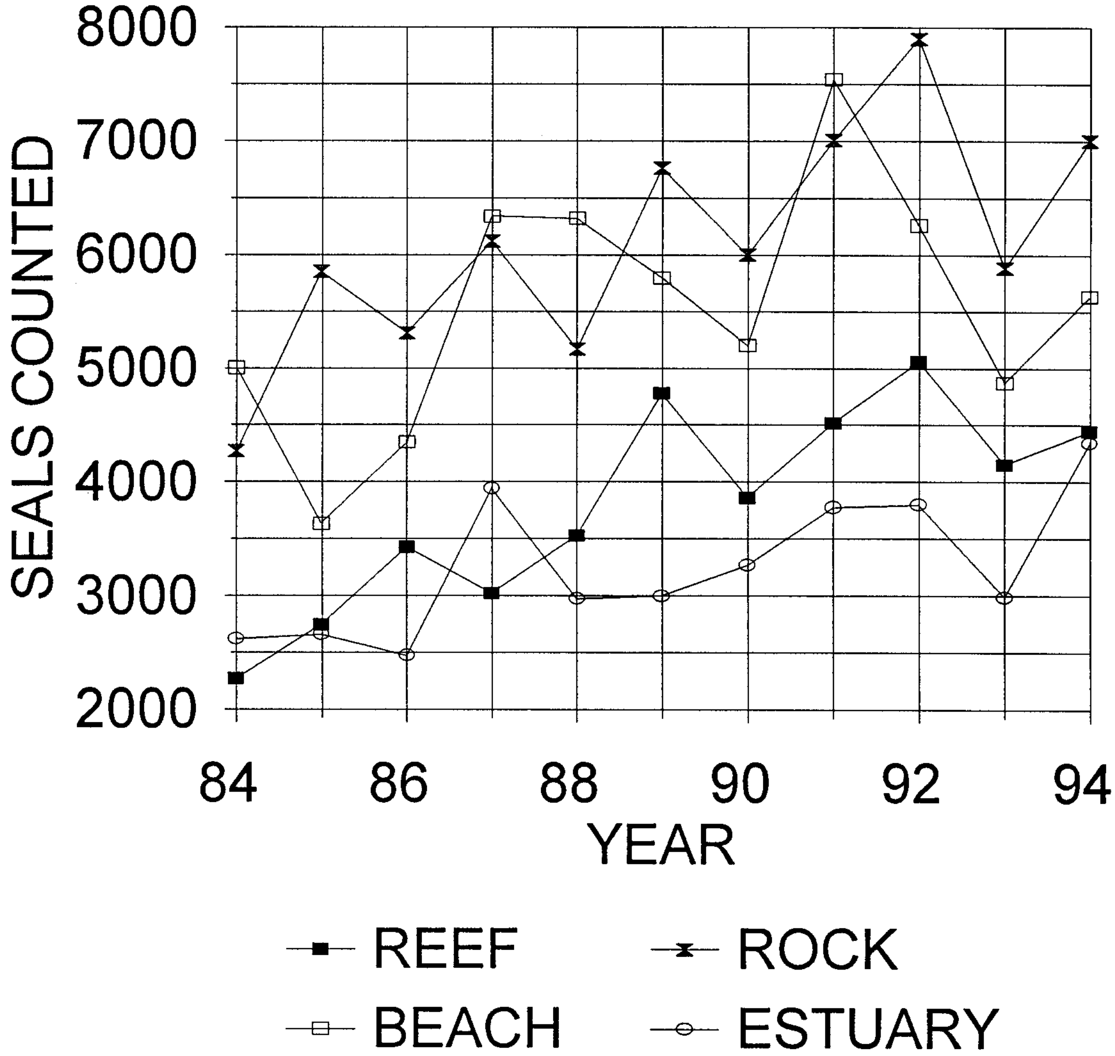
Year	Mainld	sites	%	Island	NCal	CCal	SCal	Total
1982	12,776	427	56	3,892	7,325	4,794	4,549	16,668
1983	10,945	488	38	3,472	6,611	3,031	4,942	14,417
1984	10,946	524	41	3,218	7,282	2,932	3,959	14,164
1985	12,598	580	47	2,280	8,005	3,315	3,583	14,878
1986	13,831	646	49	1,801	8,240	4,239	3,106	15,632
1987	15,124	678	46	4,322	9,263	4,631	5,553	19,446
1988	14,095	696	40	3,947	8,227	4,622	5,202	18,042
1989	16,034	711	40	4,279	8,587	5,950	5,810	20,313
1990	15,675	737	40	2,808	8,260	5,832	4,415	18,483
1991	18,346	764	40	4,743	10,658	6,195	6,040	23,089
1992	18,700	824	49	4,433	10,441	6,334	6,349	23,133
1993	14,933	848	39	3,166	7,549	6,042	4,518	18,099
1994	17,162	859	41	4,300	8,879	6,815	5,767	21,462
1995	20,297	877	43	3,005	13,038	6,059	4,205	23,302

