A Modified Theta-logistic Model with Cooperation for Understanding Species Extinction

Amiya Ranjan Bhowmick[1], Bapi Saha[2], Joydev Chattopadhyay[1] and Sabyasachi Bhattacharya[1]
[1]*Agricultural and Ecological Research Unit, Indian Statistical Institute, Kolkata*
[2]*Government College of Engineering and Textile Technology, Barrack Square, Berhampore*

SUMMARY

In general population growth models account for two apparently opposite forces (1) the natural proclivity of the species population for exponential growth, and (2) a negative density-dependent feedback governed by the environmental carrying capacity. However, the role of cooperation amongst conspecifics is a third factor that enhances population growth, and is generally ignored in currently available growth models. We consider cooperation as a fundamental aspect of population growth along with the other two factors and propose an extended family of generalized logistic growth models. Modified version of the proposed model are also discussed when cooperation is feeble. We consider stochastic counterpart of the models incorporating demographic noise to estimate the extinction measures, probability of extinction and expected time to extinction. Parameters of the proposed model are estimated using both simulated and real life data from Global Population Dynamics Database and their significance are justified in ecological context. We develop an inferential procedure to compare the biotic potential (maximum per capita growth rate) of two populations. Our analysis can have an impact in understanding extinction patterns and enable us to identify demographic threats which lead to decision making for conservation management.

Keywords: Allee effect, Grid search, Weighted least squares, Biotic potential, Global population dynamics.

1. INTRODUCTION

Every species has its own natural propensity towards unlimited growth for producing replica or offspring without considering the fate of other species sharing the same resources. If the activity of nature is silent the species grows unboundedly. With limited resources in ecological system the unlimited growth process is balanced by nature. As a result the coexistence of different species is possible. Thus for any species the overall growth mechanism can be thought of as a convolution of two apparently opposite forces: (1) the natural proclivity of the species population for exponential (Malthusian) growth, and (2) a negative density-dependent feedback governed by the environmental carrying capacity.

All growth models account for these two apparently opposite factors that govern population dynamics. However, the role of cooperation amongst conspecifics is a third factor that enhances population growth, and is generally ignored in currently available growth models. In many species, conspecific cooperation within a population is prominent in parasocial and eusocial animals (Wilson 2000), and cooperative breeding is common in diverse animal taxa (*e.g.*, spiders (Bilde *et al*. 2007), ambrosia beetle (Peer and Taborsky 2007), birds (Jetz and Rubenstein 2011), coati (Gompper 1997)). Cooperation in reproductive behavior is likely to act as a positive density-dependent feedback to population growth (Avilés 1999).

Corresponding author: Amiya Ranjan Bhowmick
E-mail address : amiya_r@isical.ac.in; amiyaiitb@gmail.com

The concept of cooperation is closely related to Allee effect (Allee *et al*. 1949), named after Prof. Warder Clyde Allee that corresponds to low per capita growth rate (hengeforth, PGR) when the abundance is small. Sufficient observational and experimental data show that cooperation is another fundamental principle in animal species (Allee *et al*. 1949). Such positive density mechanism is observed among natural populations due to some demographic forces such as mating limitations, cooperative breeding, cooperative feeding, poorer defence against predators, lower foraging efficiency, intra-specific interactions, predator-satiation etc., predominating at low densities (Dennis 1989, Kramer *et al*. 2009). In view of the empirical evidences of extinction threats and the related theoretical consequences, Allee effect received much importance in ecology and conservation biology.

In addition, populations are subject to stochastic fluctuations present in nature. Demographic stochasticity and environmental stochasticity are the main factors affecting the growth of natural populations. The demographic stochasticity is the chance variation in the number of individual births and deaths. Nevertheless demographic stochasticity is generally thought to have an important effect on dynamics only in small or sparse population *i.e.* exactly the population in which the Allee effect is expected to operate (Courchamp *et al*. 2008). However, the environmental stochasticity is also important that direct the population to low density, after which the positive density feedback starts acting. When there exists a threshold population size below which PGR becomes negative, then it becomes more sensitive towards demographic fluctuations, that increases the probability of extinction.

In this article, we consider cooperation as a fundamental aspect of population growth along with the other two factors explained above and propose an extended family of generalized logistic growth models. Modified version of the proposed model is also discussed when cooperation is feeble. We consider stochastic counterpart of the models incorporating demographic noise to estimate different extinction measures. Parameters of the proposed model are estimated using both simulated and real life data and their significance are justified in ecological context. We develop an inferential procedure to compare the biotic potential (maximum PGR) of two populations.

The different sections of the manuscript is organized as follows: Section 2 contains the information regarding the data sets used. The model formulation (both deterministic and stochastic) and corresponding ecological justification is provided in Section 3. In Section 4 the estimation procedure is discussed and a testing procedure for the biotic potential is developed in Section 5. In Section 6 the results and data analysis are described and in Section 7 we have discussed how our methods can be used as a conservation management tool. A general discussion on the findings are described in Section 8. In Section 9 we draw conclusion and provide future directions.

2. THE DATA

2.1 Simulated Data

For model illustration and to verify analytical findings we emphasize more on simulated data. By taking an arbitrary sequence of the values of the variable x and using Eq. (1), we can generate PGR values for a fixed set of parameter values. The parameter r is the intrinsic growth rate, γ denotes the coefficient of cooperation, K is the carrying capacity of the environment and θ is the strength of density dependence at carrying capacity. We know that from practical point of view PGR is generally bounded and in rare situation it may exceed 1. PGR is expected to exhibit different monotonic structures (concave, convex, linear and non-monotonic convex) for different choices of parameters (r, γ, θ, K).

$$rx^{\gamma}\left[1-\left(\frac{x}{K}\right)^{\theta}\right] \tag{1}$$

If we choose these x values as the population size at different time points, the growth curves always exhibit linear trend, which is unrealistic. As a result, for corresponding unusual PGR trends we would not get sigmoidal or exponential population trends together. To achieve this first we generate PGR and then by using the empirical estimate of PGR $R(t) = \ln\left(\dfrac{x_{t+1}}{x_t}\right)$, then using the recursive relation

$$x_{t+1} = x_t \exp(R(t))$$

we could generate population size estimates at different time points. Moreover, assuming these values as final

estimates of population size we could generate PGR for different time points by using

$$R(t) = r x_t^\gamma \left[1 - \left(\frac{x_t}{K} \right)^\theta \right]$$

To account for randomness in the data we add a stochastic component $\xi(t)$, where $\xi(t)$ is normally distributed with mean zero and variance σ^2. The randomness in $R(t)$ may appear due to randomness in environment, also termed as the process noise. The process error is used in model fitting to capture the real-world differences between population census data and the idealization of the model (Clark *et al.* 2010).

2.2 Real Data

In the present study we use population time series data from Global Population Dynamic Data base (GPDD), a vast data base containing the records of population sizes over different years of various species around the world <http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html>. The GPDD is one of the largest collections of animal and plant population data in the world, bringing together over 5000 time series in one database. The type of data contained in the GPDD varies enormously, from annual counts of mammals or birds at individual sampling sites, to weekly counts of zooplankton and other marine fauna.

The most important empirical study along this direction is done by Sibly *et al.* (2005), by fitting a generalized logistic growth curve to 3269 time series data in the GPDD, using nonlinear least squares procedure. The estimates are available in the GPDD, maintained by the National Environmental Research Council. The study concludes that, in general, the relationship between a populations growth rate and its size is concave in nature. This seminal paper elicited debates and cross debates, with a series of insights emerging from different perspectives (Getz and Lloyd-Smith 2006, Ross 2006, Doncaster 2006, Peacock and Garshelis 2006, Reynolds *et al*. 2005, Sibly *et al.* 2006a, b). For example, Getz and Lloyd-Smith (2006) have suggested that Sibly *et al*. (2005)'s method may produce biased estimates compared to the case when stochasticity is explicitly incorporated in the model and hence their regression method may not be consistent with the corresponding continuous growth equation.

According to Ross (2006), another concern of the Sibly analysis is that when the strength of density dependence (θ in Eqn. 2) is negative, the intrinsic growth rate (r in Eqn. 2) is negative for certain species but exhibit no signs of becoming extinct in the short term (Ross 2006).

We incorporate a coefficient of cooperation, (represented as an allometric power of population size) in the θ-logistic model and analyzed the database. The key findings of this study are: γ-compensated logistic model is a more appropriate description of the populations than the Eqn. 2 because (a) it explains non-monotonic concavity of several species populations; (b) does not invoke biologically unfeasible values of θ, and (c) precludes biologically meaningless (< 0) values of r. Detail findings of this study on the whole GPDD database is submitted elsewhere.

In this manuscript, for model illustration and supporting analytical results we have identified respectively 10 and 1 prominent evidences of weak and strong Allee cases in species across different taxa (Fish, Aves, Insect).

