

Predicting numbers of hauled-out harbour seals: a mathematical model

JAMES L. HAYWARD,^{1,*} SHANDELLE M. HENSON,[†] CLARA J. LOGAN,[†]
CATHERINE R. PARRIS,[‡] MATTHEW W. MEYER[†] and BRIAN DENNIS[§]

^{*}Biology Department, [†]Department of Mathematics and [‡]Department of Chemistry, Andrews University, Berrien Springs, MI 49104, USA; and [§]Department of Fish and Wildlife Resources and Division of Statistics, University of Idaho, Moscow, ID 83844, USA

Summary

1. It was once assumed that commercially important fish make up significant portions of seal diets. As a consequence, prior to the 1970s many seal populations were dramatically reduced by rampant slaughtering. Today, seals and other marine mammals are valued components of marine ecosystems and their numbers are carefully managed. To facilitate management, government statutes mandate the systematic monitoring of seal populations. Population estimates are based on counts of hauled-out seals obtained by aerial survey and radio and satellite telemetry; hence, considerable effort has been devoted to finding optimal times for such counts. We have developed a predictive mathematical model of seal haul-out to assist resource managers in the selection of optimal census times.

2. Haul-out depends on a number of environmental variables. Some of these variables, such as wind speed, can be obtained only as historical data or short-range predictions. Others, such as tide height, are deterministic and can be obtained as long-range predictions.

3. We used deterministic environmental variables to develop mathematical models that describe haul-out dynamics of harbour seals *Phoca vitulina* during the pupping season at a site in Washington, USA. A list of alternative hypotheses for environmental cues gave rise to a suite of competing models. We used information-theoretic model selection techniques to choose the best model. The selected model was a function of tide height and current direction, and explained 40% of the variability in hourly census data.

4. An assumption that the system recovers rapidly after disturbance introduced two time scales. This allowed the differential equation model to be reduced to an algebraic equation.

5. *Synthesis and applications.* This study demonstrates that resource managers can use a simple algebraic equation based on deterministic environmental variables to predict times at which to census maximal haul-out in harbour seals. At the Washington site, maximal daily haul-outs during pupping season are predicted to occur during receding tides, approximately midway between high and low tides. The largest maximal daily haul-outs during the pupping season are predicted to occur in the last week of July. The environmental factors correlated with haul-out are, however, site-specific; therefore the model developed for the Washington site will not necessarily hold for other haul-out areas. Managers should carry out the model selection procedure separately for each monitored haul-out site. The general methodology employed in this study can be used to make long-range predictions of diurnal movements for a variety of marine birds and mammals.

Key-words: Akaike information criterion, census times, current, *Phoca vitulina*, prediction, tide, Washington

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Introduction

Harbour seals *Phoca vitulina* L. live within a broad latitudinal range along the North Atlantic and North Pacific coasts (Thompson *et al.* 1997; Carretta *et al.* 2002). During the early and mid-20th century large numbers of these animals were slaughtered under the false assumption that commercially important fish such as salmon (*Oncorhynchus* sp.) formed a major component of harbour seal diets. Better understanding of the diets of harbour seals and increasing public concern over declining numbers of all marine mammals led to the 1970 Conservation of Seals Act (CSA) in the UK and the 1972 Marine Mammal Protection Act (MMPA) in the USA. These acts resulted in dramatic recoveries of seal populations (Boveng 1988; Moss 1992; Matthiopoulos *et al.* 2004).

Not only do the CSA and MMPA provide statutory protection of seals, they also mandate the systematic monitoring of seal populations. Population estimates are used by government agencies to make decisions concerning seal conservation vis-à-vis human utilization of marine fisheries and other resources. Estimates are based on aerial as well as radio and satellite telemetered counts of hauled-out seals. Significant efforts are devoted to determining the most appropriate census times to achieve maximal counts under the assumption that these numbers can be used to calculate reasonable estimates of population size (Pitcher & McAllister 1981; Stewart 1984; Thompson *et al.* 1989, 1997; Huber 1995; Thompson, Van Parijs & Kovacs 2001; Adkinson, Quinn & Small 2003; Jeffries *et al.* 2003; Matthiopoulos *et al.* 2004).

During the pupping season harbour seals divide their time between coastal waters, where they feed, and favourite haul-out sites, where they rest, interact with conspecifics, give birth and tend young (Watts 1992; Kroll 1993). They use a wide variety of habitats for hauling out, including sand and cobble beaches, rocky shelves, tidal sand and mud bars, human-made structures and drifting glacial ice (Stewart 1984). Hauling out lowers the cost of negotiating waves and currents and raises the temperature of peripheral tissues, promoting skin growth and maintenance. Timing of haul-out varies by sex, locality, individual variation and pelage dryness (Thompson *et al.* 1989, 1997; Watts 1992), as well as by a variety of environmental factors, including time of year, tide height, shoreline topography, time of day, wave intensity, disturbance, wind chill, wind speed, solar radiation and air temperature (Schneider & Payne 1983; Stewart 1984; Thompson *et al.* 1989, 1997; Watts 1992).

