TRENDS AND STATUS OF HARBOR SEALS IN WASHINGTON STATE: 1978–1999

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Abstract: In the first half of the twentieth century, harbor seal (*Phoca vitulina richardsi*) numbers were severely reduced in Washington state by a state-financed population control program. Seal numbers began to recover after the cessation of bounties in 1960 and passage of the Marine Mammal Protection Act (MMPA) in 1972. From 1978 to 1999, aerial surveys were flown at midday low tides during pupping season to determine the distribution and abundance of harbor seals in Washington. We used exponential and generalized logistic models to examine population trends and size relative to maximum net productivity level (MNPL) and carrying capacity (K). Observed harbor seal abundance has increased 3- fold since 1978, and estimated abundance has increased 7 to 10-fold since 1970. Under National Marine Fisheries Service (NMFS) management, Washington harbor seals are divided into 2 stocks: coastal and inland waters. The observed population size for 1999 is very close to the predicted K for both stocks. The current management philosophy for marine mammals that assumes a density-dependent response in population growth with MNPL > K/ 2 is supported by growth of harbor seal stocks in Washington waters.

JOURNAL OF WILDLIFE MANAGEMENT 67(1):208–219

Key words: generalized logistic, harbor seal, Marine Mammal Protection Act, maximum net productivity level, optimum sustainable population, *Phoca vitulina*, pinniped, population growth, trend, Washington.

The MMPA of 1972 established criteria for management of marine mammals by the NMFS and U.S. Fish and Wildlife Service (USFWS). These criteria stated that marine mammal populations "should not be permitted to diminish beyond the point at which they cease to be a significant functioning element in the ecosystem of which they are a part, and, consistent with this major objective, they should not be permitted to diminish below their optimum sustainable population" (16 U.S.C. 1361 Sec. 2). The intent of the MMPA was clear, but the language was too vague to provide an operational definition for management.

Eberhardt (1977) suggested that optimum sustainable population (OSP) should be interpreted as the range of population sizes from the maximum (K) down to the size that gives maximum productivity or maximum sustainable yield (MSY). The NMFS adopted the definition for OSP as a population level between K and the population size that provides the maximum net productivity level (MNPL; Federal Register, 21 December 1976, 41FR 55536). Maximum net productivity level was chosen because, unlike MSY, MNPL is independent of harvest structure (Gerodette and DeMaster 1990).

Defining OSP was a first step, but implementing the definition was difficult due to a lack of biological knowledge about population parameters and sufficiently precise data (Gerodette and DeMaster 1990, Ragen 1995). Difficulties in implementing an OSP management scheme led to the 1994 amendments to the MMPA that provided an alternative approach based on managing incidental take. In this approach, potential biological removals (PBR) must remain below a percentage of a minimum population size (Wade 1998, Read and Wade 2000). However, determinations of OSP and population status are still required by the MMPA to transfer management authority to a state government. Also, an assessment of population growth rates and status relative to MNPL can be incorporated into the calculation of PBRs in the existing management scheme.

Ragen (1995) questioned the utility of MNPL because he was unable to measure it precisely in a well-studied northern fur seal (*Callorhinus ursinus*) population. He stated that "under ideal conditions, MNPL would be determined by accurate and precise monitoring of a discrete population unit during natural growth from some level well below MNPL ... to a level above MNPL." Those ideal conditions are rare indeed, but they did exist for harbor seals in Washington state. Harbor

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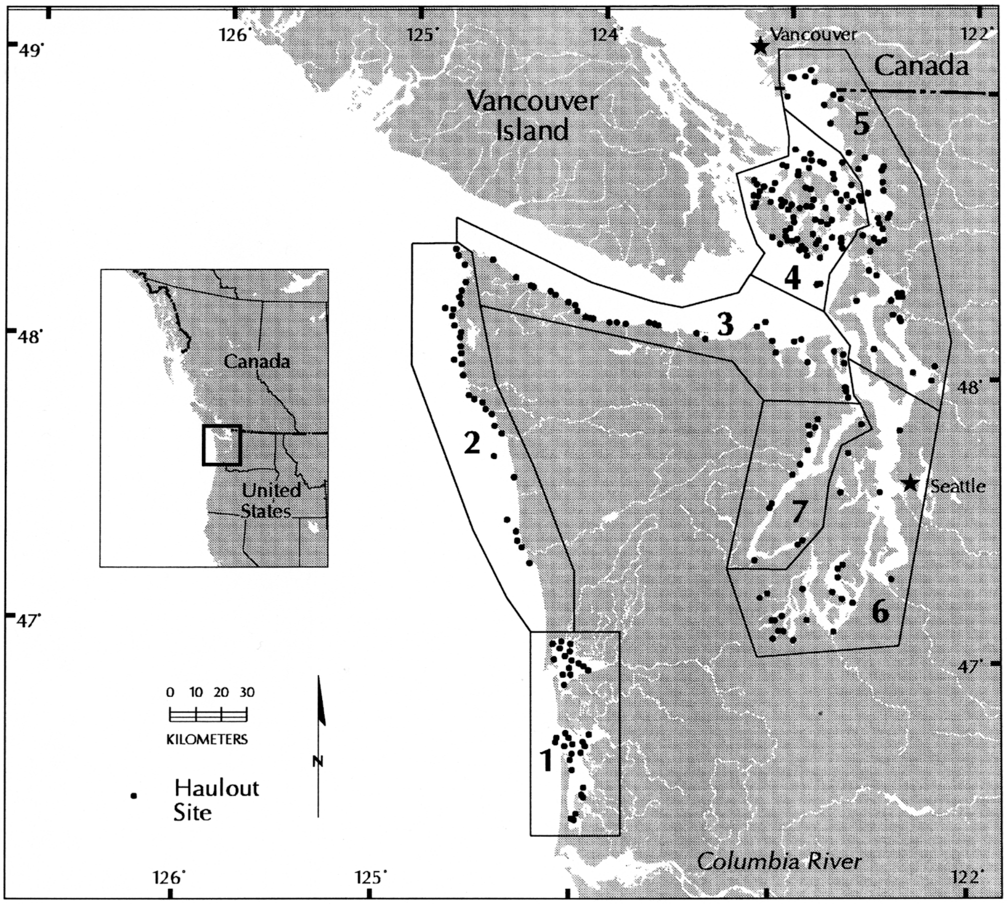

