



Resource Competition in Stage-structured Populations

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Two models are made to account for the dynamics of a consumer–resource system in which the consumers are divided into juveniles and adults. The resource grows logistically and a type II functional response is assumed for consumers. Resource levels determine fecundity and maturation rates in one model, and mortality rates in the other. The analysis of the models shows that the condition for establishment of consumers is that the product of per capita fecundity rate and maturation rates is higher than the product of juvenile and adult per capita decay rates at a resource level equal to its carrying capacity. This result imposes a minimal abundance of resource able to maintain the consumers. A second result shows an equilibrium stage structure, with a small instability when juveniles and adults mean saturation constants are different. The implications of these results for community dynamics are discussed.

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Introduction

If two or more age classes or stages exploit a limited resource, competition occurs (Cushing, 1994; Franke & Yakubu, 1996; Tschumy, 1982). The magnitude of competition between stages can change depending on the stage of the life cycle as well as the type of cycle (Ebenman, 1988). For example, in those animals that undergo metamorphosis as the endopterigote insects (flies, beetles) and the amphibians, the magnitude of competition is weak or none because the anatomic and morphologic differences make the use of a common resource difficult. On the other hand, in organisms that do not undergo metamorphosis like the exopterigote insects (aphids, grasshoppers), or in those that have an incomplete metamorphosis (hemipterans) the consumption of common resources between classes is

usual. Individuals of distinct age groups will respond differentially either to the effects of total density or to the population composition because of their anatomic, morphologic and physiologic differences.

In contrast with two-species competition, in inter-stage competition there cannot be elimination of one competitor by the other, because the two depend on each other. Most models of inter-stage competition (Leslie, 1959; Cooke & Léon, 1976; Guckenheimer *et al.*, 1977; Tschumy, 1982; Ebenman, 1987, 1988) are discrete, and assume two stages: pre-reproductive and post-reproductive, or juveniles and adults. The majority of these matrix models, however, do not take into account in an explicit way the competition for resources, that is, they do not include resource density as a variable. An exception is the model of Maynard Smith & Slatkin (1973) which includes this in a study of the stability of predator–prey systems, using a discrete time model. In it, the

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effect of the predator’s age structure on the dynamics is the consequence of the differences in hunting ability between juveniles and adults, differences that can permit the coexistence in spite of the competition for only one resource. This approach of including prey or resource density in models can also be used by ordinary differential equations (ODE) systems. As an example, Pimm & Rice (1987) study a trophic web with structure. In this study, the dynamic equations consider the instantaneous and coupled changes of the densities of resource, juvenile consumers and adult consumers. Prey densities increase maturation and fecundity rates and/or decrease mortality rates.

In this work I use ODE systems to describe a resource–consumer interaction. The consumer population is subdivided in juveniles and adults. It is assumed that the interaction with the resources increases the per capita rates of maturation and fecundity or decreases the mortality rates. Thus, the competition consists in the negative effect one class has upon the increase of the other when resource level decreases. The objective is to find conditions that warrant the coexistence in the presence of only one resource, and also to study the dynamics of this type of system.

The Models

There are two models. In the first one, it is assumed that maturation and fecundity rates increase with resource consumption. In the second one, mortality rates decrease with consumption.

MODEL 1: WHEN MATURATION AND FECUNDITY RATES DEPEND ON RESOURCE DENSITY

The interaction between juvenile consumers (N) and resources (R) produces the transition of juveniles to adults (M):

$$R + N \xrightarrow{b_n} M \tag{1}$$

at a rate b_n . This interaction eliminates a juvenile and creates an adult. The interaction between resource and adult consumer creates n new juveniles. Suppose that a fraction μ of these events

is a cause of mortality in the adults. Then

$$R + M \xrightarrow{b_m} nN, \text{ probability} = \mu, \tag{2}$$

$$R + M \xrightarrow{b_m} nN + M, \text{ probability} = 1 - \mu.$$

This will be considered later to determine the effects of a variable semelparity (μ). From eqn (1), following a “law of mass action” approach, maturation rate is proportional to the product of juvenile density and the resource quantity consumed per juvenile individual. At saturation, maturation rate can be expressed as

$$\frac{b_n R}{R_n + R} N, \tag{3}$$

using the type II functional response from Holling (1959). Here b_n is the maximal per capita rate of maturation and R_n the half-saturation constant for resource consumed. This rate of maturation should be subtracted in the dynamic equation for juveniles and added in the corresponding equation for adults. With a similar reasoning, the fecundity rate would be proportional to the product of adult density, resource consumed and the number of juveniles produced per adult or clutch size n :

$$n \frac{b_m R}{R_m + R} M, \tag{4}$$

where b_m is the maximal per capita fecundity rate to produce one recruit per consumed resource and R_m the half saturation constant for adults. This expression is the sum of the two contributions described by eqns (2), and should be added to the dynamical equation of juveniles and subtracted from the adult equation weighted by μ (probability of death as a consequence of reproduction) instead of n .

