Stability Analysis of Gompertz's Logistic Growth Equation Under Strong, Weak and No Allee Effects

J. LEONEL ROCHA
ISEL - Instituto Superior de Engenharia de Lisboa
ADM - Department of Mathematics
Rua Conselheiro Emídio Navarro, 1, 1959-007 Lisboa
PORTUGAL
jrocha@adm.isel.pt

Abstract: The interest and the relevance of the study of population dynamics and extinction phenomenon are the main motivation to investigate the induction of Allee effects in Gompertz's logistic growth equation. The stability analysis of the equilibrium points of Gompertz's logistic growth equation under strong, weak and no Allee effects is presented. Properties and sufficient conditions for the existence of strong, weak and no Allee effects for these new continuous population growth models are provided and discussed. It is established a sufficient condition to prove that the time evolution of the population density to the stable equilibria gets larger, as the Allee effects get stronger. These continuous population growth models subjected to Allee effects take longer time to reach its equilibrium states. The developed models are validated using the Icelandic herring population, with GPDD Id.1765.

Key–Words: Gompertz logistic growth equation, stability analysis, strong and weak Allee effects.

1 Introduction

For many international organizations a major concern is the extinction of species of trees, plants and mammals in the planet. In fact, species extinction is usually a major focus of ecological and biological research. The Allee effect is an important dynamic phenomenon first described by Allee in 1931, see [2]. In this work is used the concept of demographic Allee effect, which is manifested by a reduction in the *per capita* growth rate at low population sizes. Managers and biologists are usually more interested in demographic Allee effect, because they ultimately govern extinction or recovery probability of species at low densities.

The Allee effect is described as *strong* when there is a density threshold, where the *per capita* growth rate becomes null, below which the population decrease and go to extinction. On the other hand, the Allee effect is described as *weak* when population growth is slowed down for small densities but not to the point of becoming negative. The distinction between strong and weak Allee effects is very important, most authors neglect the former and almost exclusively consider the strong Allee effect. Previous studies show that the presence of Allee effects in the population growth models affects the stability analysis of the equilibrium points of these models. See, for example, [1], [6], [9], [12] and references therein.

Throughout this paper is studied the Gompertz logistic growth equation, which is given by the following Bernoulli differential equation,

$$f\left(N(t)\right) = \frac{dN(t)}{dt} = r\, N(t) \left(1 - \left(\frac{N(t)}{K}\right)^{\beta}\right)^{\gamma}, \tag{1}$$

where t is a variable representing time; $N(t)$ is a value of a measure of size or density of an organism or population; $\beta, \gamma \in \mathrm{R}^{+}$ are additional shape parameters, introduced as a power law so that it can define asymmetric curves (dimensionless scalar), considered as intraspecific competition factors; $r = \frac{\bar{r}}{\beta^{\gamma}} \in \mathrm{R}^{+}$ is the maximum intrinsic growth rate of increase of $N(t)$ and K is the carrying capacity, see [14] and [15]. The *per capita* growth rates associated to Gompertz logistic growth equation, given by the population growth rates Eq.(1), are defined as follows:

$$g\left(N(t)\right) = \frac{dN(t)}{dt}\frac{1}{N(t)} = r \left(1 - \left(\frac{N(t)}{K}\right)^{\beta}\right)^{\gamma}. \tag{2}$$

However, for certain parameter values, the *per capita* growth rates $g\left(N(t)\right)$ decreases at low densities. This is the main focus of this work, because for these parameter values the population dynamics model defined by Eq.(1) does not contemplate Allee effects.

Remark 1 *Note that the Gompertz logistic growth* *equation, given by Eq.(1), for some parameter values of β and γ, verifies particular cases of growth models:*

(i) for $\beta = \gamma = 1$, Eq.(1) is the Verhulst logistic growth equation; see [16];

(ii) for $\beta = 1$ and $\gamma \in \mathrm{R}^+$, Eq.(1) is a particular case of Blumberg's growth equation, see [4];

(iii) for $\beta \in \mathrm{R}^+$ and $\gamma = 1$, Eq.(1) is the Richards growth equation or β-logistic model, see [11].

These models have been already studied by diverse authors, see [14], [15] and references therein.

The layout of this paper is as follows. In Sec.2 is defined new Gompertz logistic growth models with and without Allee effect. The generalization that is proposed results from considering an adjustment or correction factor of polynomial type, where two parameters are considered. The use of a parameter $C \in \mathrm{R}^+$ leads the presented generalization, which yields some more flexible models with variable extinction rates. An Allee limit or threshold E^u is incorporated so that the models under study have strong or weak Allee effects, or no Allee effect. Sec.3 is devoted to the stability analysis of Gompertz logistic growth models subjected to Allee effects. Simultaneously are investigated properties and sufficient conditions for the existence of strong, weak and no Allee effects for these new continuous population growth models. The adjustment or correction factor of polynomial type introduced allow to analyze simultaneously strong and weak Allee effects, whose classification is dependent on the number of equilibrium points and the local stability of the equilibrium points $N(t) = 0$ and $N(t) = E^u$. In Sec.4 is analyzed under what conditions the Allee effects affect the local stability of the carrying capacity K, which is a stable equilibria of the Gompertz logistic growth equation subjected to Allee effects. To support the analytical results are presented several numerical simulations for the Icelandic herring dataset of 24 years (1947-1970), from the Global Population Dynamics Database (GPDD) maintained by the National European Research Council, with Main Id. 1765. Finally, in Sec.5, the results are discussed and are provided some relevant conclusions.

2 Gompertz's logistic growth models with and without Allee effects

The growth models given by Eq.(1) do not exhibit Allee effect, because the *per capita* growth rates, given by Eq.(2), decreases at low densities for $\beta \in]0,1]$ and $\forall\gamma \in \mathrm{R}^+$. In fact, considering $\forall\gamma \in \mathrm{R}^+$ it is verified that:

$$\lim_{\beta\to 1} g\left(N(t)\right) = r\left(1 - \frac{N(t)}{K}\right)^{\gamma};$$

$$\lim_{\beta\to 0^+} g\left(N(t)\right) = 0 \text{ and } \lim_{\beta\to +\infty} g\left(N(t)\right) = r. \quad (3)$$

Thus, for $\beta \in]0,1]$ and $\forall\gamma \in \mathrm{R}^+$, the *per capita* growth rates decrease at low densities ($N(t) \to 0^+$), while for $\beta \to +\infty$ the *per capita* growth rates converge to $r \in \mathrm{R}^+$, for all densities $N(t) > 0$.