3. THE MODEL

3.1 Deterministic

The PGR-density relationship is generally characterized by the θ-logistic curve, given by,

$$\frac{1}{x} \frac{dx}{dt} = r \left[1 - \left(\frac{x}{K} \right)^\theta \right] \tag{2}$$

where $x(t)$ is the population size at time t, r is intrinsic growth rate parameter, representing PGR when $x = 0$, K is the carrying capacity of the environment, and θ is the parameter describing the curvature of the relationship, also called the competition coefficient (de Valdar 2006). Convex relationships imply that PGR varies little until population size is near carrying capacity, then drops rapidly. Concavity means that PGR is initially relatively high, so small populations grow quickly, but PGR then declines rapidly as population size increases, later flattens out to reach carrying capacity in a relatively slow rate. Different shapes of PGR density relationship for varying θ is depicted in Fig. 1.
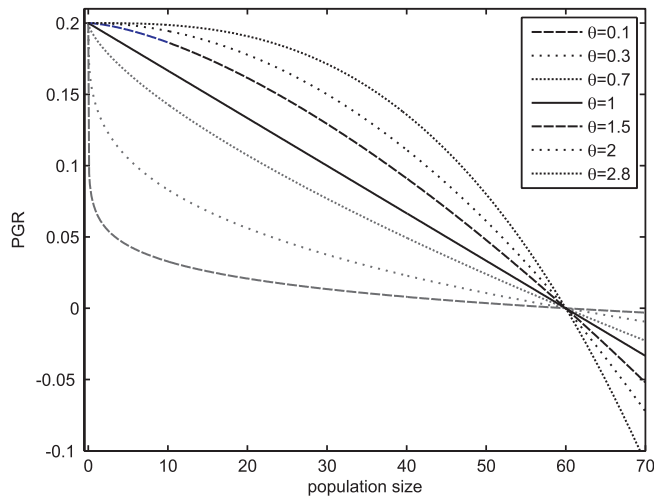
Fig. 1. Shapes of PGR profile for different values of θ. The other parameters are fixed as $r = 0.2$, $K = 60$.

As a consequence, these species' population growth rates are relatively unaffected until they are close to carrying capacity and produce a convex curve of $\theta > 1$. On the contrary, species that spend most of their time at densities much lower than carrying capacity are selected for a high maximum rate of increase. As a result, these species are affected even at relatively low densities in their abilities to acquire foods, and so the concave relationship of $\theta < 1$ between PGR and x arises (Sibly *et al.* 2005). When the population is large, the individuals may interact for resources and space and intra-specific competition decreases the species PGR. For example, in case of logistic or Ricker growth dynamics, PGR assumes highest value at low density and decreases as the population size becomes larger.

3.1.1 Model with Cooperation: Weak Allee Effect

When the abundance is low, the population is susceptible to Allee effect and PGR is reduced at low density. Under this circumstances, species may adopt some cooperative movement to save themselves from extinction. We introduce a cooperation parameter γ in the model and since the strength of cooperation is density dependent, we consider it as an allometric power of population size. Paloheimo and Dickie (1965) used a similar allometric concept in scaling of consumption and energy cost. Thus the θ-logistic model with weak Allee effect and cooperation is given by,

$$\frac{1}{x}\frac{dx}{dt} = rx^{\gamma}\left[1 - \left(\frac{x}{K}\right)^{\theta}\right] \tag{3}$$

Mathematically this model with cooperation can be treated as a special case of generalized logistic function proposed by Tsoularis and Wallace (2002). With increasing value of γ the cooperation component tries to drag the PGR value to a certain high level. Then nature's negative feedback acts as potential threat to mutual reciprocation among populations and facilitates the decline in PGR. With $\gamma > 0$, PGR exhibits increasing trend and reaches maximum (biotic potential) at an intermediate density $\left(\dfrac{\gamma}{\gamma + \theta}\right)^{\frac{1}{\theta}} K$. On the contrary in absence of the affinity parameter ($\gamma = 0$, θ-logistic), clearly indicates the negative density dependence and biotic potential is reached at minimum population size. The parameter θ is allowed to take only positive values and thus intrinsic growth rate cannot be negative, so the ecological interpretation of the parameters remains unaffected. Also we are allowing γ to assume both positive and as well as negative values. For negative γ values concavity of the PGR profile is well explained (Fig. 2).
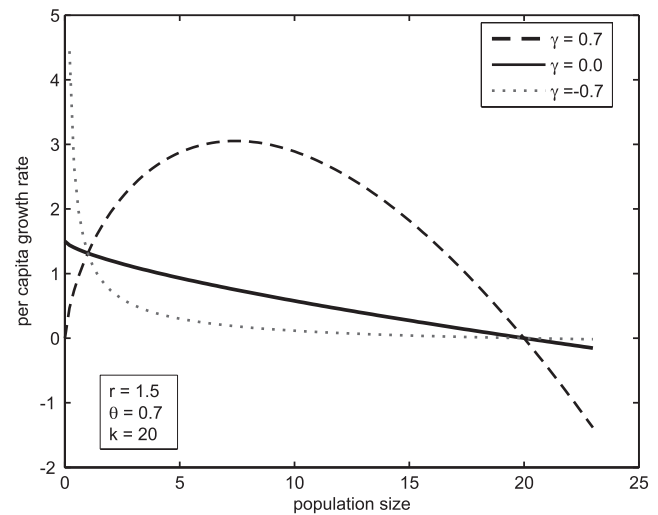

Fig. 2. Illustration of the curves generated by the γ-compensated theta-logistic equation (Eqn. (3)) for different values of γ. Population size or density is along the x-axis and per capita growth rate is along y-axis.

3.1.2 Model with Feeble Cooperation: Strong Allee

It may be possible that the abundance becomes so small that social groups are not strong enough to reproduce recovery mechanism and PGR becomes negative below a threshold population size. This phenomenon is known as the strong Allee effect. The effect of cooperation is feeble in this case. The population has a higher risk of extinction, even if, the

cooperation may be present in species life span. The model delineating the strong Allee effect is characterized by,

$$\frac{1}{x}\frac{dx}{dt} = r(x-a)\left[1-\left(\frac{x}{K}\right)^{\theta}\right], \tag{4}$$

where *a* is the Allee threshold.

We also consider the limiting model with $\lim \theta \to 0$, for fixed γ. Ignoring higher order terms in θ and $\theta \to 0$ the model approaches

$$\frac{1}{x}\frac{dx}{dt} = r\theta\ln(K)(x-a)\left[1-\frac{\ln(x)}{\ln(K)}\right]$$

Hence for a well defined model in the limit, *r* must tends to infinity so that $r\theta\ln(K)$ approaches to a finite constant, say r_0, in the limiting model (Saha *et al.* 2013), giving

$$\frac{1}{x}\frac{dx}{dt} = r_0(x-a)\left[1-\frac{\ln(x)}{\ln(K)}\right] \tag{5}$$

Linear stability analysis around the equilibria of Eqn. 4 suggest that for $\theta > 0$, the equilibrium points 0 and *K* are stable and the Allee threshold *a* is unstable; if the population falls below the level of *a*, then the population will be attracted to stable equilibria 0, that accelerates extinction, otherwise, it will reach to carrying capacity *K*.

3.2 A Discrete Version of the Model

Discrete models are mostly used in ecological context to model the population growth if the population has non-overlapping generations. The discrete version of the model may have some important ecological importance, so we take an opportunity to explain it shortly. We propose here a coefficient of cooperation, γ, which represents an allometric power of population size, x^{γ}. In our model, the population growth rate is proportional to the product of the cooperational allometric component x^{γ} and the density-dependent negative feedback function $\left(1-\left(\frac{x}{K}\right)^{\theta}\right)$.

$$\text{PGR} = rx^{\gamma}\left[1-\left(\frac{x}{K}\right)^{\theta}\right] \tag{6}$$

When $\gamma = 0$, Eqn. (6) transforms into Eqn. (2). The discrete form of the Eqn. (6) is

$$x_{t+1} = x_t \exp\left[rx_t^{\gamma}\left(1-\left(\frac{x_t}{K}\right)^{\theta}\right)\right] \tag{7}$$

