

VON BERTALANFFY'S GROWTH DYNAMICS WITH STRONG ALLEE EFFECT

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Abstract

Von Bertalanffy's model is one of the most popular differential equation used in order to study the increase in average length or weight of fish. However, this model does not include demographic Allee effect. This phenomenon is known in the fisheries literature as “depensation”, which arises when populations decline rapidly at low densities. In this paper we develop and investigate new corrected von Bertalanffy's models with Allee effects. The generalization that we propose results from considering correction factors, one of rational type and the others of polynomial type, where two parameters are considered. The use of a parameter $C > 0$ leads the presented generalization, which yields some more flexible models with variable extinction rates. An Allee limit or unstable equilibrium E^u is incorporated so that the models under study have strong Allee effect. We analyze and show the transition from the strong Allee effect to the inexistence of this effect, through by a “weakening” of the Allee effect, depending on the parameters C and E^u . Finally, we discuss the flexibility of corrected von Bertalanffy's sigmoid growth curves. So, the correspondents inflexion points are variable, i.e., the fish mass when the growth rate is maximum may be varied.

Keywords: Von Bertalanffy's model, population dynamics, Allee effect.

2010 Mathematics Subject Classification: 92D25, 92D99, 92D40.

1. INTRODUCTION AND MOTIVATION

The growth of individuals within a population is usually modeled by a function which represents the growth of an “average” individual in the population. The

growth of an individual is regarded as an increase in its length or weight with increasing age. Among the various functions or models that have been used to analyze the increase in average length or weight of fish, von Bertalanffy's model is one of the most popular, see for example [6, 8] and references therein. The mathematical model formulated by the Australian biologist von Bertalanffy is given by the differential equation,

$$(1) \quad \frac{dN(t)}{dt} = \alpha N(t)^{\frac{2}{3}} - \beta N(t).$$

This model can be considered a change of the Verhulst logistic growth curve in order to incorporate metabolic characteristics based on physiological arguments, where $N(t)$ is the fish mass as a function of time t , $N_0 = N(0)$ is the initial biomass, α is the constant of anabolism (representing the synthesis rate of mass per unit of surface area of the animal) and β is the constant of catabolism (which represents the rate of decrease in weight per unit of mass). The term $N(t)^{\frac{2}{3}}$ comes from the allometric relationship between the weight and the body surface area of the fish. For more details see [6, 8, 17] and [18].

The basic models of population dynamics consider the number of individuals in a stock, either as a whole or categorized by age group. Sometimes, instead of using the number of fish, scientists use the concept of biomass, the total weight of all the fish in a stock. The biomass can be estimated through the calculus of the average weight of a fish (either for each age class or for the stock as a whole), and then multiply that average weight by the number of individuals in the class or stock, [7]. Note that, while a population is a group of individual fish of the same species located in a given area (that can be very large as an ocean or small as a river), a stock is a group of fish of the same species in a given area that is defined as much by management concerns (such as jurisdictional boundaries or harvesting location) as by biology. A fish stock may be only one population or may encompass numerous populations.

When populations decline rapidly at low densities, i.e., when there are slow recovery rates, it is verified a phenomenon known in the fisheries literature as "depensation", which is better known throughout the ecological literature as the Allee effect. This phenomenon should be of great concern to managers and those attempting to assess risk of extinction. See for example [9] and [11].

The Allee effect is an important dynamic phenomenon first described by Allee in 1931, [3]. Stephens et al in 1999 distinguish between component Allee effects and demographic Allee effects. All mechanisms giving rise to an Allee effect (for example, difficulty finding mates or cooperative feeding) result in component Allee effects, i.e., a positive relationship between a component of individual fitness, e.g., survivorship or *per capita* reproduction, and population size or density. If these component Allee effects are not offset by negative density dependence in other

components of fitness they may cause demographic Allee effects, i.e., positive density dependence manifested at the population level, [10]. The population level consequences of demographic Allee effects are classified as either weak or strong, where a strong Allee effect results in a critical density below which *per capita* population growth rate is negative, while in the case of a weak Allee effects this critical density does not exist, see for example [10] and [16], observe Figure 1(a).

