A Mathematical Approach for Predicting Harbor Seal Haul-out

Jonathan Daniel Cowles

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ABSTRACT

A MATHEMATICAL APPROACH FOR PREDICTING HARBOR
SEAL HAUL-OUT

by

Jonathan Daniel Cowles

Co-chairs: James L. Hayward
Shandelle M. Henson
ABSTRACT OF GRADUATE STUDENT RESEARCH

Thesis

Andrews University
College of Arts and Sciences

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Harbor seals haul out in response to various environmental factors such as tide, current, time of day, wind, and surf. Mathematical modeling techniques can be used to determine which of these variables are important and to predict the number of seals that will haul-out in a given set of environmental circumstances. Haul-out counts were recorded every hour for 16 hrs per day over two 14-d tidal cycles at a site in Washington State. Deterministic environmental variables (tide height, current velocity, solar elevation, and time of day) were used to create 37 alternative models, which were then compared to the haul-out data using information theoretic model selection techniques. The best model contained the environmental variables tide, current, and time of day and
explained >45% of the observed variability. It revealed, in the morning, that maximal seal haul-out occurs several hours before low tide, and seals begin returning to the water at low tide. Higher haul-out numbers are observed in the afternoon and evening, and fewer seals reenter the water at low tides that occur in the afternoon. The results of this study are site-specific, but the methods used are portable and useful for researchers and wildlife managers interested in monitoring haul-out or population trends over time.
A MATHEMATICAL APPROACH FOR PREDICTING HARBOR SEAL HAUL-OUT

A thesis presented in partial fulfillment of the requirements for the degree Master of Science

by

Jonathan Daniel Cowles

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CHAPTER 1

INTRODUCTION

During the early 1970s, declining seal populations led several countries to begin protecting harbor seals. In 1970, for example, the United Kingdom passed the Conservation of Seals Act which provides protection during the pupping and molting seasons, and in 1972 the United States instated the Marine Mammal Protection Act (MMPA) which provides year-round protection for these animals. The MMPA required an initial estimate of marine mammal population size and growth rate and continued management to preserve optimal population sizes. In effect, this legislation mandates carrying out population estimates which provide the only means for evaluating population trends.

Aerial surveys are one of the most effective ways to census harbor seals (Thompson and Harwood 1990). These surveys are accomplished by flying over known seal haul-out sites in small aircraft or helicopters and photographing hauled-out seals. Seals in the photographs can be counted later to determine the number at each haul-out site. The disadvantage of this approach is that it fails to account for seals in the water at the time of the photograph. A combination of aerial surveys and corrections based on radio telemetry data, however, can provide more accurate estimates of total seal population.

Radio telemetry involves tagging seals with VHF radio transmitters by gluing them to the pelage (Thompson et al. 1989) or attaching them to the hind flippers (Ries et al.)
Signals picked up by radio monitoring stations indicate whether the seal in question is hauled out or not. When data are simultaneously collected for all tagged seals, the proportion hauled out is revealed. This information can be used to develop a correction factor for aerial surveys that leads to a better estimate of total population size (Huber et al. 2001).

Due to variability in environmental factors between haul-out sites, a different correction factor may be needed for each site (Baird 2001). Thus, an understanding of the factors that influence haul-out behavior is important for calibrating surveys. These factors include time of year, time of day, weather, El Niño effects, tide height, current speed, substrate, and level of disturbance (Suryan 1995; Baird 2001; Henry and Hammill 2001; Patterson and Acevedo-Gutiérrez 2008; Becker et al. 2009). Although there is general agreement on the variables that affect haul-out, it is less clear which variables exert the most impact, or if variables remain constant over different locations.

Mathematical modeling can be used to determine environmental factors that drive changes between habitats (Henson et al. 2006), and in some circumstances modeling can identify relationships between variables that statistical analyses would miss due to data averaging (Hayward et al. 2005). Modeling also can be used to forecast the number of animals occupying a habitat using environmental factors as predictors (Henson et al. 2004).

The predictive capabilities of mathematical modeling could be used to increase the robustness of seal population estimates by enabling the planning of aerial surveys during equivalent predicted haul-out patterns, even when widely spaced temporally. This would ensure that the proportion of the population hauled out during subsequent surveys is equal.
to the proportion hauled out when the correction factor was created. Thus, correction factors could be applied with more confidence. This method could benefit both wildlife managers and policy makers by decreasing the amount of error present in repeated population estimates.

In previous work, Hayward et al. (2005) used a mathematical model to predict harbor seal haul-out on Violet Point at the east end of Protection Island National Wildlife Refuge, Washington, USA. Their model was a function of tide height and current direction and it explained 40% of the variability in haul-out counts. In the present study a similar methodology was used to (1) determine environmental factors influencing seal haul-out on Kanem Point at the west end of Protection Island; (2) test the hypothesis that the Hayward et al. (2005) model is portable between these two sites, and (3) construct a site-specific haul-out model of Kanem Point.
CHAPTER 2

METHODS

Census and Environmental Data

Data were collected at Protection Island National Wildlife Refuge, WA (48° 7′ N, 122° 55′ W). Protection Island is closed to the public and covers an area of 147 ha. It serves as the breeding ground for more than 70% of the seabirds in the Puget Sound area and is an important rookery for harbor seals (Henson et al. 2004; Hayward et al. 2010). A gravel spit projects from each end of the island: Violet Point on the east end and Kanem Point on the southwest end (Fig. 1). In addition, the haul-out site on Kanem Point contains two alternate haul-out areas: the primary area on the point itself and a secondary location that consists of a gravel bar beyond the end of the point. This bar becomes submerged at high tide, leaving the main spit as the only haul-out area. Data were collected with a spotting scope from a 30m bluff overlooking Kanem Point. The bluff was sufficiently removed from the haul-out location such that seals were not significantly disturbed by the researcher’s presence.