The dynamical equations for resource, juvenile and adult consumers are then

$$\dot{R} = rR \left(1 - \frac{R}{K} \right) - \frac{a_n RN}{R_n + R} - \frac{a_m RM}{R_m + R},$$

$$\dot{N} = n \frac{b_m R M}{R_m + R} - \frac{b_n R N}{R_n + R} - d_n N, \quad (5)$$

$$\dot{M} = \frac{b_n R N}{R_n + R} - \mu \frac{b_m R M}{R_m + R} - d_m M.$$

It is supposed that the resource grows logistically in the absence of consumers. The consumption rates are shown in the resource equation multiplied by the constants a_n and a_m . The per capita death rates of juveniles and adults are d_n and d_m , respectively.

MODEL II: WHEN MORTALITY RATES DEPEND ON RESOURCE DENSITY

The difference with Model I is that juveniles mature with a constant per capita rate equal to m and that adult per capita fecundity rate is also constant, but the per capita death rates are decreasing functions of the consumed resource. Then

$$\text{for juveniles: } d'_n - \frac{c_n R}{R_n + R}, \quad (6)$$

$$\text{for adults: } d_m - \frac{c_m R}{R_m + R}. \quad (7)$$

The constants d'_n and d_m are the maximal per capita mortality rates in the absence of resource, c_n and c_m are conversion constants that relates quantity of resource consumed to the decrease in mortality. It is assumed that $d'_n > c_n$ and $d_m > c_m$, to avoid negative rates. As in model I, R_n and R_m are half-saturation constants.

The dynamical system is

$$\begin{aligned} \dot{R} &= rR \left(1 - \frac{R}{K}\right) - \frac{a_n R N}{R_n + R} - \frac{a_m R M}{R_m + R}, \\ \dot{N} &= fM - \left(m + d'_n - \frac{c_n R}{R_n + R}\right) N, \\ \dot{M} &= mN - \left(d_m - \frac{c_m R}{R_m + R}\right) M. \end{aligned} \quad (8)$$

For the sake of simplicity, we define $d_n = m + d'_n$, as the maximal per capita rate of disappearance

of juveniles (maturation + death). Model II becomes

$$\begin{aligned} \dot{R} &= rR \left(1 - \frac{R}{K}\right) - \frac{a_n R N}{R_n + R} - \frac{a_m R M}{R_m + R}, \\ \dot{N} &= fM - \left(d_n - \frac{c_n R}{R_n + R}\right) N, \\ \dot{M} &= mN - \left(d_m - \frac{c_m R}{R_m + R}\right) M. \end{aligned} \quad (9)$$

Results

For Model I all the analysis were made with $\mu = 1$, that is, supposing that all the adults that reproduce die, which means total semelparity. Later, a general result for every $\mu < 1$ is presented. The expressions for internal equilibria involve complicated parameter combinations make the interpretation of the stability conditions difficult by means of the Jacobian matrix. So the local stability analysis is applied to the trivial equilibria $(0, 0, 0)$ and $(K, 0, 0)$. Local stability of these points will determine if consumers can invade.

MODEL I

System (5) has the nullclines that are shown in Fig. 1, plotted with *Mathematica 2.2* (Wolfram Research Inc., 1991). The equations for nullclines are presented in the Appendix. A condition for a positive equilibrium is that R must be less than the carrying capacity K , and

$$n > 1 + \frac{d_n}{b_n} + \frac{d_m}{b_m} + \frac{d_n d_n}{b_n b_m}, \quad (10)$$

that is the clutch size must be greater than the unity plus three terms, which are greater as the relations between mortalities and conversion rates are higher. The solutions for the internal equilibrium are presented in the mathematical Appendix, corresponding to the intersection of the nullclines of Fig. 1.