In this work, we use the concept of demographic Allee effect, which is manifested by a reduction in the *per capita* growth rate at low population sizes. In this case, the *per capita* growth rates are higher than the population growth rate at the initial time. The definitions of strong and weak Allee effects that we are going to use are in the sense of [5, 10, 12, 14, 16] and references therein.

The layout of this paper is as follows. In Section 2, we develop and investigate new corrected von Bertalanffy's models with Allee effects. The generalization that we propose results from considering correction factors, one of rational type and the others of polynomial type, where two parameters are considered. The use of a parameter $C > 0$ leads the presented generalization, which yields some more flexible models with variable extinction rates. An Allee limit E^u is incorporated so that the models under study have strong Allee effect. In Section 3, we study the transition from the strong Allee effect to the inexistence of this effect, through by a "weakening" of the Allee effect, depending on the parameters C and E^u . This analysis gives the most interesting results of the work, Propositions 1 and 2. At the end, Section 4, we present a discussion about the flexibility of the news von Bertalanffy's sigmoid growth curves.

2. VON BERTALANFFY'S MODELS WITH ALLEE EFFECT

The von Bertalanffy model, equation (1), can be rewritten to be a special case of the Bernoulli differential equation, as follows:

$$(2) \quad f(N(t)) = \frac{dN(t)}{dt} = r N(t)^{\frac{2}{3}} \left(1 - \left(\frac{N(t)}{K} \right)^{\frac{1}{3}} \right)$$

considering $r = \frac{\alpha}{\beta}$ the intrinsic growth rate or density-independent growth rate (a growth rate that does not depend on the abundance or density of individuals in the stock; the stock size will change at a constant rate regardless of the size of the stock, [7]) and $K = r^3$ the carrying capacity (the maximum upper limit to the size of a stock, determined by the availability of prey, the presence of predators or other limitations of the habitat, [7]). The equation (2) is designated by von

Bertalanffy's growth equation, which has solution

$$(3) \quad N(t) = K \left[1 - \left[1 - \left(\frac{N(t_0)}{K} \right)^{\frac{1}{3}} \right] e^{-(rt/3K^{1/3})} \right]^3.$$

The *per capita* growth rate, associated to this growth model, is given by

$$(4) \quad g(N(t)) = \frac{f(N(t))}{N(t)} = r N(t)^{-\frac{1}{3}} \left(1 - \left(\frac{N(t)}{K} \right)^{\frac{1}{3}} \right).$$

In fact, the von Bertalanffy model is the classic model for predicting how a fish grows as it ages, which assumes that fish grow most quickly when they are young. Growth slows gradually as the individual gets older, and eventually stops. The size at which the fish stop growing is referred to as carrying capacity (K).

Note that, the fish mass $N(t)$ at the inflexion point of von Bertalanffy's sigmoid curve, defined by equation (3), is given by $N_{inf} = \frac{8}{27}K$, [15]. These inflexibility of the inflection point can be a limitation of von Bertalanffy's model, which leads to consider the fish mass, when the growth rate is maximum, always constant, see Figure 3. The corrected von Bertalanffy models, that we develop and investigate in this paper, have the great advantage of consider that the fish mass, when the growth rate is maximum, can be variable. See the discussion presented at Section 4.

