Detecting Density Dependence in Recovering Seal Populations

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Abstract Time series of abundance estimates are commonly used for analyses of population trends and possible shifts in growth rate. We investigate if trends in age composition can be used as an alternative to abundance estimates for detection of decelerated population growth. Both methods were tested under two forms of density dependence and different levels of environmental variation in simulated time series of growth in Baltic gray seals. Under logistic growth, decelerating growth could be statistically confirmed after 16 years based on population counts and 14 years based on age composition. When density dependence sets in first at larger population sizes, the age composition method performed dramatically better than population counts, and a decline could be detected after 4 years (versus 10 years). Consequently, age composition analysis provides a complementary method to detect density dependence, particularly in populations where density dependence sets in late.

Keywords Density-dependent population growth · Age-structured populations · Population management · Detecting population trends · Environmental stochasticity

INTRODUCTION

The population growth rate is perhaps the most important parameter in population ecology as it reflects vital information about the condition of a population, such as current age-specific fecundity and mortality. However, despite its significance in population analyses the causative mechanisms behind the status of population growth are generally difficult to determine (Murdoch 1994; Dennis et al. 2006).

One important factor controlling population growth is density, and density dependence in form of food shortage

as populations grow has been demonstrated in many species (e.g., Stenseth et al. 1998; Turchin 1999). The most common way to test for effects of increasing density is to use autoregressive analysis and correlate long-term trends of declines in population growth with increasing population size (Murdoch 1994; Stenseth et al. 1998; Turchin 1999; Bjornstad and Grenfell 2001; Sibly and Hone 2002). Time series of abundance data can also be used to evaluate if a population has reached or is fluctuating around its carrying capacity (Lande et al. 2002; Saether and Engen 2002). However, these patterns are obscured by environmental stochasticity that introduces variation in population size independent of density (Tuljapurkar 1990; Lande 1993; Murdoch 1994; Bjornstad and Grenfell 2001; Lande et al. 2002). Furthermore, census errors in abundance estimates will lead to artificially inflated estimates, which may conceal early signs of density dependence (Shenk et al. 1998; Dennis et al. 2006; Freckleton et al. 2006).

Seals are long-lived mammals with high adult survival and relatively low fecundity. Most seal populations therefore comprise large proportions of adults, and the intrinsic population growth rate is usually low (Fowler 1981; Boveng et al. 1998; Harkonen et al. 2002). This makes seal populations comparably resistant to short-term changes in the environment. Population dynamics of seals are primarily affected by intra- and inter-specific competition and predation (Boveng et al. 1998; Mathews and Pendleton 2006), disease (Heide-Jørgensen et al. 1992; Harding et al. 2002), and reduced diversity or abundance of prey species (Innes et al. 1981; Merrick et al. 1997; Krafft et al. 2006; Bowen et al. 2007).

Seal populations show age-specific responses to changes in density. Juvenile survival rate often decreases rapidly with increasing density, whereas adult survival is relatively constant (Lett et al. 1979; Bowen et al. 2007), which can

lead to changes in age composition in growing populations (Caughley 1974; Eberhardt 1977; Caswell 2001). Higher density also affects fecundity if food becomes scarce, since females show delayed age at sexual maturity and resorb fetuses if energy reserves are low (e.g., Bengtsson and Siniff 1981; Kjellqwist et al. 1995; Bowen et al. 2007). Moreover, it has been suggested that both males and female mature later when food is limiting (Krafft et al. 2006). As a consequence, the reproductive output declines rapidly under harsh conditions, and increasing densities in seal populations tend to change the age structure toward higher proportions of adults (Harwood and Prime 1978).

Declining growth rates can thus indicate that a population is approaching its carrying capacity, and detection of such changes and their reasons is crucial for management strategies aiming at attaining natural abundances of seal species (HELCOM web portal, www.helcom.fi). Indicators of density dependence other than population growth would be valuable, and we investigate if changes in age composition can be a useful estimator. First we model population growth in Baltic gray seals for different scenarios of density dependence and extract the resulting data series on population size and fraction of adults over time. As if unaware of the underlying processes, these time series are sub-sampled and analyzed statistically. We investigate how the statistical power to detect underlying density dependence depends on the length of the time series, the chosen growth function, and on the degree of environmental variability.

METHODS

The Model

Let N_i denote the number of female seals at the end of their i th year of age, where $i = 0$ is a newborn pup and $i = c$ is the maximum age (Fig. 1). We assume even sex ratios for

Fig. 1 General age-structured life cycle of a seal population, where m is the age at which a seal starts reproducing, and c is the maximum age

all age classes (Harding et al. 2007). The mean age at first parturition is termed age m (Fig. 1).

