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Putting long-term, population monitoring data to good use: The Causes of Density Dependence in UK grey seals

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Summary

In a recent proposal submitted to NERC, members of SMRU and SCOS put forth the best solution to the fundamental problem confronting many long-term, population monitoring studies: The fact that monitoring a single component of the population ultimately leads to unreliable conclusions about its current and future state. We proposed the independent collection of calibration population data and the use of state-space models that have been developed specifically to deal with partially observed systems. In this briefing paper, we present the proposal and some of the criticisms levied against it.

1 Rationale

Many populations of large vertebrates are monitored either because of concerns about their conservation status or because their population dynamics are thought to provide a proxy for other processes within the ecosystem, such as changes in the size of prey populations. Most monitoring schemes involve regular counts of the most easily observed component of the population such as the number of territorial males or the number of offspring produced in a year. Assumptions about population structure are then used either to scale individual counts into population estimates or draw demographic inferences from the count time series. However, assuming a simple, multiplicative relationship between monitoring counts and total population size, is not valid in the presence of density dependence. Density dependence can operate on different demographic processes (e.g fecundity or age-specific survival) and therefore differentially affect specific components of the population. Paradoxically, this means that some of the longest time-series in ecology can no longer be used for the purposes for which they are being collected. If monitoring data are to be useful for scientific prediction and practical management, it is essential that they are calibrated with independent information on demography and that the causes of variation in these data are interpreted correctly by means of realistic population models. Such models need to properly account for systematic and environmental stochasticity and make use of known facts about the animals' behaviour and life-history. Here, this problem is examined within the context of the dynamics of UK grey seals, an increasing population that has been monitored globally for more than 20 years, studied locally at fine spatiotemporal scale and now showing evidence of density dependence. It is also the focus of many urgent issues in marine conservation and management.

With this proposal we sought to combine fundamental ecological research with an immediate application. We aimed to demonstrate how remote observation (both aerial and satellite) can be used to quantify population structure, calibrate estimates of population size obtained from monitoring data and pinpoint the proximate, demographic causes of density dependence in a population of large vertebrates.

2. Scientific Objectives

This proposal aimed to:

1. Identify and collect supporting population data that can help calibrate estimates based on monitoring counts by providing additional information about population size and structure.
2. Develop statistical models of those aspects of life history and individual behaviour that influence the calibration process.
3. Establish a flexible, fully stochastic model of grey seal population dynamics that can assimilate all available information and use it to estimate current population size, identify the demographic causes of density dependence and predict future trends.

3. Programme and Methodology

The proposal focused on grey seals (*Halichoerus grypus*) using the long-term, spatially explicit, population time series of pup production whose continuation is seen as essential by SMRU, SCOS and NERC. In recent years, the steady 7% annual increase in pup production that had been observed for decades has slowed down (to 0.5% in 2004).

It is possible that the population is approaching the environmental carrying capacity and, therefore, showing greater sensitivity to annual fluctuations in environmental covariates. Since seals feed at the upper levels of marine food chains there is a strong likelihood that they will be affected by changes in the distribution and abundance of food that could result from ocean warming, changes in the structure of the coastal seas around the UK and human exploitation of the marine environment.

In response to this, SMRU has developed and fitted to the pup-production time-series a Bayesian, state-space model aiming to 1) estimate total grey seal population size and 2) identify the demographic causes of density dependence. A state-space model, is composed of a state process, which models the true, but unknown, state of the population (i.e., the number of animals in each age group and region in each time period), and an observation process, which models how the survey data are generated given the true states. The model appears to provide a reasonable fit to the regional data (Thomas & Harwood 2003).