The von Bertalanffy growth model, equation (2), do not exhibit the Allee effect, because the *per capita* growth rate decreases at low densities, see the graphic of $g(N(t))$ in Figures 1(a) and 2(a). However, this drawback can be corrected using suitable corrections, similarly to what was done by the authors in [1, 2] and [13], with respect to particular cases of Blumberg's model. Therefore, we defined the corrected von Bertalanffy models or population growth rates by the differential equations,

$$(5) \quad f_i^*(N(t)) = \frac{dN(t)}{dt} = r_i N(t)^{\frac{2}{3}} \left(1 - \left(\frac{N(t)}{K} \right)^{\frac{1}{3}} \right) T_i(N(t))$$

with intrinsic growth rates $r_i > 0$ and $i = 1, 2, 3$, where K is the carrying capacity and the correction factors that adjust the Allee effect are defined by

$$(6) \quad T_1(N(t)) = \frac{N(t) - E^u}{N(t) + C}, \quad T_2(N(t)) = \frac{N(t) - E^u}{K + C}$$

and $T_3(N(t)) = \frac{N(t) - E^u}{E^u + C}$

(a) <i>Per capita</i> growth rates	(b) Population growth rates
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Figure 1. Strong Allee effect: *per capita* growth rates $g_i^*(N(t))$ and corresponding von Bertalanffy's population growth rates $f_i^*(N(t))$, at $r_i^* = 95, K = 10, C = 3$ and $E^u = 2$.

with $E^u < K$ and $C > 0$, where E^u is the rarefaction critical density or Allee limit. The parameter C allows us to define and study more flexible models, with variable extinction rates. Consequently, the respective *per capita* growth rates are defined by

$$g_i^*(N(t)) = \frac{f_i^*(N(t))}{N(t)}.$$

Generally, the *per capita* growth rates $g_i^*(N(t))$, with $i = 1, 2, 3$, associated to the corrected von Bertalanffy models, that describes the Allee effect, are unimodal maps, where the maximum rate is obtained for only one positive dimension. Below this “optimal” population size, positive effects of the presence of individuals of the same species prevail and $g_i^*(N(t))$ are increasing. While above this “optimal” population size, the negative dependence of the population size dominates and so the *per capita* growth rate $g_i^*(N(t))$ are decreasing. In order to analyze the stability, the values of the *per capita* growth rate $g_i^*(N(t))$ should have small oscillations near the equilibrium point (slightly increasing until the equilibrium point, and slightly decreasing soon after this value), and should be a continuous function for other values of the population size $N(t)$, see Figures 1(a) and 2(a).

In the next section, we discuss and analyze the type, existence or inexistence of Allee effects, depending on the parameters that are considered in the corrected von Bertalanffy models proposed.

3. TRANSITION FROM STRONG TO INEXISTENCE OF ALLEE EFFECTS

The transition from the strong Allee effect to the inexistence of the Allee effect, through by a “weakening” of this effect, depending on the parameters C and E^u , gives the most interesting results of the paper. The presence of strong Allee effects is presumed in many theoretical predictions about the role and importance of Allee effects, especially predictions concerning extinction and colonization rates. This makes understanding the strength of Allee effects at observed population densities as important to ecological theory and management decisions as the ability to detect their presence. Strong Allee effects occurred in multiple taxonomic groups and were caused by mate limitation, predator satiation and cooperative defense, see [10] and references therein.

The existence of strong Allee effect can be characterized by an extinction/survival scenario, which is the most usual consequence of the Allee effect, and the issue of extinction or survival of the population is of utmost practical relevance, see [4] and [13]. At this stage the Allee effect appears at moderate levels, i.e., the *per capita* growth rates $g_i^*(N(t))$, with $i = 1, 2, 3$, considering $0 < E^u < K$, $C > 0$ and for every $r_i^* > 0$, are negative for very low or very high values of the population size $N(t)$, i.e.,

$$g_i^*(N(t)) < 0 \Leftrightarrow 0 < N(t) < E^u \vee N(t) > K,$$

but are positive for intermediate values of $N(t)$, i.e.,

$$(7) \quad g_i^*(N(t)) > 0 \Leftrightarrow E^u < N(t) < K,$$

see Figure 1(a). It means that the *per capita* growth rates increase with population size at low densities. This phenomenon is characterized by strong Allee effect, see [5, 16] and references therein.