Figure 1. Estimated harbor seal abundance by time 1927 - 1995.



Harbor Seal Estimates
25000
20000
15000
10000
5000
0
1920
1940
1960
1980
2000
YEAR
MAINLAND
ISLANDS
TOTAL

Figure 2. Pacific harbor counts by substrate type for years 1984-1994 combined.



8000
7000
6000
5000
4000
3000
2000
SEALS COUNTED
84
86
88
90
92
94
YEAR
REEF
ROCK
BEACH
ESTUARY

Figure 3. Rates of growth by region north, central, and southern California.

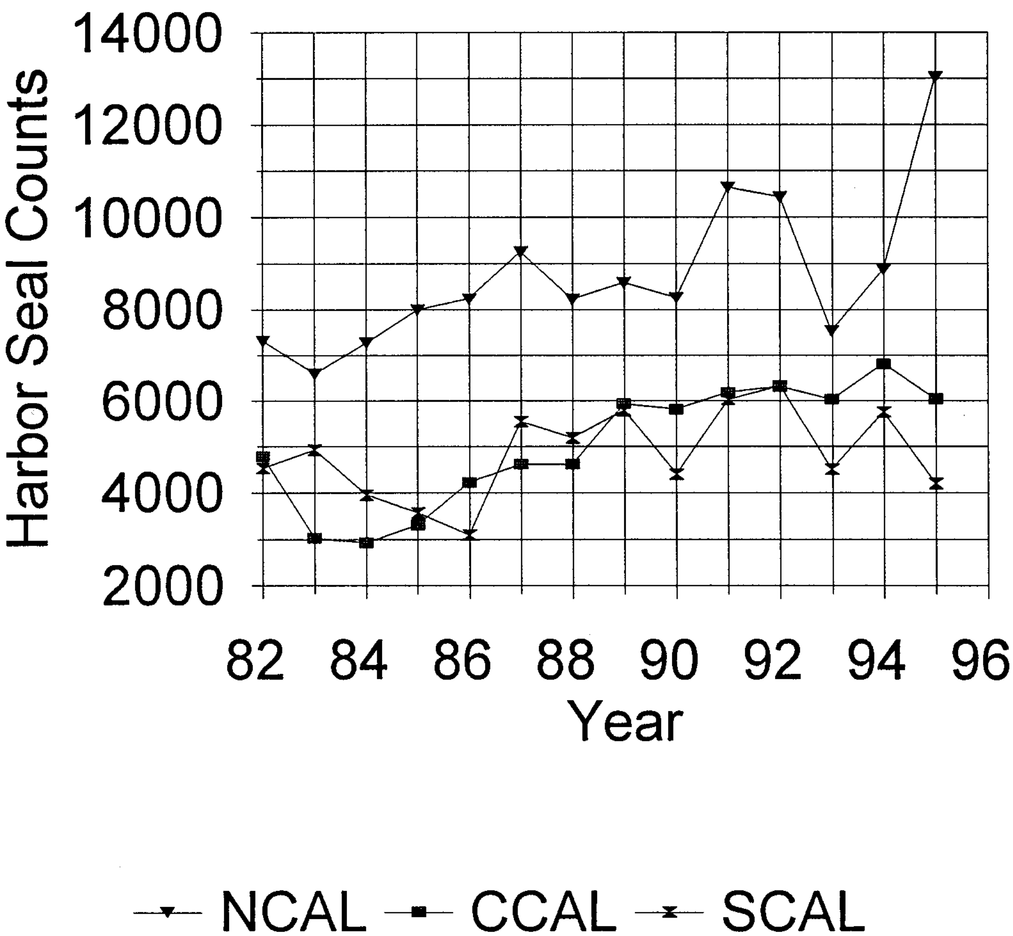

14000
12000
10000
8000
6000
4000
2000
Harbor Seal Counts
82 84 86 88 90 92 94 96
Year
NCAL
CCAL
SCAL

Figure 4. Harbor seal counts and linear regression fit (1982-1995).

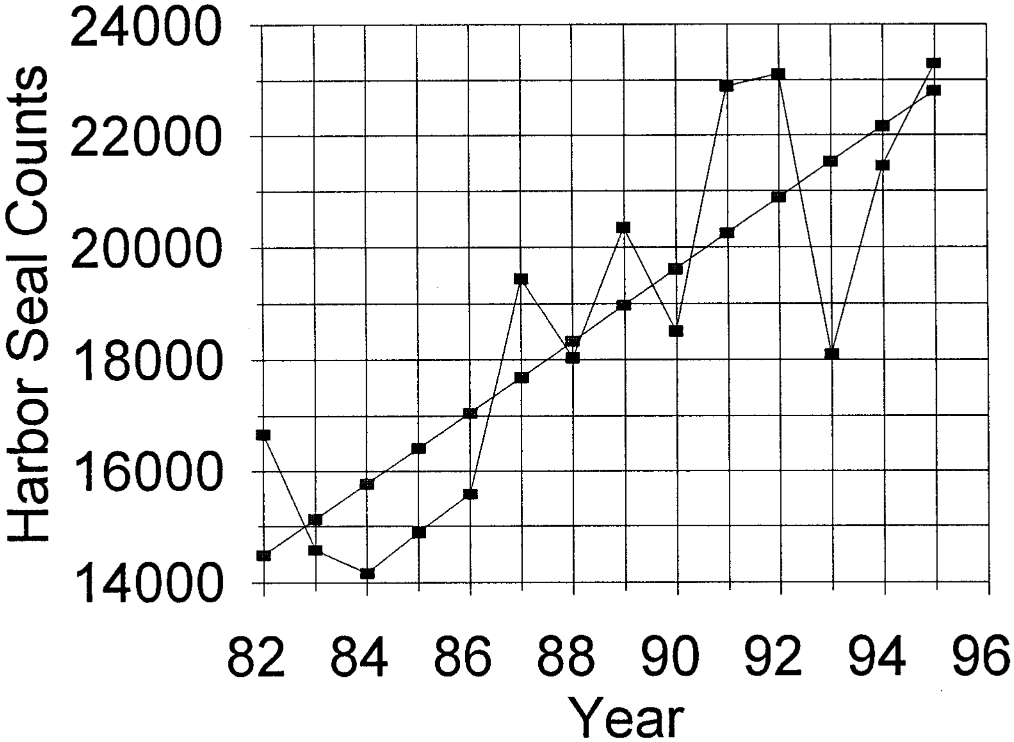
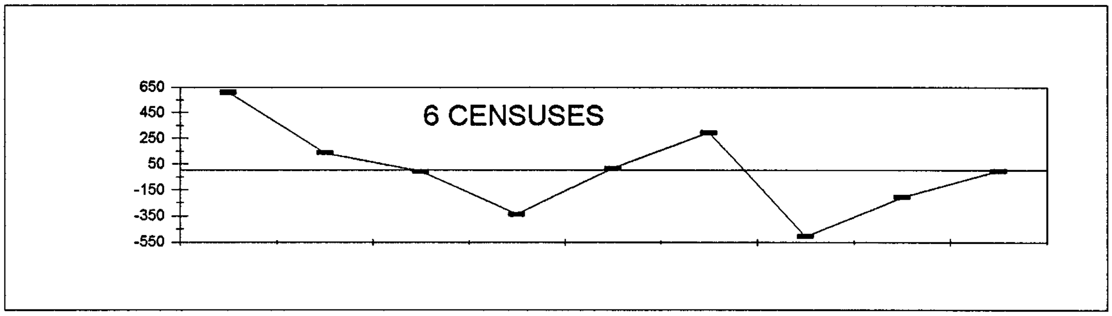
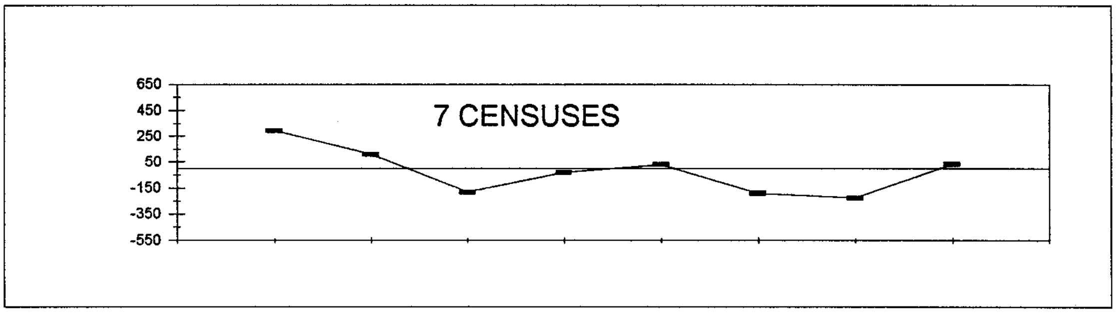

