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Master thesis

Impacts of predation on dynamics of an age-structured population: mathematical modelling and applications

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Abstract:

Predation is one of the basic mechanisms of population growth control. Using a mathematical model, we explore the impact of predation in a prey population structured into two age classes, juveniles and adults, assuming a generalist predator. The specific predation pressure is represented for each of the two age classes by either no predation or Holling type II or Holling type III functional responses in various combinations. We distinguish two scenarios. In the first one, we seek for potential Allee effects or multiple stable states in the prey population, and explore the conditions at which the predation is more effective on juveniles than adults and vice versa. The most interesting finding here is the occurrence of bistability, or a predator-pit-like behaviour, when predators consume only juvenile prey, via a Holling type II functional response, an observation not described previously. In case only adults or both age classes are killed by predators exhibiting a type II functional response, the Allee effect occurs frequently. Multiple positive stable states are commonly observed if one of the age classes is exploited via a type III functional response. In the second scenario, we assume that the prey feeds on a resource and that the resource together with the prey undergoes outbreak dynamics, and we examine possibilities of control of such outbreaks using age-specific predation. Predation was proven to be able to suppress the prey population successfully. In some cases, an oscillation-free resource-prey-predator coexistence was detected.

Hereby I declare that this master thesis was written exclusively by Viola Pavlová, using cited literature only. I agree with publishing of the abstract of this thesis in the university internet database.

České Budějovice, 29. 4. 2009

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1 Introduction

Predation is one of the mechanisms that can crucially impact prey population dynamics. It is widely recognized that generalist predators often mediate the top-down control of prey (Begon et al. 2006), given that the predation pressure is persistent and the predator population does not respond to potential fluctuations in prey density. Understanding the mechanisms that enable predators to regulate density of their prey may help us in efficient population management, be it pest biocontrol, harvesting of economically important species or endangered species protection. For example, Erlinge et al. (1983) supposed predation to be a regulating factor of small rodents with non-cyclic dynamics.

In this thesis, we study the impacts of predation on dynamics of a prey population separated into two age classes – juveniles and adults – consumed by different predators. Predation or escape from predation in one of the prey stages sometimes has important influence on the whole population dynamics. For example, the lack of predation on juveniles is suspected to cause outbreaks of the prey species as in the winter moth (Raymond et al. 2002) or the reduced predation on fawns due to removal of foxes in Sweden allowed the deer population to increase rapidly (Jarnemo & Liberg 2005). On the contrary, Reeve (1997) described the importance of predation on adults of bark beetles for the regulation of this pest species.

In this thesis, we model two possible scenarios of prey–predator interactions. In the first one, we assume that juvenile and/or adult prey are exploited each by a specific predator and study how prey population dynamics vary with diverse predator functional responses. In particular, we search for possible occurrence of a demographic Allee effect, a population-dynamic feature with important consequences for population viability (such an Allee effect has been demonstrated to be driven by predation under some circumstances; see Section 1.3), and ask about possibility of prey population suppression or even complete eradication. We refer to this scenario as the **P-P** (prey–predator) **model** further on. In the second scenario, the age-structured prey is again consumed by a predator but in addition to that it feeds on an explicitly modelled resource; the corresponding model is referred to as the **R-P-P** (resource-prey-predator) **model** further on. We assume that in this scenario, model parameters are set up so that in the absence of predation the system undergoes oscillations in the resource and prey densities, in the form of recurrent outbreaks, and ask about possibility of an outbreak regulation via predation. Results of both models can thus have interesting implications for population management.

1.1 Allee effects

The phenomenon of positive density dependence of the per capita population growth rate has already been documented in a wide range of species and the mechanisms that lead towards such a “demographic” Allee effect are quite diverse (Courchamp et al. 1999, 2008, Berec et al. 2007). Through the so-called “component” Allee effects these mechanisms trigger a positive relationship between a component of individual fitness and population size or density (Stephens et al. 1999, Berec et al. 2007). However, component Allee effects might be out-weighted by other, negatively density-dependent mechanisms and therefore do not necessarily accelerate the population growth rate (e.g. Angulo et al. 2007).