Fig. 1. Map of harbor seal haulout sites and survey regions for Washington, USA, coastal and inland stocks. The Washington coastal stock includes Coastal Estuaries (1) and Olympic Peninsula (2). The inland stock includes Strait of Juan de Fuca (3), San Juan Islands (4), Eastern Bays (5), Puget Sound (6), and Hood Canal (7).

seal numbers were severely reduced in the early 1900s by bounty hunters under a state-financed program that considered harbor seals to be predators in direct competition with commercial and sport fishermen. After the bounty program ceased in 1960 and MMPA was passed in 1972, Washington harbor seals began to recover. Newby (1973) estimated that 2,003,000 harbor seals resided in Washington state in the early 1970s. Beginning in 1978, systematic surveys of Washington's harbor seal population were initiated by Washington Department of Fish and Wildlife (WDFW) and continued through 1999.

This 22-year time series of systematic surveys provided a unique opportunity to describe an unharvested marine mammal's population growth. Because a large number of harbor seals haul out onto land in discrete aggregations at specific times, we were able to count a large proportion of the population to provide an index of population trends. We described population growth using exponential and generalized logistic models.

METHODS

Study Area

As managed by NMFS, harbor seals in Washington and Oregon have been separated into coastal and inland stocks because of differences in cranial morphology, pupping phenology, and genetics (Temte 1986, Lamont et al. 1996). The Washington inland stock includes all harbor seals in U.S. waters east of a line extending north-south between Cape Flattery on the Olympic Peninsula and Bonilla

Point on Vancouver Island (Fig. 1). Harbor seals on the outer coast of Washington are part of a stock that includes seals in Oregon, from the Columbia River southward to the Oregon/California border.

Interchange between inland and coastal stocks is unlikely, since no radiomarked seals from the inland stock (n = 140) were observed in coastal areas or vice versa (n = 188). Harbor seal haulout sites in Washington state were combined into 7 survey regions: Coastal Estuaries, Olympic Coast, Strait of Juan de Fuca, San Juan Islands, Eastern Bays, Puget Sound and Hood Canal (Fig. 1). In the Strait of Juan de Fuca, seals were counted annually in the eastern portion of the strait (east of Port Angeles). The western portion—where few suitable haulout sites exist and few pups are born—was surveyed only twice and was excluded from our analysis. Survey regions were determined by pupping phenology and a geographic area that could be surveyed within a 34 hr tidal window.

Survey Methods

Harbor seal aerial surveys were flown at low tide during the pupping season when maximum numbers were onshore. All known haulout sites were surveyed and potential new sites were examined on each survey. Seals in the water were not counted. Because of differences in pupping phenology among regions, surveys were flown in late May to mid-June for the coastal stock and August through September for the inland stock. Surveys were scheduled as closely as possible (tides permitting) to the time when peak number of pups were expected to be present. All regional surveys occurred within a week of peak pupping for each region (Huber et al. 2001). Surveys were flown between 2 hr before low tide to 2 hr after low tide in a single engine plane at 700–800 ft altitude at 80 knots. To provide consistency in data collection, about 80% of pupping season surveys were flown by 1 observer, while the others were flown by a second observer. Data collected during surveys included date, time, location, a visual estimate of seal numbers, and photographs of all sites with ≥25 seals. We took photographs with a 35mm SLR camera with 70210 mm lens, using 200 or 400 ASA Ektachrome film, and shutter speeds of 1/500 to 1/1,000 s. We counted the seals (including pups) at each site from slides. Evidence of recent disturbances (haulout marks on the beach or seals milling in the water off the haulout site) also was noted.

We scheduled at least 2–3 surveys for each region during annual survey windows, although some surveys were canceled because of inclement weather. A complete survey of each region was attempted in 1 day; if this was impossible, we combined surveys from 2 to 3 days. We excluded surveys with low counts (due to disturbance on a haulout or bad weather, and surveys outside the survey window were discarded. In some years, no count was available for ≥1survey regions.