Harbor Seal Counts
24000
22000
20000
18000
16000
14000
82
84
86
88
90
92
94
96
Year

Figure 5. Plots for moving intervals of six, seven, and eight censuses. Second order regression coefficients plotted against midpoint of census interval.


6 CENSUSES
650
450
250
50
-150
-350
-550


7 CENSUSES
650
450
250
50
-150
-350
-550

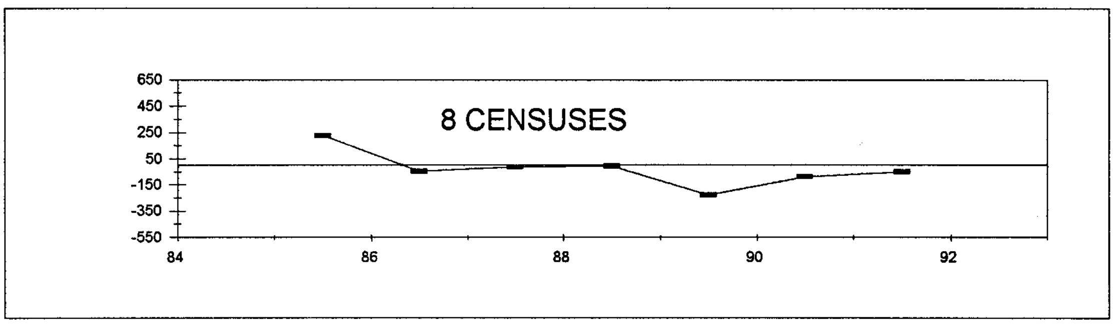
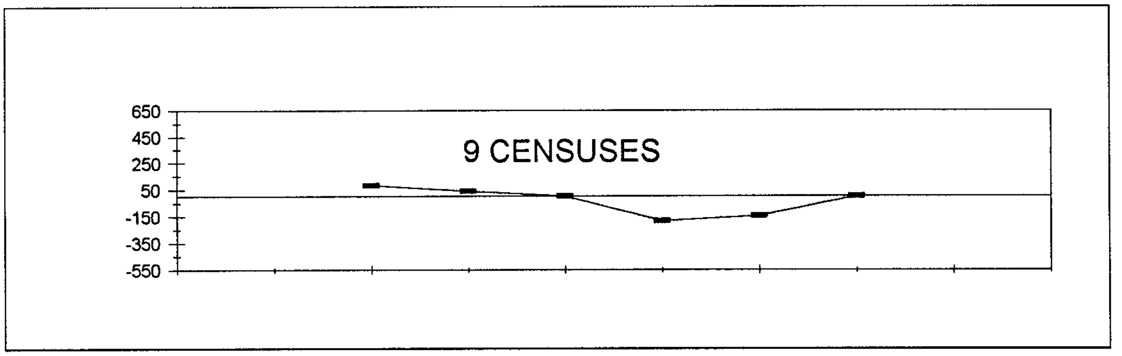
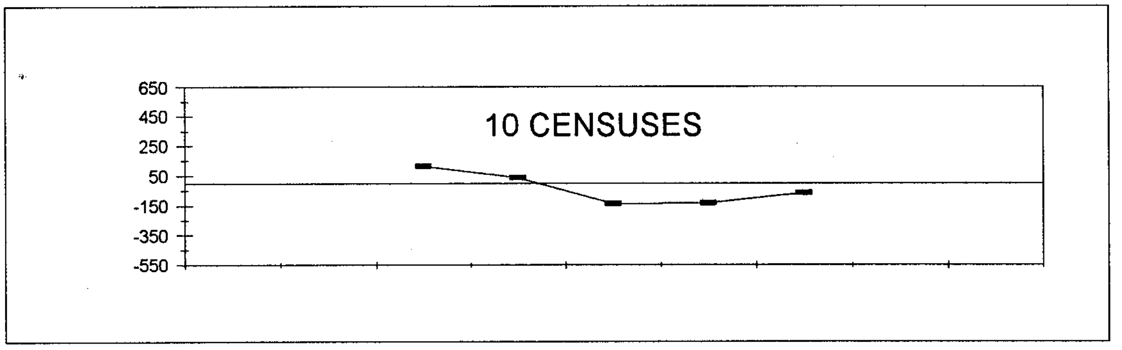

8 CENSUSES
650
450
250
50
-150
-350
-550
84
86
88
90
92

Figure 6. Plots for moving intervals of nine, ten, and eleven censuses. Second order regression coefficients plotted against midpoint of census interval.