The results of the limits given by Eq.(3) are one of the main motivations of the present work. The principal idea is to introduce in Eq.(1), with $\beta \in]0,1]$ and $\forall\gamma \in \mathrm{R}^+$, a new adjustment or correction factor, denoted by $T\left(N(t)\right)$, in such a way that the *per capita* growth rates, denoted by $g^*\left(N(t)\right)$, given by

$$\frac{dN(t)}{dt}\frac{1}{N(t)} = r^*\left(1 - \left(\frac{N(t)}{K}\right)^{\beta}\right)^{\gamma} T\left(N(t)\right), \quad (4)$$

be negative as soon as the population size $N(t)$ gets smaller than the Allee limit or threshold. Alternatively, the *per capita* growth rates are increasing with density from low densities, starting with a positive value, or are decreasing for all densities.

The correction factor that is proposed in this work is defined as follows:

$$T\left(N(t)\right) = \frac{N(t) - E^u}{K + C}, \quad (5)$$

with $|E^u| < K$ and $C \in \mathrm{R}^+$. E^u is the Allee limit or threshold. As in [1], [5] and [12], the use of the parameter C allows us to define and study more flexible models, with variable extinction rates. This parameter can be used for other explanations such as migration, trophic interactions or autocorrelations in environmental factors.

Biological facts lead us to the following assumptions on $T\left(N(t)\right)$:

(T1) if $N(t) = 0$ and $\forall 0 < E^u < K$ then $T(0) = \frac{-E^u}{K+C} < 0$; that is, there is no reproduction without partners (critical depensation exist). If $N(t) = 0$ and $\forall -K < E^u \leq 0$ then $T(0) = \frac{E^u}{K+C} > 0$; that is, there is reproduction (no critical depensation);

(T2) $T'\left(N(t)\right) = \frac{1}{K+C} > 0$ for $\forall N(t) > 0$; that is, Allee effects decreases as density increases;

(T3) $\lim_{N(t)\to K} T\left(N(t)\right) = \frac{K - E^u}{K + C}$, if $K \to +\infty$ then $T\left(N(t)\right) \to 1$; that is, Allee effects vanishes at high densities.

This correction factor imply the appearance of a new equilibrium point ($N(t) = E^u$) that changes the structural stability of the population system, thus causing changes in stability of the initial equilibrium points of Eq.(1) ($N(t) = 0$ and $N(t) = K$). The Allee limit E^u or the minimal population size corresponds to a null growth rate, which allow that the population maintains exactly its dimension at a fixed value. At this density E^u the population is incapable to grow up and maintains its equilibrium value until some disturbance happens, leading either to extinction or to growth. So, this value is an unstable equilibrium value of the population growth rate and is smaller than the carrying capacity K.

The correspondent population growth rates to Eq.(4) or Gompertz logistic growth models with and without Allee effects are defined by the following non-linear differential equation:

$$f^*(N(t)) = N(t)g^*(N(t))$$
$$\Leftrightarrow \frac{dN(t)}{dt} = r^* N(t)\left(1 - \left(\frac{N(t)}{K}\right)^{\beta}\right)^{\gamma} T(N(t)), \tag{6}$$

with $r^* \in \mathrm{R}^+$, $\beta \in]0, 1]$ and $\gamma \in \mathrm{R}^+$, the other parameters have the same meaning as explained in Eq.(1). The parameter value $\beta \in]0, 1]$ means that for small population densities the *per capita* growth rates are relatively high, but decreases rapidly as population densities increase. Note that the proposed models are a generalization of the model presented in [13], with important applications in conservation management of herring fish populations.

Remark 2 *Note that the Gompertz logistic growth models under Allee effects, with the correction factor $T(N(t))$, Eq.(6), for some parameter values of β and γ, verifies particular cases of growth models with strong and weak Allee effects and without Allee effect:*

(i) for $\beta = 1$ and $\gamma \in \mathrm{R}^+$, Eq.(6) is a particular case of Blumberg's growth equation with strong and weak Allee effects and without Allee effect, see [1];

(ii) for $\beta \in \mathrm{R}^+$ and $\gamma = 1$, Eq.(6) is the Richards growth equation with strong and weak Allee effects and no Allee effect, see [12] and [13].

3 Stability analysis of Gompertz's logistic growth models subjected to the correction factor $T(N(t))$

In recent decades, the study of Allee effect has attracted much attention in population dynamics. In particular, Allee effects have played an important role in the stability analysis of the equilibrium points of population dynamics models. See, for example, [1], [6], [9], [12] and references therein. Determining whether strong, weak or no Allee effects are more common in natural populations will rely on improved study design and analytical techniques. One of the greatest contributions of this work are the next results, where is studied under what conditions the Allee effects, given by $T(N(t))$, affect the stability of the equilibrium points of the Gompertz logistic growth equation, Eq.(1).

3.1 Strong Allee effect

The study of the Allee effect has been widely recognized in conservation biology, because when the Allee effect is sufficiently strong there is a critical threshold below which populations experience rapid extinction. Strong Allee effects occurred in multiple taxonomic groups and were caused by mate limitation, predator satiation and cooperative defense. The setting extinction/survival is the most familiar consequence of the Allee effect and the issue of extinction or survival of the population is of utmost practical relevance, see [5], [8] and references therein. In this scenario, the Allee effect appears at moderate levels, that is, the *per capita* growth rates $g^*(N(t))$ are negative for very low or very high values of the population size $N(t)$, but are positive for intermediate values of $N(t)$, see Fig.1. See, also, for example, [1], [3], [10], [12] and references therein.

In this section are discussed properties and sufficient conditions for the existence of strong Allee effect in the Gompertz logistic growth models, given by Eq.(6).