A distinguishing feature of sufficiently strong demographic Allee effects is a critical threshold of population size or density, also called the Allee threshold. In deterministic population models, this threshold materializes through the existence of an unstable, non-zero equilibrium state of the population which divides the space of population sizes or densities into two areas, one in which all populations go extinct and one for which all populations persist and often approach a non-zero stable equilibrium corresponding to an environmental carrying capacity of the population (Courchamp et al. 2008). The difference between these two non-zero equilibrium points can express an ecological stability of the population. In particular, the greater is the distance between these equilibria, the more resistant is the population to any disturbances (Beisner et al. 2003).

1.2 Allee effects in applied ecology

From the conservation biology point of view, existence of the Allee threshold might be regarded as a threat to endangered species. For example, the critical pack size of four pack members was observed in the obligatory cooperative African wild dog *Lycaon pictus* (Courchamp & Macdonald 2001) and the critical density necessary for successful reproduction in the Queen Conch *Strombus gigas* was determined to be around 50 conch per hectare (Stoner & Ray-Culp 2000). Also, demographic Allee effect is a phenomenon often discussed in relation to animal (re)introductions (Deredec & Courchamp 2007) as well as successful releases of biocontrol agents (Grevstadt 1999), for the same reasons as in the case of endangered species.

However, an existence of the Allee threshold might be of a benefit to population management as well as this population feature can be used to prevent unwanted spread of invasive or explosive species. Researchers have already noticed that Allee effects might prevent a newly introduced non-native species from establishing a persistent population in the early stages after invasion. One of the mechanisms might be the mate-finding Allee effect in the gypsy moth *Lymantria dispar*, an outbreaking invasive species of North America (Grey et al. 2008, Robinet et al. 2008). Liebhold & Bascompte (2003) were among the first who suggested Allee effects to be useful in exotic species eradication and provided an illustrative example, again on the gypsy moth. The results provided by their model reveal that to achieve eradication, more than 80% of the population needs to be removed as long as population densities are relatively low.

1.3 Predation-driven Allee effect and predator functional responses

Gascoigne & Lipcius (2004) suggested remarkable “side effects” of predator’s response to prey density. If the predator functional response is of Holling type II (or of so-called saturation foraging behaviour type), a (demographic) Allee effect in the prey population emerges as a consequence of the fact that at some level of prey density predator’s killing rate becomes virtually constant and therefore the higher is the prey density, the lower is the probability of each prey individual to be killed. One of the examples of such a predation-driven Allee effect is the woodland caribou (Wittmer et al. 2005). Since there is typically one animal killed per each predator-herd encounter, in smaller herds there is a higher probability of each individual to be killed. Also, salmon juveniles had a better survival in streams with resident predators if released in greater numbers (Ward et al. 2008).

In contrast, the Holling type III functional response, representing a sort of switching foraging behaviour whereby the predator switches to another food source if prey becomes too sparse, does not induce an Allee effect (Gascoigne & Lipcius 2004). This is because low densities of the prey population provide refuge from predation to prey individuals and thus their survival probability increases.

The Holling type II functional response belongs to the most frequently exhibited foraging behaviour but the type III functional response is not uncommon as well (Skalski & Gilliam 2001, Jeschke et al. 2002). A number of studies on predators and parasitoids have detected either a type II or type III functional response. Reay-Jones et al. (2005) found both types of functional responses in their trials with the parasitoid *Trichogramma chilonis* and its prey *Galleria mellonella* or *Chilo sacchariphagus.* The type III response was also found by Shenk & Bacher (2002) in their rare field study on predatory behaviour of the paper wasp *Polistes dominulus* on the beetle *Cassida rubiginosa* and by Lauman et al. (2008) in their comparative study on the *Trissolcus* species. (The less usual type I functional response has been documented in *Trichogramma* and *Eretmocerus* (Mills & Lacan 2004) but it will not be considered in this thesis as it is generally much less common.)

1.4 Predation in age-structured populations

The interesting fact is that the results of experiments on predation on a community of size-structured prey by Rudolf (2008) did not allow any description of the predator functional response by the commonly used simple terms. As Rudolf suggested, prey population structure can have important influence on the predator functional response. We can expect that implications of age structure can be comparable to size structure in prey (assuming that juveniles are different in size from adults), which supports our aim to develop a more realistic model by using separate functional responses for each age class of prey.