650
450
250
50
-150
-350
-550
9 CENSUSES


650
450
250
50
-150
-350
-550
10 CENSUSES

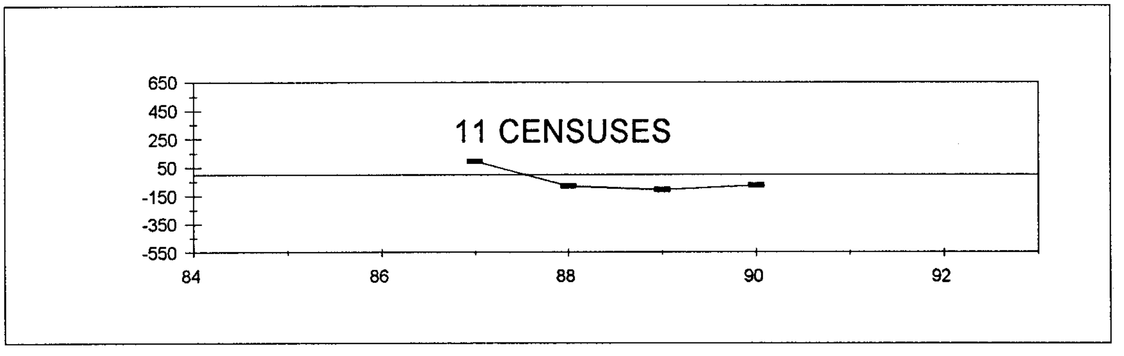

650
450
250
50
-150
-350
-550
11 CENSUSES
84
86
88
90
92

Figure 7. Log-linear fit of Pacific harbor counts (1982-1995, solid triangles) and northern elephant seal pup counts (1982-1991, solid squares) at Año Nuevo Island.