Property 3 *Let $f^*(N(t))$ be the Gompertz logistic growth models under Allee effects, Eq.(6), $T(N(t))$ be the correction factor, Eq.(5), with $\beta \in]0, 1]$, $\gamma \in \mathrm{R}^+$ and $r^* \in \mathrm{R}^+$. If $0 < E^u < K$ and $C \in \mathrm{R}^+$, then $f^*(N(t))$ has three equilibrium points for all population size $N(t) \geq 0$: $N(t) = E^0 = 0, N(t) = E^u$, $N(t) = E^s = K$; and it is verified that:*

(i) $N(t) = E^0 = 0$ is an equilibrium point locally stable;

(ii) $N(t) = E^u$ is an equilibrium point locally unstable;

(iii) $N(t) = E^s = K$ is an equilibrium point locally stable.

Proof: Let us consider $f^*(N(t))$ be the population growth rates, such that $0 < E^u < K$ and $C \in \mathrm{R}^+$. From Eq.(6) follows that $f^*(N(t))$ has

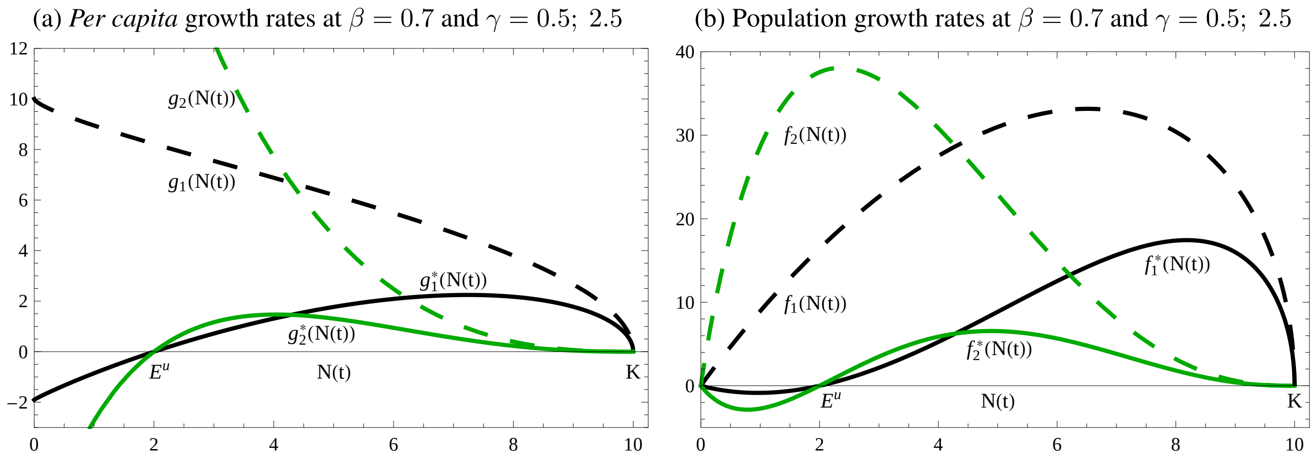

Figure 1: Strong Allee effect: (a) (Solid lines) *Per capita* growth rates $g^*(N(t))$, Eq.(4), at $\beta = 0.7$, $K = 10$, $C = 2$, $E^u = 2$ fixed parameters and $\gamma_1 = 0.5$, $\gamma_2 = 2.5$, $r_1^* = 10$, $r_2^* = 50$ for $g_1^*(N(t))$ and $g_2^*(N(t))$, respectively; (Dashed lines) $g(N(t))$ is the *per capita* growth rate without strong Allee effect, given by Eq.(2), for the same parameter values; (b) (Solid lines) corresponding Gompertz logistic growth models $f^*(N(t))$, Eq.(6); (Dashed lines) $f(N(t))$ is the population growth rate without strong Allee effect, given by Eq.(1).

three equilibrium points: $N(t) = E^0 = 0, N(t) = E^u$ and $N(t) = E^s = K$, $\forall N(t) \geq 0$. Relative to the equilibrium point $N(t) = E^0 = 0$, for any $\beta \in]0,1]$, $\gamma \in \mathbb{R}^+$ and $r^* \in \mathbb{R}^+$, it is verified that:

$$\lim_{N(t)\to 0^+} (f^*)'(N(t)) = -\frac{r^*\, E^u}{K+C} < 0.$$

So, we get the claim (i). Under the same conditions, to the equilibrium point $N(t) = E^u$ it follows that:

$$\lim_{N(t)\to E^u} (f^*)'(N(t)) = \frac{r^*\, E^u}{K+C}\left(1-\left(\frac{E^u}{K}\right)^{\beta}\right)^{\gamma} > 0.$$

Thus, the claim (ii) is proved. Finally, with respect to the equilibrium point $N(t) = E^s = K$ and considering that $\gamma \in \mathbb{R}^+$, we have for any $\beta \in]0,1]$ and $r^* \in \mathbb{R}^+$:

$$\begin{cases} \lim\limits_{N(t)\to K} (f^*)'(N(t)) = -\infty, \text{ if } 0<\gamma<1 \\ \lim\limits_{N(t)\to K} (f^*)'(N(t)) = 0^-, \text{ if } \gamma \geq 1 \end{cases} . \quad (7)$$

Consequently, the claim (iii) is proved. □

Property 4 *Let $g^*(N(t))$ be the per capita growth rates associated to the Gompertz logistic growth models under Allee effects, Eq.(4), with $\beta \in]0,1]$, $\gamma \in \mathbb{R}^+$ and $r^* \in \mathbb{R}^+$. If $E^0 = 0 < E^u < E^s = K$ and $C \in \mathbb{R}^+$, then it is verified that:*

(i) $g^*(N(t)) < 0 \Leftrightarrow 0 < N(t) < E^u \vee N(t) > E^s$*;*

(ii) $g^*(N(t)) > 0 \Leftrightarrow E^u < N(t) < E^s$.

The above results follow from Eq.(4) and Property 3. See also Fig.1 (a) and (b).