Density dependence was included by multiplying pup survival (p_p) with the density-dependent factor $(1 - (N/K))$ from the logistic equation. The number of 1-year olds (N_1) can then be estimated for each year (t)

$$N_{1(t+1)} = \left(1 - (N_{\text{tot}}/K_e)^\theta\right) p_p N_{0(t)} \quad (1)$$

where K_e is a scaling factor that determines the carrying capacity K and theta θ regulates the shape of the curve. We compare model simulations, where growth is a linearly decreasing function of density ($\theta = 1$), to simulations based on an initially weaker response to density ($\theta = 4$), i.e., density-dependent effects set in first at high population sizes (Fig. 2a). The variability in carrying capacity is commonly assumed to affect pup survival and fecundity simultaneously and to the same extent (Lett et al. 1979; Bengtsson and Siniff 1981; Kjellqwist et al. 1995; Bowen et al. 2007). The variability in carrying capacity in our

Fig. 2 **a** Pup survival (p_p) as a function of abundance for the Baltic grey seal population growing according to the logistic equation, i.e., $p_p(t) = p_p(1 - (N_t/K_e)^\theta)$, for linear density dependence, $\theta = 1$ (solid line) and initially weak density dependence, $\theta = 4$ (dashed line). **b** Abundance as a function of time for $\theta = 1$ (solid line) and $\theta = 4$ (dashed line)

model affects only pup survival since simulations reveal that this generalization has negligible effects on population size and structure.

The number of newborn pups (N_0) in the model depends on the number of adult females (N_a) and their fecundity (f) and survival (p_a)

$$N_{0(t+1)} = f_m p_s N_{m-1(t)} + f p_a N_{a(t)} \quad (2)$$

where the first factor includes the pups born by the youngest mature seals ($f_m = f/2$), and where p_s is the sub-adult survival. The number of seals in each age (i) older than 1 can be obtained by multiplying the number of seals in the previous year class ($i - 1$) the year before their survival $N_{i(t+1)} = p N_{i-1(t)}$, where p is either sub-adult or adult survival (Table 1).

We parameterize the model with age-specific survival and fertility rates for Baltic gray seals (Harding et al. 2007) (Table 1). K_e (Eq. 1) is scaled such that the realized carrying capacity K is 100,000 individuals, as given by historical population sizes (Harding and Harkonen 1999) (Table 1).

Variation in Carrying Capacity

The carrying capacity K of a population is rarely stable but varies among years depending on fluctuations in vital resources, predators, climate, and other environmental factors. For example, availability of important prey species for seals, such as young cod, often show extensive annual variations (ICES Advice 2007). Here we assume values of K to be gamma distributed, since this distribution is always positive and can easily be modified to have a range of different shapes. The gamma distribution can be used to describe the annual variation in cod abundance in the North Atlantic (Brynjarsdottir and Stefansson 2004; ICES Advice 2007), and also many other naturally occurring distributions, such as population and species abundance (Cadigan and Myers 2001; Benton et al. 2002) and species diversity

(McCain 2005; Cornell et al. 2007). The gamma distribution is a continuous probability distribution (see the Poisson distribution for a discrete counterpart) governed by two parameters, α and β , which through the gamma function, $f(x) = (1/\Gamma(\alpha)\beta^\alpha)x^{\alpha-1}e^{-x/\beta}$, where $0 < x < \infty$, determine the expected value and the variance of the distribution. We calculate the minimum and maximum time span required for detection of density dependence (dd) by adding either low or high random variation to K , which is represented by a coefficient of variation (cv_K) of 0.01 and 0.5, respectively. The high variation ($cv_K = 0.5$) is taken from the estimated annual variation in cod abundance in the Baltic Sea (ICES Advice 2007). We choose the expected value of K_e such that the realized carrying capacity K is 100,000 individuals (Table 1). In the scenario with low variation the carrying capacity is close to normally distributed where K varies between $100,000 \pm 2000$ seals in 90% of all years. The scenario with high variation allows K to vary between 40,000 and 180,000 in 90% of all years.

Trend Analysis

A trend analysis (Gerrodette 1987) was performed to investigate the following questions; first, if the population is increasing, is it increasing at the inherent maximum growth rate or is it subject to density dependence? Second, what is the statistical power to detect a decreasing slope or a change in population structure, and how does the statistical power depend on the phase of population growth and the number of years sampled? If R represents the response variable (population size or adult fraction in this study), the polynomial $\ln(R_t) = a + b_t + c_t^2$ is fitted to the data, where a is $\ln(R)$ at the start of the time window used for analysis. If the second derivative c is not significantly different from zero, then b is the exponential rate of change in growth (or age structure). If c is significantly different from zero the growth rate (or age structure) has changed over the time period of the analysis. We first look for a trend in the data (i.e., is

Table 1 Model parameters for the Baltic gray seal population, when density dependence acts on pup survival

