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The nature of density dependence in British grey seal populations

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Summary

We analysed time series of pup production estimates from 42 British grey seal colonies for evidence of density dependence. Nearly 90% of colonies showed evidence of density dependence with a 1 year time lag (likely to be caused by changes in adult survival or fecundity), whereas only 2 colonies showed evidence of density dependence with a 6 year time lag (likely to be caused by variations in first-year survival).

Introduction

In recent years, the growth rate of many grey seal colonies in Scotland has slowed considerably, suggesting that some density dependent processes are operating. The only such process that has been documented for grey seals relates to pup mortality at the Farne Islands (Harwood & Prime 1978). However, the levels of pup mortality required to explain the observed declines in growth rate are much higher than those that have recorded at any British grey seal colony (Thomas & Harwood 2003). This has led to speculation that other density dependent processes may be involved.

Fecundity and adult survival rates are notoriously difficult to estimate precisely, and it is not surprising that there is no evidence of density dependence in these demographic parameters for British grey seals. We have therefore adopted a more empirical approach to the problem by analysing the time series of pup production estimates from individual grey seal colonies, using an approach developed by Dennis and Taper (1994). The way that density dependence is formulated in this approach means that any relationships that are detected cannot be incorporated directly into process models of grey seal population dynamics. However, we believe that it is a useful diagnostic tool for identifying those density dependent processes that are likely to be most important. Density dependence in adult survival or fecundity will affect growth rate with a 1 year time lag, whereas density dependence in pup survival will affect growth rate with a time lag of approximately 6 years (the mean age at which females breed for the first time – Harwood & Prime 1978).

Material and Methods

Dennis and Taper (1994) developed a test for detecting density dependence in a time series of observations of population abundances. The null hypothesis is that the population is undergoing stochastic exponential increase, stochastic exponential decline, or a random walk. The basic model is a Ricker equation of the form:

$$N_t / N_{t-1} = \exp(\beta_0 + \beta_1 N_{t-1} + \beta_2 N_{t-6} + \sigma Z_t)$$

where N_t is pup production in year t, and σZ_t represents random variation in the population growth rate (the Z_t are independent Normal(0,1) deviates). Values of β_1 or $\beta_2 \leq 0$ are taken as evidence of density dependence.

Transforming the model to a logarithmic scale and rearranging gives the following linear relationship:

$$X_t = X_{t-1} + \beta_0 + \beta_1 \exp(X_{t-1}) + \beta_2 \exp(X_{t-6}) + \sigma Z_t$$

where $X_t = \ln(N_t)$. We fitted this relationship to data on the estimated pup production at 42 British grey seal colonies between 1984 and 2002. Data from 10 other colonies were excluded, either because of missing data points or because the colonies were first surveyed after 1984.

Simple linear regression provides unbiased estimates of the parameters of this model, but estimates of uncertainty are biased because of the non-independence of the dependent and independent variables in the regression. To overcome this, we estimated confidence limits about the parameter estimates using a parametric bootstrap. After fitting each model, we generated 2000 simulated datasets from the estimated model

$$X_t = X_{t-1} + \hat{\beta}_0 + \hat{\beta}_1 \exp(X_{t-1}) + \hat{\beta}_2 \exp(X_{t-6}) + \hat{\sigma} Z_t^{[i]}$$

where $Z_t^{[i]}$ is a pseudo random Normal(0,1) deviate generated independently for each time point *t* and simulation *i*. We then re-fit the model to each of these 2000 simulated datasets to obtain 2000 bootstrap estimates of the model parameters. To calculate 95% two-sided confidence intervals on each model parameter, we ordered the 2000 bootstrap estimates, and selected the 50th and 1951st We declared the estimate of that parameter to be statistically significant if this confidence interval did not include 0.0.

Results

Table 1 summarizes the results of the analysis. Thirty-seven of the 42 colonies showed evidence of density dependence with a 1 year time lag, whereas only two colonies showed evidence of a 6 year lag. However, 15 colonies showed evidence of a **positive** relationship between pup-productions separated by 6 years. This implies that survival of pups may be enhanced in years of high production.

Table 1. Results of time series analysis of density dependence in British grey seal colonies

Parameter β_1 (1-year lag)

	n	negative	positive	not significant
All colonies	**42**	**37**	**0**	**5**
North Sea	3	3	0	0
Inner Hebrides	9	9	0	0
Outer Hebrides	11	8	0	3
Orkney	19	17	0	2

Parameter β_2 (6-year lag)

	n	negative	positive	not significant
All colonies	**42**	**2**	**15**	**25**
North Sea	3	0	3	0
Inner Hebrides	9	1	2	6
Outer Hebrides	11	0	4	7
Orkney	19	1	6	12

Discussion

Our results suggest that the predominant form of density dependence in British grey seal populations operates with a 1 year time lag. This is most likely to be the result of changes in adult survival or fecundity. Harwood & Rohani (1996) concluded that there are few obvious sources of density-dependent adult survival. We have therefore modified the model we use to estimate grey seal population size to include density dependent fecundity as well as density dependent first-year survival.

Dennis and Taper's (1994) method assumes that there is no observation error. However, it is well known that the presence of observation error produces an inflated Type I error rate, so we expect the frequency of false positive results in Table 1 to be higher than the nominal 5% level. Shenk *et al.* (1998) performed extensive simulations to assess the effect of observation error on the performance of this and other methods. Their Figure 6 indicates that a coefficient of variation (CV) of 10% results in only a small increase in the Type I error rate, although this increases sharply at a CV of 40% and greater. Duck et al. (in prep.) report that the CV of grey seal pup production estimates is around 7%. We therefore conclude that ignoring observation error did not have a major effect on our results.

References

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