Proposition 5 *Let $f^*(N(t))$ be the Gompertz logistic growth models under Allee effects, Eq.(6), $T(N(t))$ be the correction factor, Eq.(5), $g^*(N(t))$ be the associated per capita growth rates, Eq.(4), with $\beta \in]0,1]$, $\gamma \in \mathbb{R}^+$ and $r^* \in \mathbb{R}^+$. If $E^0 = 0 < E^u < E^s = K$ and $C \in \mathbb{R}^+$, then $f^*(N(t))$ has strong Allee effect.*

Proof: Let us consider $f^*(N(t))$ be the population growth rates and $N(t) \geq 0$, such that $E^0 = 0 < E^u < E^s = K$ and $C \in \mathbb{R}^+$. The following conditions are satisfied:

(i) from Property 3 (ii) exists a population threshold corresponding to the equilibrium point $N(t) = E^u$, that is, $\lim\limits_{N(t)\to E^u} f^*(N(t)) = 0$;

(ii) from Property 4 (i) and (ii) it follows that there is a subinterval $I \subset]0,K]$, such that the *per capita* growth rates verifies the inequality,

$$g^*\left(\tilde{N}(t)\right) > (f^*)'(0^+) < 0,\ \forall \tilde{N}(t) \in I,$$

that is, the population exhibits an Allee effect;

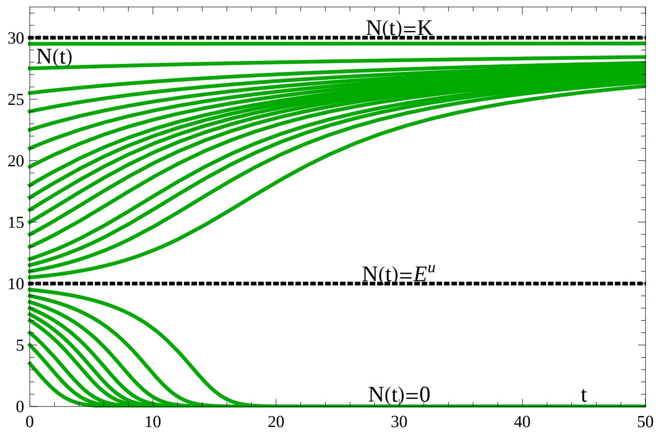

Figure 2: Gompertz's logistic sigmoid growth curves with strong Allee effect: (solid lines) numerical solutions of the Gompertz logistic growth models $f^*(N(t))$, Eq.(6), for different initial population sizes, at $\beta = 0.6$, $\gamma = 2.5$, $K = 30$, $C = 40$, $E^u = 10$, $r^* = 8$; (dashed lines) local unstable equilibria $N(t) = E^u$ and local stable equilibria $N(t) = K$. Any initial population size $N(t_0)$ starting above the critical threshold $N(t) = E^u$ converges to the stable equilibria $N(t) = K$, the carrying capacity, when $N(t_0)$ is below the critical threshold $N(t) = E^u$, then it converges to the stable equilibrium point $N(t) = 0$.

(iii) the Allee effect is strong, that is,

$$\lim_{N(t)\to 0^+} (f^*)'(N(t)) < 0.$$

This result follows from Property 3 (i). In fact, the respective *per capita* growth rates $g^*(N(t))$ increases with density from low densities, starting with a negative value.

Therefore, is proved that the Gompertz logistic growth models $f^*(N(t))$ have strong Allee effect. □

In Fig.1 (a) and (b) are presented numerical simulations of the *per capita* growth rates $g^*(N(t))$, given by Eq.(4), and of the population growth rates $f^*(N(t))$, given by Eq.(6), both with strong Allee effect, respectively, for different parameter values. Note the significant difference in the behavior of the presented cases, in particular the variation of the parameters values r^* ($r_1^* = 10$ and $r_2^* = 50$) and γ ($\gamma_1 = 0.5$ and $\gamma_2 = 2.5$).

Generically, the previous results characterize the phenomenon of strong Allee effect for the Gompertz logistic growth models subjected to the correction factor $T(N(t))$. In this case, populations with fluctuating dynamics and a strong Allee effect are especially vulnerable to extinction (will be attracted to the stable equilibrium point $E^0 = 0$) as the fluctuations may drive their densities below the critical threshold E^u.

Otherwise, the population size $N(t)$ will grow as the time t increases until it establish on the value of carrying capacity $E^s = K$. If the initial population size is equal to the Allee limit or critical threshold E^u, then the population size remains constant equal to this value over time t, see Fig.2.

3.2 Weak Allee effect

In the presence of weak Allee effect the populations do not exhibit any thresholds, that is, this scenario is characterized by an unconditional survival or establishment of the populations. The *per capita* growth rates are positive for all the population size $N(t) \geq 0$ and are increasing at low densities. See, [1], [3], [5], [10], [12] and references therein, see also Fig.3.

Property 6 *Let $f^*(N(t))$ be the Gompertz logistic growth models under Allee effects, Eq.(6), $T(N(t))$ be the correction factor, Eq.(5), with $\beta \in]0,1]$, $\gamma \in \mathrm{R}^+$ and $r^* \in \mathrm{R}^+$. If $-K < E^u \leq 0$ and $C \in \mathrm{R}^+$, then $f^*(N(t))$ has two equilibrium points for all population size $N(t) \geq 0$: $N(t) = E^0 = 0$, $N(t) = E^s = K$; and it is verified that:*

(i) $N(t) = E^0 = 0$ is an equilibrium point locally unstable;

(ii) $N(t) = E^s = K$ is an equilibrium point locally stable.

Proof: Let us consider $f^*(N(t))$ be the population growth rates, such that $-K < E^u \leq 0$ and $C \in \mathrm{R}^+$. From Eq.(6) follows that $f^*(N(t))$ has two equilibrium points: $N(t) = E^0 = 0$ and $N(t) = E^s = K$, $\forall N(t) \geq 0$. Relative to the equilibrium point $N(t) = E^0 = 0$, for any $\beta \in]0,1]$, $\gamma \in \mathrm{R}^+$ and $r^* \in \mathrm{R}^+$, let us see in what conditions this equilibrium point is locally unstable, that is,

$$\lim_{N(t)\to 0^+} (f^*)'(N(t)) > 0. \quad (8)$$

Considering Eqs.(4) and (6), and from $-K < E^u \leq 0$ and $C \in \mathrm{R}^+$, we have,

$$\lim_{N(t)\to 0^+} g^*(N(t)) = -\frac{r^* E^u}{K + C} > 0. \quad (9)$$

Thus, to verify Eq.(8) it is sufficient that the following condition is satisfied,

$$\lim_{N(t)\to 0^+} (g^*)'(N(t)) > 0. \quad (10)$$

Given the derivative of $g^*(N(t))$, in order to verify Eq.(10), we obtain the following implicit inequality:

$$\lim_{N(t)\to 0^+} \left(1 - \left(\frac{N(t)}{K}\right)^{\beta}\right)^{\gamma-1} \left(\frac{N(t)}{K}\right)^{\beta-1} T(N(t))$$