The point $(0, 0, 0)$ will be locally unstable whenever a non-trivial equilibrium exists, and that is easy to demonstrate. Suppose that R ,

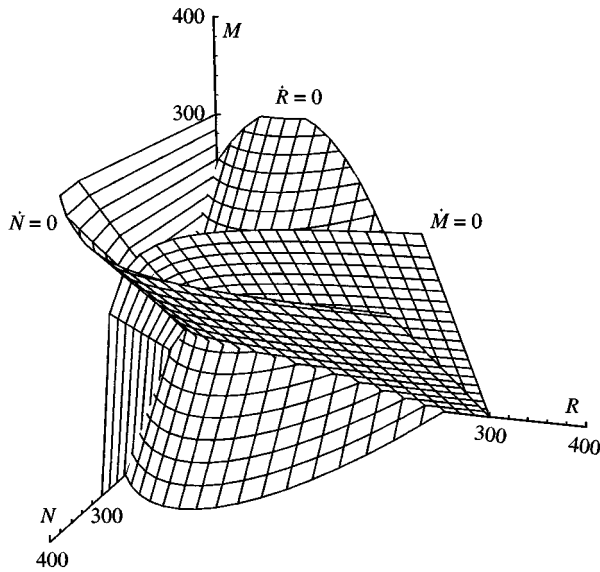


FIG. 1. Nullclines of Model I. $r = 0.5$, $K = 250$, $a_n = a_m = 0.2$, $R_n = R_m = 100$, $n = 2$, $b_n = b_m = 1$, $d_n = d_m = 0.1$.

N and M tend to zero. This makes the second-order terms RN , RM and R^2 (from logistic) negligible in system (5). Then the equations can be linearly approximated by

$$\begin{aligned} \dot{R} &\approx rR, & \dot{N} &\approx -d_n N & \text{and} \\ \dot{M} &\approx -d_m M. \end{aligned} \tag{11}$$

So the trajectory in the phase space RNM will approach initially the point $(0, 0, 0)$, and then go away in the R direction. The trivial equilibrium is a saddle point.

For the $(K, 0, 0)$ point, the Jacobian of eqn (5) has a positive eigenvalue when the following inequality is satisfied (see Appendix):

$$\begin{aligned} \left(n \frac{b_m K}{R_m + K} \right) \left(\frac{b_n K}{R_n + K} \right) &> \left(\frac{b_n K}{R_n + K} + d_n \right) \\ &\times \left(\frac{b_m K}{R_m + K} + d_m \right). \end{aligned} \tag{12}$$

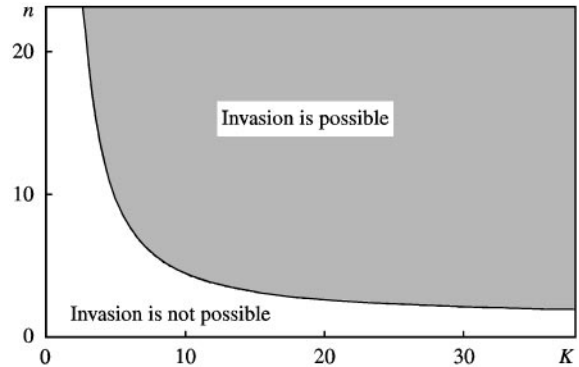


FIG. 2. Parameter space for Model I. $a_n = a_m = 0.2$, $R_n = R_m = 100$, $b_n = b_m = 1$, $d_n = d_m = 0.1$.

Establishment is possible when the product of the fecundity and maturation per capita rates is higher than the product of the per capita rates of disappearance of both stages at the resource density K . A parameter space that relates n and K with this condition is shown in Fig. 2. In this graph, the boundary between the stability regions is a function that has a horizontal asymptote equal to the l.h.s. of eqn (10). If $0 < \mu < 1$, that is, a fraction of the adults do not die as a result of reproduction, this condition changes to

$$\begin{aligned} \left(n \frac{b_m K}{R_m + K} \right) \left(\frac{b_n K}{R_n + K} \right) &> \left(\frac{b_n K}{R_n + K} + d_n \right) \\ &\times \left(\mu \frac{b_m K}{R_m + K} + d_m \right). \end{aligned} \tag{13}$$

If conditions (12) and (13) are met, the $(K, 0, 0)$ point behaves as a saddle point. This detail is important when examining the global dynamics of the system.

MODEL II

System (9) has a positive equilibrium that corresponds to the intersection of the nullclines shown in Fig. 3 plotted with *Mathematica* 2.2 (Wolfram Research Inc., 1991). Nullcline equations are presented in the Appendix. A condition for a positive equilibrium is that R must be less than K (see the Appendix), and