However, the posterior distributions for the demographic parameters indicate that the estimates of juvenile survival and fecundity are almost completely determined by the prior distributions used to describe the density dependent processes Thomas & Harwood 2005). As a result, SMRU's current estimates of the size of the entire British grey seal population have a much higher level of uncertainty than those provided to SCOS during the period of pure exponential increase. This is because different hypotheses about the density-dependent processes that are presumed to be responsible for the slow-down in population growth cannot be distinguished reliably with the existing monitoring data. It has become evident that this would require, either direct measures of fecundity and juvenile survival, or a new estimate of grey seal population size that is independent of the pupping data. Neither of these can be achieved with current resources without severely disrupting the annual pupping survey. Furthermore, even with additional resources, it is not feasible to measure either fecundity or juvenile survival precisely enough to distinguish between alternative causes of density dependence, because it is technically impossible to conduct mark-recapture studies with the broad spatial scale and recapture rates necessary for this purpose.

In contrast, it has been shown by simulation that including a new independent estimate of population size in the existing models would critically enhance our ability to distinguish between models involving different sources of density dependence. Outside the breeding season, the only other opportunity to count a large subset of the population is at their coastal haul-out sites. An independent population estimate is therefore achievable by aerial survey of these sites. It would be expensive and impractical to survey these sites annually as a replacement for the pup production time series. This one-off survey, and its incorporation within the modeling framework for the grey seal population, formed the central undertaking of the proposal.

A fundamental problem with this approach is that not all animals are hauled-out and available to be photographed at any one time. However, this could be estimated from the survey counts by using reliable estimates of the proportion of animals hauled-out on shore at any one time. SMRU has led the development and implementation of technology for the collection of satellite telemetry data from seals. To date, movements of 212 grey seals have been tracked, including adult females, adult males and juveniles from all around the UK coast. These data, equivalent to over 20,000 seal-days, are an invaluable source of information for how animals apportion their time between land and sea.

Pilot attempts to estimate population size from haul-out data have already been made based on older haul-out counts, from the period of exponential growth, the opportunistic by-product of a common seal (*Phoca vitulina*) survey. These counts were used in conjunction with concurrent telemetry data within a model which assumed that haul-out patterns do not vary between different animals, different locations, time of day, or seasons (Matthiopoulos *et al.* 2004). One or more of these assumptions was patently violated because the population point estimate was significantly lower than the number obtained from scaling-up pup count data. Although there is bound to be some inaccuracy and imprecision in estimates based on pup data, they, at least set a minimum to population size (1 pup per mother). Furthermore, recent studies on related species have shown that haul-out behaviour varies considerably between different types of animals and is therefore likely to bias population estimates. This indicates the need for modelling the covariates of haul-out behaviour in different classes of grey seals. We aimed to exploit the long-term and large-scale telemetry data on individual movement to build such models.

In order for these behavioural models to be useful for population estimation, it is also necessary to quantify the probability of misclassification of different classes of animals from the air. A local, ground-truthing survey carried out in parallel with the aerial survey can address this requirement. From the estimated proportions of time spent on-shore by different classes of seals and the matrix of misclassification probabilities it will be possible to calculate the likelihood of the aerial survey data occurring under particular combinations of population size and structure. By incorporating the haul-out time-balances and misclassification probabilities into the observation part of the existing state-space population model, the proposed haul-out counts will yield a clear picture of grey seal population structure. This would enable us to generate robust population predictions for the future management and conservation of the species.

Our proposed approach to each of the three scientific objectives was as follows:

Scientific Objective 1: *To identify and collect supporting population data that can help calibrate estimates based on monitoring counts by providing additional information about population size and structure.*

We would initially complete a comprehensive map of haul-out locations around the UK coasts. This information is available to SMRU from historical data. A helicopter equipped with a thermal imager would be used to survey the grey seal haul-outs along the Scottish coast. The map of haul-out locations would be used to design the aerial survey route. The survey would aim to cover all known haul-outs; i.e. all those known to be currently used by seals or to have been used in the recent past. Thermal imaging allows for rapid searching of the entire coast between known locations, giving a very high probability of locating individuals or small groups at previously unknown haul-outs. Twin-engine, fixed-wing aircraft would be used to survey the East coast where grey seals haul-out at discrete well-documented locations, and for remote offshore sites in North and West Scotland that are beyond the safe operating range of light helicopters. A preliminary survey in August 2005 showed that this was an effective and efficient survey method for these sites.