Besides possible variation in functional responses of one predator to two age classes of one prey species, the even more common feature of species life history is a different predator species feeding on juveniles and adults of the prey species. There might be not only a difference in predatory species, but also in genera or even classes and therefore the completely different foraging behaviour of different predators on different age classes is a quite reasonable assumption. For example, predation on *Daphnia* is size-specific: fish feeding on zooplankton select large ovigerous females, while invertebrate predators prey mostly on young or juvenile non-ovigerous females (Manca et al. 2008). The two types of predation have been found to change population dynamics and structure. According to Hoogland et al. (2006) the juvenile prairie dogs are more prone to predation by northern goshawks, whereas adults, especially pregnant females, are more often killed by foxes. A quite complicated situation appears to arise in insects where eggs may be a breakfast for a beetle, larvae a lunch for a parasitoid fly, pupae a dinner for a rodent and imago (adult) an anytime meal for a bird or bat or frog, not speaking of numerous other species where the juveniles are temporally and/or spatially separated from adults.

1.5 Why age-structured models?

The importance of age-structured models for getting more realistic predictions of predator–prey dynamics has been suggested also by Dostalkova et al. (2002) even though in their study they rather focused on the issue of age structure in predators. Other authors likewise used stage- or age-structured models to model predator-prey interactions. For example, de Roos et al. (2003) explored a continuous-time predator-prey model with age-structured prey, observing an emergent Allee effect in the predator, Jang (2007) analyzed a discrete-time host–parasitoid model with age-structure in the host, and Wikan (2001) examined a discrete-time, age-structured, density-dependent prey-predator model. To our best knowledge, however, there has been no study that would explore potential for a demographic Allee effect in an age-structured population of prey due to consumption by generalist, age-specific predators.

In the first part of this thesis, we explore the impacts of various predator functional responses on dynamics of an age-structured population of prey. We will focus on their potential to generate a demographic Allee effect or more generally multiple stable equilibria in prey, phenomena that can be exploited for successful biocontrol of pest species.

1.6 Predation in biocontrol of pests

Native or introduced natural enemies have been excessively used for controlling pests since the second part of the 20th century. It has proven to be a wise solution compared to the common use of chemical agents. There is a number of reasons why it got popular, including costs comparable to those of chemical protection, no problems with resistance occurrence, healthier working space and products, and general public approval. Production of biocontrol agents has grown into quite a big industry, with more than 100 commercially produced biocontrol species for greenhouse crop protection (in the year 2000) and a mass production of up to 50 million individuals per week (van Lenteren 2000). Costs of production of the biocontrol agents and their optimal performance in regulating pests is therefore of utmost importance to the greenhouse and field growers and to the ecosystem managers. Modelling species interactions in biocontrol, even though with many simplifying assumptions and various disputable aspects, provides valuable insights into dynamics of controlling and controlled species. Murdoch & Briggs (1996) recommended using stage-structured models in biocontrol and gave some examples where models had been helpful for making optimal decisions about the choices of biocontrol agents.

1.7 Pest species eradication and economic thresholds

In this thesis, we view the prey species as a pest and its control by predators as a positive effect. It is understandable that a 100% eradication of some pest species is generally very difficult, if not impossible, to achieve under natural conditions. As already discussed in Section 1.2, the existence of an Allee effect and an implied Allee threshold in population size or density might significantly contribute to successful eradication (Liebhold & Bascompte 2003), which might be of importance especially for invasive non-native species. However, in biocontrol practice a 100% eradication is often not achieved and not even aimed for. A lot of pests of economically important organisms naturally share a common habitat. Therefore, in most cases the aim of the pest management is to keep the pest population size or density below an economic threshold or level of tolerance, which represents a balanced state between the costs of pest suppression and possible economic losses due to the damage caused by the pest. The economic threshold can be defined as the pest population size or density at which management action should take place (Bor 1995).

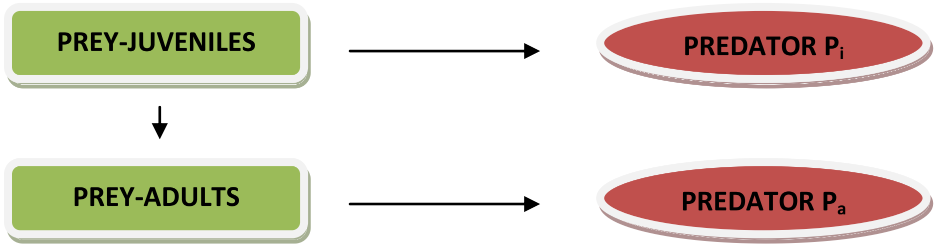
1.8 Generalist vs. specialist predators and pest biocontrol