3.3 Stability and Chaotic Regime

If the system is dominated by positive feedback (with cooperation among individuals), then overcompensation may lead the population to chaos
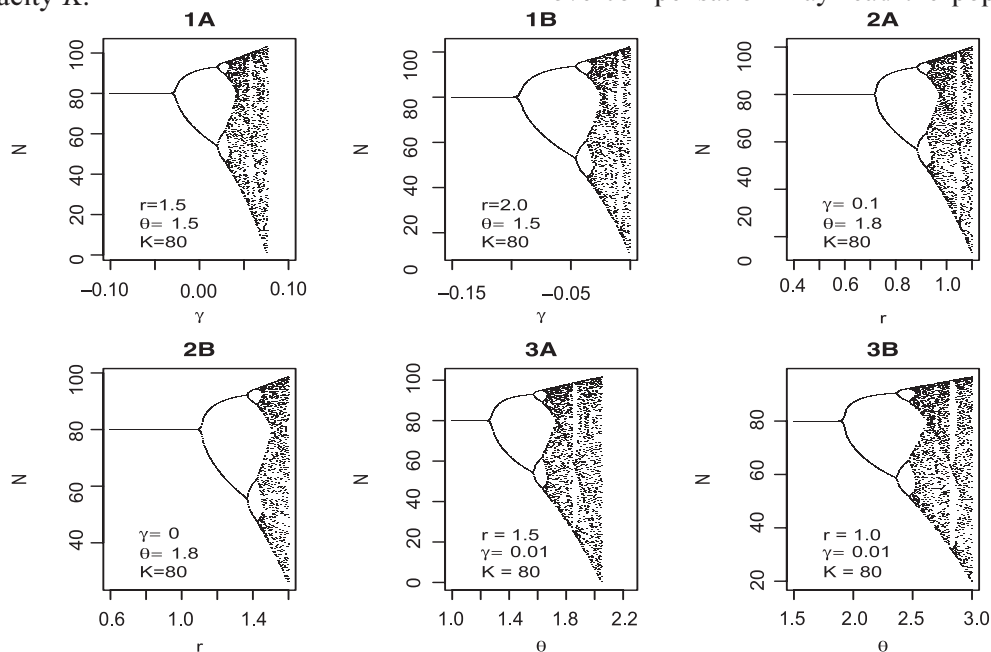

Fig. 3. Bifurcation plot with respect to model parameters γ, *r* and θ and their interplay in population process. (Fig. 1A - 1B): Parameter θ is kept fixed, with fixed *r* the bifurcation with respect to γ is plotted. Note that in 1B increase in *r* lead the system to chaotic region with low values of γ than in Fig. 1A, supporting the strong qualitative synergism between *r* and γ. (Fig. 2A - 2B): A similar result is obtained but with respect to intrinsic growth rate *r*, and with decreasing γ. (3A - 3B): *r* value is decreased in Fig. 3B and chaotic regime is shifted to the right, supports the qualitative interpretation of *r* and θ.

(Berryman and Millstein 1989). Therefore, higher values of $\gamma (> 0)$ has a strong synergistic effect on the intrinsic growth rate, and even at low values of r, the population may shift to a chaotic regime (see Fig. 3). Similarly at large values of r, a similar chaotic behavior will be observed for $\gamma = 0$ and $\theta = 1$ (May *et al.* 1974).

The system described in Eqn. (7) will be stable if $0 < r\theta K^\gamma < 2$. With $\gamma = 0$, the stability condition reduces to $0 < r\theta < 2$ (Thomas *et al.* 1980). With constant r and γ the population may collapse at a large value of θ. However, with a decreasing r, the onset of bifurcation and the appearance of Feigenbaum window occur only at higher values of θ and higher values of γ (Fig. 3).

3.4 Stochastic Model

The variability between individual's survival and reproduction causes the demographic stochasticity. Although the population process may be perturbed by random environmental changes, but at low population density demographic stochasticity is more prevailing. Thus while analyzing the extinction process of certain population, it can not be adequately analyzed without inclusion of demographic disturbances. While modeling Allee effect, most recent reviews suggest that stochastic influences should not be a part of it except stochastic variation in sex ratio (Courchamp *et al.* 1999 and Dennis 2002). In addition demographic stochasticity alone cause the most of sample paths in small populations to decrease and becomes more severe if it is coupled with stochastic variation in sex ratio (Lande 1998).

Many stochastic models of growth of biological populations can be approximated by diffusion process (including discrete time birth-death process). This generally takes the form,

$$dx(t) = \mu(x(t)) \, dt + \sqrt{v(x(t))} dW(t), \qquad (8)$$

where $dx(t)$ is the approximate population size change in time interval dt, and where $dW(t)$ has a normal distribution with zero mean and variance of dt. The infinitesimal mean $\mu(x(t))$ specifies the underlying deterministic tendencies, while the infinitesimal variance $v(x(t))$ corresponds to stochastic fluctuations. Engen *et al.* (1998) showed that, $v(x) = \sigma_d^2 x$ corresponds to demographic stochasticity and $v(x) = \sigma_e^2 x^2$ corresponds to environmental stochasticity, and these have become a vital tool in modeling

populations in stochastic environments. Incorporating demographic stochasticity in models (6) and (4), we have,

$$\frac{dx}{dt} = rx^{\gamma+1}\left[1 - \left(\frac{x}{K}\right)^\theta\right] + \sigma_d \sqrt{x}dW_t, \qquad (9)$$

$$\frac{dx}{dt} = rx(x-a)\left[1 - \left(\frac{x}{K}\right)^\theta\right] + \sigma_d \sqrt{x}dW_t. \qquad (10)$$

Next we compute the stationary distribution of the above equations and fit them to real data.

3.5 Stationary Density

Let $\{X(t), t \geq 0\}$ be a regular time homogeneous diffusion process on $[0, \infty)$ with transition density $p(t, x, y)$ for $t > 0$. The transition density satisfies the Kolmogorov's forward equation,

$$\frac{\partial p(t, x, y)}{\partial t} = \frac{1}{2}\frac{\partial^2}{\partial x^2}[\sigma^2(x)p(t, x, y)] - \frac{\partial}{\partial x}[\mu(x)p(t, x, y)] \qquad (11)$$

where $\mu(x)$ and $\sigma^2(x)$ are infinitesimal mean and variance of the process. If there exists a stationary density $f(y)$ necessarily satisfies

$$f(x) = \int f(y)p(t, x, y)dy \quad \text{for all } t > 0$$

and $\lim_{t \to \infty} p(t, x, y) = f(x)$ and f satisfies the Kolmogorov's forward equation. Putting $\partial f / \partial t = 0$, we have the following equation,

$$0 = \frac{1}{2}\frac{\partial^2}{\partial x^2}[\sigma^2(x)f(x)] - \frac{\partial}{\partial x}[\mu(x)f(x)]$$

Integrating we have,

$$\frac{d}{dx}\left[\frac{\sigma^2(x)}{2f(x)}\right] - \mu(x)f(x) = \frac{1}{2}C_1,$$

where C_1 is a constant. Multiplying with the integrating factor

$$s(x) = \exp\left\{-\int^x \left[\frac{2\mu(\xi)}{\sigma^2(\xi)}\right]d\xi\right\},$$

We can write in the compact form

$$\frac{d}{dx}s(x)\sigma^2(x)f(x) = C_1 s(x).$$

Another integration with $S(x) = \int^x s(y)dy$ gives

$$f(x) = C_1 \frac{S(x)}{s(x)\sigma^2(x)} + C_2 \frac{1}{s(x)\sigma^2(x)} = m(x)[C_1 S(x) + C_2].$$

C_1 and C_2 are determined so that, $f(x) \geq 0$ and $\int_0^\infty f(x)dx = 1$. In our case $\mu(x)$ is a non-linear function and it is difficult to get compact expression for extinction time. So we use numerical method to solve the differential equation and to compute different extinction measures.

3.6 Expected Time to Extinction

Diffusion approximation is often used to describe the population fluctuation accurately for discrete time models. For the present analysis the infinitesimal mean is $\mu(x) = rx\,(x - a)\,(1 - (x/K)^\theta)$, and the infinitesimal variance is $v(x) = \sigma_d^2 x$. We define extinction of population to occur when $x = 1$. The mean time to extinction can be derived from the distribution of the sojourn time- that is, the expected time spent at each population size before extinction, given by the following Green's function (Karlin and Taylor 1981),

$$G(x; x_0) \ = 2m(x)\,S\,(x) \text{ for } x < x_0$$
$$= 2m(x)\,S\,(x_0) \text{ for } x \geq x_0, \quad (12)$$

where,

$$S(x) = \int_1^x s(u)du,$$

$$s(u) = \exp\left[-2\int_1^u \frac{\mu(z)}{v(z)}dz\right] = \exp\left[-2\int_1^u \frac{\mu(z)}{\sigma_d^2 z + \sigma_e^2 z^2}dz\right],$$

$$m(x) = \frac{1}{v(x)s(x)},$$

If we consider the extinction of the population at $x = 1$, then the required expected time to extinction is given by,

$$\int_1^\infty G(x; x_0)dx = \int_1^{x_0} G(x; x_0)dx + \int_{x_0}^\infty G(x; x_0)dx$$

3.7 Probability of Extinction

The first passage probability (*i.e.* the probability of attaining a large population size before attaining a small one); and the mean time to extinction are commonly used to evaluate viability of stochastic populations (Drake and Lodge 2006). We are interested in evaluating the probability of extinction with different initial population size. Let $\xi\,(n; a, b)$ be the probability that the population reaches a before reaching an upper size b, starting at n, where $0 < a \leq n \leq b$. A standard formula gives,

$$\xi(n; a, b) = \frac{\int_n^b \exp[-\varphi(x)]dx}{\int_a^b \exp[-\varphi(x)]dx},$$

where

$$\varphi(u) = 2\int \frac{m(u)}{v(u)}du.$$

In the above expression the (exponentiated) constant of integration cancels in numerator and denominator. As a function of n, $\xi\,(n; a, b)$ is equal to 1 when, $n = a$, is strictly monotone decreasing in the interval (a, b), and is equal to 0 when $n = b$. The probability of extinction starting from population size n under this model is found from by letting $a \to 0$ and $b \to \infty$. An explicit analytical form of the probability of extinction is not available due to intricate form of the chosen PGR model.

