

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

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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



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:

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.

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.

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

Given the first three assumptions, this becomes:

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:

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:

eqn 4

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

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):

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

eqn 5

The square-root transformation arises as a method of analysing data from a stochastic birth-and-death process. Suppose the number

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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:

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

where n is the number of observations, $\hat{\sigma}^2 = \text{RSS}(\hat{\theta})/n$ 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 $\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$, 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:

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

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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):

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.

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

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 pre-

Of course, this does not imply that E_{12} and E_{21} = T' . 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:

eqn 7

eqn 8

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 C_p ($T_{13.9}(l_e t) - 4.29(1)$). *Theu, witappear*

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

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