



An Age-structured Resource-Consumer Dynamical Model

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Received December 30, 2006; revised May 4, 2007; accepted May 16, 2007

Abstract

Many dynamical systems in population biology in which agents compete for resources may exhibit chaotic fluctuations. This short letter develops Gamarra and Solé's previous work. We briefly review a classical model of population with complex dynamics, and proceed to study the dynamics of an age-structured resource-consumer model, in which the fertility coefficients are density independent. Implicit or first integral solutions of the model are obtained, and conditions for which they are stable given. It is observed that resource availability at any time depends on the number of potential consumers present.

Key words: Age-structure, population dynamics, resource-consumer model, stability of solutions

AMS Classification: 34C28, 92D25, 92D40

1. Introduction

The most basic framework for understanding the dynamics of biological populations recognizes that changes in population numbers are the result of two types of processes - on the one hand, there is the deterministic component of population dynamics that results from interactions between individuals and other predictable ecological processes - on the other, there is stochastic component of population dynamics that results from random variations in birth and death rates, for instance owing to the direct effects of weather or disturbance (Freckleton and Watkinson, 2002). It is fundamental to understand the dynamics of any population in order to determine the relative roles of these two processes in a year-to-year variation in population numbers. We shall consider the former in the present study.

This paper is motivated by the fact that one of the most important development in ecology during the 1970s was the recognition that, even in the absence of stochastic variations, entirely deterministic systems are capable of producing patterns of population change that are apparently indistinguishable from random noise (May and Oster, 1976). This form of dynamics results when density dependence within populations is overcompensating, and the growth of populations from low densities is high (Freckleton and Watkinson, 2002). From this low level, growth is then rapid, and high levels are soon reached. Consequently, populations fluctuate around a long term average, and in the extreme, these patterns of fluctuations may be entirely unpredictable. The existence of

such dynamics could thwart attempts to predict population dynamics from one year to the next. However, partially inspired by ideas of this kind, we propose a resource-consumer mechanism structured by age, and in which a time lag is introduced to account for the time it takes individuals to adapt to changes (in their feeding pattern, environmental changes etc...). Recently, Rao and Rao (2006), Murdoch *et al.*, (2003) studied the stability of resource-consumer dynamic models involving distributed delays. They do not ¹take into account the age parameter. Various age-structured consumer-resource models in the form of predator-prey dynamics have been analyzed in the literature (Thomson, 1975; Cushing and Saleem, 1982; McCauley et al., 1996 to name just a few and the references therein). No coupled consumer-resource age-structure model has been analyzed previously, except by simulation in the context of predator-prey interaction between fishes of different species in lakes (de Roos and Persson, 2002).

Therefore, in this short letter, within-generation dynamics of and age-structured resource-consumer interactions developing in time units t is studied. In writing this short note which develops and naturally extends Gamarra and Solé (2002) previous work, we ask: *Does age-dependent vital rates play any important role in the dynamics of resource-consumer model?* The proposed model is interesting in its own right, at least from the mathematical point of view. Also, some resources are more vulnerable to consumers at juvenile age, and this gives a biological relevance to this study.

1.1 An Example

The concept of chaos (a term first coined by May, 1974) or complex behavior in ecological population is widely known for non-overlapping generations. The classical approach uses very simple models consisting of time discrete, first-order difference equations of the form

$$N_{t+1} = bN_t f(N_t), \quad (1)$$

or simply

$$N_{t+1} = g(N_t) . \quad (2)$$

$f(N_t)$ is the so-called *density regulation factor* which must be prescribed in such a way as to reflect the basic biology (fertility, mortality and growth rates) of the particular species being described (Cushing, 1988). More often than not, the population N_t may either exhibit the *Allee effect* (Allee, 1931, 1938), or some typical effect of saturation in reproduction due to scarcity of resources. Thus, a stage is reached when the demands made by the existing population on the resources preclude further growth and the population is then at its *saturation level*, a value determined by the *carrying capacity* of the environment (Pielou, 1969). In general $f(N_t)$, has various forms, for instance, in Gamarra and Solé (2002), $f(N_t) = g(N_t, \dots, N_{t-\tau})$, which represents some non-linear function describing some degree of density-dependence, τ defines a within-generation