(a) *Per capita* growth rates at $\beta = 0.7$ and $\gamma = 0.5;\ 1.5$

(b) Population growth rates at $\beta = 0.7$ and $\gamma = 0.5;\ 1.5$

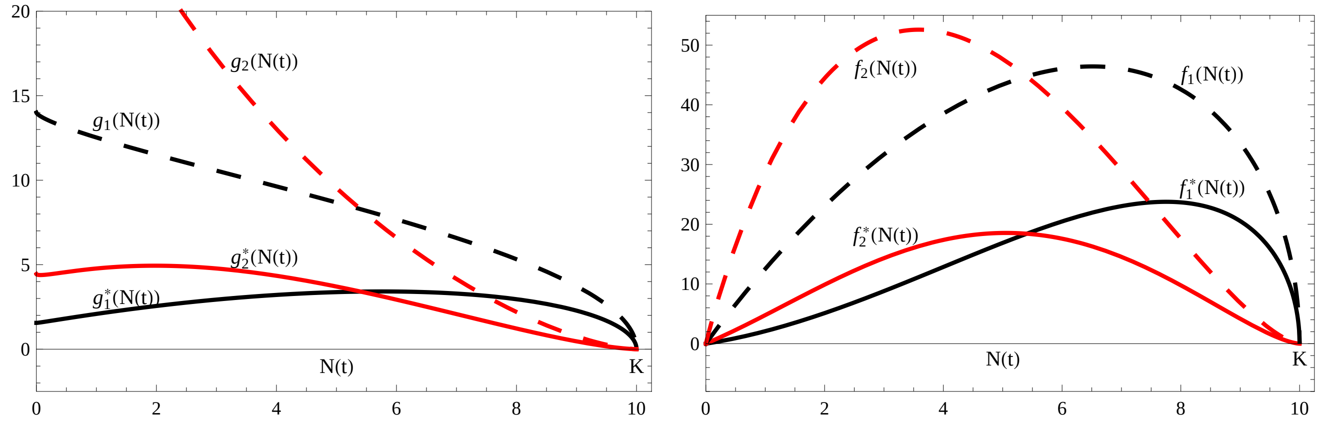

Figure 3: Weak Allee effect: (a) (Solid lines) *Per capita* growth rates $g^*(N(t))$, Eq.(4), at $\beta = 0.7,\ K = 10,\ C = 8,\ E^u = -2$ fixed parameters and $\gamma_1 = 0.5,\ \gamma_2 = 1.5,\ r_1^* = 14,\ r_2^* = 40$ for $g_1^*(N(t))$ and $g_2^*(N(t))$, respectively; (Dashed lines) $g(N(t))$ is the *per capita* growth rate without weak Allee effect, given by Eq.(2), for the same parameter values; (b) (Solid lines) corresponding Gompertz logistic growth models $f^*(N(t))$, Eq.(6); (Dashed lines) $f(N(t))$ is the population growth rate without weak Allee effect, given by Eq.(1).

$$< \frac{K}{\beta\gamma(C+K)}. \qquad (11)$$

Therefore, under the above conditions the equilibrium point $N(t) = E^0 = 0$ is locally unstable.

Finally, with respect to the equilibrium point $N(t) = E^s = K$ and considering that $\gamma \in \mathrm{R}^+$, in a similar way to Eq.(7), follows that this equilibrium point is locally stable. □

In this case, the unstable equilibrium point E^u vanishes in the population growth rates $f^*(N(t))$, the trivial equilibrium point $E^0 = 0$ becomes unstable and the population stabilizes at $E^s = K$. See also, for example, [5] and [12]. Thus, for parameter values $-K < E^u \leq 0$ and $C \in \mathrm{R}^+$, the population growth rates $f^*(N(t))$ have not a population threshold in $[0, K]$. Fig.3 (a) and (b) illustrates this situation. Note that the implicit inequality established at Eq.(11) depends on all six real parameters. The sufficient condition given by Eq.(10) relating to instability of the equilibrium point $N(t) = E^0 = 0$ is decisive in the desired results of this section.

Considering Eq.(9), follows that $g^*(0^+) > 0$. Under this conditions and from Eq.(4), the next result is proved.

Property 7 *Let $g^*(N(t))$ be the per capita growth rates associated to the Gompertz logistic growth models, Eq.(4), with $\beta \in]0,1]$, $\gamma \in \mathrm{R}^+$ and $r^* \in \mathrm{R}^+$. If $-K < E^u \leq E^0 = 0$ and $C \in \mathrm{R}^+$, then*

$$g^*(N(t)) > 0 \Leftrightarrow E^0 = 0 \leq N(t) < E^s = K. \qquad (12)$$

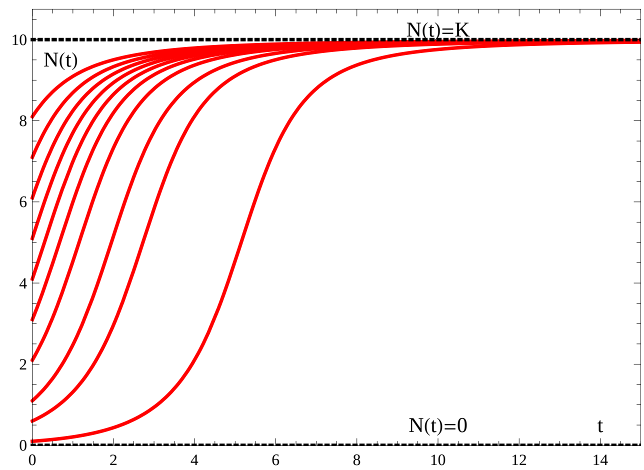

Figure 4: Gompertz's logistic sigmoid growth curves with weak Allee effect: (solid lines) numerical solutions of the Gompertz logistic growth models $f^*(N(t))$, Eq.(6), for different initial population sizes, at $\beta = 0.7,\ \gamma = 1.5,\ K = 10,\ C = 28,\ E^u = -2,\ r^* = 14$; (dashed lines) local unstable equilibria $N(t) = 0$ and local stable equilibria $N(t) = K$. Any initial population size $N(t_0)$ starting above the stable equilibrium point $N(t) = 0$ converges to the stable equilibria $N(t) = K$, the carrying capacity.