However, the population growth rates $f_i^*(N(t))$, with $i = 1, 2, 3$, exhibit two equilibrium values: the smaller one, that corresponds to the rarefaction critical dimension or Allee limit, which is unstable, denoted by E^u ; and the larger, that corresponds to the carrying capacity K , which is locally stable and is denoted by E^s . The population size at the initial instant, denoted by E^0 , designated by trivial equilibrium, is locally stable, see Figure 1(b). The populations whose dimension at initial instant is smaller than the value E^u will decline to extinction. In particular,

$$\lim_{N(t) \rightarrow 0} g_i^*(N(t)) = -\infty,$$

which imposes higher extinction rates on small populations. Otherwise, for dimension at initial instant greater than the value E^u , the population size stabilize at the value E^s , see Figure 1(a). The next result illustrates what happens, in this scenario, with the corresponding population growth rates.

Proposition 1. *Lets $f_i^*(N(t))$ be the corrected von Bertalanffy models, defined by equation (5), with $r_i^* \in \mathbb{R}^+$ and $T_i(N(t))$, with $i = 1, 2, 3$, be the correction factors, defined by equation (6). If $0 < E^u < K$ and $C > 0$, then $f_i^*(N(t))$ have strong Allee effect.*

Proof. Under these conditions, the population growth rates $f_i^*(N(t))$ satisfies the following conditions:

- (i) the population growth rates have a population threshold, i.e.,

$$\lim_{N(t) \rightarrow E^u} f_i^*(N(t)) = 0;$$

- (ii) from equation (7) it follows that there is a subinterval $I_i \subset]0, K]$, for each $i = 1, 2, 3$, such that is verified the inequality

$$g_i^*(\tilde{N}(t)) > (f_i^*)'(0) < 0, \quad \forall \tilde{N}(t) \in I_i,$$

i.e., the population exhibits an Allee effect;

- (iii) this Allee effect is strong, i.e., $\lim_{N(t) \rightarrow 0} (f_i^*)'(N(t)) < 0$, for any $r_i^* \in \mathbb{R}^+$ and $i = 1, 2, 3$, the value of this limits are:

$$\lim_{N(t) \rightarrow 0} (f_1^*)'(N(t)) = -\frac{r_1^* E^u}{C}; \quad \lim_{N(t) \rightarrow 0} (f_2^*)'(N(t)) = -\frac{r_2^* E^u}{K + C}$$

$$(8) \quad \text{and} \quad \lim_{N(t) \rightarrow 0} (f_3^*)'(N(t)) = -\frac{r_3^* E^u}{E^u + C}.$$

Therefore, the population growth rates $f_i^*(N(t))$, with $i = 1, 2, 3$, have strong Allee effect, as desired. \blacksquare

When the Allee effect gets weaker, in the population growth rates $f_i^*(N(t))$ the unstable equilibrium E^u vanishes, the trivial equilibrium E^0 becomes unstable and the population stabilizes in E^s . The *per capita* growth rates $g_i^*(N(t))$, with $i = 1, 2, 3$, are positive for all the population size $N(t) > 0$ and are increasing at low populations sizes. This description corresponds to a weak Allee effect, see [16] and references therein.

In particular, we remark that, for $E^u = E^0 = 0$ and $C > 0$, the population growth rates $f_i^*(N(t))$ have no a population threshold. Nevertheless, the following conditions are verified:

$$\lim_{N(t) \rightarrow 0} (f_i^*)'(N(t)) = 0,$$

(a) <i>Per capita</i> growth rates	(b) Population growth rates
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Figure 2. Inexistence of Allee effect: *per capita* growth rates $g_i^*(N(t))$ and corresponding von Bertalanffy's population growth rates $f_i^*(N(t))$, at $r_i^* = 15, K = 10, C = 4$ and $E^u = -2$.

and attending that $g_i^*(N(t)) > 0 \Leftrightarrow r_i^* > 0 \wedge 0 < N(t) < K$, with $i = 1, 2, 3$, there is a subinterval $I_i \subset]0, K[$, such that:

$$g_i^*(\tilde{N}(t)) > (f_i^*)'(0) = 0, \forall \tilde{N}(t) \in I_i.$$

Therefore, at the point $E^u = 0$ there is a transition between the strong Allee effect and the inexistence of this effect. We consider that, at the point $E^u = 0$, there is a kind of "weakened" Allee effect. However, we can not claim that there is weak Allee effect for the proposed models.