¹ A population experience *Allee effect* when the per capita growth rates decrease as a population decrease. When there is some sort of density-dependence, per capita growth rates also decrease when population increases. This creates a one-hump curve when the per capita rate is plotted against population size.

term for consumption and mortality. A commonly used density function is $f(N_t) = e^{-bN_t}$, $b > 0$. The well-known equation describing a full range of dynamics was developed by Ricker (1954)

$$N_{t+1} = \sigma N_t e^{-bN_t} \quad (3)$$

σ is the discrete initial growth rate, $b > 0$ is the death modulus, or the measure of density-dependent regulation; e.g., cannibalism, intra-specific interactions, etc. Ricker (1954) assumed that adults cannibalize their own young so that the system is implicitly age-structured. As early as 1953, Slobodkin demonstrated that neither age nor size of *Daphnia* taken separately was sufficient information to predict its physiological reactions.

In view of this, it should be more interesting to introduce age dependence explicitly into Gamarra and Solé's (2002) model. They used a hybrid continuous-discrete model, but I will use a purely continuous model. The modification of $f(N_t)$ given by

$$f(N_t) = \eta N_t^{\omega-1} e^{bN_t}, \quad (4)$$

allows for an *Allee effect* when $\omega > 1$, and for models of the form $N_{t+1} = \beta N_t^\omega e^{-bN_t}$ ($\beta = b\eta$), the graph of the right hand side has *one hump* (Cushing *et al.*, 1996).

2. The Consumer-Resource Model

The model presented in this section generalizes Gamarra and Solé's (2002). By assuming a homogeneous interaction at any continuous time t , and by using the notation of Gamarra and Solé (2002), where R stands for resources and C for consumers, we have

$$\begin{aligned} \frac{dR(t)}{dt} &= \gamma - C(t) \frac{R(t)}{\Gamma}; \quad R(0) = R_0, \\ \frac{dC(t)}{dt} &= \lambda - m \left(1 - \frac{R(t)}{\Gamma} \right) C(t); \quad C(0) = C_0, \end{aligned} \quad (5)$$

where $\lambda > 0$ stands for the renewal of resources, and $\lambda > 0$ is a constant growth/renewal rate depicting some immigration of consumers from external pool. m represents the intrinsic death modulus in the absence of resources. $\Gamma = \lim_{t \rightarrow \infty} R(t)$ as $t \rightarrow \infty$ is the carrying capacity of the environment in terms of resources or the maximum available resource ($R \leq \Gamma$), a limit which holds only in the absence of consumers.

Equation (5) is soluble, since the functions involved are continuous in \mathbb{R}^+ and integrable. Indeed, $R(t), C(t) \in L^1(\mathbb{R}^+; \mathbb{R}^+)$. System (5) is a system of couple differential equations. Considering the first equation in (5) independently (this is a crude assumption), using a freshman integration, its first integral is of the form

$$R(t) = R_0 + \gamma \exp \left\{ -\frac{1}{\Gamma} \int_0^t C(u) du \right\} \int_0^t \exp \left\{ -\frac{1}{\Gamma} \int_0^s C(u) du \right\} ds \quad (6)$$

where u follows the limit described only in the absence of consumers. Equation (6) may be used in estimating the quantity of resources if the number on consumers is known *a priori*. The growth of any population in a restricted environment must eventually be

limited by a shortage of resources (Pielou, 1969). If production depends on previous resources, then system (5) now reads

$$\begin{aligned}\frac{dR(t)}{dt} &= \left(\gamma - \frac{C(t)}{\Gamma} \right) R(t), \\ \frac{dC(t)}{dt} &= \left[(\lambda - m) \left(1 - \frac{R(t)}{\Gamma} \right) \right] C(t),\end{aligned}\quad (7)$$

where $m > \lambda < 1$. Otherwise, for $m > \lambda$, consumers will grow in the absence of resources. This may be due to an implicit assumption that consumers may grow from consumption of alternative resources when the common resources are scarce, a biologically reasonable condition as it relates directly to the adaptation of species. A more detail study on this can be found in Ma and Levin (2006). λ and m are the growth rate and the intrinsic mortality rate in the absence of resources, respectively.