$$mf > (d_n - c_n)(d_m - c_m). \tag{14}$$

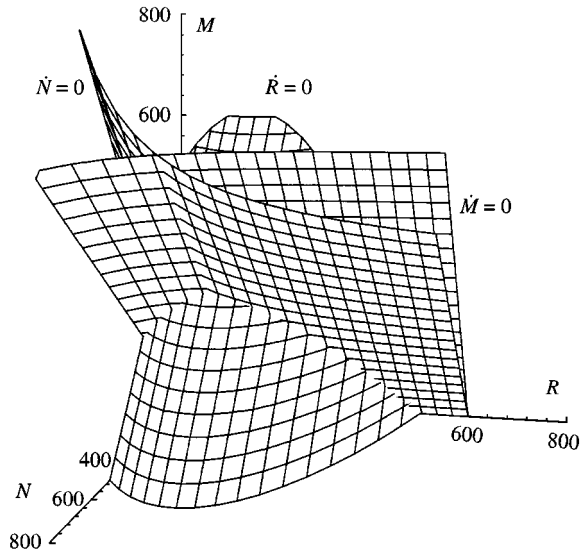


FIG. 3. Nullclines of Model II. $r = 0.5$, $K = 500$, $a_n = a_m = 0.2$, $R_n = R_m = 200$, $m = f = 1.5$, $d_n = d_m = 1.1$, $c_n = c_m = 1$.

To analyse the stability of the trivial equilibrium $(0, 0, 0)$ we consider that when R , N and M approach zero, the higher order terms, RN , RM and R^2 will be negligible, and system (9) can be linearly approximated by

$$\dot{R} \approx rR, \quad \dot{N} \approx fM - d_nN \quad \text{and}$$

$$\dot{M} \approx mN - d_mM,$$

$$\dot{N} + \dot{M} \approx (m - d_n)N + (f - d_m)M. \quad (15)$$

R tends to grow near $(0, 0, 0)$ and $N + M$ to decrease, because this sum depends on R . The point will be a saddle.

In relation to point $(K, 0, 0)$, the Jacobian has a positive eigenvalue (see Appendix) if

$$mf > \left(d_n - \frac{c_n K}{R_n + K} \right) \left(d_m - \frac{c_m K}{R_m + K} \right). \quad (16)$$

This result is similar to that of Model I. The establishment, by instability of $(K, 0, 0)$, is possible if the product of the fecundity and maturation per capita rates is higher than the product of the per capita rates of disappearance at resource density K . A parameter space is shown in Fig. 4.

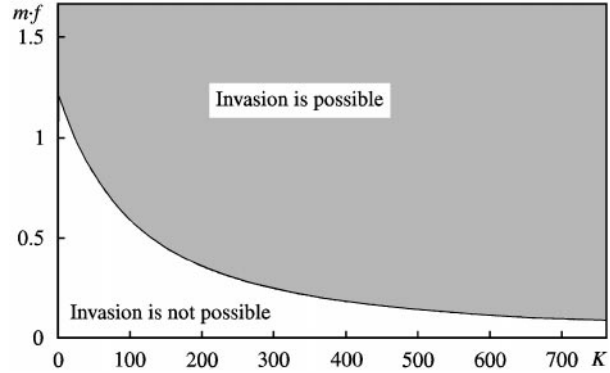


FIG. 4. Parameter space for Model II. $a_n = a_m = 0.2$, $R_n = R_m = 200$, $d_n = d_m = 1.1$, $c_n = c_m = 1$.

As in Model I, a function separates the regions of stability, this function has a horizontal asymptote equal to the l.h.s. of eqn (14).

In both models we have a condition for a positive equilibrium provided that $R_e < K$ and conditions (10) (for Model I) and (14) (for Model II). The l.h.s. of eqns (10) and (14) are the values of the horizontal asymptotes for the functions that separates the conditions of invasion (Figs 2 and 4), then as K becomes larger conditions (10) and (14) becomes also invasibility conditions. But conditions (12) and (16) are the more general because states that if they meet, then a positive interior equilibrium exists and invasion is possible.

GLOBAL STABILITY

Looking over the NM plane, the nullcline level curves are straight lines [Figs 5(a)-(c)]. We can graph nullclines for different values of R between 0 and K . Signs of \dot{R} , \dot{N} and \dot{M} result in vector field directions. The rules are these: R increases in the triangular region closed by $\dot{R} = 0$ and the axes N and M ; N increases between $\dot{N} = 0$ and the M -axis; and M increases between $\dot{M} = 0$ and the N -axis.