Proposition 8 *Let $f^*(N(t))$ be the Gompertz logistic growth models under Allee effects, Eq.(6),*

$T(N(t))$ be the correction factor, Eq.(5), $g^*(N(t))$ be the associated per capita growth rates, Eq.(4), with $\beta \in]0,1]$, $\gamma \in \mathrm{R}^+$ and $r^* \in \mathrm{R}^+$. If $-K < E^u \leq 0$, $C \in \mathrm{R}^+$ and is verified Eq.(11), then $f^*(N(t))$ has weak Allee effect.

Proof: Considering Property 7 there is a subinterval $I \subset]0,K]$, such that the generalized *per capita* growth rates $g^*(N(t))$ verifies the following inequality:

$$g^*\left(\tilde{N}(t)\right) > (f^*)'(0^+) > 0, \ \forall \tilde{N}(t) \in I, \quad (13)$$

that is, the population exhibits an Allee effect. Clearly, considering Eqs.(12) and (13), and the arguments from Eq.(11), established in Proof. of Property 6, i.e.,

$$\lim_{N(t)\to 0^+} (g^*)'(N(t)) > 0,$$

follows that the generalized Gompertz logistic growth models $f^*(N(t))$ have weak Allee effect. □

As can be seen in Fig.3 (a) and (b), the generalized *per capita* growth rates with weak Allee effect $g^*(N(t))$, Eq.(4), and the corresponding Gompertz logistic growth models $f^*(N(t))$, Eq.(6), displays a highly diversified behavior according to the variation of the diverse parameters. Under weak Allee effect, populations experience lower *per capita* growth rates at low densities but they are always positive, hence there is no critical threshold to be exceeded for the population to survive. Any initial population size $N(t_0)$ starting above the stable equilibrium point $N(t) = 0$ converges to the carrying capacity $N(t) = K$, the stable equilibria, see Fig.4.

3.3 No Allee effect

There are several studies of population growth models, for which the existence of Allee effect has no evidence, see for example [7], [8] and references therein. In this case the *per capita* growth rates are decreasing for all densities $N(t) \geq 0$, see also [1] and [12].

Remark 9 *Under the conditions of Property 6, i.e., $-K < E^u \leq 0$ and $C \in \mathrm{R}^+$, it was proved that $f^*(N(t))$ has two equilibrium points for all population size $N(t) \geq 0$: $N(t) = E^0 = 0$ an equilibrium point locally unstable and $N(t) = E^s = K$ an equilibrium point locally stable. However, to prove that the equilibrium point $N(t) = E^0 = 0$ is locally unstable, i.e.,*

$$\lim_{N(t)\to 0^+} (f^*)'(N(t)) > 0, \quad (14)$$

it is sufficient that the following condition is satisfied:

$$\lim_{N(t)\to 0^+} (g^*)'(N(t)) < 0. \quad (15)$$

This condition is necessary for the models $f^*(N(t))$ have no Allee effect. In fact, considering the expression of the derivative $(g^*)'(N(t))$, if $r^* \in \mathrm{R}^+$, $\beta \in]0,1]$ and $\gamma \in \mathrm{R}^+$, then there are parameter values for which the following implicit inequality is verified,

$$\lim_{N(t)\to 0^+} \left(1 - \left(\frac{N(t)}{K}\right)^{\beta}\right)^{\gamma-1} \left(\frac{N(t)}{K}\right)^{\beta-1} T(N(t)) > \frac{K}{\beta\gamma(C+K)}. \quad (16)$$

Proposition 10 *Let $f^*(N(t))$ be the Gompertz logistic growth models under Allee effects, Eq.(6), $T(N(t))$ be the correction factor, Eq.(5), $g^*(N(t))$ be the associated per capita growth rates, Eq.(4), with $\beta \in]0,1]$, $\gamma \in \mathrm{R}^+$ and $r^* \in \mathrm{R}^+$. If $-K < E^u \leq 0$, $C \in \mathrm{R}^+$ and is verified Eq.(16), then $f^*(N(t))$ has no Allee effect, for all population size $N(t) \geq 0$.*

Proof: Considering the population growth rates $f^*(N(t))$, given by Eq.(6), and Remark 9, Eq.(15), it is verified the following condition:

$$f^*(N(t)) \leq N(t)\,(f^*)'(0) < +\infty, \ \forall N(t) \in [0,K]. \quad (17)$$

On the other hand, the respective no Allee effect *per capita* growth rates $g^*(N(t))$ are decreasing for all densities $N(t) \geq 0$. This result follows from Eq.(16) and also it is found that,

$$\lim_{N(t)\to K^-} (g^*)'(N(t)) < 0.$$

We can claim that $(g^*)'(N(t))$, $\forall N(t) \in [0,K]$, is a function with decreasing exponential behavior. Thus, we conclude that,

$$(g^*)'(N(t)) < 0, \ \forall N(t) \in [0,K]. \quad (18)$$

So, given the results of Eqs.(17) and (18), the desired results follows. □

Remark 11 *Note that under the conditions of Proposition 10, i.e., $-K < E^u \leq 0$ and $C \in \mathrm{R}^+$, the parameter values for which is obtained the implicit equality in Eq.(16), corresponding to*

$$\lim_{N(t)\to 0^+} (g^*)'(N(t)) = 0,$$

define the transition from weak Allee effect to no Allee effect for the models studied in this work.