Studies of haul-out patterns typically utilize statistical approaches such as canonical correlation, linear regression and analysis of variance, which are designed to identify significantly correlated independent variables (Schneider & Payne 1983; Stewart 1984; Thompson *et al.* 1989; Moss 1992; Watts 1992). Statistical studies are useful for understanding patterns in historical data, but they provide limited predictive capability. In

contrast, in addition to the description of past patterns, mathematical modelling allows the prediction of future patterns and the identification of probable driving forces for these patterns (Levin 1992; Hastings 1997).

In previous work, Henson *et al.* (2004) used a differential equation model to predict, with surprising accuracy, diurnal habitat occupancy patterns in marine birds on Protection Island National Wildlife Refuge, Washington, USA. Deterministic environmental variables, including tide height, solar elevation and day of year, were used to create long-range predictions. In this study, we used similar methodology, but a different set of environmental variables, to model harbour seal haul-out on a beach at Protection Island, Washington, USA.

Methods

DATA COLLECTION

During the pupping season, hourly counts of harbour seals hauled out on the north beach of Violet Point, Protection Island (48°08'N, 122°55'W), were made on 1 day per week from 05.00 to 20.00 Pacific Standard Time, during July and August of 1995 and 1997–99. All counts were made from a 33-m bluff overlooking Violet Point; counts made within 30 min after a major disturbance were discarded. A seal was considered to be hauled out if its body was resting on the substrate, even when partially submerged. Hourly counts yielded samples at a temporal scale appropriate for detection of tidal and diurnal periodicities (Hunt & Schneider 1987). Tides in the adjacent Strait of Juan de Fuca are semi-diurnal with strong diurnal inequalities in the lows. 'Nodes' of minimal tidal amplitude occur approximately every 14 days (Fig. 1; arrows). Patterns in counts tended to recur during similar times within this biweekly tidal cycle.

MODELLING ASSUMPTIONS

One principle of mathematical modelling is to identify a parsimonious set of simplifying assumptions that captures the main dynamics of a system. The model proposed in this study is formulated from five assumptions.

Assumption 1

The numbers of seals that haul out in the study area during daylight hours can be described with a two-compartment model consisting of the haul-out site and a remote location (everywhere else).

Assumption 2

Seals move back and forth between these two compartments in direct response to deterministic environmental variables. Specifically, seals leave the haul-out site for the remote location at a per capita rate proportional to a function $E_{21}(t)$ of deterministic environmental variables, and return to the haul-out site at a per capita rate

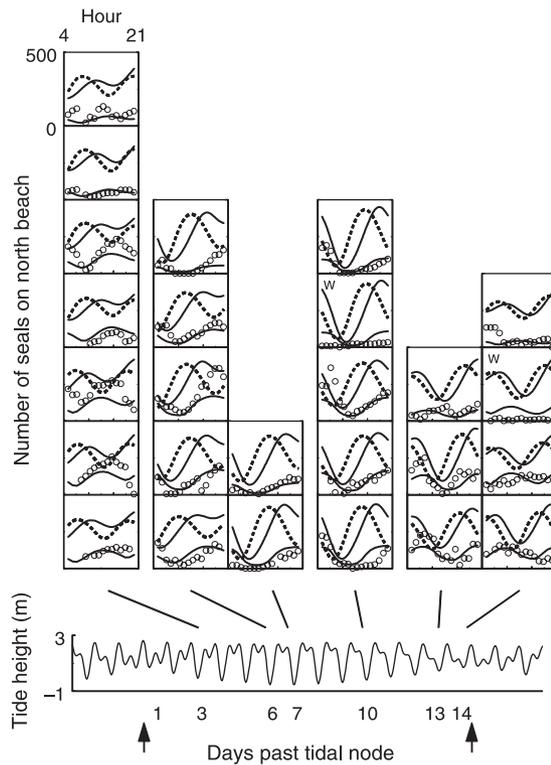


Fig. 1. Model prediction (lower solid curve), seal haul-out data (circles), tidal curve (upper solid curve) and current velocity (dashed curve). Each panel corresponds to 1 day. Tide height is graphed on a vertical scale of -1 to 3 m, and current velocity on a scale of -2 to 1.5 knots. A typical 14-day tidal period for Protection Island is shown at the bottom; tidal nodes are indicated with arrows. Data from days occurring during the same time in the tidal period are stacked vertically. The data in a given column show similar diurnal patterns. Days preceded by high, sustained winds are designated W (see the Discussion). The following are dates for days in each of the six columns, left to right, top to bottom: first column, 6 July 1995, 7 July 1999, 20 July 1995, 21 July 1999, 3 August 1995, 4 August 1999, 18 August 1999; second column, 2 July 1997, 16 July 1997, 30 July 1997, 5 August 1998, 13 August 1997; third column, 8 July 1998, 22 July 1998; fourth column, 13 July 1995, 14 July 1999, 27 July 1995, 28 July 1999, 11 August 1999; fifth column, 9 July 1997, 23 July 1997, 6 August 1997; sixth column, 1 July 1998, 15 July 1998, 29 July 1998, 12 August 1998.