The integral representation of equation (7)₁ is

$$R(t) = R_0 e^{\gamma t} \exp \left\{ -\frac{1}{\Gamma} \int_0^t C(u) du \right\}, \quad (8)$$

Which can be interpreted as: in the absence of consumers, resources will keep on growing, but will not exceed the carrying capacity Γ , and as a result of overcrowding, will start declining. For instance, plants compete for light, and those that cannot emerge fast die out. Similarly, equation (7)₂ yields

$$C(t) = C_0 e^{(\lambda - m)t} \exp \left\{ -\frac{\lambda - m}{\Gamma} \int_0^t R(u) du \right\}. \quad (9)$$

By allowing γ in equation (5)₁ to depend on time, an equation similar to that of concentration of drug in the blood stream (Hoppensteadt and Murray, 1981) is obtained, the drug being introduced in dosages $\gamma(t)$ and removed at a rate proportional to $R(t)$. The

main difference is that the constant of proportionality $k := -\frac{C(t)}{\Gamma}$, is not a constant. This

is extremely important, especially for seasonal or periodic resources. In such cases, it could be assumed that $\gamma(t)$ is periodic, i.e., $\gamma(t - T) = \gamma(t) = \lambda(t + T)$ where T is the period; and the initial resource (stock) depends on T such that $R_0 = R_0(T)$ gives the initial resource at the beginning of each period T .

Also, any periodic change of climate will tend to impose its period upon oscillations of internal origin (Lalli and Zhang, 1994), and incorporating the periodicity of environment (seasonal effects, food supplies, mating habits...) into equation (8) yields

$$R(t + T) = R_0(T) \exp \left\{ \int_0^t \left[\gamma(s - T) - \frac{C(s)}{\Gamma} \right] ds \right\}. \quad (10)$$

As mention earlier, age structure is capital in the Resource-Consumer model because in the case of a food web, it takes some time for the plants to get mature for a proper interaction to take place. It is therefore vital to account for this time retardation. More so, it takes a certain unit of time for consumers to respond to changes in the population size or environment (Wangerskey and Cunningham (1956/57), Lalli and Zhang (1994)). Aiyelo and Tchuenche (2005) referred to this process as adaptation parameter.

It is of interest to note however that true age of a biological entity is a matter of which sites are active. Hence, true age is a multidimensional variable, and this multidimensional characterization is called physiological age by biologists (Brewer, 1989). By the continuity law, the evolution equations in (5) with some little modifications take the form of a system of non-linear first order partial differential equations of the McKendrick type, given by

$$\frac{\partial R(t, a)}{\partial t} + \frac{\partial R(t, a)}{\partial a} = -k(t, a)R(t, a); \quad R(0, a) = R_0(a), \quad R(t, 0) = B_R(t) \quad (11)$$

$$\frac{\partial C(t, a)}{\partial t} + \frac{\partial C(t, a)}{\partial \alpha} = -m \left(1 - \frac{R(t, \alpha)}{\Gamma} \right) C(t, \alpha); \quad C(0, \alpha) = R_0(\alpha), \quad C(t, 0) = B_C(t) \quad (12)$$