Although specialist predators used to be believed to be optimal for biocontrol, a recent study by Symondson et al. (2002) gives a number of examples of successful biocontrol by generalist predators. There are many advantages in omnivorous predatory species, namely their ability of persistence in the ecosystem and their potential to regulate more pest species. Besides, a clever use of native generalists may prevent harmful introductions of exotic species as has been documented for the invasive *Harmonia axyridis* whose introduction to North America was followed by a decline of populations of a native coccinellid beetle species (Snyder et al. 2004). Introduction of non-native biocontrol agents is accompanied with further risks to non-target species, and unexpected effects on community and ecosystem level (Simberloff & Stiling 1996). Symondson et al. (2002) also suggested to use communities of generalist predators as their synergistic impact might be more effective. Among the strongest arguments against the generalists is the possibility of intraguild predation, which might lessen the effect of biocontrol (Rosenheim et al. 1995). Besides predators *sensu stricto*, parasitoids are frequently used in as biocontrol agents. Even though they are often specialists, there are exceptions: as an example, the parasitic fly *Compsilura concinnata*, a natural enemy of the gypsy moth *Lymantria dispar*, is a generalist (Grey et al. 2008). In this thesis, to keep things simple, interactions such as intraguild predation, cannibalism or competition will be neglected and in both examined scenarios we will assume only generalist predators.

2 The Prey-Predator (P-P) model

2.1 Model development

Fig. 2.1.1: The P-P model scheme



The P-P system to be modelled is schematically depicted in Fig. 2.1.1. Population dynamics of prey is described by a system of two differential equations (case 0) discerning juvenile and adult classes. Only adults are able to reproduce. The population growth is assumed limited by an environmental carrying capacity:

$$f1 = \frac{dJ}{dt} = bA - mJ - d_j J\left(1 + \frac{J}{K_j}\right) \qquad (1)$$

$$f2 = \frac{dA}{dt} = mJ - d_a A\left(1 + \frac{A}{K_a}\right)$$

where *J* and *A* represent juvenile and adult density, respectively, *b is the* per capita birth rate, *m the* maturation rate, d_j (d_a) *is the* per capita mortality rate of juveniles (adults) due to factors other than consumption by modelled predators, and K_j (K_a) *is the* environmental carrying capacity for juveniles (adults).

In order to explore the influence of age-selective predation and of predator functional responses on prey population dynamics, we consider terms expressing predation. Recall that we assume generalist predators whose dynamics are not interconnected with prey population dynamics and whose density is assumed constant. We use five different combinations of no predation on an age class, a Holling type II ("saturation") functional response:

$$P_j = L_j J/(1 + B_j J), P_a = L_a A/(1 + B_a A)$$

and a Holling type III ("switching") functional response (see Table 2.1.1):

$$P_j = L_j J^2/(1 + B_j J^2), P_a = L_a A^2/(1 + B_a A^2)$$

Table 2.1.1: Combinations of predator functional responses used in cases A, B, C1-C3

Case	**Juveniles – P_j**	**Adults – P_a**
A	Type II	no predation
B	no predation	Type II
C1	Type II	Type II
C2	Type III	Type II
C3	Type II	Type III

In these expressions, L_j is the maximum attack rate of predator sat low juvenile densities and B_j is the inverse of juvenile density (type II) or of square of juvenile density (type III) at which the attack rate reaches 50% of its maximum value; in the case of type II response, B_j can represent the efficiency of behavioural response of juveniles (e.g. herding or sentinel behaviour) which increases with increasing B_j. Parameters L_a and B_a have an analogous interpretation with respect to adults. For the full systems of equations containing predation terms and corresponding to cases A-C3 see Table 2.1.2.