proportional to a function $E_{12}(t)$ of deterministic environmental variables. There are no density-dependent effects; that is, $E_{12}(t)$ and $E_{21}(t)$ do not depend on the seal density in either compartment.

Assumption 3

The upper bound $M(t)$ for the number of seals that may haul out at the study area during pupping season can be approximated by:

$$M(t) = \beta e^{-\gamma(\text{day of year} + t/24 - \delta)^2} \quad \text{eqn 1}$$

where t is the hour of the day and β , γ and $\delta > 0$ are positive constants. The functional form in this assumption was suggested by the maximal weekly haul-out counts, as shown in Fig. 2. Three points should be emphasized.

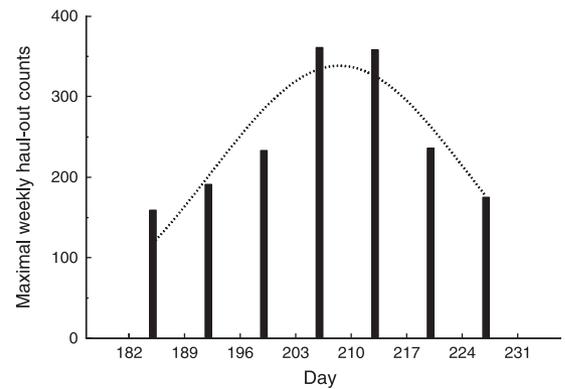


Fig. 2. Maximal counts at the haul-out site during 1 July-18 August. Each bar represents 1 week. The height of each bar is the mean maximal count recorded at the haul-out site for that week, averaged over the years 1995 and 1997-99. Based on this graph, the function $M(t)$ was assumed proportional to a normal curve. The dotted normal curve shown is not $M(t)$; see assumption 3 in the text.

First, $M(t)$ is not the population size but is simply a functional form assumed to describe the upper bound for the number that haul out at the study area. Seal monitors use various techniques to estimate population sizes from haul-out counts (Pitcher & McAllister 1981; Thompson & Harwood 1990; Moss 1992; Watts 1992; Huber 1995; Matthiopoulos *et al.* 2004) but we did not address or model population size in this study. Secondly, $M(t)$ is not the normal curve fitted to the data in Fig. 2. The parameters β , γ and δ in equation 1 were estimated, along with the rest of the model parameters, from census time series data as described in the section on model parameterization. Thirdly, the functional form of $M(t)$ depends on the seasonal context. Maximal counts do not follow a normal curve throughout the year.

Assumption 4

The system recovers rapidly after disturbance. Specifically, the values of $M(t)$, $E_{12}(t)$ and $E_{21}(t)$ remain approximately constant during the time it takes the system to return to 'steady state' dynamics.

Assumption 5

The main source of noise in the census data is demographic stochasticity, which can be modelled with a stochastic 'birth-and-death' (arrival-and-departure) process, as detailed below in the section on the stochastic model. This assumption was motivated by a post-hoc inspection of model residuals.

GENERAL DETERMINISTIC MODEL

The dynamics of 'compartmental models' are typically described by differential equations of the form:

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

Given the first three assumptions, this becomes:

$$\frac{dN}{dt} = [aE_{12}(t)(M(t) - N)] - [bE_{21}(t)N] \quad \text{eqn 2}$$

Here $N(t)$ is the number of seals hauled out at hour t , $M(t)$ is the upper bound for the number that may haul out as given in equation 1, $E_{12}(t)$ and $E_{21}(t)$ are the functions of environmental variables to be determined, and the parameters a and $b > 0$ are constants of proportionality. Given assumption 4, it can be shown by the methods of multiple time scale analysis (Hoppensteadt 1974; Tikhonov, Vasil'eva & Sveshnikov 1985; Lin & Segel 1988) that, in the absence of disturbance, the solution of the differential equation 2 is well approximated by the algebraic equation:

$$N(t) = \frac{M(t)}{1 + \frac{bE_{21}(t)}{aE_{12}(t)}} \quad \text{eqn 3}$$

Note that equation 3 depends on the ratio of the two environmental functions and the ratio of the parameters b and a . Replacing the ratios in equation 3 by $\alpha = b/a$ and $E(t) = E_{21}(t)/E_{12}(t)$, and substituting the expression for $M(t)$ from equation 1, yields the deterministic mathematical model:

$$N(t) = \frac{\beta e^{-\gamma(\text{day of year} + t/24 - \delta)^2}}{1 + \alpha E(t)} \quad \text{eqn 4}$$

where α , β , γ and $\delta > 0$ are constant parameters to be estimated from data.