Variable	Value	Description
f	0.75/2	Adult fertility (adults of age m has fertility $f/2$)
p_p	0.7	Pup survival without density dependence
p_s	0.938	Sub-adult survival
p_a	0.9562	Adult survival
m	5	Age at first parturition
c	44	Maximum age
K	100,000	Carrying capacity
K_e	139,000 ($\theta = 1$, $cv_K = 0.01$)	K_e (Eq. 1) is scaled such that mean carrying capacity K is 100,000 for two types of density dependence and different levels of environmental variability
	152,000 ($\theta = 1$, $cv_K = 0.5$)	
	109,000 ($\theta = 4$, $cv_K = 0.01$)	
	101,000 ($\theta = 4$, $cv_K = 0.5$)	

c significantly different from zero) and second, we check if the slope is increasing or decreasing with time, which in our model is equivalent to that the population growth (N_{t+1}/N_t) and/or the adult fraction ($N_{a,t+1}/N_{tot,t+1}$) varies with N_t . The trend is analyzed by estimating the growth rate or the adult fraction from a number of subsequent counts (in the range from 2 to 40 years).

The fecundity in our model is static, and the stochastic variability in K is conveyed to the population through density-dependent pup survival. In real seal populations, however, environmental variability affects fecundity as well as pup survival. This does not affect the adult and sub-adult ratio of the population, but may lead to large fluctuations in the proportion of pups (Kjellqwist et al. 1995). It is therefore difficult to use pups in age composition analysis even when estimates are accurate. Here we exclude pups from the age composition estimates and calculate the fraction of adults to adults and sub-adults, i.e., $N_{a,t}/(N_{a,t} + N_{s,t})$. The age structure is determined by randomly selecting individuals from 1% of the population, and the number of seals classified to belong to each age class is therefore binomially distributed. All simulations are repeated 1,000 times to calculate the probability of detecting a trend in population growth and structure. We then compare the power (i.e., the proportion of the trials where the underlying trend is discovered) to detect the presence of density dependence during low and high variation in K with the two different methods.

RESULTS

The population age composition changes gradually as population density increases. At small population sizes and during exponential growth adults comprised $\approx 60\%$ of the population for both types of density dependence (set by θ). As density dependence began to act on pup survival and the population growth rate dropped, the proportion of adults started to increase. The slope in the adult fraction increased most just before the population reached carrying capacity (at about year 100 in the simulations, Fig. 2). The proportion of adults changed to $\approx 80\%$ at carrying capacity for both forms of density dependence. The rate of change in age composition was greater for an initially weak density dependence compared to logistic growth with linear density dependence.

Fitting the second-order polynomial to the logarithm of the number of seals, three regions of growth can be classified; (region 1) exponential growth, where the curve is approximately linear with a significantly positive slope and a second derivate close to zero; (region 2) density-dependent growth, where a significant positive slope in combination with a significant negative second derivative

characterizes the transition from the exponential growth regime to the asymptotic plateau; and (region 3) asymptotic growth, where a zero slope cannot be rejected, and where the population fluctuates around the carrying capacity K .

Analyzing the logarithm of the population size under logistic growth ($\theta = 1$), the power to detect density dependence was highest during the latter time period of growth (region 2), and a measurement window of 16 or more years was required during low variation in K (Fig. 3a). Power decreased dramatically with decreasing window size (Fig. 3a). When variation in K is high, the power dropped significantly, and a measurement window of 35 or more years was required to detect density dependence (Fig. 3b). Power was slightly higher using the initially weak growth function ($\theta = 4$), and power was highest for measurement windows of 10 years or more (Fig. 3c). When variation was added to K similar effects appeared as for the linear growth function, and a measurement window of at least 37 years was required to detect density dependence (Fig. 3d).

Time series of age structure revealed density dependence with a slightly, to much higher probability compared to time series of population size (Fig. 4a–d versus 3a–d). Using logistic growth ($\theta = 1$), a measurement window of at least 15 years was required to detect density dependence (Fig. 4a). Power was relatively high even for measurement windows down to 8 years. When adding environmental variation to carrying capacity K a measurement window of 38 or more years was required to detect density dependence (Fig. 4b). However, for the initially weak growth function ($\theta = 4$) probability of detecting a trend was as short as 4 years (Fig. 4c). It was also possible to detect a sudden decrease in the fraction of adults, which occurred as a result of overcompensation just after reaching K (Fig. 4c). Power decreased quickly when environmental variation was added to K , and a measurement window of at least 38 years was now required to detect retarded growth (Fig. 4d).