where a is the age of resources while α is the consumer's age. Since resource depletion is caused by consumption, the effect of consumers on resources of age a at time t can be generalized to take into account its age structure, and this will depend on how a consumer distributes its consumption effort among different ages of the resource population. In general, if we let $k(t, a) = k_1 \int_0^\infty p(a, \alpha) C(t, \alpha) d\alpha$ (with $k_1 := \frac{1}{\Gamma}$), then, the per capita loss rate of resources at time t will depend on the probability distribution $p(a, \alpha)$. This distribution defines the age-specific resource-consumer coupling. For mathematical convenience, we assume that this distribution is Dirac's δ , so only consumer of age a predate on resources of the same age (a very crude assumption!), that is $k(t, a) = k_1 \int_0^\infty p(a - \alpha) C(t, \alpha) d\alpha$ and consequently, this reduces to $k(t, a) = \frac{C(t, a)}{\Gamma}$. a is the age of resources while α is the consumer's age. $B_C(t)$ and $B_R(t)$ represent the recruitment or renewal of consumers and resources, respectively; $C_0(\alpha)$ and $R_0(a)$ are the appropriate initial densities.

Equations (11) and (12) can readily be solved via the Laplace transform method if the right-hand sides are modified to be of convolution type. The method of characteristics can best be applied if it is heuristically assumed that $k(t, a)$ above is age-independent. In this case the solution is given by

$$R(t, a) = \begin{cases} R_0(a-t) \exp \left\{ - \int_0^t k(\tau+a-t) d\tau \right\}; \\ B_R(-a) \exp \left\{ - \int_0^a k(\alpha-a+t) d\alpha \right\}; \end{cases} \quad (13)$$

Similarly, by letting $\frac{C(t, a)}{\Gamma} = k(t, a)$, the same method of solution yields

$$R(t, a) = \begin{cases} R_0(a-t) \exp\left\{-\int_0^t k(\tau, \tau+a-t) d\tau\right\}; \\ B_R(-a) \exp\left\{-\int_0^a k(\alpha-a+t, \alpha) d\alpha\right\}; \end{cases} \quad (14)$$

Equation (12) has a similar solution of the form (14) if $k(t, a) := \left(1 - \frac{R(t, a)}{\Gamma}\right)$. In order to apply the Laplace transform technique (see Watson, 1981), it is convenient to introduce a time lag as follows:

$$\frac{\partial R(t, a)}{\partial t} + \frac{\partial R(t, a)}{\partial a} = -C(t, a) \frac{R(t - \tau, a)}{\Gamma}; \quad (15)$$

$$\frac{\partial C(t, a)}{\partial t} + \frac{\partial C(t, a)}{\partial a} = -m \left(1 - \frac{R(t, \alpha)}{\Gamma}\right) C(t - \tau, \alpha); \quad (16)$$

Depletion of resources is a consequence of random encounters of consumers and resources at time t in a well mixed scenario (mass-action principle). However, equation (15) above is biologically fuzzy since it says that the loss of resources is proportional to the product of consumers and resources of similar ages a and α , but at different times. For this reason, we only accept this equation as a phenomenological ad-hoc assumption that allows for some analytical progress. The introduction of the same time lag swiftly renders the equations analytically tractable if the right hand side is of convolution type.

Let \mathcal{L} represents the operator of Laplace transform, while \hat{R} is the transform of R with respect to t and $p \in \mathbb{C}$ the transform variable. Then, equation (15) yields

$$\mathcal{L}[R_t + R_a + \frac{1}{\Gamma} C(\tau, a) R(t - \tau, a)] = 0. \quad (17)$$

That is,

$$\frac{d\hat{R}(p, a)}{da} + \left(p + \frac{1}{\Gamma} \hat{C}(p, a)\right) \hat{R}(p, a) + R_0(a), \quad (18)$$

which implies,

$$\begin{aligned} \hat{R}(p, a) = e^{-pa} \exp\left\{-\frac{1}{\Gamma} \int_0^a \hat{C}(p, \alpha) d\alpha\right\} \int_0^a R_0(\xi) e^{p\xi} \exp\left\{\frac{1}{\Gamma} \int_0^\xi \hat{C}(p, \alpha) d\alpha\right\} d\xi + \\ + K(p) \exp\left\{-\int_0^a \left(p + \frac{1}{\Gamma} \hat{C}(p, \alpha)\right) d\alpha\right\}, \end{aligned} \quad (19)$$

where $K(p)$ is the constant of integration given by the boundary condition $\hat{B}_R(p)$. By letting

$$\sigma(a) := \exp\left\{-\frac{1}{\Gamma} \int_0^a \hat{C}(p, \alpha) d\alpha\right\}, \quad (20)$$

equation (19) now reads

$$\hat{R}(p, a) = \sigma(a) \left\{ \int_0^a e^{-p(a-\xi)} \frac{R_0(\xi)}{\sigma(\xi)} d\xi + \hat{B}_R(p) e^{-pa} \right\}. \quad (21)$$