In an extreme case, when $E^u < 0$ and $C > |E^u|$, the models defined do not exhibit the Allee effect and we establish the next result, see also Figure 2.

Proposition 2. *Lets $f_i^*(N(t))$ be the corrected von Bertalanffy models, defined by equation (5), with $r_i^* \in \mathbb{R}^+$ and $T_i(N(t))$, with $i = 1, 2, 3$, be the correction factors, defined by equation (6). If $E^u < 0$ and $C > |E^u|$, then $f_i^*(N(t))$ have no Allee effect.*

Proof. Considering $E^u < 0$ and $C > |E^u|$ the influence of the Allee effect becomes weak, i.e., with the proposed correction the unstable equilibrium E^u vanishes. The corresponding *per capita* growth rates decreases with the density $N(t)$, which means that, considering equation (8) is verified:

$$g_i^*(N(t)) \leq (f_i^*)'(0) = +\infty, \forall N(t) \in [0, K]$$

see Figure 2(a). This proves that, in the conditions considers, the generalized models $f_i^*(N(t))$ have no Allee effect, as advertised. ■

4. CONCLUSIONS AND DISCUSSION

As we claim, the inflexibility of the inflection point of von Bertalanffy's sigmoid curve, defined by equation (3), can be a limitation of this model. The corrected von Bertalanffy models, equation (5), define new sigmoid growth curves, in which the rate of growth increases as size increases from low values, reaches a maximum at a point of inflexion and then decreases towards zero at an upper asymptote, see

(a) Strong Allee effect	(b) Inexistence of Allee effect
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Figure 3. Corrected von Bertalanffy's sigmoid growth curve. Strong Allee effect: $K = 30, E^u = 6, C = 20$ and $N(0) = 5.85$ (thin dotted lines), $N(0) = 6$ (thick dashed line), $N(0) = 6, 2$ (solid lines). Inexistence of Allee effect: $K = 30, E^u = -6, C = 20$ and $N(0) = 0$.

Figure 3. Nevertheless, the models that we proposed and analyzed in this paper have the great advantage of consider that the fish mass $N(t)$, when the growth rate is maximum, can be variable.

Once, the model presented by von Bertalanffy, equation (2), can be seen as a special case of the Bernoulli differential equation is possible to obtain an explicit solution $N(t)$, given by equation (3). For the new corrected models defined, we can not explicitly determine their solutions. We can only plot numerical approximations of these solutions, whose values are determined by interpolation, see Figure 3. In this figure, we can observe sigmoid growth curves for the case of strong Allee effect (Figure 3(a)), and also for the case in which there is no Allee effect (Figure 3(b)).

The corrected models with strong Allee effect, model three types of growths, depending on the value of the initial population size. In the case of this value be less than the Allee limit or unstable equilibrium, the population size tends to zero as the time t increases, but according to three different behaviour. In all cases, the population will become extinct, see the graphics of the thin dotted lines in Figure 3(a). If the initial population size is equal to the Allee limit, then the population size remains constant equal to this value over time, for the three models corrected, see the thick dashed line in Figure 3(a). In the case of the initial population size be higher than the Allee limit, the population size will grow as the time t increases until it establish on the value of carrying capacity, see the graphics of the solid lines in Figure 3(a). Beyond this range of behaviour, even the models without Allee effect are more flexible in relation to von Bertalanffy's model, Figure 3(b), because they all have variable inflection points. Therefore, the new corrected von Bertalanffy models proposed are theoretical credible alternatives in the modeling of the mass fish growth over time, allowing the possibility of extinction.

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