4. PARAMETER ESTIMATION PROCEDURE

Statistical Modeling and inference plays a central role in addressing the way how density dependence acts by testing theoretical models against time series data (Polansky *et al.* 2008). We follow the convention in denoting the vector valued parameter $\beta = (r, a, \theta, K)$ in the space Θ of all admissible parameter values. Let $\{x_t\}_{t=1}^n$ be the given time series data and the fluctuations in data are modeled in the log transformed scale. We have estimated PGR by $\log\left(\frac{x_{t+1}}{x_t}\right)$ in the interval $(t, t + 1)$ and consider it as response variable, say y_t. For strong and weak Allee models (4) and (3), the regression of y on x is represented by

$$\mathbb{E}(Y|x) = \mu(x, \beta) = r(x - a)\left[1 - \left(\frac{x}{K}\right)^\theta\right]$$

and

$$\mu(x, \beta) = rx^\gamma\left[1 - \left(\frac{x}{K}\right)^\theta\right],$$

respectively. The distribution of y_t conditional on x_t is assumed to be normally distributed with mean $\mu(x_t, \beta)$. In a constant environment, $Var(y_t) = \frac{\sigma_d^2}{x_t}$ where σ_d^2 is the demographic stochasticity, caused by variation among individuals in fitness (Saether *et al.* 1998 and

Melbourne 2013). This defines a nonlinear regression model together with the assumption that observations are independent. Hence the covariance matrix is a diagonal matrix with off-diagonal entries are zero. The demographic stochasticity in PGR is most important among small populations, because the individual levels of variations tend to average out in large populations (Dennis *et al*. 1991). The apparent advantage of the use of PGR modeling and its applications are elaborately explained by several other authors (Sibly *et al*. 2005 and Bhattacharya *et al*. 2009). We use nonlinear least squares method (NLS) to estimate the fixed but unknown parameter β by minimizing the residual sum of squares function,

$$\text{RSS}(\beta) = \sum_{t=1}^{n} x_t [y_t - \mu(x_t, \beta)]^2,$$

with weights $w_t = x_t$. The asymptotic normality of the weighted least square estimates follows from the Weisberg (2005) and Seber and Wild (2003).

We use Gauss-Newton algorithm to minimize the residual sum of squares implemented in R-package for statistical computing. Convergence of this iterative algorithm heavily depends on the initial choices of the model parameters. Convergence of the least-square procedure sometime may be uncertain while fitting real data to highly nonlinear models. Grid Search Method may be an alternative option for parameter estimation as well as choosing initial guess for NLS.

Given the initial range of parameter values, each range is divided into equal number n of partitions. With $(n + 1)$ points in the partition of the space of each of the four parameters, $(n + 1)^4$ quadruplets (r, a, θ, K) of parameter combinations are available. For best fitting, we compute error sum of squares at each of these combinations and choose the quadruplet having the minimum error sum of squares. The grid points may be selected in such a way that the parameter estimates can be found with desired accuracy level.

We can use the standard asymptotic properties of NLS estimates for statistical testing when we have reasonable size of data. For small samples, one can estimate the uncertainty in parameters by simulating repeated datasets from the given data matrix using bootstrap. For these bootstrap samples, we have B bootstrap estimates of the model parameter vector using NLS. A nonparametric CI can be constructed accordingly from the percentiles of the bootstrap sampling distribution (see Section 6).

5. STATISTICAL TEST FOR EQUALITY OF BIOTIC POTENTIAL

Let us recall that, biotic potential is the population size at which the maximum per capita growth rate is achieved. For example, in logistic/Ricker growth law, it is achieved at small population size, but in general models with cooperation PGR will be maximum at some intermediate density. Let us consider the theoretical solutions of the population size at which biotic potential is reached are x_1^* and x_2^* for two different populations. Biotic potential is an important ecological concept, which is quantified by the maximum value of the population PGR. We have developed the test procedure through simulated data. In mathematical notation, the hypothesis based on the population size where the biotic potential is maximized can be stated as

$$H_0: \left(\frac{\gamma_1}{\gamma_1 + \theta_1}\right)^{\frac{1}{\theta_1}} K_1 = \left(\frac{\gamma_2}{\gamma_2 + \theta_2}\right)^{\frac{1}{\theta_2}} K_2 \text{ against } H_1: \text{ not } H_0$$

Let $\beta_i = (\gamma_i, \theta_i, K_i)'$ for $i = 1, 2$. Relying on the large sample distribution of the parameter estimates to be normal, then NLS estimates and maximum likelihood estimates are equivalent (Seber and Wild 2003). Let $\hat{\beta}_i = (\hat{\gamma}_i, \hat{\theta}_i, \hat{K}_i)'$ are the corresponding parameter estimates and asymptotically normally distributed, $\hat{\beta} \sim N(\beta, \hat{\Sigma})$, where $\hat{\Sigma}$ is given by,

$$\begin{pmatrix} var(\hat{\gamma}) & cov(\hat{\gamma}, \hat{\theta}) & cov(\hat{\gamma}, \hat{K}) \\ cov(\hat{\theta}, \hat{\gamma}) & var(\hat{\theta}) & cov(\hat{\theta}, \hat{K}) \\ cov(\hat{K}, \hat{\gamma}) & cov(\hat{K}, \hat{\theta}) & var(\hat{K}) \end{pmatrix}$$

Let us consider the application of Delta method in estimating the asymptotic variance of $g(\hat{\beta}) = \left(\frac{\hat{\gamma}}{\hat{\gamma} + \hat{\theta}}\right)^{\frac{1}{\hat{\theta}}} \hat{K}$. $\text{Var}(g(\hat{\beta}))$ is given by,

$$\left[\frac{\partial g(\hat{\beta})}{\partial \hat{\beta}}\right] \hat{\Sigma} \left[\frac{\partial g(\hat{\beta})}{\partial \hat{\beta}}\right]'$$

where,

$$\frac{\partial g(\hat{\beta})}{\partial \hat{\beta}} = \left[\frac{g(\hat{\beta})}{\partial \hat{\gamma}} \; \frac{g(\hat{\beta})}{\partial \hat{\theta}} \; \frac{g(\hat{\beta})}{\partial \hat{K}} \right]$$

5.1 Test Statistic

For simulation results (including bootstrap regression estimates) we have asymptotic normality of the parameter estimators. The test statistic under H_0 is given by,

$$T = \frac{g(\hat{\beta}_1) - g(\hat{\beta}_2)}{\sqrt{\widehat{Var(g(\hat{\beta}_1))} + \widehat{Var(g(\hat{\beta}_2))}}}. \quad (13)$$

Here $T^n \sim N(0,1)$. So H_0 is rejected at $\alpha\%$ level of significance if $|T| > \tau_{\alpha/2}$. One may also interested in one-sided test, whether one species achieves its biotic potential at larger population size than the other.