Population Growth Models

Two simple non-age-structured deterministic models of population growth were considered to represent the growth in the harbor seal stocks: exponential and generalized logistic (Pella and Tomlinson 1969, Gilpin et al. 1976). These models are discrete in nature with an annual time step to represent the annual pupping pulse. Exponential growth assumes that the population grows without limit at a constant annual rate (R_{max}):

$$N_t = N_{t-1} + N_{t-1}R_{\max} \quad (1)$$

Clearly, the exponential model cannot be true forever, but populations can experience exponential growth prior to approaching K. Therefore, the exponential model can be used as a null model to test for density dependence. In the generalized logistic growth model, the rate of increase is a function of the population size relative to the maximum population size K:

$$N_t = N_{t-1} + N_{t-1}R_{\max}\left[1-\left(\frac{N_{t-1}}{K}\right)^z\right] \quad (2)$$

Annual net production is the difference in consecutive population sizes and the MNPL is the value of N_{t-1} when annual net production is maximized. The shape of the growth curve and the per capita production curve is governed by the exponent z, which determines the timing of the density dependent effect and the position of MNPL relative to K:

$$\frac{N_t - N_{t-1}}{N_{t-1}} = R_{\max}\left[1-\left(\frac{N_{t-1}}{K}\right)^z\right] \quad (3)$$

The standard logistic curve is obtained when z = 1: per capita production is a linear function of N and MNPL/K = 0.5. If z >1, per capita production is a concave nonlinear function of N and MNPL/K > 0.5 and if z < 1, per capita production is a convex nonlinear function of N and MNPL/K < 0.5.

An approximate relationship between MNPL/K and z (Polachek 1982) is given by:

$$\mathrm{MNPL}/K \approx (z+1)^{-1/z} \quad (4)$$

Incorporating z into the growth model is important for harbor seal populations because long-lived marine mammals are expected to demonstrate the strongest density-dependent effect as N approaches K (z >1; Eberhardt and Siniff 1977, Fowler 1981). However, in most cases, survey data were not sufficiently precise to estimate z adequately (Goodman 1988, Hilborn and Walters, 1992, Ragen 1995). The parameters R_{max} and z have a strong negative correlation in the model and diametrically opposed parameter values can yield nearly identical population trajectories for portions of the overall trajectory (Fig. 2). Without precise population estimates, z will almost surely be poorly estimated. The correlation between R_{max} and z is lessened by observing the population over a wide range of growth.

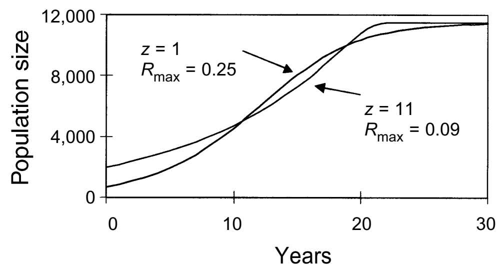

Fig. 2. Two similar generalized logistic growth curves of harbor seals in Washington, USA, achieved by choosing different values for z, R_{max}, and initial population size. Discriminating between these 2 growth curves would be nearly impossible if the population were observed from year 10 and beyond. However, if the population is observed from year 0, the parameters would be estimated more precisely as the 2 models imply different starting population sizes.

Growth Model Fitting

Our survey count data represented some variable proportion of the population (Jeffries 1985, Huber et al. 2001). Fitting growth models to the harbor seal count data involved finding parameter values that provided the best fit to the data. The best fit depended on the assumed statistical model for the observed data. We used deterministic population growth models (i.e., given the parameter values, the population size in year N_t determined exactly the size in year N_{t+1}) but the observed count C_t of harbor seals represented some unknown and variable proportion of the population abundance N_t:

$$C_t = N_t p_t \quad (5)$$

If p_t has a normal distribution with expectation p and variance s^2, the statistical model for the counts can be expressed as:

$$C_t = N_t(p+\delta_t) = N_t p + N_t\delta_t = N_t p + \varepsilon_t \quad (6)$$

where the distribution for δ_t is $N(0, s^2)$, and the distribution for $\varepsilon_t = N_t\,\delta_t$ is $N(0, s^2N_t^2)$. Thus, the coefficient of variation (c) of the errors ε_t is constant:

$$\mathrm{c} = \mathrm{CV}(\varepsilon_t) = \frac{sN_t}{pN_t} = \frac{s}{p} \quad (7)$$

An estimate of p requires additional data (e.g., radiomarking; Huber et al. 2001). If p had been estimated for each region and year, the growth model could have been based on estimates of population size. However, estimates of p were only available for 2 regions in different years. Thus, we fitted growth models to the count data and our inference to population growth depends on the assumption no temporal trend in p_t exists.

Based on these assumptions, we used the following statistical model:

$$C_t = N_t + \varepsilon_t \quad (8)$$

where N_t is now the size of the population onshore at time t as specified by the generalized logistic or exponential growth model, and ε_t are independent normal errors with zero expectation and constant coefficient of variation. The growth model parameters are R_{max}, K, z, and an intercept N_0, which is an initial size of the population onshore for some arbitrarily chosen time designated as $t = 0$. We only used counts to fit the growth models, but to express N_0 and K in terms of the population we multiplied N_0 and K by the correction factor (CF) of 1.53 (Huber et al. 2001), which is the reciprocal of the average proportion ashore (p) for an assumed age–sex structure. The parameters R_{max} and z remain unchanged by the constant scaling but would be affected by any trends in p_t.