N and M decrease if $R < R_e$ [Fig. 5(a)], and increase if $R > R_e$ [Fig. 5(c)]. At $R = R_e$, the straight lines of the N and M nullclines coincide with the R nullcline and there is a positive equilibrium [point e in Fig. 5(b)]; vector fields tend to move any trajectory to the nullclines of N and M . Thus, combining Figs 5(a)-(c), we can conclude that the dynamic is periodic, with $(0, 0, 0)$ and

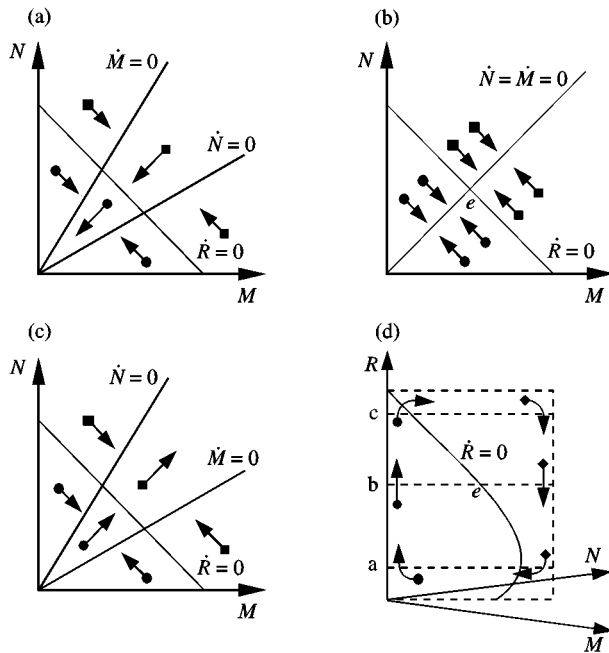


FIG. 5. (a)–(c) Nullclines of Model I or Model II in the NM plane for increasing values of R : (a) $R < R_e$, (b) $R = R_e$, (c) $R > R_e$. (d) The R nullcline is drawn over the plane formed by the R -axis and the point of equilibrium e . (●→) R increases; (◆→) R decreases.

$(K, 0, 0)$ as saddle points. This is depicted in Fig. 5(d), where the vector field is drawn over a plane formed by the R -axis and the straight line where the nullclines of N and M coincide [at $R = \mathbf{b}$ in Fig. 5(d)].

To study the stability of the equilibrium point (R_e, N_e, M_e) , a projection of the R nullcline is made over the plane formed by the R -axis and the straight line of coincidence for the nullclines of N and M . Over this plane the projection of the R nullcline is a parabola, as in the classic predator–prey model (with logistic dynamics in the prey, and type II functional response), and the positive equilibrium is also on this plane [point e in Fig. 5(d)]. If the half-saturation constants of juveniles and adults are below the value of the carrying capacity, then the parabola has a “hump” in the positive octant, and the possibility of eigenvalues with positive real parts for the interior point arises. The prediction is: if the position of the hump in the R -axis is below R_e , then the interior point is stable [this case is depicted in Fig. 5(d)], but if the hump is above R_e , the

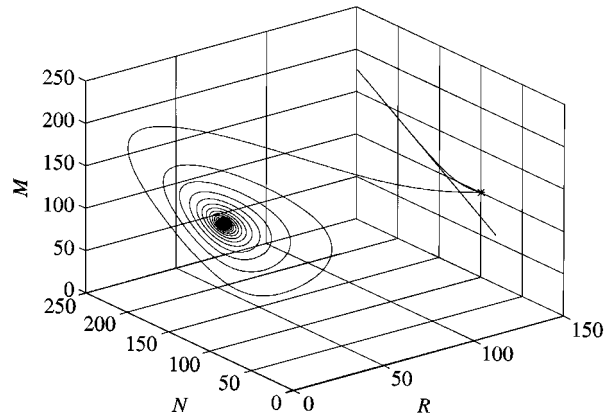


FIG. 6. Numerical solution of Model I. $r = 0.5$, $K = 150$, $a_n = a_m = 0.2$, $R_n = R_m = 100$, $n = 2$, $b_n = b_m = 1$, $d_n = d_m = 0.1$. Initial conditions: $R = 150$, $N = 100$, $M = 100$. System converges to equilibrium passing through a regime of damped oscillations, and a stable juvenile and adult composition is approached (looking at the NM plane).

interior point is unstable and limit cycles appear. If carrying capacity becomes larger, the hump moves for larger values of R and the second possibility is likely to occur.

If the interior point is stable, then we hope a stable stage structure. If it is not stable and limit cycles appear, the trajectories must approach the plane formed by the R -axis and the interior point due to the influence of the vector field [Fig. 5(b)], and there is a tendency for a stable stage structure, with a limit cycle bounded to a plane perpendicular to the NM plane.

Making numerical simulations of Model I with a fourth-order Runge–Kutta algorithm using MATLAB 5 (The Mathworks Inc., 1997), it is found that the dynamic is periodic, there are damped oscillations for a small value of K (Fig. 6) and a limit cycle for a large K (Fig. 7). In Fig. 8, there is a small deviation of a stable stage structure, that probably arises due to asymmetries in the nullcline shapes.