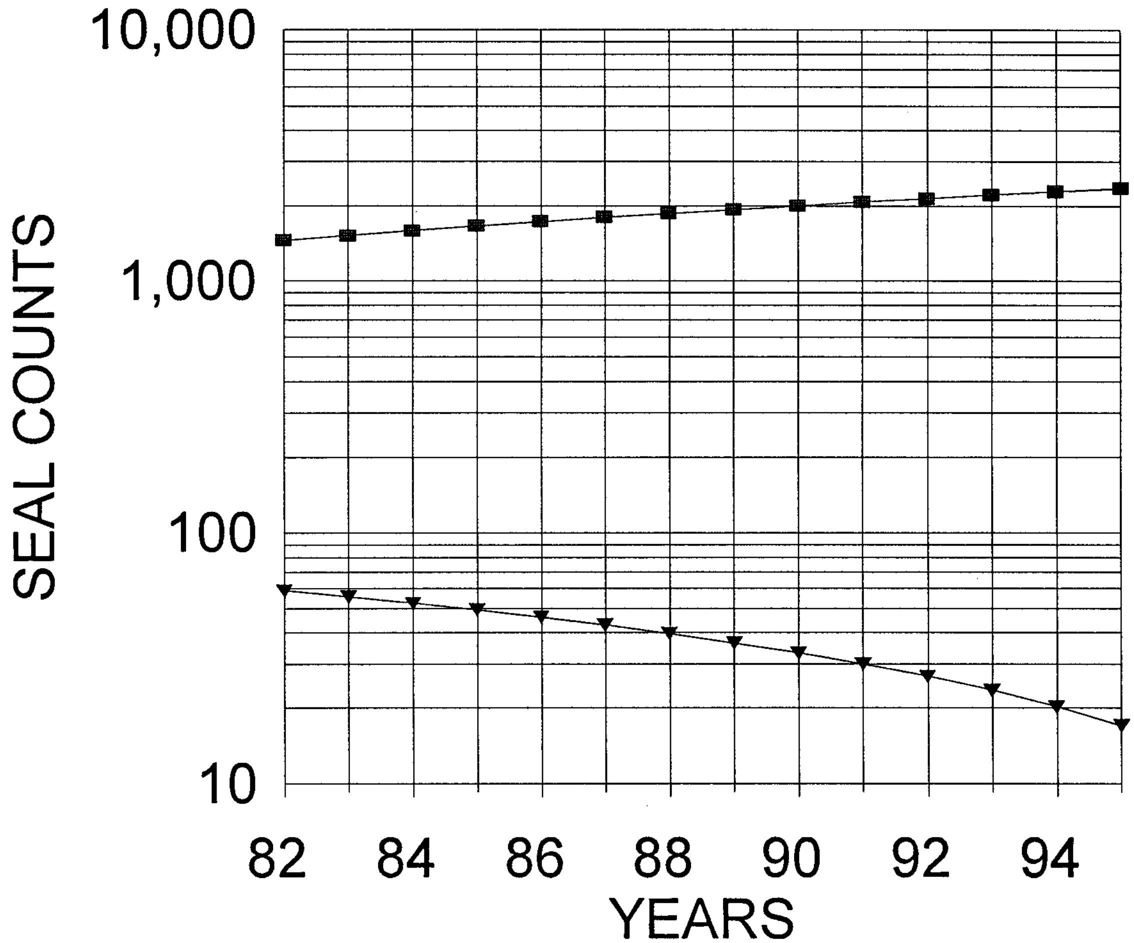
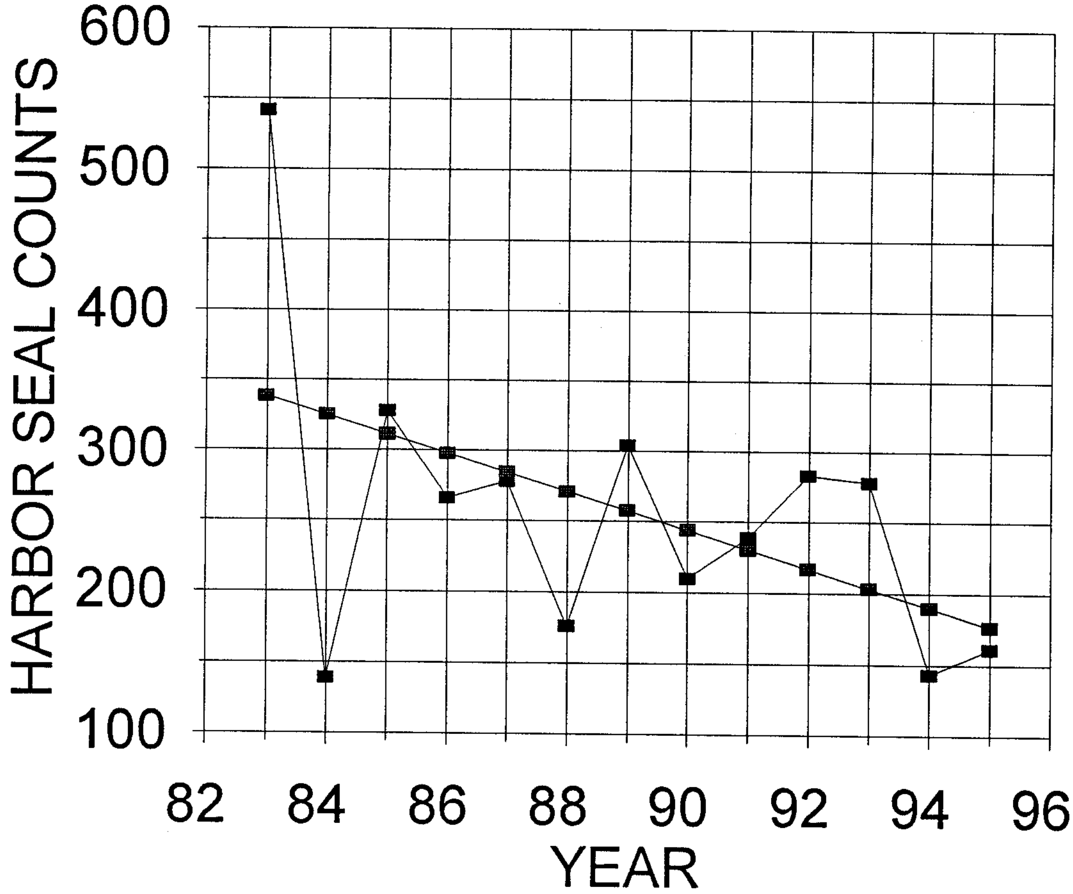

10,000
1,000
100
10
SEAL COUNTS
82
84
86
88
90
92
94
YEARS

Figure 8. Pacific harbor seal counts and linear regression (1982-1995) at Castle Rock, California.


600
500
400
300
200
100
HARBOR SEAL COUNTS
82
84
86
88
90
92
94
96
YEAR