Table 2.1.2: Full systems of equations corresponding to cases A, B, C1-C3

Case	**Model**	**Remarks**
A	$\frac{dJ}{dt} = bA - mJ - d_jJ\left(1 + \frac{J}{K_j}\right) - \frac{L_jJ}{1 + JB_j}$ $\frac{dA}{dt} = mJ - d_aA\left(1 + \frac{A}{K_a}\right)$	predation only on juveniles
B	$\frac{dJ}{dt} = bA - mJ - d_jJ\left(1 + \frac{J}{K_j}\right)$ $\frac{dA}{dt} = mJ - d_aA\left(1 + \frac{A}{K_a}\right) - \frac{L_aA}{1 + AB_a}$	predation only on adults
C1	$\frac{dJ}{dt} = bA - mJ - d_jJ\left(1 + \frac{J}{K_j}\right) - \frac{L_jJ}{1 + JB_j}$ $\frac{dA}{dt} = mJ - d_aA\left(1 + \frac{A}{K_a}\right) - \frac{L_aA}{1 + AB_a}$	Holling type II predation on both age classes
C2	$\frac{dJ}{dt} = bA - mJ - d_jJ\left(1 + \frac{J}{K_j}\right) - \frac{L_jJ}{1 + JB_j}$ $\frac{dA}{dt} = mJ - d_aA\left(1 + \frac{A}{K_a}\right) - \frac{L_aA^2}{1 + A^2B_a}$	predator exhibits switching foraging behaviour on adults and saturation functional response on juveniles
C3	$\frac{dJ}{dt} = bA - mJ - d_jJ\left(1 + \frac{J}{K_j}\right) - \frac{L_jJ^2}{1 + J^2B_j}$ $\frac{dA}{dt} = mJ - d_aA\left(1 + \frac{A}{K_a}\right) - \frac{L_aA}{1 + AB_a}$	predator exhibits switching foraging behaviour on juveniles and saturation functional response on adults

2.2 Parameters

In this thesis, we focus on the impact of predation and question it in relation to the prey maturation rate *m*, that is, inner dynamics of the age-structured prey population; see also Section 2.3 below. Therefore, the focal parameters we consider are L_j, L_a and *m*. All the other parameters remain positive constants and their values were chosen in a heuristic way following reasonable assumptions about age-structured populations, e. g. lower mortality of adults than of juveniles or lower environmental carrying capacity for adults than for juveniles. The values of model parameters we use in this chapter are presented in Table 2.2.1.

Table 2.2.1: Parameter values

Parameter	Meaning	Value
b	per capita birth rate	1
d_j	per capita mortality rate of juveniles	0.02
d_a	per capita mortality rate of adults	0.01
K_j	parameter scaling carrying capacity for juveniles	5
K_a	parameter scaling carrying capacity for adults	3
B_j	behavioural response to predators for juveniles	0.8
B_a	behavioural response to predators for adults	0.5

2.3 Maturation rate as population characteristic, parameter or variable?

In the **P-P model** we use *m*, the prey maturation rate, as a focal parameter. This parameter might be perceived as a factor describing prey population dynamicity and we can compare on its basis different populations of the same or different species. We have chosen four values of *m* across four orders of magnitude (m = 0.01, 0.1, 1 and 10), which we found in the pre-tests to be sufficient in order to describe the spectrum of behaviour of the model. It is known that the maturation rate may be a function of temperature or food availability (see Section 5.3) but this is neglected in the P-P model in order to demonstrate baseline dynamics only.

2.4 Model analysis

As can be easily checked, the point $E^0 = [0,0]$ solves model (1) and any of the models listed in Table 2.1.2 and corresponding to all the examined cases, and will be referred to as the extinction equilibrium further on. Stability analysis of the extinction equilibrium $E^0 = [0,0]$ proceeds as follows. In general, an equilibrium point is locally asymptotically stable if and only if, at this point,

$$Det(J) > 0 \; and \; Tr(J) < 0,$$

where J is the Jacobian of the system of equations under study ($f1 = \frac{dJ}{dt}, f2 = \frac{dA}{dt}$):

$$J = \left[\begin{array}{cc} \frac{\partial f1}{\partial J} & \frac{\partial f1}{\partial A} \\ \frac{\partial f2}{\partial J} & \frac{\partial f2}{\partial A} \end{array} \right]$$

The trace *Tr(J)* of the Jacobian (see Table 2.4.1) stays in all cases always negative, for any parameters $m > 0$, $d_j > 0$, $d_a > 0$, $L_j > 0$, $L_a > 0$, $b > 0$, hence the stability conditions derive from the sign of the determinant *Det (J)*. The results are summarized in Table 2.4.1.