6. RESULTS AND DATA ANALYSIS

6.1 Simulated Data

As per the method discussed in Section 2 we have simulated two data sets. Dataset 1 is simulated using the parameter values fixed as $r = 1.5$, $\gamma = 0.6$, $\theta = 0.5$,

Table 1. NLS and bootstrap estimates of the model parameters for simulated Dataset 1

Parameters	NLS estimate	CI	bootstrap estimate	CI bootstrap
$\hat{r}$	1.4858	(0.087, 2.885)	1.399	(.944, 2.09)
$\hat{\gamma}$	0.4771	(−0.182, 1.136)	0.469	(0.2467, 0.7619)
$\hat{\theta}$	0.9299	(−1.059, 2.919)	1.3356	(0.3505, 2.377)
$\hat{K}$	78.9304	(76.773, 81.088)	77.80	(77.55, 80.0355)

Table 2. NLS and bootstrap estimates of the model parameters for simulated Dataset 2

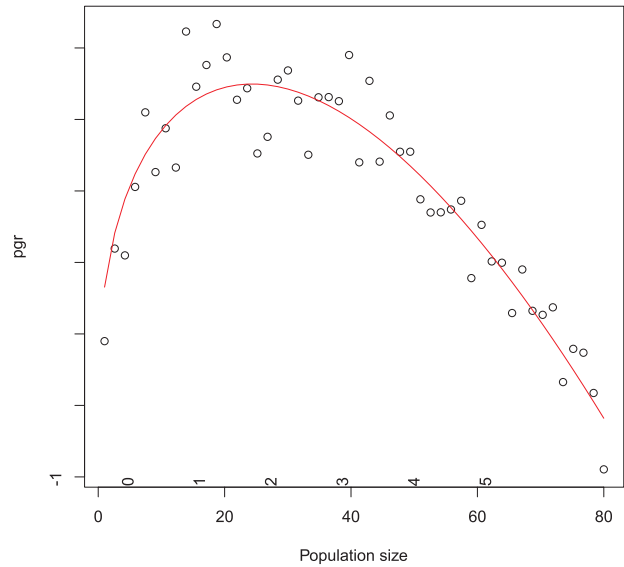| Parameters	NLS estimate	CI	bootstrap estimate	bootstrap CI
$\hat{r}$	1.6253	(0.145, 3.106)	1.882	(1.372, 2.755)
$\hat{\gamma}$	0.5799	(0.072, 1.087)	0.5345	(0.3454, 0.7975)
$\hat{\theta}$	0.8706	(-0.593, 2.334)	1.07	(0.3053, 1.792)
$\hat{K}$	128.7397	(126.533, 130.946)	128.2	(125.4138, 131.7557)

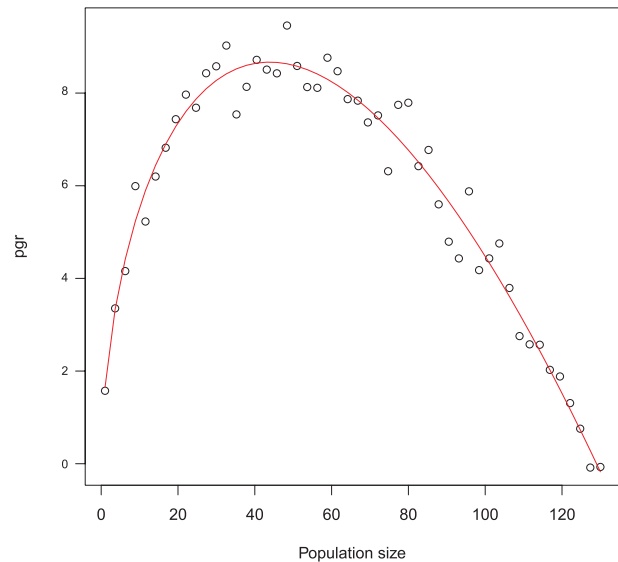**Fig. 4.** NLS fit for the simulated data sets 1.

Fig. 5. NLS fit for the simulated data sets 2.

$K = 80$ and Dataset 2 by using $r = 1.5$, $\gamma = 0.7$, $\theta = 0.4$, $K = 130$ (see Fig. 4 and Fig. 5). We used NLS method to estimate the model parameters. We found that, the 95% CI of the estimated parameter values contain the true value of the parameters. We also performed bootstrap regression and obtain the bootstrap estimates of the parameters with associated CI. We computed the bootstrap confidence intervals for the model parameters by curtailing the lower 2.5 % and the upper 2.5 % observations from the ordered vectors of bootstrap estimates computed from B bootstrap samples. The bootstrap CI contains the true parameter values. CI obtained from NLS is wider than the CI obtained from bootstrap regression.

We perform the test to compare the expected population size of these two datasets at which the biotic potential is achieved. The estimated population size at which PGR is maximized for Dataset 1 and 2 are $x_1^* = 25.28$ and $x_2^* = 45.57$ respectively. The observed value of the test statistic T is 7.31 and the test is rejected at 5% level of significance. It indicates that, two populations in different locations may not be able to achieve the biotic potential at same population sizes (they may be populations of same kind).

6.2 Real Data

We have considered 10 datasets of aves (GPDD Id. 1149, 6644, 6649), fish (GPDD Id. 1634, 1944), insects (GPDD Id. 2864, 3001, 3232, 3652, 3856) for model illustration. PGR profiles for such species clearly shows the evidence of Allee effect, although the NLS

Table 3. Table for list of identified species demonstrating Allee effect in their growth profile. The parameters are estimated through grid search procedure.

GPDD Id	r	γ	K	θ	γ-critical
1149	0.85	1.05	10.00	0.154	1.18
6644	0.609	0.548	19.54	0.161	1.01
6649	2.89	1.38	3.86	0.081	1.76
1634	1.31	1.014	198.60	0.011	0.94
1944	0.034	0.857	897.33	0.067	1.00
2864	0.373	1.45	40.14	0.027	1.43
3001	0.11	0.875	25.00	2.400	0.63
3232	0.93	0.51	250.00	0.101	0.56
3652	1.45	1.58	475.00	0.001	1.54
3856	1.95	0.86	52.83	0.034	0.86

estimates are not available due to convergence failure in NLS routine. We used Grid Search Method to compute the parameter estimates using the model (3). Estimated parameter values are provided in Table 3.

We have identified a specific strong Allee case from GPDD (GPDD Id. 1765) for illustration of model 4 using profile plot of PGR. Although there are other evidences of strong Allee cases in GPDD. We used NLS
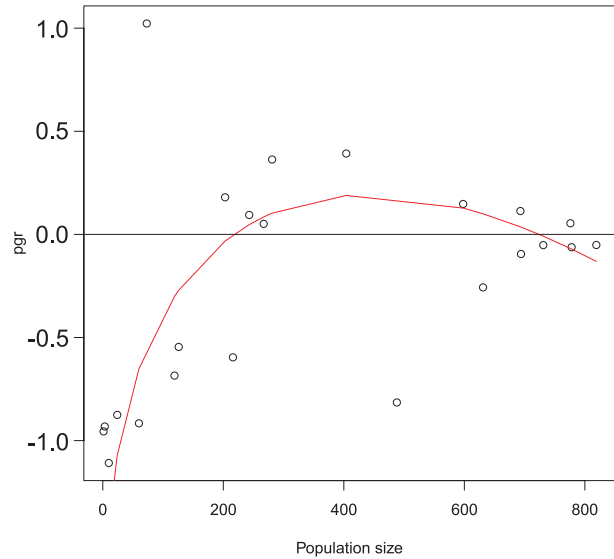

Fig. 6. Assuming the limiting model, the model predicted values are plotted in the scatter plot of PGR and population size, GPDD Id 1765