By inspection (see Tchenche, 2006),

$$R(t, a) = B_R(t - a)\sigma(s)H(t - a) + R_0(a - t)\sigma(t)H(a - t) \quad (22)$$

where $\sigma(t) := \frac{\sigma(a)}{\sigma(a - t)}$; $H(\cdot)$ is the Heaviside function which forces solutions to be right continuous. Hence, they are positive and biologically relevant. Integrating equation (17) with respect to a gives

$$\widehat{R}(p, a) = e^{-pa} \int_0^a e^{-ps} \left\{ R_0(s) - \frac{1}{\Gamma} \widehat{C} \widehat{R} \right\} ds + \widehat{B}_R(p) e^{-pa}.$$

(23) Evaluation of the inverse of the first and last expressions on the right-hand side of equation (23) is done by inspection. The middle term is a convolution integral whose inversion is immediate, and a little rearrangement of the solution yields

$$R(t, a) = \left(1 - \frac{C(t, \alpha)}{\Gamma + C(t, \alpha)} \right) \{ B_R(t - a)H(t - a) + R_0(a - t)H(a - t) \}. \quad (24)$$

It is important here to note the absence of the survival function $\sigma(\cdot)$ in equation (24).

Nevertheless, this may be taken care of by the expression $\left(1 - \frac{C(t, \alpha)}{\Gamma + C(t, \alpha)} \right) < 1$. The interpretation of equation (24) is not so obvious, but an intuitive look tells us that the quantity of resources available at time t depends on the number of consumers $C(t, \alpha)$ who actually go for the available resources. Also, if $C(t, \alpha)$ is very large, then the resources $R(t, a)$ will decrease very fast.

In order to buttress further the motivation behind this study, we note that the passenger pigeon was present in the United States in vast numbers until late in the nineteenth century. It was heavily hunted for sport and for food and consequently its numbers were drastically reduced by the 1880s (Austin, 1983). Unfortunately, the passenger pigeon could apparently breed successfully only when in a large concentration. The precipitous decline in the passenger pigeon population from huge numbers to extinction calls for great concern and this seems to be one of the basic factors which contributed to the quest for species conservation. Therefore, a study related to resource consumption is ecologically meaningful.

3. Stability

In the regulation of population growth, boundedness and stability are two concepts to be given prominence (Sowunmi, 2002). Though it is a *jeu d'esprit* to show that all the solutions obtained above are bounded, local stability is considered in its entirety.

Equilibrium solutions are often of interest because they are easy to analyze qualitatively, and they often provide important information about the dynamical behavior of the system (Tchuente, 2002). At equilibrium,

$$C(t, \alpha) = C(\alpha); R(t, a) = R(a). \quad (25)$$

That is, C and R are time independent. Densities of these types will satisfy

$$\frac{dR(a)}{da} = -C(\alpha) \frac{R(a)}{\Gamma}; R(0) = B_{R0} \quad \text{and} \quad (26)$$

$$\frac{dC(\alpha)}{d\alpha} = -m\left(1 - \frac{R(\alpha)}{\Gamma}\right)C(\alpha); \quad C(0) = B_{C_0} \tag{27}$$