Table 2.4.1: Conditions on local stability of the extinction equilibrium $E^0 = [0,0]$. *Note: case 0 corresponds to model (1), that is, the absence of predation*

Case	Determinant and trace of the Jacobian at $E^0 = [0,0]$	Conditions on local stability of $E^0 = [0,0]$
0	$Det(J) = md_a - d_j d_a - bm$ $Tr(J) = -(m + d_j + d_a)$	$m < \frac{d_j d_a}{b - d_a}, for \; b - d_a > 0$ $m > \frac{d_j d_a}{b - d_a}, for \; b - d_a < 0$
A	$Det(J) = md_a + d_a d_j + L_j d_a - bm$ $Tr\,(J) = -(m + d_j + L_j + d_a)$	$L_j > \frac{bm - md_a - d_j d_a}{d_a}$ $m < \frac{L_j d_a + d_j d_a}{b - d_a}$, *for* $b - d_a > 0$ $m > \frac{L_j d_a + d_j d_a}{b - d_a}$, *for* $b - d_a < 0$

B	$Det(J) = md_a + L_a m + d_j d_a + d_j L_a - bm$ $Tr(J) = -(m + d_j + d_a + L_a)$	$L_a > \frac{bm - md_a - d_j d_a}{m + d_j}$ $m < \frac{L_a d_j + d_j d_a}{b - d_a - L_a}, for \quad b > d_a + L_a$ $m > \frac{La d_j + d_j d_a}{b - d_a - La}, for \quad b < d_a + La$
C1	$Det(J) = (-m - d_j - L_j)(-L_a - d_a) - bm$ $Tr(J) = -(m + d_j + L_j + d_a + L_a)$	$L_a > \frac{bm - md_a - d_j d_a}{m + d_j + d_a + L_j}$ $m < \frac{L_a(d_j + d_a + L_j) + d_j d_a}{b - d_a - L_a}$ $for \quad b > d_a + L_a$ $m > \frac{L_a(d_j + d_a + L_j) + d_j d_a}{b - d_a - L_a}$ $for \quad b < d_a + L_a$
C2	$Det(J) = md_a + d_j d_a + L_j d_a - bm$ $Tr(J) = -(m + d_j + L_j + d_a)$	$Lj > \frac{bm - md_a - d_j d_a}{d_a}$ $m < \frac{L_j d_a + d_j d_a}{b - d_a}, for \quad b - d_a > 0$ $m > \frac{L_j d_a + d_j d_a}{b - d_a}, for \quad b - d_a < 0$
C3	$Det(J) = md_a + mL_a + d_j d_a + d_j L_a - bm$ $Tr(J) = -(m + d_j + d_a + L_a)$	$La > \frac{bm - md_a - d_j d_a}{m + d_j}$ $m < \frac{L_a d_j + d_j d_a}{b - d_a - L_a}, for \quad b > d_a + L_a$ $m > \frac{L_a d_j + d_j d_a}{b - d_a - L_a}, for \quad b < d_a + L_a$

Further analyses were performed using the MATLAB software (The MathWorks, Inc.). The non-zero equilibrium states were searched for numerically as the roots of a higher-order polynomial by the function *roots* and their stability was then assessed using the above given rule.

3 Results

Figures 3.I – 3.VI show the non-zero equilibrium states (stable and unstable) of juveniles and adults corresponding to all the examined cases. The equilibria were searched for different maturation rates m (0.01, 0.1, 1, 10) and predation parameters L_j (case A), L_a (case B) or both (C1, C2, C3).

We can observe several types of influence of predation and of different maturation rates on the prey population dynamics. There are either just one branch of stable equilibria and the increasing predation pressure (via parameters L_j or L_a) causes a decline in the value of stable population density (such as case A, m = 10), or an additional branch of unstable equilibria arises, representing the Allee threshold of population survival and hence implying occurrence of a demographic Allee effect (such as case A, m = 0.01; see also Fig. 3.1a). In some cases, there are even two branches of stable equilibria with an unstable equilibrium branch in between (such as case A, m = 1; see also Fig. 3.1b). This last situation might represent a phenomenon called the predator pit, suggesting that the prey population is able to persist at two alternative stable population densities. Once a population is suppressed below the critical density represented by the unstable equilibrium, it would attain a low-density stable equilibrium because the extinction equilibrium remains unstable in this case. In some species, this might be a reason for the lack of recovery after a rapid decline (Courchamp et al. 2008). These multiple stable states occur quite often; quite surprisingly, we have even found several cases where triple stable states co-occur of which one is the extinction equilibrium (case C3, see below).