routine to fit model to the given data. We observed that NLS estimate of θ (0.003) is not statistically significant at 5% level and obviously pretty close to zero. So for this specific case the limiting form (5) of this model (4) might be a suitable choice. We fit the data to model (5) and observed that, all the model parameters namely growth rate ($\hat{r} = 0.11 \pm 0.03$ [SE]), Allee threshold ($\hat{a} = 214.4 \pm 0.39$), carrying apacity ($\hat{K} = 723.3 \pm 0.37$) are significant (the value of the test statistics are, $z = 3.514$, $z = 5.414$, $z = 19.188$ for r, a, K respectively and $P < .001$). The bootstrap confidence intervals (CI's) of parameters are $\hat{r}_b = 0.011171$, (0.0047, 0.017); $\hat{a}_b = 226.1$ (150.25, 414.69); $\hat{K}_b = 719.9$ (617.1963, 781.28). The estimated demographic variance is 3.413. The fitted curve is shown in Fig. 6 and corresponding bootstrap histogram and confidence intervals are depicted in Fig. 7. We have used numerical algorithm Runge-Kutta method of order 4 to solve the differential equation numerically to compute the stationary density. For this we have used ode45 routine implemented in MATLAB for solving differential equation numerically. The plot of stationary density and probability of extinction is depicted in Fig. 8 and Fig. 9 respectively. The expected time to extinction is calculated as 206 years.
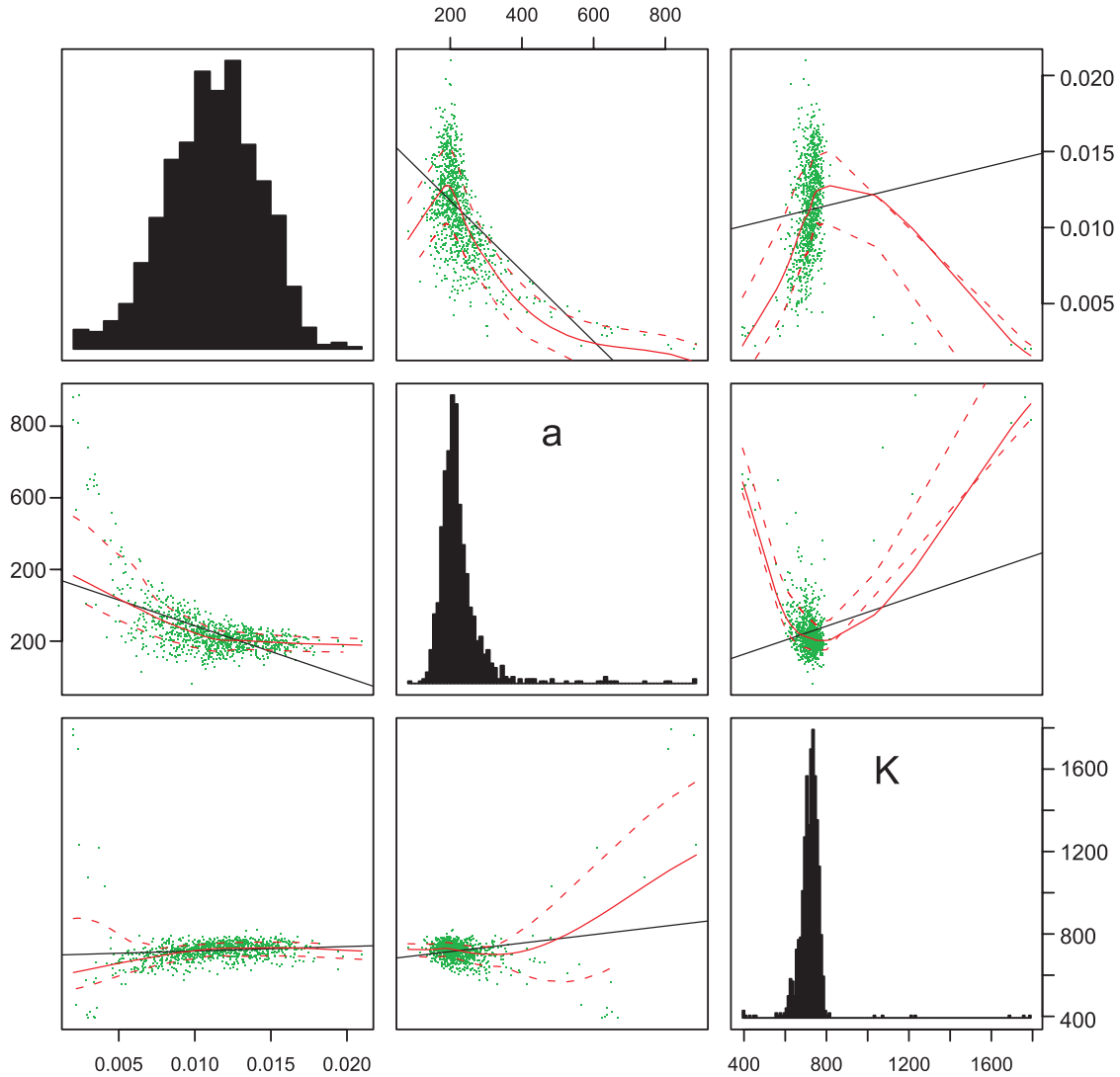
Fig. 7. Scatterplot matrix of bootstrap estimates of the Atlantic herring data in Canada. GPDD ID 1765
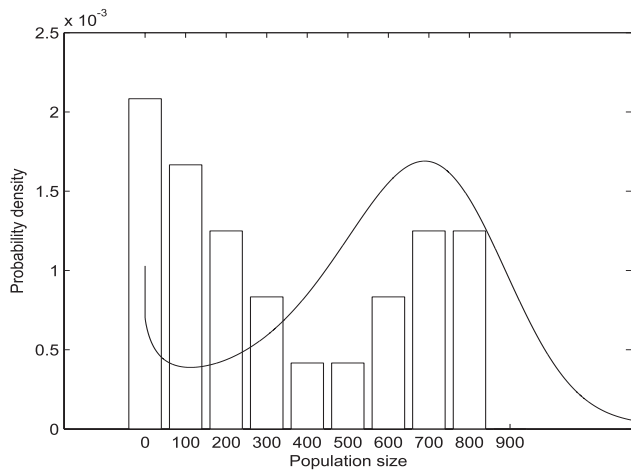

Fig. 8. Histogram of the data for Herring population, GPDD Id 1765 and corresponding fit of the stationary density based on the fitted model.
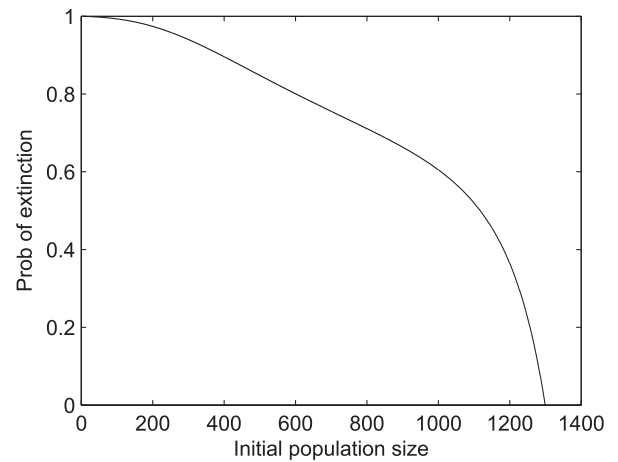

Fig. 9. $\xi(n; a, b)$ the probability of reaching population size a before size b, graphed as a function of initial population size n, for (lower line) population growth model (4) with critical depensation with demographic variance $\sigma_d^2 = 3.413$

7. CONSERVATION

Bifurcation plot with respect to model parameters γ, r and θ play an important role in understanding the population dynamics of model (3) (see Fig. 3). If the parameter θ is kept fixed, with fixed r the bifurcation with respect to γ is plotted in Fig. 3 (1A - 1B). Note that in 1B increase in r lead the system to chaotic region with low values of γ than in Fig. 1A, supporting the strong qualitative synergism between r and γ. A similar result is obtained but with respect to intrinsic growth rate r, and with decreasing γ (Fig. 2A - 2B). When the value of r is decreased and chaotic regime is shifted to the right, supports the qualitative interpretation of r and θ (3A - 3B). We suggest the following conservation management scheme:

[Conservation Scheme]

1. For a given population time series data $\{x_t\}$ obtain the estimate of parameters r, γ, K and θ and their variances based on nonlinear regression or grid search using model 7.

2. Estimate x^* (say, $\hat{x}*$), the population density where PGR is maximum. A confidence interval for $x*$ will be more appropriate. Variance of $\hat{x}*$ can be computed using Delta method.

3. Plot bifurcation diagram with respect to γ keeping other parameters r, K and θ fixed as obtained in step 2.

4. Identify the threshold value of the cooperation parameter (γ^*) from the bifurcation diagram by computing the Lyapunov exponent. In other words, γ^* is the minimum value of γ for which the Lyapunov exponent is positive.

5. If the estimated $\gamma(\hat{\gamma})$ is greater than the threshold $\gamma(\gamma^*)$, we predict that, the species is under extinction risk.

6. A potential conservation approach to minimize the risk of extinction is to introduce a mosaic of cooperators/individuals into the population (up to the level x^*) so that the population will be maintained at a density, where it has the highest growth rate (biotic potential), hence highest fitness to survive.

For the fish species *Coregonus hoyi* (bloater, GPDD ID. 1634) are $r = 1.31$, $\gamma = 1.014$, $\theta = 0.011$, $K = 198$ (see Table 3 and Fig. 10). Brown *et al.* (2005) presents the biomass and age structure data for this species. They also describe a superabundance of predator alewife pushing this population downward. When the alewife population leveled off and started to decline, the bloaters increased. So, this is not case of a
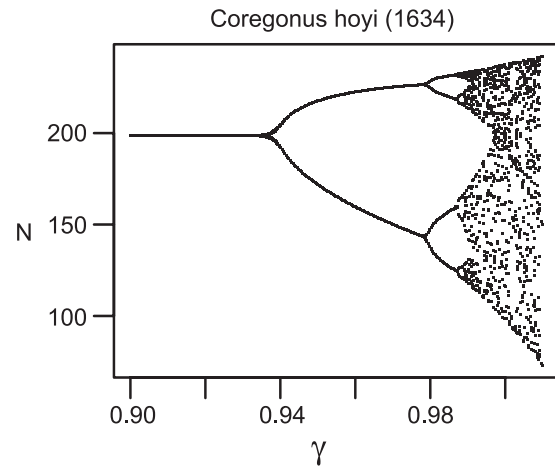

Fig. 10. We note that for the species *Coregonus Hoyi,* the estimated (1.014) exceeds its threshold value = 0.94 and severely suffering from extinction threats.

low population unable to maintain itself (Allee effect), but a combination of fishing and invasive predation pressure. This population is found to be in the chaotic region of the bifurcation diagram with respect to γ. This species is already declared as Vulnerable in the IUCN Red Data. The parameter γ can be used as a measure of assessing extinction risk for a species population. We denote the γ-critical as the value of γ from where the first bifurcation occurs.