DISCUSSION

Mammals with low mortality and low fecundity, such as seals, respond slowly to environmental variability, facilitating detection of density-dependent changes in population composition compared to animals with more rapid life cycles (Fowler 1981; Saether et al. 2005). By adjusting recognized modeling techniques and theory (Gerrodette 1987; Caswell 2001; Sibly et al. 2005) to empirically based simulations, this study shows that seal population structure as well as population growth rate are feasible parameters for detecting logistic growth using Gerrodette's (1987) polynomial. As in all similar studies,

data must either be representative of the population or the range and direction of the census error should be known. This allows a population trend analysis in cases where abundance data are lacking, but more precise data on population structure are available (Forcada 2000; Taylor et al. 2007). However, similar age structure patterns may occur as a result of different mechanisms, and care must be taken when analyzing trends in historical records where sampling bias (e.g., by hunting) in age ratio is unknown (Caughley 1974; Holmes and York 2003; Taylor et al. 2007).

Obviously, it can be difficult and time-consuming to identify significant trends if census error is large, since a directional bias increases the risk of detecting false trends (Gerrodette 1987; Shenk et al. 1998; Dennis et al. 2006; Freckleton et al. 2006). Dennis et al. (2006) proposed a method that would account for census error, but this method requires density dependence to be described by a Gompertz function. Our approach allows the growth function to be more flexible, so that increasing variability in population growth as the population approaches

K can mimic the effects from natural variations in prey abundance (Brynjarsdottir and Stefansson 2004; ICES Advice 2007). Density dependence was therefore described by the theta logistic function (e.g., Turchin 2003). Error is instead accounted for by the binomial sampling of 1% of the population, which in combination with a varying K provides a moderate and unbiased estimate of sampling error. In practice this means that the error increases rapidly when the population approaches carrying capacity and the variation in K become apparent.

Density dependence (dd) also acts on adult and sub-adult survival. However, adult survival is often affected in a later phase of population growth, i.e., close to or at carrying capacity K (Eberhardt 1977). Stochastic fluctuations are generally large at K , and at this point neither population size nor age structure is a useful parameter for detecting dd. Furthermore, since adult seals have long life spans and reproduce several times during their lifetimes, dd has been shown to primarily affect pup survival and fertility (e.g., Lett et al. 1979; Bengtsson and Siniff 1981; Kjellqvist et al. 1995).

Fig. 3 The probability to detect a significant trend in time series of abundance data (as given by the gray scale of the shaded area) for a population growing from low numbers at year 1 to carrying capacity in years 100–200 (as depicted in Fig. 2). During this time, population size is estimated from subsets of the data and analyzed for signs of density dependence. As the measurement window of the sub-sampled

time series is increased (y-axis), the probability to detect a significant trend increases. **a, b** Illustrate the case when an ordinary “symmetric” logistic growth function is applied. **c, d** Illustrate a skewed, initially weak, density dependence. **a, c** Show cases of low environmental variability whereas **b** and **d** show cases of high environmental variability

Fig. 4 This figure is directly analogous to Fig. 3, but instead of trends in population size the data sampled here is age structure (adult proportion as a ratio to total population size excluding pups). Window size is the number of years over which the sub-sampling is performed (y-axis). The intensity of the gray scale represents the probability to

detect a significant trend in a time series of age composition data during logistic growth (a, b), during initially weak density dependence (c, d) and for low (a, c) and high (b, d) environmental variability

Whether population size or age structure should be used to look for changes in trends depends on the amount of error in both estimates. For example, externally imposed mortality, such as hunting, can give biased age ratios, unless the hunt is performed during times of the year when the population composition on land is representative of the population, or when the expected population composition is known (Kokko et al. 1997; Thompson et al. 2007). Determining age structure from censuses can be difficult because of differences in haul-out behavior among age groups and seasons, except for species where the age- and sex-specific behavior is known (Harkonen and Harding 2001; Carlens et al. 2006). Pup production can vary dramatically among years (see Jussi et al. 2008 for an example where poor ice years affect ringed and gray seal pup survival), which is reflected in the number of sub-adults the subsequent year. However, effects of error can be minimized by always performing the census or hunt during the same time of the year (Harkonen and Harding 2001; Carlens et al. 2006), and by excluding age or stage

structures that are most sensitive to environmental variability from the trend analysis.

The EU Habitat Directive and the 2006 HELCOM seal recommendation state that Baltic seal populations should have “natural abundances,” which is interpreted as: populations should be close to their carrying capacities (HELCOM web portal, www.helcom.fi). Censuses of gray seal abundance in the Baltic are focused on numbers hauled out during their peak molting period. A possible approach to study changes in age composition for these seals is to investigate if the ratio of numbers of pups born to numbers of seals hauled out during molt changes over time given that the accuracy of estimates is moderate to high. Consequently, analysis of changes in age structure can be a useful complement to abundance data in identifying density dependence. However, long and accurate time series are still required for successful analyses, since both population growth and age structure are sensitive to environmental variability and census error. We therefore recommend collection of data on both abundance and age

structure whenever possible, and certainly, to maintain long-term monitoring programs.

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