Hourly counts of hauled-out seals were made at the top of the hour, from 06:00 to 21:00 hrs Pacific Standard Time (PST), 30 June to 27 July 2010 (excluding 10 July), and during all weather conditions except fog, which obscured the point. The study period was chosen to coincide with the pupping season and the previous study on Violet Point. A seal was considered hauled-out if any part of its body was resting on the substrate, even if
largely submerged. Only adult and subadult seals were counted; pups birthed in 2010 were omitted so that haul-out behavior would not be confounded with reproduction. The time, type, and relative intensity of seal disturbances also were recorded. Any event which caused seals to bolt into the water was considered a disturbance. Counts occurring ≤ 30 min after a disturbance were not included in the analysis.

Tide height, current velocity, and solar elevation data were downloaded from the National Oceanic and Atmospheric Administration (NOAA) websites
http://tidesandcurrents.noaa.gov/curr_pred.html, http://tidesandcurrents.noaa.gov/ and http://www.srrb.noaa.gov/highlights/sunrise/azel.html. Current velocity data were for Kanem Point, whereas tide height data were for Port Townsend. Using the normalization technique in Hayward et al. (2009), tide height $T(t)$, current velocity $C(t)$, solar elevation $S(t)$, and hour of day $H(t)$ were nondimensionalized so that

$$1 \leq S(t), T(t), C(t), H(t) \leq 2.$$  

(1)

Tides in the Strait of Juan de Fuca are semi-diurnal, with two unequal high (and low) tides per day. The amplitudes of the high tides vary from day to day in a 14-d cycle between “nodes” of minimal tidal range (Fig. 2, arrows). Because of the possibility that seals respond to whether the tide is high or low rather than to actual tide height, another tidal variable $T_e(t)$ was constructed from tide height $T(t)$ in the following way. Each local tidal maximum was assigned a value of 2, each local minimum was assigned a value of 1, and the oscillation was splined between these points to create the “equalized tide” $T_e(t)$. The same process was used to create an “equalized current” variable $C_e(t)$.
Deterministic Model

The general model is a “two-compartment” model in which one compartment is the haul-out site and the other compartment consists of all locations other than the haul-out site. A compartment model is a “balance equation” that quantifies the net rate of change of hauled-out seals as the difference between the rates at which seals arrive at and leave the beach. If \( N(t) \) is the number of hauled-out seals, the compartment model is

\[
\frac{dN}{dt} = [\text{inflow rate}] - [\text{outflow rate}],
\]

where the inflow and outflow rates to and from the beach must be specified by means of modeling assumptions. The assumptions in this study are the same as those in Hayward et al. (2005); they are repeated here for convenience.

Assumption 1. Movement of seals between the two compartments is in direct response to changes in environmental variables. Seals leave the haul-out site at a per capita rate proportional to a function \( E_{21}(t) \) of environmental variables, and arrive at the haul-out site at a per capita rate proportional to a function \( E_{12}(t) \) of environmental variables. Neither of these rates depends on the number of seals in either compartment; that is, these movements are density-independent.

Assumption 2. The maximum number \( M(t) \) of seals that are eligible to haul-out during the study period is approximated by

\[
M(t) = \beta e^{-\gamma \left(\text{day of year} + t/24 - \delta\right)^2},
\]

where \( t \) is the hour of the day and \( \beta, \gamma \) and \( \delta > 0 \) are positive constants that were estimated from the maximal daily counts as described in the model parameterization section (Fig. 3).
This functional form is based on previous work on Violet Point (with a much larger data set), which suggests the maximal weekly haul-outs over the study period are proportional to a normal distribution (Hayward et al. 2005). Note that $M(t)$ does not represent the population size, but is simply a function used to describe the seasonal envelope of the maximum number of seals that haul out in the study area.

Given these two assumptions, model (2) can be specified as

$$\frac{dN}{dt} = [aE_{12}(t)(M(t) - N)] - [bE_{21}(t)N].$$

(4)

In equation (4), the inflow rate is the per capita rate $aE_{12}(t)$ at which seals haul out (assumption 1) multiplied by the number of seals $M(t) - N$ eligible to haul out (assumption 2). The outflow rate is the per capita rate $bE_{21}(t)$ at which seals leave the haul-out site multiplied by the number of seals $N$ eligible to leave. The parameters $a, b > 0$ are constants of proportionality.