Discussion

In both models the conditions for the establishment of consumers at low densities with resource level at carrying capacity is that the product of the per capita rates of maturation and fecundity has to be higher than the product of the

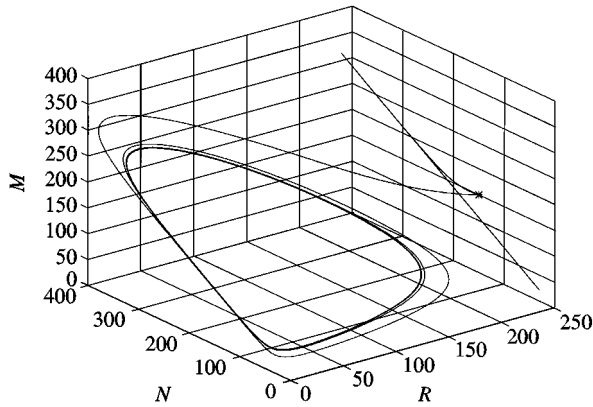


FIG. 7. Numerical solution of Model I. $r = 0.5$, $K = 250$, $a_n = a_m = 0.2$, $R_n = R_m = 100$, $n = 2$, $b_n = b_m = 1$, $d_n = d_m = 0.1$. Initial conditions: $R = 250$, $N = 150$, $M = 150$. There is a limit cycle with a stable juvenile and adult composition (looking at the NM plane).

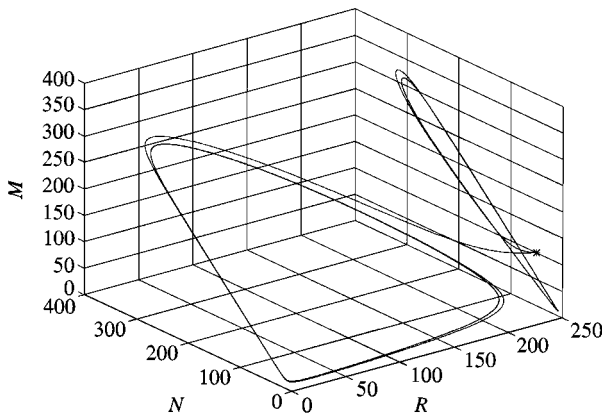


FIG. 8. Numerical solution of Model I. $r = 0.5$, $K = 250$, $a_n = a_m = 0.2$, $R_n = 50$, $R_m = 100$, $n = 3$, $b_n = b_m = 1$, $d_n = d_m = 0.1$. Initial condition: $R = 250$, $N = 50$, $M = 100$. The result is a limit cycle where the juvenile and adult composition also oscillates (looking at the NM plane).

per capita rates of disappearance of juveniles (that also include maturation) and adults. This is stated in inequalities (12) and (16). This is a logical result, and is also in agreement with a former result of the Tschumy (1982) discrete model with two age classes. Tschumy (1982) found that extinction is avoided if the product of fecundity and survivorship of juveniles is greater than unity. The result does not depend on the stability of the internal equilibrium, but depends on the existence of that equilibrium. This can be inferred from Figs 2 and 4 provided that conditions for

positive equilibrium are the same as for invasibility at higher values of K . That is to say, n or $m \cdot f$ is over the horizontal asymptote. The invasibility region defines also the regions of positive equilibrium.

In Model I, the possibilities for positive equilibrium and for coexistence increase when the ratio between maximal conversion rates and mortalities (b_n/d_n and b_m/d_m) increases. The same happens, when mean saturation densities (R_n, R_m) decrease. In Model II this happens when conversion efficiencies (c_n, c_m) increase in relation to mortality rates (d_n, d_m).

The most important effect of variable semelparity in Model I is to change the magnitude of adult mortality. When semelparity (μ) decreases the product of maturation and fecundity rates is higher, making invasion easier. This means that iteroparity favours invasion provided the fecundity rates are not affected, that is to say, that increasing survivorship does not decrease the energy or resources allocated to reproduction.