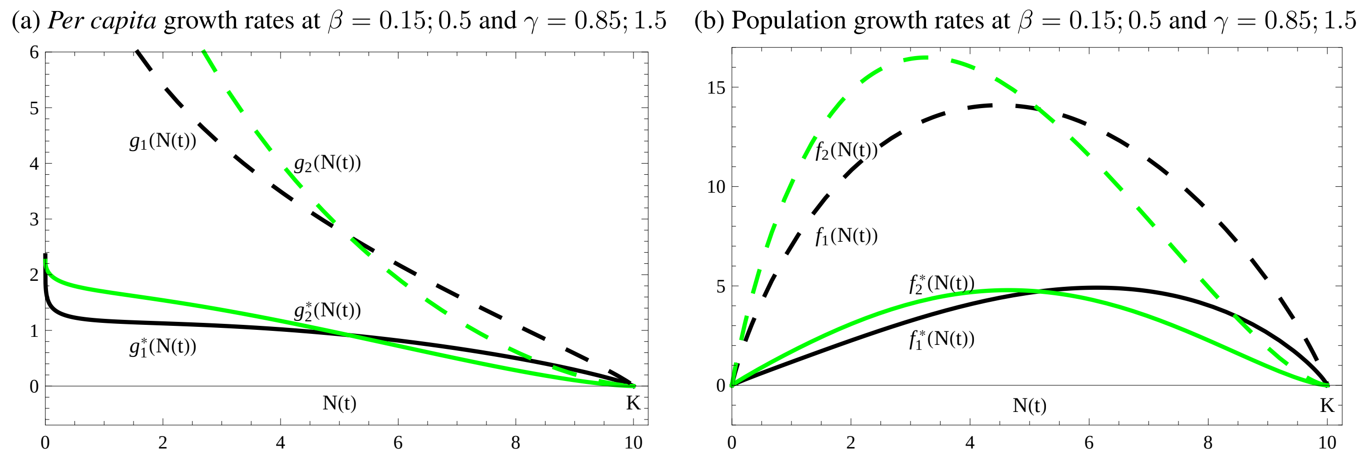

Figure 5: No Allee effect: (a) (Solid lines) *Per capita* growth rates $g^*(N(t))$, Eq.(4), at $K = 10,\ C = 14,\ E^u = -3$ fixed parameters and $\beta_1 = 0.15,\ \beta_1 = 0.5,\ \gamma_1 = 0.85,\ \gamma_2 = 1.5,\ r_1^* = 20,\ r_2^* = 18$ for $g_1^*(N(t))$ and $g_2^*(N(t))$, respectively; (Dashed lines) $g(N(t))$ is the *per capita* growth rate with no Allee effect, given by Eq.(2), for the same parameter values; (b) (Solid lines) corresponding Gompertz logistic growth models $f^*(N(t))$, Eq.(6); (Dashed lines) $f(N(t))$ is the population growth rate with no Allee effect, given by Eq.(1).

In a similar way, as mentioned in the previous sections, in Fig.5 (a) and (b) are presented numerical simulations of the *per capita* growth rates $g^*(N(t))$ and of the population growth rates $f^*(N(t))$, both with no Allee effect, for different parameter values of r^*, β and γ. The variation of admissible parameters illustrates the wide possible modeling with the proposed models.

4 Impact of $T(N(t))$ on the local stability of the carrying capacity K

In this section is studied the impact of Allee effects, given by the correction factor $T(N(t))$, Eq.(5), on the local stability of the stable equilibria $N(t) = K$, the carrying capacity of the population growth models.

Proposition 12 *Let $f(N(t))$ be the Gompertz logistic growth models, Eq.(1), $f_w^*(N(t))$ and $f_s^*(N(t))$ be the Gompertz logistic growth models under weak and strong Allee effects, respectively, Eq.(6), $T(N(t))$ be the correction factor, Eq.(5), with $\beta \in]0,1], \gamma, r, r^*, C \in \mathrm{R}^+$, $|E^u| < K$ and K be the positive equilibrium point of Eqs.(1) and (6). If $r^*T(K) < r$, then*

$$f'(K) < (f_w^*)'(K) < (f_s^*)'(K).$$

Proof: Considering the Gompertz logistic growth models $f^*(N(t))$, given by Eq.(6), its derivative with respect to $N(t)$, with $|E^u| < K$, is given by,

$$(f^*)'(N(t)) =$$

$$\frac{r^*}{r}\left(f'(N(t))\,T(N(t)) + f(N(t))\,T'(N(t))\right).$$

Let $N(t) = K$ be the positive equilibrium point of Eqs.(1) and (6), easily it is verified that,

$$(f^*)'(K) = \frac{r^*}{r} f'(K)\,T(K).$$

If $r^*T(K) < r$ and by the conditions of Eq.(7), follows that

$$f'(K) < (f^*)'(K), \text{ with } |E^u| < K. \quad (19)$$

It is clear from Propositions 5 and 8 that, for $C \in \mathrm{R}^+$:

- if $0 < E^u < K$, then $T_s(K) = \frac{K-E^u}{K+C} < \frac{K}{K+C}$;
- If $-K < E^u \leq 0$, then $T_w(K) = \frac{K+E^u}{K+C} > \frac{K}{K+C}$;

Using conditions of Eq.(7) once more one may write the inequality,

$$\frac{r^*}{r} f'(K)\,T_w(K) < \frac{r^*}{r} f'(K)\,T_s(K)$$

$$\Leftrightarrow (f_w^*)'(K) < (f_s^*)'(K). \quad (20)$$

From Eqs.(19) and (20), we obtain the desired results. □

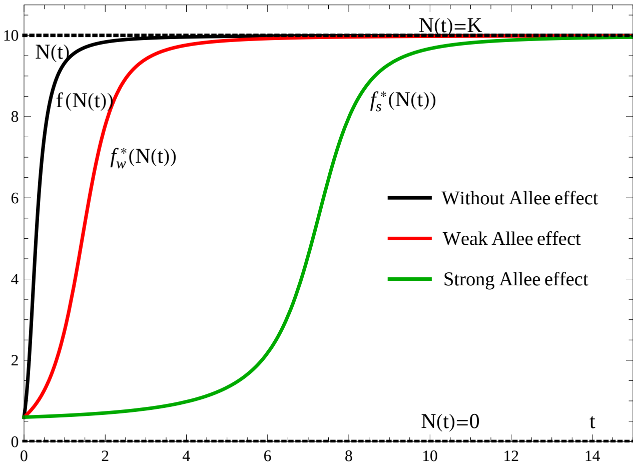

Figure 6: Gompertz's logistic sigmoid growth curves with strong, weak and without Allee effects: (solid lines) numerical solutions of the Gompertz logistic growth models $f(N(t))$, Eq.(1), $f_w^*(N(t))$ and $f_s^*(N(t))$, Eq.(6), for the same initial population size $N(t_0) = 0.6$, at $\beta = 0.7$, $\gamma = 1.5$, $K = 10$, $C = 10$, $r = r^* = 14$, $E^u = -2$ (weak), $E^u = 0.5$ (strong); (dashed lines) local unstable equilibria $N(t) = 0$ and local stable equilibria $N(t) = K$. The trajectories of the Eqs.(1) and (6), $f(N(t))$, $f_w^*(N(t))$ and $f_s^*(N(t))$, Proposition 12, show that the time length gets larger for the models as the Allee effects get stronger.