GENERAL STOCHASTIC MODEL

Noise is ubiquitous in ecological systems. In order to link the model represented by equation 4 to data, one must first model the departure of the data from the deterministic predictions. Under assumption 5, the noise is approximately additive on the square-root scale (Dennis *et al.* 2001):

$$\sqrt{N(t)} = \sqrt{\frac{\beta e^{-\gamma(\text{day of year} + t/24 - \delta)^2}}{1 + \alpha E(t)}} + \sigma \epsilon(t)$$

Here the $\epsilon(t)$ are standard normal random variables uncorrelated in time, and $\sigma > 0$ is a constant parameter. This yields the stochastic model:

$$N(t) = \left(\sqrt{\frac{\beta e^{-\gamma(\text{day of year} + t/24 - \delta)^2}}{1 + \alpha E(t)}} + \sigma \epsilon(t) \right)^2 \quad \text{eqn 5}$$

The square-root transformation arises as a method of analysing data from a stochastic birth-and-death process. Suppose the number N of seals hauled out is a discrete stochastic birth-and-death process with a linear arrival (birth) rate of the form $\phi - \eta N$ and a proportional departure (death) rate μN . In other words, in a small interval of time Δt , the approximate probability of an arrival is $(\phi - \eta N)\Delta t$, and the approximate probability of a departure is $\mu N\Delta t$, given that the current number of seals hauled out is N (Taylor & Karlin 1984).

The equilibrium probability distribution for N is then a generalized binomial (ϕ/η , $\phi/(\eta + \mu)$) distribution (binomial with non-integer number of trials, reducing to an exact binomial if ϕ/η is a positive integer) with mean $\phi/(\eta + \mu)$ (Boswell, Ord & Patil 1979). If ϕ , η and μ are slowly varying functions of time, the distribution of N will equilibrate towards the binomial evaluated at the current values of ϕ , η and μ . The birth and death model is a stochastic version of the deterministic model (equation 2), with $\phi = aE_{12}(t)M(t)$, $\eta = aE_{12}(t)$ and $\mu = bE_{21}(t)$. The equilibrium binomial is well-approximated by a Poisson distribution with mean $\phi/(\eta + \mu)$. In turn, to a good approximation, the square-root of a Poisson random variable is normally distributed with a mean $[\phi/(\eta + \mu)]^{1/2}$ and with a constant variance that does not depend on the value of the mean (Rao 1973). Thus, by transforming the observations and model to the square-root scale, statistical inferences can be accomplished with standard approaches based on the normal distribution. On the square-root scale, model fitting (parameter estimation) was done with non-linear least-squares, and model diagnostic analyses focused on the residuals, as explained below in the sections on model parameterization and model selection. Transforming a Poisson model to the square-root scale has an added advantage: least-squares parameter estimates have some theoretical robustness to departures of the data from distributional assumptions.

ALTERNATIVE MODELS

A suite of competing models, having the form of equation 5, was proposed based on an array of hypotheses about the environmental function $E(t)$. Solar elevation $S(t)$ and tide height $T(t)$ data were obtained from the National Oceanic and Atmospheric Administration (NOAA), USA, web sites <http://www.srrb.noaa.gov/highlights/sunrise/azel.html> and <http://co-ops.nos.noaa.gov>, and current speed predictions $C(t)$ were obtained from the University of South Carolina, USA, web site <http://tbone.biol.sc.edu/tide/>. These environmental variables exhibit temporal aperiodic oscillations; they were non-dimensionalized and normalized so that:

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

The tidal oscillation exhibits high and low tides of widely varying magnitudes (Fig. 1; bottom). Given that the animals might respond in the same way to all tidal highs and lows regardless of exact values, another environmental variable was constructed: tide height $T_e(t)$ with 'equalized extrema'. To construct $T_e(t)$ from $T(t)$, all local maximum values of $T(t)$ were set equal to 2, all minimum values were set equal to 1, and the oscillation was splined between these points. An equalized extrema current variable $C_e(t)$ was constructed from $C(t)$ in the same manner. Twenty-three possibilities for $E(t)$ involving powers of the environmental variables $S(t)$, $T(t)$, $T_e(t)$, $C(t)$ and $C_e(t)$ were posed, which gave rise to 23 alternative mathematical models (Table 1).