Thus, we recover Gamarra and Solé's (2002) model equations given in terms of age, but with different initial conditions. Assume that the renewal equations are given by

$$B_i(t) = \beta \int_{w_1}^{w_2} i(t, a) da + F_i(t), \tag{28}$$

with i representing R or C , and $F(t)$ being added for technical reasons to allow for renewal to those already alive at the beginning of the process (Rubinov, 1972), (w_1, w_2) is the fecundity interval with $w_1 < w_2$; then

$$B_{R_0} = \beta \int_{w_1}^{w_2} R_0(a) da + F_{R_0}, \tag{29}$$

$B_{C_0} = \tilde{\beta} \int_{w_1}^{w_2} C_0(\alpha) d\alpha + F_{C_0}$, (30) β and $\tilde{\beta}$ represent the birth rate of resources and consumers, respectively. In order to solve equations (26) and (27), we assume that the age of a consumer is biologically different from that of a resource. More so, their domains, although subsets of \mathbb{R}^+ are also different; that is $a \in [0, \Omega]$, $\alpha \in [0, w]$ where Ω and w are the life spans of resource and consumers, respectively. The relationship between Ω and w cannot be generalized, but for any specific and well-known resource-consumer relationship, we may either have $w > \Omega$ or $\Omega > w$. Equality may hold in very few restrictive and exceptional cases.

Integrating equations (26) and (27) with respect to their respective variables yields

$$R(a) = R_0 \exp\left\{-\frac{a}{\Gamma} C(\alpha)\right\}, \tag{31}$$

$$C(\alpha) = C_0 \exp\left\{-m\alpha \left[1 - \frac{R_0}{\Gamma} \exp\left\{-\frac{a}{\Gamma} C(\alpha)\right\}\right]\right\} \tag{32}$$

For the sake of completion, let $\max(w, \Omega) = L$ such that $a, \alpha \in [0, L] \subset \mathbb{R}^+$, then equations (31) and (32) become

$$R(a) = R_0 \exp\left\{-\frac{1}{\Gamma} \int_0^a C(\alpha) d\alpha\right\}, \tag{33}$$

$$C(\alpha) = C_0 \exp\left\{-m \int_0^a \left[1 - \frac{R_0}{\Gamma} \exp\left\{-\frac{1}{\Gamma} \int_0^s C(\alpha) d\alpha\right\}\right]\right\} \tag{34}$$

If $m = 1$, then using a discrete unit age step of the standard Runge-Kutta fourth-order approach for ODEs integration, equation (3) of Gamarra and Solé (2002) is recovered. At this point we can affirm that age-structure has an effect on the dynamics of both resources and consumers as seen from both equations (31) and (32).

Equations (32) and (33) in matrix form read

$$\begin{bmatrix} R_a \\ C_a \end{bmatrix} = -C(\alpha) \left[\frac{R(a)}{\Gamma} \begin{pmatrix} 1 \\ -1 \end{pmatrix} + m \begin{pmatrix} 0 \\ 1 \end{pmatrix} \right], \quad (35)$$

where $R_a := \frac{dR(a)}{da}$ for simplicity. By writing

$$\frac{dC(\alpha)}{d\alpha} := H(R, C); \quad \frac{dR(a)}{da} := G(R, C), \quad (36)$$

we obtain a system of two simultaneous differential equations with $G(R, C)$ and $H(R, C)$ continuous (in their variables) and having continuous partial derivatives in $C^1(\mathbb{R}^{2+}, \mathbb{R}^+)$; $a, \alpha \in [0, L]$ so that $G, H \in C^1(\mathbb{R}^{2+} : L^1([0, L, \mathbb{R}^+))$. If (R_0, C_0) is a point in the domain of G and H in the RC -plane, then there exists a unique solution $R(a) = \phi(a)$, $C(\alpha) = \psi(\alpha)$ of (36) satisfying the initial conditions

$$R(a_0) = R_0; \quad C(\alpha_0) = C_0; \quad (37)$$

where a_0 and α_0 are the initial ages at which both processes started.