The previous results state that when one imposes the Allee effects into the Gompertz logistic growth models, Eq.(1), either the local stability of the positive equilibrium point $N(t) = K$ decreases (see Figs.1 (b), 3 (b), 5 (b)) or the population system takes longer time to reach its equilibrium state. On the other hand, the speed of the time evolution of the population density to the equilibrium state $N(t) = K$, of the models with strong Allee effect is less then the models with weak Allee effect. Thus, the Allee effects enlarge the time length in which the population system tries to reach the carrying capacity K. Fig.6 is a numerical simulation that illustrates this analysis.

Remark 13 *Note that under the sufficient condition of Proposition 12, i.e., $r^*T(K) < r$, and from (T3), where is established that for high densities $K \to +\infty$, the Allee effects vanishes, i.e., $T(N(t)) \to 1$, it is claimed that $r^* < r$ is sufficient at high densities for that the Allee effects enlarge the time length in which the population system tries to reach the stable equilibrium $N(t) = K$.*

5 Discussion and conclusions: Icelandic herring population

In this work is defined new continuous population growth models: Gompertz's logistic growth models subjected to Allee effects, given by Eq.(6). The motivation for this study comes from the fact that the *per capita* growth rates $g(N(t))$, Eq.(2), of the Gompertz logistic growth equation, Eq.(1), decrease at low densities, for $\beta \in]0, 1]$ and $\forall \gamma \in \mathrm{R}^+$. This means that the population dynamics model defined by Eq.(1) does not contemplate Allee effects. The analysis presented stems from the consideration of an adjustment or correction factor of polynomial type $T(N(t))$, given by Eq.(5), which allow the induction of Allee effects in the Gompertz logistic growth equation, Eq.(1). An Allee limit E^u is incorporated so that the models under study have strong, weak or no Allee effects.

It is already known from previous studies that the presence of Allee effects is crucial on the stability analysis of equilibrium points of a population dynamics system. In Sec.3 is studied under what conditions the Allee effects, given by $T(N(t))$, affect the stability of the equilibrium points of the Gompertz logistic growth equation. Properties 3 and 6 and Remark 9 set the stability analysis of the equilibrium points in the Gompertz logistic growth equation subjected to strong, weak and no Allee effects, respectively.

One of the crucial points of this study is the establishment of properties and sufficient conditions for the existence of strong, weak and no Allee effects in the Gompertz logistic growth equation. These results are presented in Propositions 5, 8 and 10, where it stands out particular attention to the implicit inequality given by Eq.(11), which establishes a sufficient condition for the occurrence of weak Allee effect. The transition from strong Allee effect to no Allee effect, passing through the weak Allee effect, depending on all parameters given by the implicit condition Eq.(11), gives us some of the unexpected results of the paper. This condition reflects how the weak Allee effect is complex and meticulous to detect in these population dynamics models.

Another central point of this investigation is the study of the impact of Allee effects, given by the correction factor $T(N(t))$, Eq.(5), on the local stability of the stable equilibria $N(t) = K$, the carrying capacity of the models. Proposition 12 provides a sufficient condition, a relation between the intrinsic growth rates r and r^* of the Eqs.(1) and (6), respectively, and the value of $T(K)$, for which the local stability of the positive equilibrium point $N(t) = K$ decreases, when is imposed Allee effects in the Gompertz logistic growth equation. Thus, the population system subjected to Allee effect takes longer time to reach its equilibrium

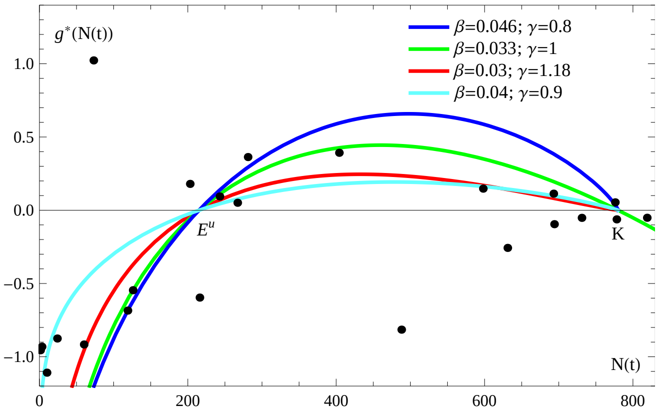

Figure 7: Icelandic herring dataset (GPDD Main Id. 1765) and *per capita* growth rates $g^*(N(t))$, Eq.(4), at fixed parameters $K = 780$ and $E^u = 215$ (strong Allee effect), (blue line) $\beta = 0.046, \gamma = 0.8, r^* = 80, C = 750$; (green line) $\beta = 0.033, \gamma = 1, r^* = 105, C = 220$; (red line) $\beta = 0.03, \gamma = 1.18, r^* = 120, C = 120$; (light blue line) $\beta = 0.04, \gamma = 0.9, r^* = 28, C = 320$. The simple units are given in thousand tonnes.

state. Under the same conditions is proved that as the Allee effects get stronger, the time evolution of the population density to the stable equilibria gets larger.

Conclusively, the present study show that the presence of Allee effects in the Gompertz logistic growth equation play a vital role in the stability analysis of these new continuous population growth models. This work is validated using Icelandic herring dataset of 24 years (1947-1970), from NERC Center for Population Biology, Imperial College (1999), The Global Population Dynamics Database, http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html, with GPDD Main Id. 1765. Fig.7 shows that the plot of the *per capita* growth rates for the Icelandic herring population dataset exhibits a behavior of strong Allee effect, see also [13]. The numerical simulations presented in the fitted curves at Fig.7, for several parameter values at Eq.(4), prove how these population growth models may be important in conservation management of herring populations and other fishing species at risk of extinction.

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