Resource competition can be analysed by the effect that different parameters have on equilibrium densities. This is seen in eqns (A.6) or (A.13) and (A.7) or (A.14), of the Appendix. They can be written succinctly as

$$N_e = \frac{r(1 - R_e/K)}{\alpha_{NN} + \alpha_{NM}},$$

$$M_e = \frac{r(1 - R_e/K)}{\alpha_{MM} + \alpha_{MN}}.$$

Equilibrium densities of both classes are always proportional to the resource per capita rate of renewal. The denominators of both expressions are composed of terms that can be considered as competition coefficients. Thus, α_{NN} and α_{MM} express the intraclass effects and α_{NM} and α_{MN} the interclass effects. Intra- and interclass effects are proportional to the maximal rates of consumption a_n and a_m , since a higher consumption means a lower availability of resource. But interclass effects include also conversion parameters, mortalities and the clutch size. Thus, an increase of mortality in relation to conversion in one class favours the other class. Finally, the relations between the coefficients determine the equilibrium

composition:

$$\frac{N_e}{N_e + M_e} = \frac{\alpha_{MM} + \alpha_{MN}}{\alpha_{NN} + \alpha_{NM} + \alpha_{MM} + \alpha_{MN}}, \quad (17)$$

$$\frac{M_e}{N_e + M_e} = \frac{\alpha_{NN} + \alpha_{NM}}{\alpha_{NN} + \alpha_{NM} + \alpha_{MM} + \alpha_{MN}}. \quad (18)$$

Nullcline analysis reveals that the dynamics of both models are periodic, and that $(0, 0, 0)$ and $(K, 0, 0)$ are saddle points, which is typically in predator-prey models. Numerical results show that the regimes can pass from damped oscillations to limit cycles when carrying capacity is increased. (Figs 6 and 7), which is similar to the “paradox of enrichment” (Rosenzweig, 1971). It is also found that if saturation parameters (R_n and R_m) differ substantially between juveniles and adults, a temporal variation in stage composition can occur (Fig. 8, see the NM plane). This result is similar to that encountered by Hsu *et al.* (1978) for a system of two predators with type II functional response. If this does not happen the composition becomes stable according to eqns (17) and (18).

The fact that limit cycles are possible perhaps is due to the existence of an implicit lag because of maturation time.

The results of this study can be related to those of inter-specific competition. Mc Arthur & Levins (1964) demonstrated that two-competitors coexistence is possible when there are at least as many distinct resources as consumers. Hsu *et al.* (1978) found that, with type II functional response, coexistence on one resource is possible when one consumer is a r -strategist while the other is a K -strategist. In a population with age structure, permanent exclusion for one class is impossible because coexistence is hold by a mutual dependence between classes (one class gives rise to the other) which can be called “facilitation” of one class by the other. This leads to the idea that some type of facilitation between competitors can hold coexistence at low diversity of resources. An example of this are the dynamical systems called hypercycles (Eigen & Schuster, 1979), in which mutual cooperation, although “selfish”, can be able to maintain coexistence between his elements (RNA replicators).

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APPENDIX

Nullclines and Equilibrium Points of Model I

Setting $\dot{R} = \dot{N} = \dot{M} = 0$ in system (5) gives the nullclines:

$$r(1 - (R/K)) = \frac{a_n}{R_n + R} N + \frac{a_m}{R_m + R} M, \quad (A.1)$$

$$N = \left(\frac{nb_m R / (R_m + R)}{b_n R / (R_n + R) + d_n} \right) M, \quad (A.2)$$

$$M = \left(\frac{b_n R / (R_n + R)}{b_m R / (R_m + R) + d_m} \right) N, \quad (A.3)$$

Combining eqns (A.2) and (A.3) gives a quadratic equation for resource at equilibrium R_e :

$$\left[\frac{(n-1)b_n b_m}{d_n d_m} - \frac{b_n}{d_n} - \frac{b_m}{d_m} - 1 \right] R_e^2 - \left[\left(\frac{b_n}{d_n} + 1 \right) R_m + \left(\frac{b_m}{d_m} + 1 \right) R_n \right] R_e - R_n R_m = 0. \quad (A.4)$$

For a positive R_e to exist the second-order coefficient must be positive, which means that (by Descartes's rule of signs)

$$n > 1 + \frac{d_n}{b_n} + \frac{d_m}{b_m} + \frac{d_n d_m}{b_n b_m}. \quad (A.5)$$

Expressions for N_e and M_e are obtained substituting eqns (A.3) and (A.4) into eqn (A.1), and are shown as functions of R_e :

$$N_e = \frac{r(1 - R_e/K)}{a_n / \underbrace{(R_n + R_e)}_{\alpha_{NN}} + \underbrace{a_m / (R_m + R_e) (b_n R_e / (R_n + R_e) / ((b_m R_e / (R_m + R_e)) + d_m))}_{\alpha_{NM}}}, \quad (A.6)$$

$$M_e = \frac{r(1 - R_e/K)}{a_m / \underbrace{(R_m + R_e)}_{\alpha_{MM}} + \underbrace{a_n / (R_n + R_e) (nb_m R_e / (R_m + R_e) / ((b_n R_e / (R_n + R_e)) + d_n))}_{\alpha_{MN}}}, \quad (A.7)$$