If the system recovers rapidly after a disturbance, the well-known mathematical technique of time-scale analysis (Hoppensteadt 1974; Tikhonov et al. 1985; Lin and Segel 1988) can be used to approximate the solution of differential equation (4) in the absence of disturbance. Previous work by Suryan (1995) revealed that haul-out numbers could rebound to pre-disturbance levels within 7 min, whereas previous work on Protection Island extended the threshold for recovery to 30 min (Hayward et al. 2005). Observations in this study confirmed that seals often recover rapidly from disturbance. This leads to assumption 3.
**Assumption 3.** System dynamics recover rapidly after disturbance. That is, the values of \( M(t), E_{12}, \) and \( E_{21} \) remain relatively constant as the system returns to “steady state” dynamics.

Given Assumption 3, it can be shown that the solution of differential equation (4) is approximated by the algebraic equation

\[
N(t) = \frac{M(t)}{1 + \frac{bE_{21}}{aE_{12}}}.
\] (5)

Note that equation (5) depends on the ratio of parameters \( b \) and \( a \) and on the ratio of the two environmental functions \( E_{12}E_{21} \) and \( E_{12} \). Defining \( \alpha = b/a \) and \( E(t) = E_{21}/E_{12} \) and substituting the full expression for \( M(t) \) from equation (3) leads to the model analyzed in this study:

\[
N(t) = \frac{\beta e^{-\gamma (day\ of\ year + t/24 - \delta)^2}}{1 + \alpha E(t)}.
\] (6)

Here \( \alpha, \beta, \gamma, \delta > 0 \) are constant parameters to be estimated from data.

**Stochastic Model**

Ecological systems are noisy. The goal in mathematical modeling is to capture the deterministic trend (signal) sufficiently well so that the departures of model from data (residuals) can be considered stochastic events (noise) that are normally distributed around zero. In general, one must first transform data and model predictions (for example, with a logarithmic or square root transformation) in order to obtain normally distributed residuals. Different types of stochasticity require different transformations. Demographic
stochasticity is approximately additive on the square root scale, whereas environmental
stochasticity is approximately additive on the log scale (Cushing et al. 2002; Dennis et al.
2001; Hayward et al. 2005).

Given that in this study the major environmental correlates were incorporated
directly into the deterministic model, noise was expected to be largely demographic, that
is, due to variability in the haul-out decisions of individual animals. Thus, the signal plus
noise was expressed as

$$\sqrt{N(t)} = \frac{\beta e^{-\gamma (\text{day of year} + t/24 - \delta)^2}}{1 + aE(t)} + \sigma \varepsilon(t)$$  \hspace{1cm} (7)

where $\sigma > 0$ is a constant parameter and $\varepsilon(t)$ is standard normal random variable
uncorrelated in time. Squaring both sides yields the stochastic model

$$N(t) = \left( \frac{\beta e^{-\gamma (\text{day of year} + t/24 - \delta)^2}}{1 + aE(t)} + \sigma \varepsilon(t) \right)^2$$  \hspace{1cm} (8)

where the right-hand side is taken to be zero whenever the quantity inside the square is
negative. A post hoc examination of model residuals (Fig. 4) confirmed that the square
root transformation was appropriate (see results).

Model Parameterizations and Model Selection

The two best models from Hayward et al. (2005) plus 37 additional alternative
models, based on combinations of powers of the environmental variables $T(t)$, $C(t)$, $S(t)$,
$H(t)$, $T_e(t)$, and $C_e(t)$, were fitted to the data (Table 1). Alternative models were created in
a step-wise approach. Each environmental variable was tested in both the numerator and
the denominator of a single-factor environmental function to determine which yielded highest goodness-of-fit. This, in turn, informed the creation of increasingly more complex models based on previous variable combinations. If a subsequent model form showed very poor goodness-of-fit, it was removed from consideration, and no further models were created from it. These discarded models do not appear in Table 1.

The seasonal envelope function \( M(t) \) was fitted directly to the daily maximal haul-out counts using the method of nonlinear least squares (LS). This yielded the parameter estimates \( \beta = 259.29, \gamma = 0.00028856 \) and \( \delta = 218.31 \) (Fig. 3). The remaining model parameters were estimated from the time series hourly counts by minimizing the sum of squared residuals

\[
RSS(\theta) = \sum_{\text{data}} \left( \sqrt{\text{observation}} - \sqrt{\text{model prediction}} \right)^2
\]

as a function of the vector \( \theta \) of model parameters.

In order to select the best model one should consider the number of parameters as well as the goodness-of-fit; models with more parameters should be penalized for overfitting. This was accomplished by using the Akaike Information Criterion (AIC), an information-theoretic model selection index used to select the best model from a group of alternatives (Burnham and Anderson 2002; Peek et al. 2002; Gibson et al. 2004; Rushton et al. 2004). For LS parameters the criterion is equivalent to

\[
AIC = n \ln \hat{\sigma}^2 + 2\kappa
\]

where \( n \) is the number of observations, \( \hat{\sigma}^2 = \frac{\text{RSS(\hat{\theta})}}{n} \) is the variance of the likelihood function as estimated from the residuals, \( \hat{\theta} \) is the vector of LS parameter estimates, and \( \kappa \) is
the number of model parameters, including \( \sigma^2 \). The model with the lowest AIC value, denoted \( \text{AIC}_{\text{min}} \), is considered the best model. Models are ranked by the AIC differences \( \Delta_i = \text{AIC}_i - \text{AIC}_{\text{min}} \) with the best model having \( \Delta_i = 0 \). Models with \( \Delta_i > 10 \) usually are deemed significantly worse than the best model and can be rejected (Burnham and Anderson 2002).