The initial-value problem given by equations (36) and (37) can be written in the well-known vectorial form

$$\frac{dX}{da} = f(X); \quad X(a_0) = X^0 \quad (38)$$

where $X = R\vec{i} + C\vec{j}$, $f(X) = G(R, C)\vec{i} + H(R, C)\vec{j}$ and $X^0 = R_0\vec{i} + C_0\vec{j}$ (\vec{i}, \vec{j} are the unit vectors in the Cartesian plane). In this case, the solution is expressed as

$$X = \phi(a)\vec{i} + \psi(a)\vec{j}. \quad (39)$$

Let $\|\cdot\|$ represents the usual L^1 -norm (with $L^1 := (\mathbb{R}^+, \mathbb{R}^+)$), define

$$\|X\|_{L^1} = \|R\|_{L^1} + \|C\|_{L^1}. \quad (40)$$

The isolated critical points of equations (11) and (12), which also satisfy (35) are $(0,0)$ and (R^*, C^*) .

A critical point of (35) is said to be stable if given $\varepsilon > 0$, there exists a $\delta > 0$ such that every solution X of system (38) which at $a = 0$ satisfies $\|X(0) - X^*\|_{L^1} < \delta$ exists, and also satisfies $\|X(a) - X^*\| < \varepsilon$. In particular, $R^* = R(a)$, and $\|R(0, a) - R(a)\| < \delta$, whenever $|t - a| < \varepsilon$. Similarly, $\|C_0(\alpha) - C(\alpha)\| < \delta$, whenever $|t - a| < \varepsilon$.

Some algebraic manipulations coupled with the application of the classical Gronwall's Lemma (Bainov and Simeonov, 1992) yield

$$C(t) \leq C^0 e^{(1-l)t} \quad (41)$$

where $C^0 = \int_t^\infty C_0(a-t)da$ and $l \geq 1$ is the common lower bound of the natural rate of resource depletion and consumer's death modulus.

The value $l = 1$ defines a bifurcation point, and both fixed points are conditionally convergent. Thus, the non-trivial equilibrium points are exponentially asymptotically stable for $l > 1$, and may become unstable as $l < 1$ implies unbounded growth, which in turn implies high demand of resources. In general, non-zero and asymptotically bounded

population models are structurally unstable (Dilao and Domingos, 2001). Real populations are far from equilibrium (Hastings et al., 1993; Ario and Pimm, 1995). In fact, complex fluctuations ($l < 1$) are found in most species which have characteristic lifespan. The steady state solutions of equations (11) and (12) are

$$R_0(a) = B_{R_0} \exp\left\{-\int_0^a k_0(s)ds\right\} := B_{R_0}\pi(a) \quad (42)$$

$$C_0(\alpha) = B_{C_0} \exp\left\{-m\int_0^\alpha \left(1 - \frac{B_{R_0}\pi(s)}{\Gamma}\right)ds\right\} = B_{C_0} \exp\left\{-m\left(a - \frac{B_{R_0}}{\Gamma}\right)\right\}. \quad (43)$$

Equation (43) is obtained under the assumption that (without any ambiguity and without loss of reality)

$\exp\left\{\int_0^a k_0(s)ds\right\} := \pi_0(a)$ is a non-negative, non-increasing and monotone integrable function, and $\int_0^a \pi_0(s)ds = 1$. That is, $\pi_0(\cdot)$ is normalized (Tchuenche, 2006).

In a study which is closely related to the present one in spirit, Dilao and Domingos (2001) found that in the case of non-trivial bounded solutions, the discrete evolution equations are not structurally stable, a result which perfectly agrees with the conclusion of Hastings *et al.*, (1993) and Ario and Pimm (1995).

In the absence of consumers, resources are auto-regulated by factors external to the population and evolve in time. For instance, the simplest situation is when resources attain a stable equilibrium (when they are not consumed).

For $R = \Gamma > 0$, $f(R,0)$ is strictly monotone and predation drops to zero in the absence of consumers (Cushing and Saleem, 1982), with $\frac{\partial f}{\partial R}(0,0) > 1$, while $\frac{\partial f}{\partial R}(\Gamma,0) < 1$. Thus,

$R = 0$ is an unstable fixed point. This may be due to fluctuations which can be highly variable, and in some cases have been identified as evidence of deterministic chaos (Schaffer, 1985; Gamarra and Solé, 2000). From the aforementioned, the following two conditions are immediate consequences.