To obtain parameter estimates for the growth curve, we used maximum likelihood. For k counts conducted at years $t_1, t_2, ..., t_k$, the log-likelihood is:

$$\ln L = -\frac{k}{2}\ln\left(\sum_{i=1}^{k}\left[\frac{C_{t_i} - N_{t_i}}{N_{t_i}}\right]^2\right) \qquad (9)$$

The log-likelihood is a function of the growth curve parameters which define the values for N_t from equations (1) or (2). Maximizing (9) is equivalent to minimizing the sum of squared proportional residuals:

$$\sum_{i=1}^{k}\left[\frac{C_{t_i} - N_{t_i}}{N_{t_i}}\right]^2 \qquad (10)$$

Use of the normal distribution probably is reasonable as long as p is not close to 0 or 1 and c^2 is sufficiently small such that there is little area in the tails of the distribution >1 or <0. A more complex alternative model could be constructed by assuming p_t follows a Beta distribution, which is bounded between 0 and 1, and C_t follows a binomial distribution with parameters N_t and p_t (or normal approximation).

Parameter estimates were obtained by using an optimization search algorithm in a FORTRAN program to find the values which maximize (9) or likewise minimize (10). We estimated variances and confidence intervals based on parametric bootstrapping (Efron and Tibshirani 1993). We implemented a parametric bootstrap by using the estimated parameters to construct a single "true" population trajectory. For each bootstrap, we constructed a data set by adding a random set of residuals drawn from the fitted error distribution to the true population trajectory. The model was then fitted to the new bootstrap data. We repeated the bootstrapping process 1,000 times to develop a distribution of parameter estimates.

One of the complications in the harbor seal data was missing counts. A count for each year was unnecessary. Ideally, however, for any year, the entire range should have been counted completely. In certain instances, some regions were not surveyed due to bad weather, disturbance, logistical problems, or lack of funding. In other instances, surveys began in 1 region and then expanded into other regions over time. For example, in Washington, the Coastal Estuaries were surveyed as early as 1975 but surveys of the Olympic coast region were not begun until 1980 (Table 1). Although counts for inland waters for 1978 were available (Calambokidis et al. 1979), consistent counts for all regions in the inland waters stock did not begin until 1983. A simple solution was to limit counts to years in which seals were counted in all regions. However, this would have wasted valuable data and severely restricted the survey time frames.

Instead, we fitted separate growth curves for each of the 7 regions (Fig. 1) using counts that were available for each region. Fitting separate growth models to the regions used only observed data but required more parameters that applied to the regions and not the entire population. Any random movement between regions would create additional variation in counts and any directed movement (i.e., permanent emigration/immigration) would be reflected in the parameters of regional growth models.

Separate growth models for each of the 7 regions were fitted by maximizing the sum of the regional log-likelihoods (9) assuming separate and independent regional error models:

$$\ln L = -\frac{1}{2}\sum_{j=1}^{r} k_j \ln\left(\sum_{i=1}^{k_j}\left[\frac{C_{t_{ij}} - N_{t_{ij}}}{N_{t_{ij}}}\right]^2\right) \qquad (11)$$

where k_j is the number of surveys in the j^{th} region and r is the number of regions. Because the predicted abundance for survey i in region j (N_t) may be determined by unique regional parameters, the number of estimated parameters expands substantially. However, some of the parameters could be held constant for some or all of the regions. In general, z is difficult to estimate (Hilborn and Walters 1992), and our data would not likely support a different z for each region. Also, R_{max} was likely to be constant among regions unless there was a strong movement component. However, K and N_0 were unlikely to be constant across regions because of differences in region size and habitat quality.

We fitted a series of models for each of the 5 regions in the inland Washington stock and separately for the 2 regions in the coastal stock. For each model, we assumed that N_0 and K (for the logistic model only) were different for each region. We fitted exponential models that assumed R_{max} was constant or varied by region. Likewise, we fitted logistic models that assumed R_{max} and z were either constant or varied by region. After selecting the best logistic model for each stock, we also explored whether R_{max} and z varied by stock.

We used the small sample Akaike Information Criterion ($AIC_c = -2\ln L + 2m + 2m[m+1]/[n - m - 1]$, where m is the number of parameters and n is the number of surveys) to choose the most

Table 1. Average annual harbor seal haulout counts for 2 regions in the coastal stock and 5 regions in the inland stock of Washington, USA, 1975–1999.

	Coastal stock		Inland stock				
Year	Coastal Estuaries	Olympic Peninsula	Strait of Juan de Fuca	San Juan Islands	Eastern Bays	Puget Sound	Hood Canal
1975	1,694						
1976	1,742						
1977	2,082						
1978	2,570		417	852	755	337	732
1979							
1980	2,864	1,639					
1981	4,408	1,677					
1982	5,197						
1983	4,416	2,359	883	1,688	1,347		
1984	4,203		1,025	2,308	1,727		
1985	6,008		1,288	1,859	1,416	732	
1986	4,807	1,789	849	2,193	1,613		
1987	7,600	3,204	1,016	2,179	1,751		
1988	6,796		1,518	2,847	1,902		
1989	6,475	3,667	1,402	2,884	1,839		
1990			1,142	3,157			
1991	8,681	3,832	1,238	3,510	1,939	891	1,206
1992	7,761	4,191	1,580	3,640	2,102	708	989
1993	8,161	3,544	2,154	4,524	2,175	972	592
1994	5,786	3,505	1,488	4,529	2,144	854	
1995	6,492	4,867	2,281	4,852	2,068		
1996	7,191	3,124	1,988	5,330	2,521	1,119	975
1997	7,643	4,221	2,284	4,277	2,008	1,060	695
1998			1,734	4,441	1,810	1,026	577
1999	7,117	3,313	1,752	3,588	1,873	1,025	711

parsimonious model (Burnham and Anderson 1998). We evaluated the model goodness of fit with the Kolmogorov-Smirnov test to examine whether the standardized residuals were normally distributed. For graphical display of the growth curve for each stock and the entire state, we summed the predicted values across regions. For observed values, we summed the average of regional counts for years in which 1 counts were available for each region. To supplement the observed values for the entire state, we added predicted counts for a few years with missing counts in 1 or 2 areas.