The generalized \( R^2 \)

\[
R^2 = 1 - \frac{RSS(\hat{\theta})}{\sum_{\text{data}}(\sqrt{\text{observation}} - \text{mean})^2}
\]  

was used to compute goodness-of-fit. Here “mean” refers to the mean of the square roots of the observations. The \( R^2 \) indicates, on the square-root scale, the proportion of the variability that is explained by the model. Thus, higher \( R^2 \) values are associated with better fits, with \( R^2 = 1 \) indicating a perfect fit.
CHAPTER 3

RESULTS

Seal census data are listed as time-series in Table 3 and graphed as time-series in Figure 2. It is difficult to determine by visual inspection the exact relationships between the environmental variables and seal haul-out; hence the model selection procedure in this study. However, the time-series data, as well as scatter-plots of the data against environmental variables, do suggest the following trends.

First, maximal daily haul-out varied throughout the study period (Fig. 3), suggesting that day of year is a predictor of haul-out. Maximal daily haul-out was lowest near the beginning of the study, generally increasing until day 200 (19th July).

Second, haul-out was often minimal or completely lacking at 06:00, suggesting that it was related to either time of day (Fig. 2), or solar elevation (Fig 5). Following the morning lull, seals began to haul out in greater numbers over the course of the day, often with highest haul-out observed in the afternoon or evening (e.g., Fig. 2, day 193, day 184). Higher haul-out late in the day suggests that time of day is a better predictor than solar elevation, which decreases following noon.

Third, increased haul-out often was observed around low tide (e.g., Fig. 2, day 205, day 197), which suggests that tide height is a predictor of haul-out (Fig. 2). Seal numbers often decreased shortly after low tide, and this effect was magnified by seals getting forced off the secondary haul-out location on the gravel bar as it submerged. Seals
began returning to the beach midway between high and low tide (e.g., Fig. 2, day 187, day 207).

Finally, the data suggested that current is associated with haul-out (Fig. 2). This connection could not be observed directly in the field, but a scatter-plot of haul-out against current data revealed a general trend. Haul-out began to increase around slack current following flood current (e.g., Fig. 2, day 190). Seals started returning to the water between the slacking of ebb current and midway through flood current (e.g., Fig. 2, day 183, day 207).

The trends suggested above were tested and quantified by the model selection procedure. The $R^2$, AIC, and $\Delta$ for the group of alternative models are shown in Table 1. The model with the lowest AIC ($\Delta = 0$) and highest $R^2$ (0.460) had the environmental function

$$E(t) = \frac{T^r(t)C^q(t)}{H^s(t)}$$

(Table 1). The model with

$$E(t) = \frac{T^g(t)C^q(t)}{S^u(t)H^s(t)}$$

ranked a close second with $\Delta = 4.3$ and an $R^2$ of 0.457, and the model with

$$E(t) = \frac{T^g(t)C^q(t)}{S^u(t)H^s(t)}$$

ranked a close third with $\Delta = 4.7$ and an $R^2$ of 0.456. The gap between the third and fourth models was larger with $\Delta = 25$ and an $R^2$ of 0.419. The three best models were
the only ones considered because the others had $\Delta_i$ values $> 10$ and were thus rejected. Of
the three best models, the one with the environmental function (12) was chosen as the
most parsimonious. This gave the final deterministic model

$$N(t) = \frac{\beta e^{-\gamma(t + \frac{24 - \delta}{24})^2}}{1 + \alpha \frac{T_r(t) C^a(t)}{H^a(t)}}.$$  

(15)

Simulations of model (15) using the LS parameters $\alpha = 0.69842$, $\beta = 259.29$, $\gamma = 0.00028856$, $\delta = 218.31$, $r = 3.98277$, $q = 2.75273$, and $s = 7.22788$ are shown in Figure 2.

The model simulations reveal that similar haul-out patterns occur during comparable parts of the tidal cycle (Fig. 2). In addition, they predict that seal numbers are universally low in the early morning, increasing as the day progresses. Seals begin to haul out at high tide, and begin to re-enter the water several hours before low tide. Thus, maximal haul-out precedes low tide by several hours, whereas minimal haul-out occurs at high tide (Fig. 6). Although these patterns are generally true, the dynamics are a complicated superposition of the environmental cycles of tide height, current, and time of day. For example, low tides in the afternoon or evening cause deviation from the standard pattern of seals returning to the water at low tide. In this case, the seals remain on the beach instead of returning to the water, which leads to larger numbers of seals hauled out in the evening as additional seals arrive at the next high tide. Seal haul-out is also seasonally dependent with the daily maximal number of seals hauled-out increasing over the majority of the study (Fig. 3).
Residuals, resulting from fitting equation (15) to the data under different transformations, were tested for normality using several quantitative normality tests, all of which failed. The quantitative approach was abandoned in favor of Q-Q plots, which enable visual comparison between the distribution in question and a normal distribution (Fig. 4). The Q-Q plots confirmed that the square root transformation was appropriate.
CHAPTER 4

DISCUSSION

Deviations from Model Predictions

The modeling methodology identified a relatively robust deterministic “signal” in the time-series data. Deviation from the deterministic signal could be due to demographic noise, environmental noise, count errors, and/or errors due to the simplifying nature of the model assumptions. Each of these is now discussed in turn.