Nullclines and Equilibrium Points of Model II

Setting $\dot{R} = \dot{N} = \dot{M} = 0$ in system (9) gives the nullclines:

$$r(1 - (R/K)) = \frac{a_n}{R_n + R} N + \frac{a_m}{R_m + R} M, \quad (A.8)$$

$$N = \frac{fM}{d_n - c_n R / (R_n + R)}, \quad (A.9)$$

$$M = \frac{mN}{d_m - c_m R / (R_m + R)}. \quad (A.10)$$

Combining eqns (A.9) and (A.10) gives a quadratic equation for resource at equilibrium R_e :

$$[mf - (d_n - c_n)(d_m - c_m)]R_e^2 + [(mf - d_n d_m)(R_n + R_m) + d_n c_m R_n + d_m c_n R_m]R_e + (mf - d_n d_m)R_n R_m = 0. \quad (A.11)$$

For a positive R_e to exist the second-order coefficient must be positive, and the zero-order negative, which means that

$$mf > (d_n - c_n)(d_m - c_m) \quad \text{when } R \rightarrow \infty, \quad (A.12)$$

$$mf < d_n d_m \quad \text{when } R = 0.$$

Expressions for N_e and M_e are obtained substituting eqns (A.10) and (A.11) into eqn (A.8), and are shown as functions of R_e :

$$N_e = \frac{r(1 - R_e/K)}{a_n / \underbrace{(R_n + R_e)}_{\alpha_{NN}} + \underbrace{a_m (m / ((d_m - c_m)R_e + R_m d_m))}_{\alpha_{NM}}}, \quad (A.13)$$

$$N_e = \frac{r(1 - R_e/K)}{a_n / \underbrace{(R_n + R_e)}_{\alpha_{NN}} + \underbrace{a_m / (R_m + R_e) (b_n R_e / (R_n + R_e) / ((b_m R_e / (R_m + R_e)) + d_m))}_{\alpha_{NM}}}, \quad (A.6)$$

$$M_e = \frac{r(1 - R_e/K)}{a_m / \underbrace{(R_m + R_e)}_{\alpha_{MM}} + \underbrace{a_n / (R_n + R_e) (nb_m R_e / (R_m + R_e) / ((b_n R_e / (R_n + R_e)) + d_n))}_{\alpha_{MN}}}, \quad (A.7)$$

$$M_e = \frac{r(1 - R_e/K)}{a_m / \underbrace{(R_m + R_e)}_{\alpha_{MM}} + \underbrace{a_n (f / ((d_n - c_n)R_e + R_n d_n))}_{\alpha_{MN}}}, \quad (A.14)$$

Local Stability of the $(K, 0, 0)$ Point

Models I and II have the same basic structure for the Jacobian matrix evaluated at $(K, 0, 0)$:

$$\mathbf{J}_{(K, 0, 0)} = \begin{bmatrix} -r & -A_n & -A_m \\ 0 & -\Delta_n & \Phi \\ 0 & M & -\Delta_m \end{bmatrix}. \quad (\text{A.15})$$

r is the maximal per capita rate of growth for resource, A_n and A_m are consumption rates of resource per juvenile and adult, respectively, at resource density of K . They are the same in both models:

$$A_n = \frac{a_n K}{R_n + K}, \quad A_m = \frac{a_m K}{R_m + K}. \quad (\text{A.16})$$

Δ_n and Δ_m are per capita rates of disappearance for both classes at a resource density of K . In Model I they are equal to d_n and d_m , but in Model II they are

$$\Delta_n = d_n - \frac{c_n K}{R_n + K}, \quad \Delta_m = d_m - \frac{c_m K}{R_m + K}, \quad (\text{A.17})$$

respectively. M and Φ are per capita rates of maturation and fecundity, respectively. In Model I they are, at resource level K :

$$M = n \frac{b_m K}{R_m + K}, \quad \Phi = \frac{b_n K}{R_n + K}. \quad (\text{A.18})$$

In model II they coincide with m and f . The characteristic equation for the Jacobian is

$$(r + \lambda) \begin{vmatrix} -(\Delta_n + \lambda) & \Phi \\ M & -(\Delta_m + \lambda) \end{vmatrix} = 0. \quad (\text{A.19})$$

A first eigenvalue is always $\lambda = r$. The matrix of rank 2 formed by the second and third rows of C1 gives the second and third eigenvalues, of which at least one is positive if

$$M\Phi > \Delta_n \Delta_m. \quad (\text{A.20})$$

Substituting the greek symbols by his equivalents, the invasibility conditions (12) and (16) are obtained.