Status Determination

A harbor seal stock was considered to be at OSP if the current predicted population size was above MNPL. We determined whether OSP > MNPL by comparing population sizes as a proportion of K, because (4) provides a simple computation of MNPL/K. For each parametric bootstrap, we compared $\hat{N}_{1999}/K$ to MNPL/K. If <5% of the replicates were below MNPL/K, we concluded that the stock was at OSP. We also constructed bootstrap confidence intervals for $\hat{N}_{1999}/K$, MNPL/K, and $\hat{N}_{1999}$/MNPL. A similar approach was taken by Wade (1999) to investigate whether a spotted dolphin population was above or below MNPL.

Proportion Ashore

Our growth model based on seal counts would only reflect population growth if no trend in the proportion of seals ashore existed. A trend in p could occur if, over the 2 decades of surveys, the seals spent more or less time ashore as the population increased. A plausible scenario would be a decrease in the time ashore because more time could be required for foraging as the population increased and food resources decreased.

We examined whether the proportion ashore changed in Grays Harbor or Boundary Bay during the 1990s. Huber et al. (2001) applied VHF radio-transmitters to harbor seals in 1991 at Grays Harbor (GH; coastal stock) and in 1992 at Boundary Bay (BB; inland stock) to estimate p. We applied the same techniques as Huber et al. (2001) at GH in 1999 and BB in 2000. In each survey, all seals

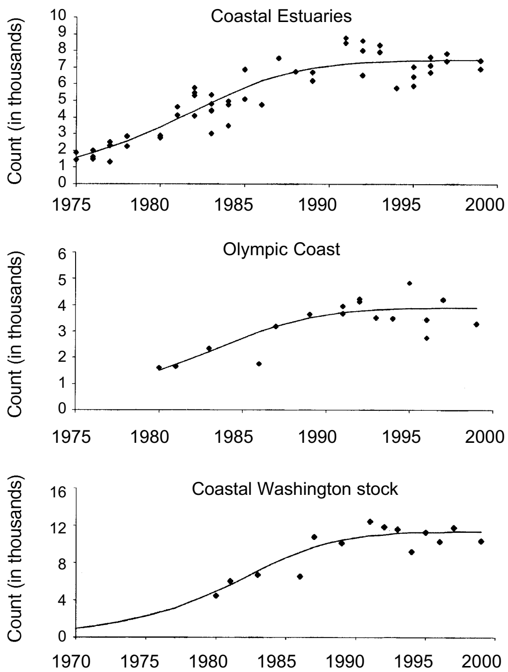

Fig. 3. Generalized logistic growth curves of harbor seals in Washington, USA, portion of the coastal stock for coastal estuaries and outer Olympic Peninsula coast regions and their sum.

with active tags were determined to be either ashore or not. Using each seal as a sample, we modeled the number of surveys the seal was ashore using a generalized linear model based on a binomial distribution and logit link function.

We fitted models that included 4 age–sex categories (adult female, adult male, pup subadult), year (1991– 1992 vs. 1999– 2000), and region (GH or BB) and the interaction of these parameters. Using the most general model with all interactions, we estimated an overdispersion scale (residual deviance/df; McCullagh and Nelder 1991) to adjust model selection using minimum $QAIC_c$ (Burnham and Anderson 1998). We also examined whether any observed annual differences in the proportion ashore would influence our conclusion regarding population growth.

RESULTS

Aerial Surveys

Between 1978 and 1999, counts of harbor seals in Washington state increased nearly 3-fold, from 6,786 to 19,379. The earliest surveys began in 1975 in the Coastal Estuaries (Table 1). By 1978, surveys had begun in all areas (Calambokidis et al. 1979) except the outer coast of the Olympic Peninsula where surveys began in 1980 (Table 1). Consistent surveys of inland waters did not begin until 1983 (Figs. 3, 4). The regions were not always surveyed annually nor were they surveyed an equal number of times/year. Growth between 1978 and 1999 was not evenly distributed throughout all regions. Most growth occurred in the San Juan Islands and the Strait of Juan de Fuca, and the least growth occurred in Hood Canal (Table 1).

Growth Model

The generalized logistic model with constant R_{max} and z was clearly the best model (Table 2) to describe inland and coastal seal stock population growth. The large discrepancy in AIC_c between exponential and logistic models provides strong evidence for a density dependent response in population growth (Table 2). When we examined models that shared R_{max} and z parameters between stocks the choice was less clear.

We selected the model with separate parameters for each stock because these stocks are genetically different and unlikely to be demographically linked. As expected, we estimated N_0 and K of the onshore population with reasonable precision, whereas less precision was achieved for R_{max} and z (Tables 3, 4). The initial size estimates, using 1970 as the base year, were quite consistent with counts for 1970– 1972 by Newby (1973), with the exception of San Juan Islands region (Tables 3, 4). The growth curves demonstrate the growth rate slowing as numbers approached K (Figs. 3– 5) and demonstrate a reasonable fit. Pooled standardized residuals did not differ from the assumed normal distribution ($KS = 0.05$, $P = 0.21$).