- $f(R,C)$ is a smooth and decreasing function of C , with $f(R,C) \rightarrow 0$ as $C \rightarrow \infty$, and $\frac{\partial f}{\partial C} < 0$, for $C > 0$.
- $f(R,0)$ is a smooth and increasing function of R , with one stable fixed point at $R = \Gamma$, $0 < \Gamma < \infty$, and one unstable fixed point at $R = 0$.

Dilao and Domingos (2001) for their resource-consumer map used a prototype separable function of the form $f(R,C) = g(R)h(C)$. In a future study, the use of the concept of saturable interactions as a framework for modeling resource-consumer interactions will be explored. The first step will be to assume that the function $f(R,C)$ satisfies the generalized law of the minimum (Sowunmi, 1988), because it seems safe to assume that such interactions are saturable processes.

4. Concluding Remarks

The consumer-resource interaction is a fundamental issue in ecology (Mac Arthur, 1972) due to the fact that living organisms do not survive or reproduce without resources (Dilao and Domingos, 2001). To derive the functional form of a robust population dynamics model with resources, we started with a well-known classical example and proceeded with an age-structured model, which extends Gamarra and Solé's model. The reason for choosing a specific functional form $f(R, C)$ (which is a smooth function of its variables R and C , with $f(R, C) \rightarrow 0$ as $C \rightarrow \infty$) is because resources have an independent dynamics if they are not consumed. Indeed, the simplest assumption one can make about a population is that it dies out without resources, resources evolve in time, and its dynamics depends on its availability and on the total population number.

The derivation of the age-structured model describing the dynamical interactions between populations of consumers and resources began with a generalization of the non-linear Gamarra and Solé's (2002) model, where the fertility coefficients are resource and consumer independent. That is, the effect of overcrowding which often causes fluctuations is not considered. It is generally followed in parallel with depletion of resources, leading to drastic changes of population numbers (Dilao and Domingos, 2001). But luckily, this problem has been analyzed from the point of view of consumer choices (MacArthur, 1972, Chapter 3), which depends on the evolutionary history and adaptability of populations. This adaptability justifies the introduction of a time lag in equations (15) and (16), which is necessary to describe the units of time it takes the resource/consumer to respond to changes in the population size or environment.

The interdependence between resource availability and survival of the population (consumers) can be incorporated into equation (7)₂. In such a case, the intrinsic growth rate $r = \lambda - m$, say, takes the form $r = r(R(t))$ such that in the complete absence of resources i.e., for $R(t) = 0$, $r(0) = r_0 < 0$, and consumers die out. Otherwise, they relocate to new sites (favorable localities) by migration. Thus in a follow up study, we shall introduce diffusion or advection into the model equations in order to account for the possible migratory effect.

The model derived herein is not only an extension, but a study of a resource-consumer model structured by age in its own right. The following biological conclusions can be derived from our analysis:

- When the non trivial steady state of the population is reached, resources also reaches a constant value R^* , say where $0 < R^* < \Gamma$. Therefore, the existence of resource-free steady state is not conceivable (Dilao and Domingos, 2001), except when the species (resource) goes extinct.
- Equation (24) tells us that the quantity of resources available at any time t depends on the number of potential consumers present at that same time. The available resources $R(t, a)$ depend on the number of consumers $C(t, \alpha)$. If $C(t, \alpha)$ is large, depletion of available resources is fast, and if this does not keep pace with renewal, there

might be scarcity 14 of the former and consumers will be forced to look for alternative if they can adapt, or some will die out from intra and inter-competition for food.

- Comparing equations (8), (13) and (24), it is an easy matter to note that the age parameter has an important effect on the dynamics of the model. In most cases, older individuals consume more resources than their juvenile counterparts. This is taken care of as the age of resources and consumers are different (cf. 24).

Our model view differently may be considered as predation, where the prey is the resource and the consumers the predators with or without other external resource forms.

Acknowledgement

Thanks to the reviewers for their comments and suggestions.

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