8. DISCUSSION

A few instances of non positive values of θ can be found in (Saether *et al*. 2002). For the insect population *Xylina vetusta* (GPDD Id. 6321), Sibly *et al*. estimated the K and θ as 512 and –2 respectively. Ross (2006) analyzed when N is approximately 1200, PGR is approximately –0.5. Thus using the θ-logistic equation (2), r is approximately –0.61. Therefore, if θ is allowed to take negative values r must also be negative. So its physical interpretation is lost and endangers an unrealistic scenario in population dynamics. However in our model (3), the estimated values of K, θ and γ are 600, 0.38 and –0.1 respectively. In this case, the biological meanings of the parameters are preserved.

We have analyzed the population time series data of herring populations from the Icelandic regions. The evidence of a strong Allee effect is prominent in this population. Many commercially important fish species, including herring, possess the characteristics of group defense and schooling (Courchamp *et al*. 2008). Species having such characteristics are at an increased risk of extinction due to the Allee effect when severe exploitation occurs. Harvested fish populations are highly subjected to the existence of critical threshold. It is to be noted that in Fig. 9, the change in extinction probability with the change in initial population size is significant around the unstable equilibrium point (Allee threshold). So the species is at the risk of extinction when the population size lies below the critical level. In the quasi-stationary state the herring population is more likely to stay close to the extinction state due to Allee effect. As demographic variance decreases the probability of the herring population, to stay around the stable equilibrium (carrying capacity *K*), increases (see Fig. 12).
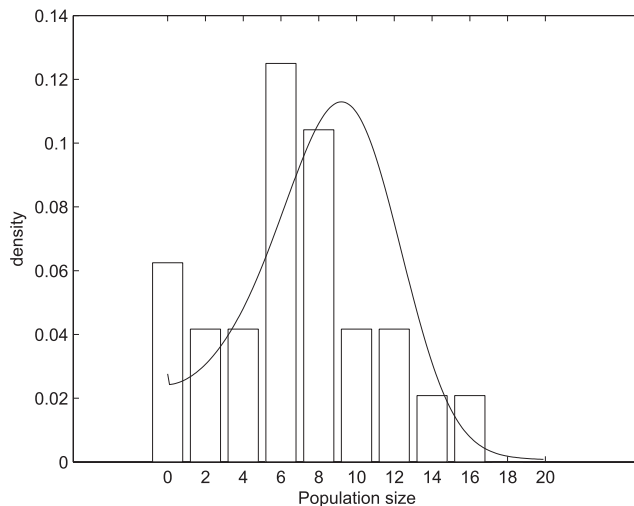

Fig. 12. Plot of stationary distribution with varying demographic variance σ_d^2. As σ_d^2 increases the mode at carrying capacity becomes low and hence the risk of extinction increases.

Fig. 11. Histogram of the data for GPDD Id 1149 and corresponding fit of the stationary density based on the fitted model.

If the sample size is very short, noisy, contains missing values, standard procedures like NLS or Maximum likelihood estimation may fail to fit a suitable model. In those cases grid search may perform well. Although this method lacks the asymptotic properties of parameter estimates from inferential view point. But, non-parametric type bootstrap confidence interval can be constructed for the parameter by
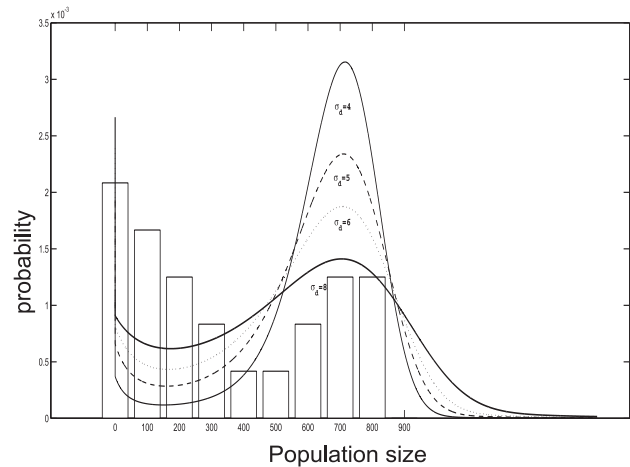
resampling the data matrix a large number of times, and running grid search procedure for each of the bootstrap sample. It requires a significant amount of computational effort. The performance of the parameter estimates can be cross-checked by plugging the estimates in density function to approximate the quasi-stationary distribution of population sizes (Saha *et al*. 2013). For example, quasi-stationary distribution of population size is well approximated if we plug-in the grid search estimates in density function (see Fig. 11) that supports the accuracy of grid search estimates.

9. CONCLUSION

It is likely that adding more parameters to the θ-logistic equation might fit the data better to the growth model. Basically, in almost all previous works (Sibly *et al*. 2005 and Ross 2006) the influence of cooperation in population dynamics remained unexplored. The proposed model provides a more suitable description of population growth rates, hence evaluation of extinction status based on this model will be more accurate. Thus our model may be used as a possible tool to make predictions regarding population level consequences, as it considers both intraspecific competition and cooperation. In addition the detection of the Allee effect is important in assessing the risk of extinction and failure to detect could lead to an overoptimistic assessment of threat status, hence wrong/ erroneous decision making in conservation management to use proper recovery plans.

The model not only shows Allee effect and compensatory dynamics, but suggests that while analyzing population database we need to consider both positive and negative feedback mechanisms in species populations. Because the model takes into account intraspecific cooperation that enhances reproductive success of breeding pairs, it can depict the population growth profiles more realistically than logistic models describing density dependent negative feedback alone.

Note that at low population density demographic stochasticity is more prevailing. We feel that, our analysis can have a huge impact on understanding extinction patterns and enable us to identify demographic threats and decision making in conservation management. Our analysis indicates that species having estimated γ close to its threshold value require the nourishment from management decisions that can be taken by $\gamma - \theta$ trade-off. A population with γ in chaotic region is under severe extinction threat and requires urgent investigation. Before ending the article we like to mention that exploratory data analysis based on complete GPDD will provide more insights in understanding the species growth behavior and its associated extinction pattern.

REFERENCES

Allee,W., Emerson, A., Park, O., Park, T. and Schmidt, K. (1949). *Principles of Animal Ecology*. W.B. Saunders, Philadelphia, 365

Avilés, L. (1999). Cooperation and non-linear dynamics: An ecological perspective on the evolution of sociality. *Evol. Ecol. Res.,* **1**, 45-77.

Berryman, A. and Millstein, J. (1989). Are ecological systems chaotic - and if not, why not? *Trends Ecol. Evol*., **4**, 26-28.

Bhattacharya, S., Basu, A. and Bandyopadhyay, S. (2009). Goodness-of-fit testing for exponential polynomial growth curves. *Commu. Statist. Theory Methods*., **38**, 1-24.

Bilde, T., Coates, K., Birkhofer, K., Bird, T., Maklakov, A., Lubin, Y. and Avilés, L. (2007). Survival benefits select for group living in a social spider despite reproductive costs. *J. Evol. Biol.,* **20(6)**, 2412-2426.

Brown, C., Gardner, C. and Braithwaite, V.A. (2005). Differential stress responses in fish from areas of high and low-predation pressure. *J. Comparative Physiol.,* **B175**, 305-312.

Clark, F., Brook, B.W., Delean, S., Akcakaya, H.R. and Bradshaw, C.J.A. (2010). The theta-logistic is unreliable for modeling most census data. *Methods Ecol. Evol.,* **1**, 253-262.

Courchamp, F., Berce, L. and Gascoigne, J. (2008). *Allee Effects in Ecology and Conservation.* Oxford University. Press, Oxford, UK.

Courchamp, F., Clutton-Brock, T. and Grenfell, B. (1999). Inverse density dependence and the allee effect. *Trends Ecol. Evol.,* **14,** 405-410.

de Valdar, H.P. (2006). Density-dependence as a size-independent regulatory mechanism. *J. Theo. Biol.,* **238**, 245-256.

Dennis, B. (1989). Allee-effects: population growth, critical density, and the chance of extinction. *Natural Resour. Modeling,* **3**, 481-538.

Dennis, B. (2002). Allee effects in stochastic populations. *Oikos,* **96**, 389-401.

Dennis, B., Munholland, P. and Scott, J. (1991). Estimation of growth and extinction parameters for endangered species. *Ecol. Monographs,* **61(2)**, 115-143.