Status Relative to Optimal Sustainable Population

Although the evidence is not strong, the growth models of both stocks agree with the speculation that MNPL is indeed $>K/2$ (Table 5; Eberhardt and Siniff 1977, Fowler 1981). The predicted population size for 1999 is very close to K for both stocks (Table 5), and none of the bootstrap replicates predicted a 1999 population size that was below MNPL. The coastal stock recovered earlier than the inland stock, as evidenced by the status of the stocks in 1990 (Table 5).

Proportion Ashore

We radiomarked 29 seals and conducted 5 surveys at GH in 1999. We radiomarked 43 seals and

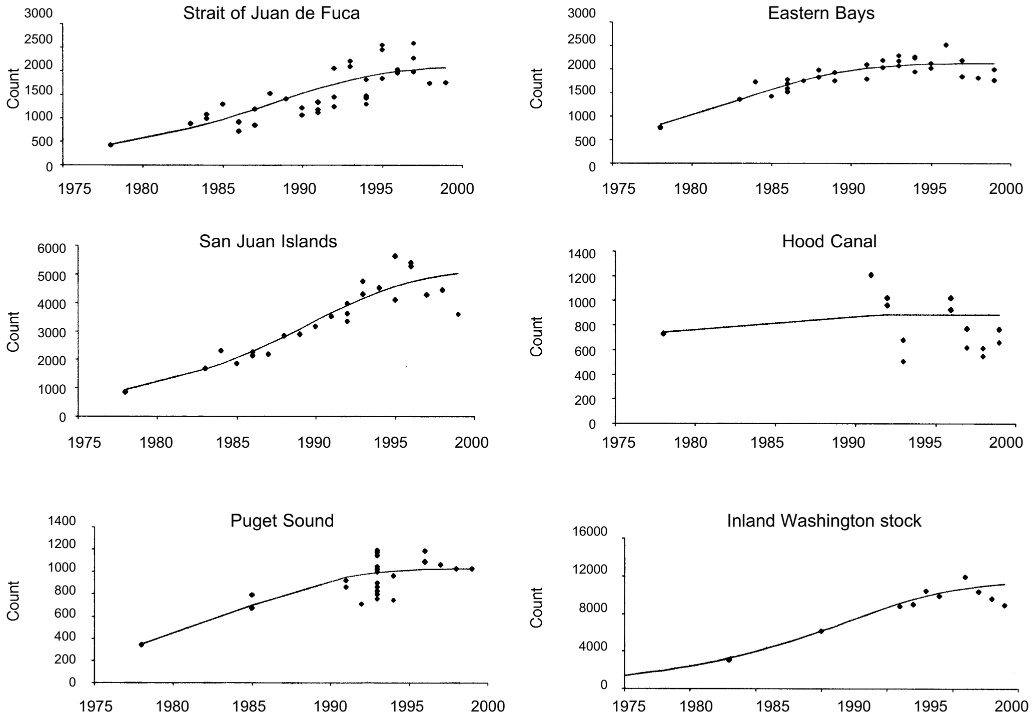

Fig. 4. Generalized logistic growth curves of harbor seals in the Washington, USA, inland stock for Strait of Juan de Fuca, Eastern Bays, San Juan Islands, Hood Canal, and Puget Sound regions and their sums.

conducted 7 surveys at BB in 2000 (Table 6). As expected during the pupping season, adult males and subadults spent considerably less time ashore than adult females and pups (Fig. 6). The full model with 16 parameters for age–sex, year, region, and parameter interactions explained 59% of the deviance. The residual deviance/df (124.82/113 = 1.11) suggested a minor amount of overdisper-

Table 2. Model selection results for exponential and generalized logistic growth models of inland and coastal harbor seal stocks in Washington, USA, 1975–1999. In addition to R_{max} and *z*, the number of parameters *m* includes initial size and carrying capacity (for logistic models) for each region.

Stock	Model	R_{max}	*z*	*m*	AIC_c
Inland	Exponential	Constant	NA	6	26.8
		Region	NA	10	–3.8
	Generalized logistic	Constant	Constant	12	–39.9
		Region	Constant	16	–28.7
		Constant	Region	16	–28.6
		Region	Region	20	–13.9
Coastal	Exponential	Constant	NA	3	68.7
		Region	NA	4	70.9
	Generalized logistic	Constant	Constant	6	20.5
		Region	Constant	7	23.3
		Constant	Region	7	23.5
		Region	Region	8	25.0
Both	Generalized logistic	Constant	Constant	16	–20.2
		Stock	Constant	17	–19.3
		Consant	Stock	17	–20.4
		Stock	Stock	18	–19.9

Table 3. Generalized logistic growth model for counts of all harbor seals in the Washington, USA, inland stock: parameter estimates and bootstrap standard errors and percentile confidence intervals (1,000 replicates). The 1970–1972 counts were obtained from Newby (1973).