Whereas large groups of seals may behave in predictable ways, individuals show considerable variation in their behavior, resulting in demographic stochasticity. For example, a radio-tagging study by Thompson et al. (1989) revealed that one male was hauled out 45% of the time while another spent only 26% of his time on shore. In addition, considerable variation was found between individual responses to tide. Some seals showed diurnal haul-out patterns, while others did not (Thompson and Miller 1990). Seals also show differences in site fidelity and home range, although these are more pronounced for seals that haul out on rocky reef substrate (Hardee 2008).

Seals are affected by environmental factors besides those included in model (15), giving rise to environmental stochasticity. For example, seals may haul out to warm up in the sun, although too much solar radiation will cause them to overheat and return to the water (Watts 1992). Weather factors also are important, especially wind and wave intensity (Schneider and Payne 1983; Henry and Hammill 2001). These types of
environmental variables were not included in the deterministic model because they cannot be predicted far in advance. Excluding them may reduce the goodness-of-fit between model and data, but enables the model to predict seal haul-out into the future. Another source of environmental noise is disturbance. Seals may take longer than the model assumes to recover from disturbance. Previous work has shown that it requires 7-117 min for recovery (Suryan 1995). However, an intermediate value of 30 min after disturbance was chosen as the threshold for discarding data in this study, as this seemed to strike the best balance between improved model fit and loss of data (Table 2).

Counting-errors provide another source of stochasticity. At the beginning of the study the observers calibrated their counting styles to reduce differences to <10%. Although this reduced count-error between individuals, there were other sources of error. For example, groups of seals usually oriented themselves in a similar direction, often at an angle perpendicular to the line of view, making it difficult to distinguish individuals. This was especially true when observing seals on the gravel bar, due to the shallower angle and greater distance from the observation point. Previous work suggests that counting seals is difficult when the angle of observation is <8° from the horizontal (Hayward et al. 2005).

Finally, model error results from the simplifying assumptions on which models are built. For example, alternate haul-out sites are available on Protection Island within 2 km of Kanem Point, the largest of which is Violet Point. Although seals show significant site fidelity (Yochem et al. 1987), the model does not address the possibility of seals hauling out at alternative sites. Interestingly, in the Hayward et al. (2005) model for
Violet Point, tide height appeared in the denominator of \( E(t) \) (Table 1: second to last model) whereas in the model for Kanem Point, tide height appears in the numerator of \( E(t) \). This begs the question of whether seals move between these haul-out locations as the tide changes. Furthermore, the secondary haul-out location on the gravel bar gradually became submerged as the tide rose, forcing hauled-out seals into the water. Although seals displaced from the gravel bar usually moved to the point, often there was a considerable time lag between these events. This action led to “dips” in haul-out numbers on rising tides. The dynamics between these two locations were not accounted for in the model. The model also does not consider the effect of density-dependent factors such as crowding or social facilitation. Substrate availability at high tide did not appear to play a role, as seals moved farther up the beach into the driftwood if space was limited.

**Model Portability**

The two best models from the study by Hayward et al. (2005) on Violet Point are found at the end of Table 1. The low \( R^2 \) values obtained when these Violet Point models were applied to Kanem Point data indicate that they do a poor job of explaining the dynamics observed on Kanem Point. The Violet Point and Kanem Point models differ in three ways.

First, the Violet Point models have tide height in the denominator of the environmental function \( E(t) \), whereas the best model for Kanem Point has tide height in the numerator of \( E(t) \) (see equation [12]). Note that \( E(t) \) itself is in the denominator of model (6). Thus, holding all other factors constant, Violet Point haul-out increases as tide height increases, whereas Kanem Point haul-out decreases as tide height increases. Current, however, plays a similar role on both spits; holding all other factors constant,
haul-out decreases as current (or “equalized” current) increases. That tide plays opposite roles on the two spits but current plays the same role seems contradictory since, from an idealized point of view, current is related to the rate of change of tide height. However, the complexity of local ocean basin topography relative to the NOAA tide and current stations complicates the relationship between the tide and current data.

Second, the Violet Point model incorporates the “equalized” current $C_e(t)$, whereas the Kanem Point model utilizes the non-equalized current $C(t)$, suggesting the possibility that both current direction and velocity are important on Kanem Point, whereas current direction, more than velocity, influences haul-out on Violet Point. Current direction is important because food availability presumably peaks during flood current. However, current velocity also may be important as high current speed may disrupt interactions between mothers and pups in the water, as pups are weak swimmers. Lower flood current speeds near Kanem Point may account for the presence of current velocity in this model. Collection location may also play a role in the differences in current between the two models: Current data in the Violet Point study were collected at the mid-channel buoy some distance from Protection Island, whereas current data for Kanem Point were predicted for the immediate location.

Third, although the most parsimonious model for Violet Point does not contain hour of day or solar elevation as a variable, the alternative best model contains solar elevation in the numerator of $E(t)$. In the afternoon this is consistent with the present model which includes hour of day in the denominator of $E(t)$; that is, both spits are predicted to have increasing haul-outs as the day progresses. In the morning, however, the predictions for the two spits are inconsistent. On Violet Point, haul-out is predicted to
be high in the morning (low solar elevation), whereas on Kanem Point haul-out is predicted to be low.