All seals encountered during the flights would be photographed. Oblique, high-resolution digital photography, using image-stabilised zoom lenses would provide both group shots, to facilitate accurate counting, and high-resolution close-up shots, to facilitate identification of sex and age class. This technique was tested in August 2005 with good results. We intended to conduct the grey seal survey during early August 2006, in conjunction with annual surveys of harbour seal populations. Preliminary examination of satellite telemetry data from grey seals indicates that the proportion of the population hauled out is as high then as at any other time with the exception of the annual moult. However, there is little telemetry data available for the moult and therefore surveying at that time would produce maximum uncertainty in the predictions of the haul-out behaviour model.

The photographs would enable us to identify the composition of haul-outs at the time of the survey. This is not an error-free process. Due to their position, orientation and pelage patterns some animals are more clearly identifiable than others. To parameterise the matrix of misclassification probabilities (see Objective 3, below), we would carry out a series of specific aerial sorties where the sex and age group of a sample of the photographed animals would be determined by ground-truthing immediately after the over-flight.

Scientific objective 2: *To develop statistical models of those aspects of life history and individual behaviour that influence the calibration process.*

We would collate auxiliary information for each haul-out site such as tidal cycles, land cover and slope, accessibility to sea, proximity to prey hotspots, breeding colonies and other haul-outs, susceptibility to wind and waves. The available satellite tag data would then be pre-processed using a standard set of algorithms developed by SMRU. This involves treating ARGOS error, identification of haul-out events by using data from the tags' wet/dry sensor and allocation of these events to the appropriate haul-out sites on the basis of concurrent location data. Since it is likely that animals of different age and sex display different haul-out pattern we would disaggregate our data into three different classes of animals, adult males, adult females and juveniles. We would use generalised additive models (GAMs) to regress the binary state (i.e. hauled-out v not hauled-out) of animals against global covariates (e.g. time of day), local covariates (e.g. aspect and substrate) and autocovariates (e.g. duration of current behavioural state). We would fit a separate model to data from each class of animal. By carrying out model selection we would arrive at those variables that determine haul-out behaviour of each class of animals and attempt to predict the haul-out behaviour of a "validation group" of animals not initially used for fitting. To properly account for individual variation and autocorrelation effects within telemetry data from the same individual, we would use mixed-effects GAMs. Such measures of individual variation would enhance our ability to make correct population-level inferences about the probability of hauling out.

Scientific Objective 3: *To establish a flexible, fully stochastic model of grey seal population dynamics that can assimilate all available information and use it to estimate current population size, identify the demographic causes of density dependence and predict future trends.*

Currently, the grey seal state-space model only uses as its input the estimates of pup production. We aimed to expand the model to incorporate the haul-out data collected under Objective 1. To do this, we would need to construct an observation model linking the haul-out data to the true numbers of adult males and females and of juveniles. This model must account for two sources of observation error: 1) omission of animals that were not hauled out at the time of the survey and 2) observer misclassification of those animals photographed on the beach. The empirical models of haul-out behaviour developed under Objective 2 would be directly incorporated in the observation model to deal with the first source of error and the matrix of misclassification obtained under Objective 1 would be used to deal with the second source of error. The additional data would allow us to expand the state-space model to include adult males (currently only adult females and juveniles are modelled). It would also allow us to use Bayesian model-selection methods to distinguish between the different demographic mechanisms mediating density dependence in grey seals. To enhance our ability to distinguish between the effects of density dependence and environmental variation, we would express the model's demographic parameters as functions of known environmental covariates (such as climatic trends or local primary productivity), as well as density. To enhance our ability to distinguish between the effects of density dependence and migration at a local scale we would build on the spatial component, already existing in the state-space model by 1) using a more detailed and biologically realistic spatial disaggregation and 2) using more informed priors about movement. Both of these developments would come from modelling work on seal movement already in progress in SMRU under a different project. By combining the long-term breeding data and the haul-out data, we would increase our knowledge of the demography of the seal population, and considerably reduce the uncertainty in our estimates of total population size. We would review the implications of this new model for the future of the UK grey seal population. Of particular interest would be scenarios involving climate change. Within the state-space framework, these can readily be modelled by providing the fully-fitted model with hypothetical time series for the climatic covariates of the demographic parameters.