Parameter	Region	Estimate	1970–1972 estimate	Standard error	95% confidence interval
N_{1970}	Strait of Juan de Fuca	172	150	39.2	104 to 262
	Eastern Bays	325	290	45.1	238 to 421
	San Juan Islands	361	160	82.9	216 to 541
	Hood Canal	390		123.6	156 to 628
	Puget Sound	138	210	23.9	94 to189
	All	1,386		197.8	1,033 to 1,807
K	Strait Juan de Fuca	2,121		185.5	1,920 to 2,619
	Eastern Bays	2,132		71.0	2,034 to 2,317
	San Juan Islands	5,222		472.6	4,584 to 6,450
	Hood Canal	882		60.2	819 to 1,052
	Puget Sound	1,033		49.7	972 to 1,175
	All	11,390		645.7	10,671 to 13,257
R_{max}	All	0.126		0.023	0.094 to 0.187
z	All	2.43		1.75	1.07 to 8.57
c	Strait of Juan de Fuca	0.207			
	Eastern Bays	0.088			
	San Juan Islands	0.124			
	Hood Canal	0.258			
	Puget Sound	0.135			

sion. The model with minimum $QAIC_c$ included all of the main effects and 2-way interactions ($QAIC_c$ = 145.6), although a much simpler model with only age–sex, year and their interaction had a similar value ($QAIC_c$ = 145.8). Based on $QAIC_c$, these 2 models are indistinguishable. The model with age-sex only ($QAIC_c$ = 150.3) accounted for 63% of the explained deviance of the full model.

The year influence was not consistent across the age–sex classes (Fig. 6). Females and pups spent less time ashore in 1999–2000 than in 1991–1992, whereas adult males and subadults spent more time ashore 1999–2000 than in 1991–1992. Most of the annual difference and the interaction resulted from shifts at GH. We computed an annual average proportion ashore for all seals (Table 6) by weighting age–sex specific values against the expected age–sex proportions of seals in the population (Huber et al. 2001), which adjusted for differences in sample sizes between the age–sex classes across years. The largest decrease in the average proportion ashore occurred at GH, with very little change at BB.

DISCUSSION

Aerial Surveys

Haulout behavior of harbor seals varies with season. In general, the number of seals ashore is highest during annual pupping and molt and

Table 4. Generalized logistic growth model for counts of all harbor seals in the Washington, USA, coastal stock: parameter estimates and bootstrap standard errors and percentile confidence intervals (1,000 replicates). The 1970–1972 counts were obtained from Newby (1973).

Parameter	Region	Estimate	1970–1972 estimate	Standard error	95% confidence interval
N_{1970}	Coastal Estuaries	714	800	128.8	518 to 1,019
	Olympic Coast	303	100+	73.3	184 to 487
	All	1,017		196.5	717 to 1,497
K	Coastal Estuaries	7,510		328.0	7,102 to 8,406
	Olympic Coast	3,934		206.9	3,585 to 4,398
	All	11,444		425.2	10,909 to 12,600
R_{max}	Both	0.185		0.037	0.129 to 0.268
z	Both	1.75		1.47	0.90 to 6.76
c	Coastal estuaries	0.165			
	Olympic Coast	0.154			

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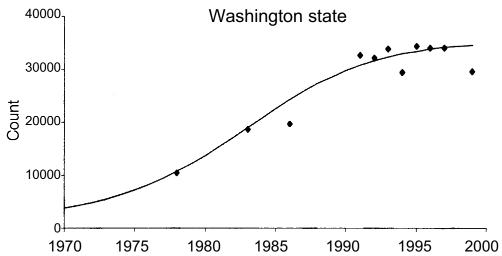

Fig. 5. Generalized logistic growth curve for harbor seals in Washington, USA, expressed population size. The observed values for 1978, 1983, 1986, 1994, and 1995 were supplemented with model predictions for regions with missing counts that accounted for 17, 12, 13, 5, and 8% of the total abundance.

lowest during winter. Many variables, such as height of tide, time of day, weather, and disturbance affect seal haulout patterns. The proportion of seals ashore during a pupping survey will depend on tide state, timing relative to peak pupping, age, sex, and reproductive condition of seals using the haulout. Several approaches exist to obtain maximum counts and reduce variability in counts within a chosen season. Some researchers have surveyed during a broad range of time and tide conditions and adjusted counts for date and tide height after the fact (Frost et al. 1999, Olesiuk et al. 1990). In contrast, we reduced variability in our counts by restricting our surveys to a narrow time frame at the peak of the pupping season in each survey region and surveying only at low tides between 2.0 and +2.0 feet, when maximum numbers of seals were hauled out.

Corrections for Proportion Ashore

Harbor seal haulout behavior varies by age, sex, and reproductive condition of seals. During pupping season, adult females and nursing pups spend 90– 100% of their time on shore during the 4– 6week nursing period (Huber et al. 2001). After weaning, pups spent an increased amount of time in the water and hauled out only infrequently, whereas males and subadults were on shore during 40– 60% of surveys. These differences in haulout behavior have strong implications for timing of surveys and the use and interpretation of correction factors associated with seasonal surveys.

We did find changes in the proportion of seals ashore during our surveys in 1991– 1992 and 1999– 2000. However, these changes do not invalidate our conclusions regarding growth and status of harbor seal stocks in Washington. The largest decrease in the proportion ashore occurred at GH, declining from 0.71 to 0.62. However, the seal counts reflected this change decreasing from 8,681 in 1991 to 7,118 in 1999. If we apply the individual annual correction factors (Table 6), we get estimates of 12,285 and 11,548, respectively. Thus, the population estimates are even closer than the counts, which is consistent with our conclusion that the population stabilized during the 1990s.

At BB little difference was noted in the average proportions ashore but the counts were not as consistent, decreasing from 797 in 1992 to 564 in 2000. However, these values are consistent with a lack of growth during the 1990s. We believe that the leveling trend in seal abundance is real and not related to a change in proportion of seals hauled out during surveys.