The similar location of the current variable in the Kanem and Violet Point models suggests the increased food availability that presumably occurs during flood current is an important driver of seal behavior across sites. Further investigations at more locations would reveal whether this relationship holds true.

The differences between models for the two haul-out sites suggest that seal populations at each haul-out site are influenced by a different combination of environmental factors; thus, a unique model must be created for each haul-out location (Huber et al. 2001; Hayward et al. 2005; Patterson and Acevedo-Gutiérrez 2008).

**Biological Significance**

The study was conducted during the pupping season, increasing the stability of seal behavior due to mothers returning to the haul-out site regularly to care for their young. The following functional hypothesis for seals using Kanem Point on Protection Island as a haul-out site is suggested by equation (15). Incoming currents associated with flood tides increase food availability, and this corresponds with the lowest haul-out numbers. Seals begin to leave the beach at the transition between ebb tide and slack tide. They remain in the water and feed throughout the incoming tidal phase; they move back to the haul-out location as the incoming current slackens. Seals prefer to haul-out diurnally (Allen et al. 1984) and forage at night (Thompson and Miller 1990), thus the number of seals hauled out is low after sunrise and increases throughout the day as seals return from their nightly foraging bouts.
Implications for Management

Understanding the factors that determine seal haul-out enables consistent surveys of hauled-out seals over long time intervals. The general methodology for using this approach can be found in Hayward et al. (2005). Several additional points should be made. First, as noted above, a new model is required for each haul-out location of interest because haul-out dynamics are site-specific. Second, the function $M(t)$ is season-specific, so measurements taken in subsequent years must be taken during the same season. Third, this process does not yield population estimates. It must be combined with other methods (such as radio tagging) in order to create estimates of population size. Fourth, mathematical models, being site-specific, are better suited to small-scale, rather than region-wide, use. Developing models for large-scale areas with tens to hundreds of haul-out locations would require a considerable time investment. Finally, lack of dynamic synchrony between haul-out locations makes universal surveys of all locations during equivalent parts of the haul-out cycle unsuitable. For example, haul-out on Kanem Point will be increasing during ebb tide, whereas haul-out on Violet Point will be decreasing under the same conditions. Repeated censuses of a few well-studied haul-out sites of the most interest would provide the most accurate estimates of seal number fluctuations. In other words, mathematical modeling can be used to reveal population trends by increasing the accuracy of repeated surveys at a few key haul-out sites.

The points above have several practical implications for harbor seal management. First, managers comfortable using mathematical modeling techniques can obtain more accurate population trends which can be used to adjust census data. Several key haul-out locations within the study area that are likely to mirror total population trends should be
chosen. Initial surveys can be conducted, and a different model created for each site. The model predictions can be used to plan later surveys at each site within similar haul-out patterns to reveal local population trends. Because haul-out patterns are similar during each survey, population trends will be more accurate than those generated via region-wide surveys. If the study sites are carefully chosen, local population trends can be compared to region-wide trends, obtained via aerial surveys, to reveal potential errors and refine region-wide population estimates.

Second, all managers should conduct future region-wide aerial surveys under environmental conditions as similar as possible to those present when the correction factor was created. Because an unknown combination of environmental variables is driving haul-out at each location, it is important for later surveys to match as many predictable variables as possible. This increases the likelihood that a similar proportion of the seal population will be hauled out at each site during subsequent surveys, thus increasing the accuracy of the correction factor. However, it should be noted that this does not enable locations to be compared, since different locations are not in equivalent parts of the haul-out cycle, as mentioned above. Location-specific correction factors must be applied before any comparisons can be made.

In summary, managers can use mathematical modeling techniques to (1) determine the environmental factors influencing harbor seal haul-out; (2) increase the accuracy of correction factors applied to subsequent aerial surveys; and (3) track population trends by modeling key haul-out locations. The modeling technique in this study cannot alone (1) indicate total population size; or (2) compare haul-out numbers at different sites during the same time interval using a single model.
Conclusion

Environmental variables driving harbor seal haul-out behavior at a given site can be determined using mathematical modeling techniques, and the resulting models provide a method for predicting future haul-out. Although specific models are not necessarily portable to new locations, they provide useful information for researchers and wildlife managers seeking to monitor haul-out behavior through time at a given location. Furthermore, population size can be determined with greater accuracy by conducting future aerial surveys during environmental conditions similar to those present when the correction factor was made.
Table 1. Model comparison. K includes $\alpha$ and $\sigma^2$ plus the environmental variables, but does not include parameters $\beta$, $\delta$, or $\gamma$ as these were computed separately. The environmental variables are tide, equalized tide, current, equalized current, solar elevation, and hour of day and are represented by $T$, $T_e$, $C$, $C_e$, $S$, and $H$, respectively. The final two entries are the best models found in Hayward et al. 2005. Due to model construction, variables in the denominator of $E(t)$ influence the numerator of the model, and variables in the numerator of $E(t)$ influence the denominator of the model. Asterisks denote best model in each group. See methods for explanation of model creation.