Doncaster, C.P. (2006). On the regulation of populations of mammals, birds, fish, and insects III - Comments. *Science.* **311**, 1100.

Drake, J.M. and Lodge, D.M. (2006). Allee effects, propagule pressure and the probability of establishment: Risk analysis for biological invasions. *Biol. Invasions,* **8(2)**, 365-375.

Engen, S., Bakke, O. and Islam, A. (1998). Demographic and environmental stochasticity-concepts and definitions. *Biometrics,* **54**, 39-45.

Getz, W.M. and Lloyd-Smith, W.O. (2006). On the regulation of populations of mammals, birds, fish, and insects I - Comments. *Science,* **311**, 1100.

Gompper, M. (1997). Population ecology of white-nosed coati (nasua narica) on barro colorado island, panama. *J. Zoology,* **241(3)**, 441-455.

Jetz, W. and Rubenstein, D. (2011). Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biol.,* **21,** 72-78.

Karlin, S. and Taylor, H.M. (1981). *A Second Course in Stochastic Process.* Academic Press, New York.

Kramer, A., Dennis, B., Liebhold, A. and Drake, J. (2009). The evidence of Allee effects. *Population Ecol.,* **51,** 341-354.

Lande, R. (1998). Demographic stochasticity and Allee effect on a scale with isotropic noise. *Oikos*, **85**, 353358.

May, R.M., Conway, G.R., Hassell, M.P. and Southwood, T.R.E. (1974). Time delays, density-dependence and single-species oscillations. *J. Anim. Ecol.,* **43,** 747-770.

Melbourne, B. (2013). *Sourcebook in Theoretical Ecology.* University of California Press, Berkeley, Chapter. Demographic Stochasticity.

Paloheimo, J. and Dickie, L. (1965). Food and growth of fishes-a growth curve derived from experimental data. *J. Fish. Res. Board Can.*, **22,** 521-542.

Peacock, E. and Garshelis, D.L. (2006). On the regulation of populations of mammals, birds, fish, and insects IV - Comment. *Science,* **313,** 45.

Peer, K. and Taborsky, M. (2007). Delayed dispersal as a potential route to cooperative breeding in ambrosia beetles. *Behavioral Ecol. Sociobiol.,* **61**, 729-739.

Polansky, L., Valpine, P., Lloyd-Smith, J. and Getz, W. (2008). Parameter estimation in a generalized discretetime model of density dependence. *Theo. Ecol.,* **1**, 221-229.

Reynolds, J., Dulvy, N., Goodwin, N. and Hutchings, J. (2005). Biology of extinction risk in marine fishes. *Proceedings of the Royal Society, Biological Science,* **272,** 2337-2344.

Ross, J.V. (2006). On the regulation of populations of mammals, birds, fish, and insects, II. *Science,* **311**, 1100.

Saether, B., Engen, S. and Matthysen, E. (2002). Demographic characteristics and population dynamical patterns of solitary birds. *Science,* 295.

Saether, B.-E., Engen, S., Islam, A., McCleery, R. and Perrins, C. (1998). Environmental stochasticity and extinction risk in a population of a small songbird, the great tit. *Ecol. Monographs,* **151(5)**, 441-450.

Saha, B., Bhowmick, A.R., Chattopadhyay, J. and Bhattacharya, S. (2013). On the evidence of an Allee effect in herring populations and consequences for population survival: A model-based study. *Ecol. Model.,* **250,** 72-80.

Seber, G. and Wild, C. (2003). *Nonlinear Regression.* John Wiley and Sons, Inc., New Jersey.

Sibly, R.M., Barker, D., Denham, M.C., Hone, J. and Pagel, M. (2005). On the regulation of populations of mammals, birds, fish, and insects. *Science,* **309**, 607-610.

Sibly, R.M., Barker, D., Denham, M.C., Hone, J. and Pagel, M. (2006a). Response to Comment on "On the regulation of populations of mammals, birds, fish, and insects". *Science,* **313,** 45.

Sibly, R.M., Barker, D., Denham, M.C., Hone, J. and Pagel, M. (2006b). Response to Comment on "On the regulation of populations of mammals, birds, fish, and insects". *Science,* **311**, 1100.

Thomas, W., Pomerantz, M., Gilpin, M. (1980). Chaos, asymmetric growth and group selection for dynamical stability. *Ecology,* **61,** 1312-1320.

Tsoularis, A. and Wallace, J. (2002). Analysis of logistic growth models. *Math. Biosci.,* **179,** 21-55.

Weisberg, S. (2005). *Applied Linear Regression.* John Wiley and Sons, Inc., New Jersey.

Wilson, E. (2000). *Sociobiology: The New Synthesis.* Harvard University Press, Cambridge MA.

Annexure

The following program is used to simulate the data and perform bootstrap regression on the simulated data.

```
library(car)
t = 50;
#Function to simulate the time series data
test <- function (theta = .5, gamma = 0.6, sigma = 0.5, rd = 1.5, N0 = 20, t=50, K = 80){
    N <- seq(1,K, length = t)
    N[1] <- N0;
p <- c(numeric(t))
for(i in 1:t-1)
    {
p[i] = rd * N[i]^(gamma) *(1 - (N[i]/K)^theta) ;
N[i+1] = N[i] * exp(p[i] + rnorm(n=1, mean = 0, sd=sigma) );
}
data <- data.frame(N[1:t], p)
    return(data)
}
#Generate the vector of population counts. Time series plot
Nts <- test()
pdf("fig1.pdf", onefile=F)
plot(Nts[,1], Nts[,2], xlab = "Population size", ylab = "PGR")
#Fitting the nonlinear regression model
pgr <- Nts[,2]
pop <- Nts[,1]
nls.out1 <- nls(pgr ~ rd * (pop^(gamma)) *(1 - (pop/K)^theta), control = nls.control(maxiter = 25),
            start = list(rd =1.5, gamma=.6 ,theta = .5, K = 130), weights = pop, trace = TRUE)
#Application of delta method to find the variance of maximum PGR
d1 <- deltaMethod(nls.out1, "K*(gamma/(gamma+theta))^(1/theta)")
lines(pop, predict(nls.out1), col =2)
summary(nls.out1)
dev.off()
#alr3 package is used to bootstrap the regression model
library(alr3)
set.seed(10131985)
s1.boot <- bootCase(nls.out1,B=999)
```

```
pdf("fig2.pdf", onefile=F)

scatterplotMatrix(s1.boot,diagonal="histogram", col=palette(),#[-1],
        lwd=0.7, pch=".", var.labels=c("r", expression(gamma), expression(theta), "K"),
        ellipse=FALSE, smooth=TRUE, level=c(.90))

dev.off()

max.pgr1 <- ((s1.boot[,2]/(s1.boot[,2]+s1.boot[,3]))^(1/s1.boot[,3]) )* s1.boot[,4]

#Simulation study for the second dataset

Nts <- test(theta = .5, gamma = 0.7, sigma = 0.5, rd = 1.5, N0 = 20, t=50, K = 130)

pdf("fig3.pdf", onefile=F)

plot(Nts[,1], Nts[,2], xlab = "Population size", ylab = "pgr")

pgr <- Nts[,2]

pop <- Nts[,1]

nls.out2 <- nls(pgr ~ rd * (pop^(gamma)) *(1 - (pop/K)^theta), control = nls.control(maxiter = 50),
        start = list(rd =1.5, gamma=.8 ,theta = .5, K = 130), weights = pop, trace = TRUE)

lines(pop, predict(nls.out2), col =2)

summary(nls.out2)

dev.off()

s2.boot <- bootCase(nls.out2,B=999)

pdf("fig4.pdf", onefile=F)

scatterplotMatrix(s2.boot,diagonal="histogram", col=palette(),#[-1],
        lwd=0.7, pch=".", var.labels=c("r", expression(gamma), expression(theta), "K"),
        ellipse=FALSE, smooth=TRUE, level=c(.90))

dev.off()

max.pgr2 <- ((s2.boot[,2]/(s2.boot[,2]+s2.boot[,3]))^(1/s2.boot[,3]) )* s2.boot[,4]

#t test for testing the equality of population size at which max. PGR is attained

t.test(max.pgr1, max.pgr2)

#Testing for equality of population size at which max. PGR is obtained

d1 <- deltaMethod(nls.out1, "K*(gamma/(gamma+theta))^(1/theta)")

d2 <- deltaMethod(nls.out2, "K*(gamma/(gamma+theta))^(1/theta)")

g1 <- d1$Estimate

Vg1 <- (d1$SE)^2

g2 <- d2$Estimate

Vg2 <- (d2$SE)^2

T <- (g1-g2)/sqrt((d1$SE)^2 + (d2$SE)^2)

pval = 2*pnorm(-abs(T))
```