Table 1. Model comparison. Least-squares (LS) parameters were estimated for each of the 23 alternative models grouped by the arrangement of variables in $E(t)$; the variance parameter σ^2 of the likelihood function was estimated from the residuals. AIC was computed from σ^2 , the number of parameters (including σ^2), denoted here by κ , and the number of data points (389). *Best model in each group. The model with $E(t) = C_e^q(t)/T^r(t)$ was selected because it was the more parsimonious of the two best-fitting models. The LS parameters for this model are $\alpha = 3.735$, $\beta = 181.6$, $\gamma = 0.001158$, $\delta = 215.2$, $q = 3.774$ and $r = 7.255$

$E(t)$	σ^2	κ	AIC	Δ_i	R^2
1	13.5	5	1023	139	0.14
T^r	13.5	6	1025	141	0.14
T_e^r	13.5	6	1025	141	0.14
$1/T^r$	11.1	6	948	64	0.30*
$1/T_e^r$	13.5	6	1025	141	0.15
S^u	12.4	6	991	107	0.22*
$1/S^u$	13.5	6	1025	141	0.14
C^q	12.4	6	991	107	0.22*
C_e^q	12.6	6	998	114	0.20
$1/C^q$	13.5	6	1025	141	0.14
$1/C_e^q$	13.5	6	1025	141	0.14
$C^q S^u$	12.3	7	989	105	0.22
$C_e^q S^u$	11.6	7	968	84	0.27*
S^u/T^r	10.5	7	927	43	0.34*
S^u/T_e^r	13.3	7	1022	138	0.16
C^q/T^r	10.2	7	919	35	0.35
C_e^q/T^r	9.5	7	890	6	0.40*
C^q/T_e^r	13.0	7	1012	128	0.18
C_e^q/T_e^r	12.0	7	981	97	0.24
$C^q S^u/T^r$	10.2	8	921	37	0.35
$C_e^q S^u/T^r$	9.3	8	884	0	0.41*
$C^q S^u/T_e^r$	13.5	8	1028	144	0.15
$C_e^q S^u/T_e^r$	12.0	8	983	99	0.24

MODEL PARAMETERIZATIONS

Parameters for each of the 23 alternative models were estimated from the data using the method of least-squares (LS) on the square-root scale. The LS method (as opposed to fitting the Poisson or binomial models directly with maximum likelihood) relaxes many of the assumptions about the distribution of the residual errors (Dennis *et al.* 2001). In this method the residual sum of squares (RSS):

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

is minimized as a function of the vector θ of model parameters. Here ‘model prediction’ refers to the prediction generated by the deterministic model given in equation 4. The minimizer $\hat{\theta}$ is the vector of LS parameter estimates for the model.

MODEL SELECTION

When comparing models, one should use a selection criterion that takes into account the number of parameters

as well as the goodness-of-fit; models having more parameters should be penalized. The Akaike information criterion (AIC) is an information-theoretic model selection index designed to select the model closest to the ‘truth’ from a suite of alternative models (Burnham & Anderson 2002; Peek, Dennis & Hershey 2002; Gibson *et al.* 2004; Rushton, Ormerod & Kerby 2004). For LS parameters the criterion is equivalent to:

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

where n is the number of observations, $\hat{\sigma}^2 = RSS(\hat{\theta})/n$ is the variance of the likelihood function as estimated from the residuals and κ is the number of model parameters, including σ^2 . The candidate model with the smallest AIC value, denoted AIC_{min} , is the model closest to the ‘truth’. Model comparison is based on relative, rather than raw, AIC values. Thus, models are ranked according to the AIC differences $\Delta_i = AIC_i - AIC_{min}$, with the best model having $\Delta_i = 0$. Models with $\Delta_i > 10$ generally are considered significantly inferior to the best model, and can be rejected (Burnham & Anderson 2002).

Goodness-of-fit was computed as:

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

where ‘mean’ denotes the mean of the square-roots of the observations. This R^2 value estimates, on the square-root scale, the proportion of the observed variability that is explained by the model. The higher the R^2 value, the better the model fit, with $R^2 = 1$ denoting a perfect fit.

The R^2 , AIC and Δ_i for the suite of candidate models are shown in Table 1.

Results

The model with the lowest AIC ($\Delta_i = 0$) and highest R^2 (0.41) was the one with the environmental function $E(t) = C_e^q(t)S^u(t)/T^r(t)$ (Table 1). The model with $E(t) = C_e^q(t)/T^r(t)$ ranked a close second best, with $\Delta_i = 6$ and $R^2 = 0.40$. The third best model lagged significantly behind, with $\Delta_i = 35 > 10$ and $R^2 = 0.35$. Thus, all models except the best two were eliminated from further consideration. The model with $E(t) = C_e^q(t)/T^r(t)$ was selected as the more parsimonious of the two best models, yielding the deterministic model:

$$N(t) = \frac{\beta e^{-\gamma(\text{day of year} + t/24 - \delta)^2}}{1 + \alpha \frac{(C_e(t))^q}{(T(t))^r}} \tag{eqn 6}$$

Simulations of equation 6, using the LS parameters $\alpha = 3.735$, $\beta = 181.6$, $\gamma = 0.001158$, $\delta = 215.2$, $q = 3.774$, and $r = 7.255$, are shown in Fig. 1.