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Violet Point Models

| $C^q/H^s$ | 12.539     | 4   | 920.9  | 50.21  | 0.37606* | $C^q_e/T^r$ | 18.238   | 4    | 1056.2 | 185.49 | 0.092505 |
| $C^q_e/H^s$ | 12.755     | 4   | 927.1  | 56.37  | 0.36532  | $C^q_e S^u/T^r$ | 18.246   | 5    | 1058.3 | 187.59 | 0.092111 |
Table 2. Effects of removing disturbances on model goodness-of-fit. Data points falling within 30 min, 1hr, and 2 hrs of a disturbance were removed. Resulting data were used to parameterize the best model (15). Removing data within 30 min of a disturbance provided the best balance between improved model fit and loss of data.

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Figure 1. Protection Island

Protection Island National Wildlife Refuge, Jefferson County, Washington, USA. The island covers 147 ha. A) denotes the observation point on the bluff overlooking Kanem Point, B) denotes the primary haul-out location along the beach on the SE side of Kanem Point, C) denotes the secondary haul-out location on the gravel bar, and D) denotes the north beach of Violet Point where the Hayward et al. (2005) study was conducted.
Figure 2. Model Predictions

Model prediction (lower solid line), seal haul-out on Kanem Point (circles), tide height (upper solid line) and current velocity (dashed line) during various parts of the tidal cycle. Each panel corresponds to 1 d. Small numbers at the top of each panel denote day of year. Tide height is graphed on a scale from -1.5 to 3.2 m and current velocity is graphed on a scale from -1.1 to 0.5 m/s. Arrows in the lower graph indicate a typical 14 d tidal cycle at Protection Island.
Figure 3. Maximal daily haul-out counts

Panel on the left is maximal weekly haul out counts on Violet Point from Hayward et al. (2005). The maximal weekly counts approximate a normal distribution (dotted line). Panel on the right is maximal daily haul-out counts on Kanem Point over the 4 wk study period starting on the 30th of June. The dotted line represents the envelope function $M(t)$, parameterized to the daily maximal haul-out which yielded the following parameters: $\beta = 259.29$, $\gamma = 0.00028856$ and $\delta = 218.31$. The maximal envelope was assumed to have the same functional form as the normal curve in the Violet Point study.
Unfortunately, the residuals for each model failed common tests for normality (Shapiro-Wilk, Kolmogorov-Smirnov and D’Agostino’s $K^2$ test). The quantitative approach was abandoned in favor of Q-Q plots, which allow visual comparison of two distributions. Q-Q plots of untransformed residuals, square root transformed residuals, and log transformed residuals were used to graphically evaluate residuals for normal distribution. Normality would be confirmed by a linear relationship between the residual and the normal distribution. Circles represent each quantile. The solid line joins the first and third quartiles.
Q–Q Plots

Natural Log Transformed Residuals

Square Root Transformed Residuals

Untransformed Residuals
Figure 5. Solar elevation

Solar elevation and seal haul-out on 2 d in different parts of the tidal cycle; the dotted line represents solar elevation and circles represent haul-out counts. Solar elevation was not present in the best models. The poor fit on day 203 provides an example of why solar elevation is not included in the best model.
Figure 6. Comparison of the effects of current and tide height on model predictions on Kanem Point and Violet Point, given that all other factors are held constant. Solid line represents predictions, upper dashed line represents tide height and lower dashed line represents current velocity. Maximal haul-out on Kanem Point occurs around low tide, whereas maximal haul-out on Violet Point occurs near high tide. Haul-out is inversely related to current on both points with decreased haul-out during flood current.
**APPENDIX A**

**DATA**

**Table 3.** Census data. Rows marked with * are within 30 min of a disturbance and were not included in the analysis.

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APPENDIX B

MATLAB PROGRAMS

Goseals2010.m

%Front end program for parameterizing seal models
%To run, type "goseals2010" at the Matlab prompt.
%authors: Shandelle Henson & Jonathan Cowles

global data pr residual

%load data set
data = load('seals2010_30min.txt');
count = data(:,3);

%set the initial parameter values for downhill method in the following order%
theta = log([0.69842
3.98277
2.75273
7.22788
]);

call nelder routine to minimize RSS
choose seal model
output = nelder(theta,'sealmodel2010');

%store best predictions
prediction = pr;

%print best parameters to screen
parameters = exp(output(1:length(output)-1))

%print stats at best parameters
RSS = output(length(output));
sigmasq = RSS/length(data(:,3))
kappa = length(theta)+1
AIC = length(data(:,3))*log(sigmasq) + 2*kappa
Rsq = 1 - RSS/sum((sqrt(count) - mean(sqrt(count))).^2)
delta = AIC - 870.71

%plot one week of data
day = (data(:,1)-min(data(:,1)));  
clf
for z=0:6
    %which of the 4 weeks of data should be plotted
    week = 1-1;
    arrayid = find(data(:,1) == 181+z+week*7);
    if (z+181+week*7 == 191)
        %skips day with no data (July 10)
    else
        xtime = (data(arrayid,2))./100;
        yseals = (data(arrayid,3));
        ypred = pr(arrayid);

        %create subplots
        dayplot(z+1) = subplot(2,4,z+1);

        %plot seal numbers
        scatter(xtime,yseals,2.5,[0 0.5 0])

        %name plot and scale axes
        axis([5 22 0 450]);
        plottitle = ['Day ',num2str(data(min(arrayid)))];
        title(plottitle);
        hold on