2. Criticisms

The salient referee comments (C) and our responses (R) to them can be summarised as follows:

C1. What is the wider applicability of this work to other species?
R1. We pointed out that this work is readily applicable to other monitoring data sets and listed five examples that would benefit from the same treatment. Each of these was linked to, at least, one of the investigators on the proposal.

C2. There is a need for an analysis of the sensitivity of population estimates on different calibration data.
R2. We drew attention to Thomas & Harwood (2005) that performed just such an analysis.

C3.Haulout probabilities are presented as fixed quantities
R3. We pointed out that the proposal acknowledged 1) spatial covariates (e.g. geomorphology of haul-outs), 2) temporal covariates (e.g. time of day), 3) autocovariates (e.g. duration of trip preceding haul-out event) and 4) individual covariates (e.g. sex, size). We did not propose to examine the effects of density, food supply and weather on haul-out probabilities because 1) the density of seals at haul-outs is remarkably constant, 2) there is very little information about the distribution of prey species at the scale of individual haul-outs, 3) the susceptibility of seals to weather is better captured by fine-scale features such as haul-out orientation rather than the larger scale processes recorded by weather stations and 4) preliminary analyses of grey seal haul-out behaviour has already indicated that much of the variability in haul-out patterns can be explained in terms of the covariates mentioned in the proposal.

C4. Objectives could be more focused and lead to a hypothesis-driven rather than descriptive data-driven project.
R4. It is was difficult to see how the proposed study could be interpreted as “descriptive” since the core of our proposal was the fitting of rival mechanistic models to large data sets using modern estimation techniques. A mechanistic model is the exact, mathematical formulation of a biological hypothesis and the proposed work was explicitly hypothesis-driven.

C5. It is unclear that there will be sufficient information in the new data to allow the desired improvements in population estimates.
R5. In response to this comment, using real data, we produced a detailed sensitivity analysis of the population estimates on a single calibration data point. This indicated that the proposed work would give considerably more accurate population predictions irrespective of the value of the calibration point. Furthermore, we showed that these improvements would be robust to measurement imprecisions in the calibration point.

C6. The value of the one-off survey may be limited for long-term predictions
R6. It is true that as the environmental covariates of population dynamics vary over time, the error in the model’s predictions will increase. Although one of the objectives of the proposal was to forecast population trends, we were not anticipating to be able to predict population size beyond a decade. Nevertheless, we did expect to resolve the demographic causes of density dependence under the current set of environmental conditions. The link between primary productivity (or other indices of prey availability) and seal population size is not yet established. However, the fine-scale foraging habitat preferences of UK seals and the multi-species functional responses of grey seals to prey availability currently form part of parallel work being conducted by SMRU.

3. Final outcome

The moderating panel made three fundamental comments (CM) to which we provide brief responses (RM) below:

CM1. The biggest contributor to uncertainty may be the method of collecting annual counts in the first place.
RM1. This is precisely why we proposed to calibrate this time series with independently collected data of a different subsection of the population.

CM2. Improvements to downstream analytical techniques applied to that data would not actually lead to significant improvement in predictive ability.
RM2. The detailed, quantitative investigation given as a response to C6 should have settled this beyond reasonable doubt.

CM3. This study would have limited application
RM3. This was a re-iteration of C1. The interpretation of the word "limited" is, of course, subjective. The equally relevant case study species we proposed in R1 were harp seals, Canadian grey seals, sea lions, Pacific salmonids and guillemots.

The proposal received an Alpha 3 grading and was subsequently rejected.

4. Current priorities

This proposal was prompted by discussions between SMRU and SCOS. Its main thrust was the perceived need for calibration of SMRU's long-term pup production time series. It must, firstly, be discussed whether, in view of more recent data, this work is still as important as previously thought.

Secondly, it must be decided whether the approach outlined above is still the most cost-effective and fruitful for the purposes of SCOS.

Finally, SMRU and SCOS may want to review the options for funding such work.

References

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