Trends and Status

Because the analysis was based on counts of seals ashore during a survey, estimated K and N_0 represent only a proportion of the entire population. To get estimates of the true population size,

Table 5. Parameter estimates for status determination of inland and coastal stocks of harbor seals in Washington, USA, with bootstrap standard errors and 95% confidence intervals.

Parameter	Stock	Estimate	Standard error	95% confidence interval
MNPL/K	Inland	0.60	0.064	0.51 to 0.77
	Coastal	0.56	0.066	0.49 to 0.74
$\hat{N}_{1999}/K$	Inland	0.98	0.025	0.90 to 1.00
	Coastal	1.00	0.004	0.99 to 1.00
$\hat{N}_{1990}/K$	Inland	0.76	0.046	0.65 to 0.84
	Coastal	0.94	0.034	0.88 to 1.00
$\hat{N}_{1999}$/MNPL	Inland	1.63	0.14	1.29 to 1.85
	Coastal	1.78	0.18	1.35 to 2.10

Table 6. Comparison of proportion of radiomarked harbor seals ashore during surveys at 2 sites 1991–1992 and 1999–2000 in Washington, USA. 1991–1992 data from Huber et al. (2001). The average proportion ashore was computed as a weighted average of the age-sex specific proportions using an assumed structure of 31% adult females, 26% adult males, 23% pups and 19% subadults.

	Grays Harbor		Boundary Bay	
	1991	1999	1992	2000
Active radio tags	33	29	24	43
Adult female	9	9	7	14
Adult male	7	7	5	16
Pup	8	8	7	8
Subadult	9	5	5	5
Number of surveys	4	5	5	7
Average proportion ashore (p)	0.71	0.62	0.69	0.72
Correction factor (1/p)	1.42	1.62	1.44	1.38

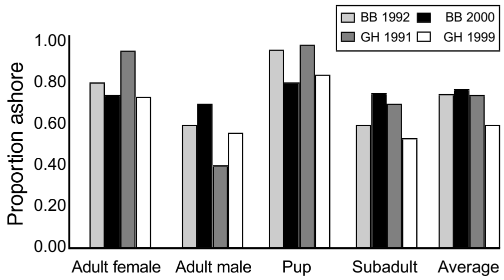

Fig. 6. Average proportion ashore for radiotagged harbor seals in each of 4 age–sex categories and a weighted average for Boundary Bay (BB) in 1992 and 2000 and Grays Harbor (GH) in 1991 and 1999, Washington, USA.

K and N_0 must be scaled by a correction factor (the inverse of the proportion ashore). Using the correction factor of 1.53 (Huber et al. 2001), we estimated that during 1999, Washington coastal stock contained 15,958 harbor seals (95% CI: 13,645 to 18,662) and the inland stock contained 13,692 seals (95% CI: 11,707 to 16,012). Because there are no records of the pre-exploitation population size in Washington, whether the present population is more or less than before is unknown. Changes that may have lowered K include decreases in harbor seal prey such as hake (*Merluccius productus*; Gustafason et al. 2000) and herring (*Clupea pallasi*; Stout et al. 2001), reduced habitat, and increased disturbance. However, we have shown that both stocks of Washington harbor seals are above MNPL and are near the current carrying capacity of the environment. These stocks can decline or be reduced by 20% and they will still be above MNPL with a high degree of certainty (Table 5).

MANAGEMENT IMPLICATIONS

Management implications for harbor seal stocks in Washington are quite clear. If formally determined to be at OSP, NMFS could return management authority for harbor seals to Washington state, if requested. Local selective removals of seals could be considered at river mouths where endangered or threatened salmonids occur, if harbor seals are consuming and threatening fish populations of concern (National Marine Fisheries Service 1997). From our analysis, selective removal of harbor seals around river mouths is unlikely to have detrimental effects on harbor seal populations in Washington state. Harbor seal stocks in Washington could decline by 20% and still be above MNPL.

The current management philosophy for marine mammals that assumes a density-dependent response in population growth with MNPL $>K/2$ is supported by growth of harbor seal stocks in Washington waters. We expect that further monitoring of other pinniped and cetacean stocks (Wade 2002) will also support this concept. Our analysis demonstrated that it was not possible to determine whether harbor seals in Washington had reached MNPL until several years after the fact. Our study highlights the importance of long-term, precise monitoring to help understand population dynamics and support management decisions.

ACKNOWLEDGMENTS

We thank J. Cubbage, K. Forbes, K. Hughes, M. Lance, D. Lambourn, B. Roca, L. Schlender, G. Steiger, J. Stein, B. Troutman, and others who counted slides or recorded data on aerial surveys. We acknowledge and thank P. Boveng, J. Breiwick, P. Olesiuk, J. Pierce, P. Wade, and D. Withrow who participated in workshops that focused on the analysis of these survey data. All research was conducted under NMFS research permit # 475 issued to WDFW or permit # 835 or permit # 782-1446 issued jointly to WDFW, ODFW, and NMML or permits # 474 or # 542 issued to Cascadia Research. Comments from P. Boveng, R. DeLong, P. Wade, and B. Wright improved this manuscript. This paper is dedicated to the memory of Dr. M. L. Johnson who provided guidance and support for our efforts to better understand the natural history of harbor seals in Washington waters.

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Received: 16 November 2001.
Accepted: 17 October 2002.
Associate Editor: Morrison.

AR032570