Simulations of equation 6 predict that seals begin to leave the beach about midway between high and low tides, and begin to return to the beach between low and high tides but before the midpoint. Thus, haul-out numbers are predicted to be highest approximately midway between high and low tides, and lowest between low

and high tides before the midpoint. Although this rule of thumb agrees with the model to within approximately 2 h, the exact timings of the maximal and minimal predictions depend, in a non-intuitive way, on the superposition of tidal and current cycles. For example, in the first column of Fig. 1 maximal predictions lag the midpoint between high and low tides by approximately 1 h, while in the fifth column maximal predictions precede the midpoint by approximately 1 h. The data are sufficiently noisy, however, that these deviations from the rule of thumb are probably insignificant. Model simulations also predict that daily haul-out patterns vary with temporal position within the biweekly tidal/current cycle. For example, during the biweekly cycle, haul-out lows are predicted to shift from earlier to later in the day, coinciding with a similar shift in tide/current fluctuations. Finally, as a consequence of the seasonally dependent $M(t)$ (Fig. 2), counts are predicted to be low in early July and to reach their maximum at the end of July, after which they once again decrease. Data trends are generally consistent with all of these predictions (Fig. 1).

Discussion

UNEXPLAINED VARIABILITY

Although the data trends generally comport with deterministic model predictions, hourly counts show considerable variability around these predictions. The following considerations should be kept in mind when interpreting these results.

Environmental stochasticity

Hauled-out harbour seals are highly sensitive to heat load. Under some conditions these animals move to the water to cool (Watts 1992), whereas under other conditions they haul out to absorb solar radiation. They respond to other environmental variables as well, such as wind speed and wave intensity. These types of environmental variables were not included in the deterministic model because they cannot be predicted far in advance. The effects of environmental stochasticity could be dramatic: contrary to predictions, on both 15 July 1998 (Fig. 1; column 6, second day from top) and 14 July 1999 (Fig. 1; column 4, second day from top), few seals were counted on the north beach. The mornings of both days, however, followed 7–8 h of sustained 38–56 km h⁻¹ north-north-west winds with gusts of up to 64 km h⁻¹ during the afternoon and evening of the previous day. Wind waves may have discouraged north beach landings and/or altered food availability. When these 2 days were deleted from the analysis, the R^2 value rose from 0.40 to 0.46.

Demographic stochasticity

Harbour seals, like many large mammals, exhibit a high degree of individual variation in behaviour (Wilson

1975). In groups of individuals that repeatedly use the same site, individual haul-out patterns may differ markedly (Brown & Mate 1983; Thompson *et al.* 1989).

Error in modelling assumptions

Alternative haul-out sites were available on Violet Point. The east and south sides commonly contained hauled-out animals that could not be seen from the observation point. Although harbour seals have preferred haul-out sites (Pitcher & McAllister 1981), it is likely that animals change sites from time to time, especially in response to disturbance, food availability and/or pupping activity (Brown & Mate 1983). These possibilities are not accounted for in the model. Furthermore, the model ignores possible density-dependent effects such as social facilitation and crowding.

Observational error

Counts made from the observation point were not as accurate as aerial counts would have been, especially under conditions of marginal light. Typically seals clumped together and faced the same direction perpendicular to the line of view and so were often difficult to distinguish or impossible to see. Observers found counting difficult if the angle of vision from the horizontal was less than about 8°.

TIME SCALE ANALYSIS AS A MANAGEMENT TOOL

Differential equations such as equation 2 are much more difficult and time consuming to simulate and parameterize than simple algebraic equations such as equation 3, especially when they depend on environmental variables. Differential equations must be integrated continuously over the past environmental history using computer software, while the algebraic equation depends only on the current state of the environment. Fast recovery time after disturbance (assumption 4) introduces two time scales into the problem, the time scale of the recovery and the time scale of the environmental variables. Multiple time scale theory then allows one to replace equation 2 by equation 3 in the absence of system disturbance. Thus, time scale reduction is a useful tool for managers.