        %plot predictions
        plot(xtime,ypred)
    end
end

sealmodel2010.m

%Computes RSS for seal model
%authors: Shandelle Henson & Jonathan Cowles

function fct = sealmodel2010(theta)
global data pr residual

%set parameters in the following order
param = exp(theta);
a = param(1);
f = param(2);
g = param(3);
k = param(4);

% create vectors of ages and measurements
day = data(:,1);
hour = data(:,2);
count = data(:,3);
T = data(:,4);
NewT = data(:,5);
C = data(:,6);
NewC = data(:,7);
S = data(:,8);

% normalize hour
hr1 = data(:,2) - min(data(:,2));
hr2 = hr1 ./ max(hr1) + 1;
normhour = hr2;

% define environmental variable function
factor = T.^f.*C.^g./normhour.^k;

% compute model predictions using hard coded parameters from envelope parameterization
pr = 2.59288617211679e+002.*exp(-2.88565782971170e-004.*(day + hour./2400 - 2.18311954452306e+002).^2)./(1 + a*factor);

% Create vector of residuals.
residual = sqrt(pr) - sqrt(count);

% Compute RSS, the sum of squared residuals
fct = sum(residual.^2);

nelder.m

function minvec=nelder(theta, ofn);

% NELDER Unconstrained function minimization.
% Nelder-Mead simplex algorithm used. Function 'ofn(theta)'
% is passed to routine and must be pre-defined, where theta
% is a vector of unknown parameters.
changes=theta.*0.1+(theta==0).*0.1;
ftol=0.000000001;
alpha=1;
betta=0.5;
gam=2.0;

% CALCULATE OBJECTIVE FUNCTION AT npar+1 INITIAL VALUES OF theta;
% PLACE ofn RESULTS IN y, A COLUMN VECTOR ((npar+1) X 1); PLACE
% VALUES OF theta AS COLUMNS OF par, A MATRIX (npar X (npar+1))
npar=length(theta);
hi=npar+1;
tha=ones(npar);
for ii=1:npar;
  thm(:,ii)=thm(:,ii).*theta;
end;
par=[theta (thm+diag(changes))];
for ii=1:hi;
  if ii==1;
    y=eval(['ofn(','par(:,1)')]');
  else;
    yx=eval(['ofn(','par(:,ii)')]');
    y=[y; yx];
  end;
end;

% SORT VALUES OF y IN ASCENDING ORDER; SORT
% CORRESPONDING COLUMNS OF par
[y,ix]=sort(y);
part=par';
part=part(ix',:);
par=part';

% GET DOWN TO BUSINESS
iter=1;
rtol=2.0*(abs(y(hi,:)-y(1,:)))/(abs(y(hi,:))+abs(y(1,:)));
while rtol>ftol & iter<=500;
  pmeans=mean(par(:,1:(hi-1))');
  pnew=(1+alpha).*pmeans-alpha.*par(:,hi);
  yfirst=eval(['ofn','('pnew')']);
  if yfirst<=y(1,:);
    pnewer=gam.*pnew+(1-gam).*pmeans;
    ysecond=eval(['ofn','('pnewer')']);
    if ysecond<=y(1,:);
      par=[pnewer par(:,1:hi)];
      y=[ysecond; y(1:hi,:)];
    else;
      iter=iter+1;
      rtol=2.0*(abs(y(hi,:)-y(1,:)))/(abs(y(hi,:))+abs(y(1,:)));
    end;
  else;
    iter=iter+1;
    rtol=2.0*(abs(y(hi,:)-y(1,:)))/(abs(y(hi,:))+abs(y(1,:)));
  end;
end;
par=[pnew par(:,1:hi)];
y=[yfirst; y(1:hi,:)];
end;
elseif yfirst>=y((hi-1,:),);
if yfirst<y(hi,:);
par(:,hi)=pnew;
y(hi,:)=yfirst;
end;
pshrink=betaa.*par(:,hi)+(1-betaa).*pmeans;
ysecond=eval([ofn,'(pshrink)']);
if ysecond<y(hi,:);
place=sum(ysecond>y)+1;
par(:,place:hi)=pshrink par(:,place:(hi-1)));
y(place:hi,:)=ysecond; y(place;(hi-1,:));
else;
par=0.5.*(par+par(:,1)*ones(1,length(par(1,:))));
ii=2;
while ii<=hi;
y(ii,:)=eval([ofn,'(par(:,ii))']);
i=ii+1;
end;
y,ix=sort(y);
part=par';
part=part(ix',:);
par=part';
end;
else;
place=sum(yfirst>y)+1;
par(:,place:hi)=pnew par(:,place:(hi-1)));
y(place:hi,:)=yfirst; y(place;(hi-1,:));
end;
rtol=2.*(abs(y(hi,:)-y(1,:))/(abs(y(hi,:))+abs(y(1,:))));
iter=iter+1;
end;
if iter>500;
minvec=0;
'did not converge'
else;
minvec=[par(:,1); y(1,:)];
end;
end;
LITERATURE CITED


Suryan, R. 1995. Pupping phenology, disturbance, movements, and dive patterns of the harbor seal (Phoca vitulina richardsi) off the northern San Juan Islands of Washington. 75 pp.