ENVIRONMENTAL CUES FOR MOVEMENT

While assumption 4 vastly simplifies model selection, parameterization and simulation, it also confounds identification of $E_{12}(t)$ and $E_{21}(t)$: equations 3 and 4 depend on the ratio of the environmental functions $E_{21}(t)$ and $E_{12}(t)$ rather than on the individual functions themselves. The results of the model selection procedure suggest that the ratio can be expressed in the form:

$$E = \frac{E_{21}}{E_{12}} = \frac{C_e^q}{T^r}$$

Of course, this does not imply that $E_{21} = C_e^q$ and $E_{12} = T^r$. The model equation 6 could have arisen from many, indeed, infinitely many, differential equations of the form given in equation 2. Three representative possibilities are those having:

$$E_{12} = \frac{1}{C_e^q} \quad \text{and} \quad E_{21} = \frac{1}{T^r} \quad \text{eqn 7}$$

$$E_{12} = T^r \quad \text{and} \quad E_{21} = C_e^q \quad \text{eqn 8}$$

$$E_{12} = \frac{T^{r/2}}{C_e^{q/2}} \quad \text{and} \quad E_{21} = \frac{C_e^{q/2}}{T^{r/2}} \quad \text{eqn 9}$$

Equation 7 would imply that seals on the beach respond primarily to tide height or to a direct correlate of tide height, while those in the water respond primarily to current or to a direct correlate of current. This seems more likely than the situations expressed in equations 8 and 9. In equation 8, seals on the beach respond primarily to current and those in the water respond primarily to tide height. In equation 9, seals on the beach and in the water respond to both tide and current. It seems unlikely that seals hauled out on the beach respond directly to current; however, indirect monitoring of current by these animals may be possible given that current is roughly the rate of change of tide height with respect to time ($C \approx dT/dt$), depending on local wind conditions, river discharges, basin shapes, and coastal geometries (Anonymous 1983; Duxbury, Duxbury & Sverdrup 2000). It was not possible to choose among equations 7–9 on the basis of the present data set. Identification of the individual functions $E_{12}(t)$ and $E_{21}(t)$ requires observation of seal numbers post-disturbance, with data collected on a temporal scale much finer than 1 h as the animals return to the beach.

Assuming the situation described by equation 7, the following functional hypothesis is suggested for seals that use the north beach of Protection Island as a haul-out site. Food availability peaks at flood current, which corresponds with low haul-out numbers. Hauled-out seals use falling tide levels as a cue to leave the beach to feed, a trend that continues until the midway point between low and high tides, when few or no seals remain on the beach. A decline in flood current, however, signals a decline in food availability so seals return to the beach.

The relationship between current and patterns of harbour seal movement has received little attention. Thompson *et al.* (1989), however, noted that harbour seals using haul-out sites in the vicinity of Eynhallow Sound, Orkney, UK, appeared to pattern their haul-out behaviours differently depending on whether the tide was rising (incoming current) or falling (outgoing current). They hypothesized that seals that spent less time on shore during rising tides were responding to increases in food availability brought about by incoming flood tides. Their observations and hypothesis are consistent with the model predictions presented here for seals using Protection Island.

It is of interest that models using C_e yielded better predictions than those using C (Table 1). Thus, it appears

that current direction may play a more crucial predictive role than current strength. This interpretation would be consistent with the functional hypothesis, given that food availability is likely to be maximal at flood current regardless of actual current speed. It is also of interest that equation 6 performed about the same as the model including solar elevation with $E(t) = C_e^q(t)S^u(t)/T^r(t)$ (Table 1). Other studies have found correlations between solar elevation (time of day) and haul-out behaviour (Stewart 1984; Watts 1992; Thompson *et al.* 1997). These correlations with time of day could be related to the fact that consecutive days have roughly similar tidal patterns; they also could be related to the effects of heat loading that commonly occur about midday and afterwards (Watts 1992).

GENERAL METHODOLOGY

The methodology employed in this study is quite general. It has been used to predict the diurnal abundance patterns of loafing seabirds in a single habitat (Henson *et al.* 2004) as well as in a system of habitats (Damania 2004), and can probably be used to predict the diurnal movements of a variety of marine birds and mammals. A general approach for modelling the occupancy dynamics of one habitat patch is as follows.

1. Habitat census data should be collected at discrete time intervals much shorter than the periods of environmental oscillations, and should be collected throughout the cycle of environmental change.
2. The per capita flow rates into and out of the habitat can be assumed to be proportional to functions $E_{12}(t)$ and $E_{21}(t)$ of environmental variables, and then incorporated into a two-compartment differential equation model in the form of equation 2.
3. The form of the function $M(t)$ that describes the maximal habitat occupancy should be based on historical maximal counts from the season of interest. The functional form of $M(t)$ for moulting season in seals, for example, would most probably be different than that for pupping season. Over short periods of time, M might be considered constant.
4. If the system recovers rapidly following disturbance, time scale analysis can reduce the differential equation model to a simple algebraic equation for dynamics in the absence of disturbance. The algebraic model will be easy to parameterize and simulate.
5. A suite of alternative hypotheses for $E_{12}(t)$ and $E_{21}(t)$ can be proposed, thereby generating a suite of candidate models. If the candidate models do not all have the same number of parameters, the best model should be selected with an information-theoretic criterion such as the AIC.
6. Parameter estimation should be based on a stochastic model that accounts for the major type of noise in the system.
7. Ideally, an independent data set (not used for model fitting) should be reserved or collected for the purpose of model validation or to test a priori model predictions.
8. If the environmental variables are largely deterministic, for example tide height, current speed, solar elevation

and hour of the day, the model can be used to make long-range predictions of habitat occupancies.

APPLICATION TO MONITORING HARBOUR SEAL HAUL-OUT

As mandated by the CSA and MMPA, significant resources are spent monitoring seal populations in the UK and USA. Much attention has been devoted to finding optimal times for such counts because seal population estimates are based on maximum haul-out counts (Pitcher & McAllister 1981; Stewart 1984; Thompson *et al.* 1989, 1997; Thompson, Van Parijs & Kovacs 2001; Adkinson, Quinn & Small 2003; Jeffries *et al.* 2003). The fact that haul-out patterns vary by season and among sites within seasons complicates this process (Sullivan 1980; Adkinson, Quinn & Small 2003; Simpkins *et al.* 2003). The modelling approach developed in this study not only provides management personnel with a powerful tool to identify more accurately optimal census times, but also enables them to identify the environmental forces correlated with local haul-out, to predict haul-out patterns into the future, and to identify times at which to minimize human disturbance.

At the Washington study site during the pupping season, managers can expect maximal daily haul-outs to occur during receding tides, approximately midway between high and low tides. The largest maximal daily haul-outs during the pupping season are expected to occur in the last week of July. Three points, however, must be emphasized. First, resource managers should note that the precise environmental function $E(t) = C_e^g(t)/T^r(t)$ identified in this study, along with the parameter estimates, are probably site- and season-specific. Each haul-out site and season may require a new application of the model selection procedure. Secondly, the modelling procedure is not designed to make predictions of population size but only numbers of hauled-out seals. Thirdly, the form of the function $M(t)$ depends on the seasonal context.

We wish to underscore two distinctive aspects of the methodology in this study. First, we used an information-theoretic criterion (in our case the AIC) instead of traditional hypothesis testing to choose the best model from a suite of a priori alternatives. This powerful and increasingly popular approach requires a more mechanistic understanding of the system, dovetails nicely with mathematical modelling, and penalizes models for overfitting. The information-theoretic paradigm for modelling species' distributions was featured in a recent series of articles (Cabeza *et al.* 2004; Engler, Guisan & Rechsteiner 2004; Frair *et al.* 2004; Gibson *et al.* 2004; Jeganathan *et al.* 2004; Johnson, Seip & Boyce 2004; Rushton, Ormerod & Kerby 2004) in the *Journal of Applied Ecology*. Secondly, our mathematical approach differs significantly from statistics-based analyses carried out by previous workers (Schneider & Payne 1983; Stewart 1984; Watts 1992; Thompson *et al.* 1997). Statistics-based analyses are useful in that they allow

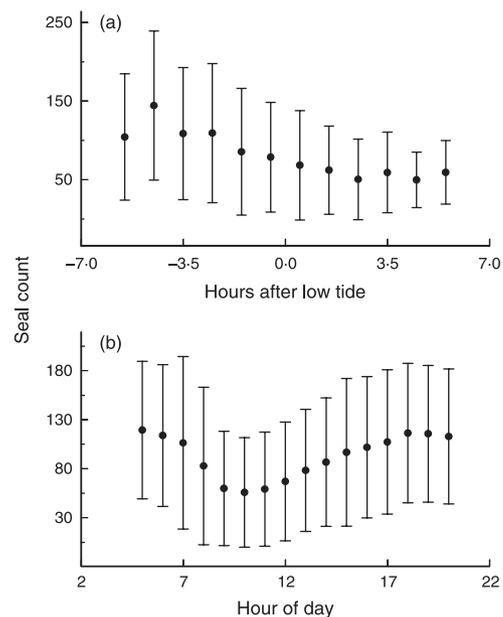


Fig. 3. Haul-out counts averaged in relation to (a) hours before and after low tide and (b) hours of day. Error bars depict standard deviations.

identification of environmental factors correlated with dependent variables. Commonly, however, such analyses entail data averaging, a procedure that can mask important relationships among variables. Figure 3 shows a graph generated when the data were averaged in relation to (a) hours before and after low tide and (b) hour of the day. Apparent patterns emerge, but the biweekly shift in count minima and maxima, daily haul-out pattern variability and seasonal haul-out pattern variability disappear, a result reflected in the large standard deviations (compare Figs 1 and 3). Moreover, haul-out censuses are often reported as proportions of the maximum number of seals hauled out at a site (Schneider & Payne 1983; Stewart 1984; Watts 1992); this can also mask informative differences among daily patterns.

For resource personnel who make management decisions about marine bird and mammal populations, we believe the mathematical methodology outlined in this study (in tandem with preliminary statistical exploration) can offer a distinct advantage over purely statistics-based recommendations.

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