Figure 3.1: Branch of stable (solid lines) and unstable (dashed lines) equilibria for a demographic Allee effect (a) and two positive stable states (b), with marked limit points (stars) at which the number of equilibria changes as the system undergoes here a global bifurcation

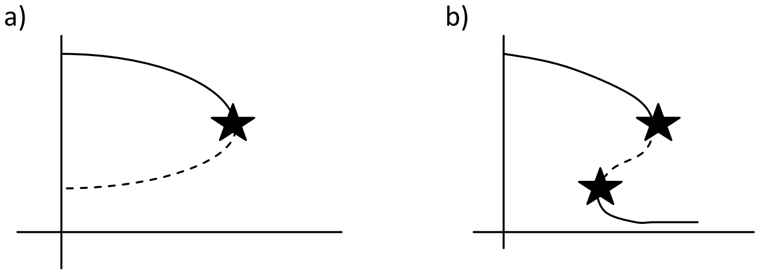


Fig. 3.I: ***CASES A, A in LOG (y) SCALE, and B:*** *Stable (solid line) and unstable (dashed line) density equilibria of juveniles (blue) and adults (red) for various values of parameters m and* L_j *or* L_a*. For other parameters see Table 2.2.1.*

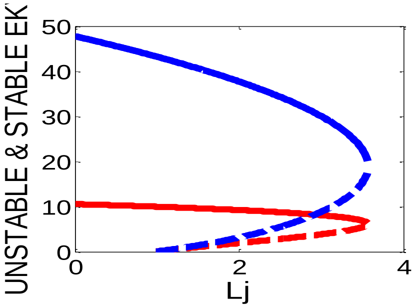
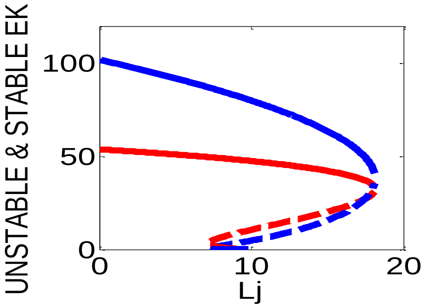
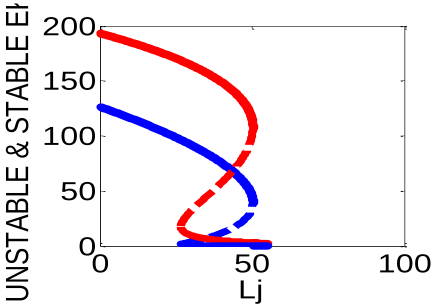
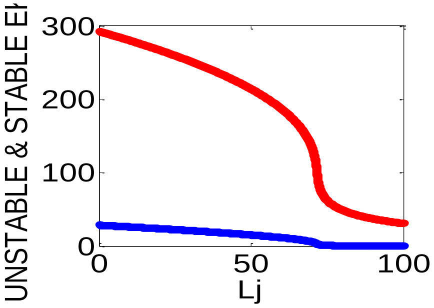
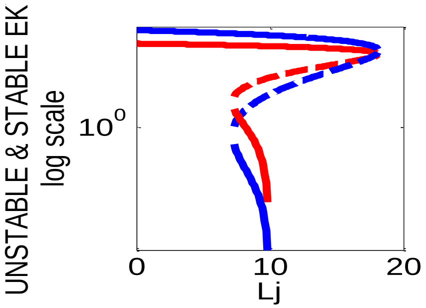
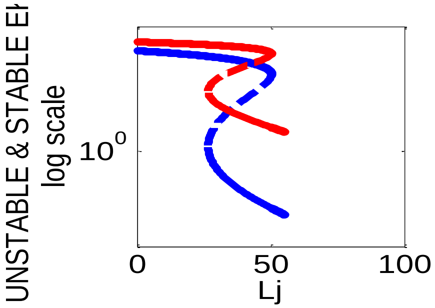
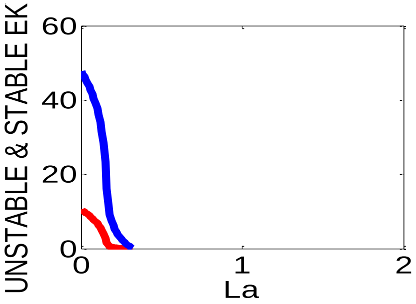
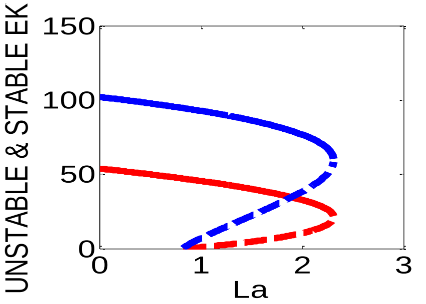
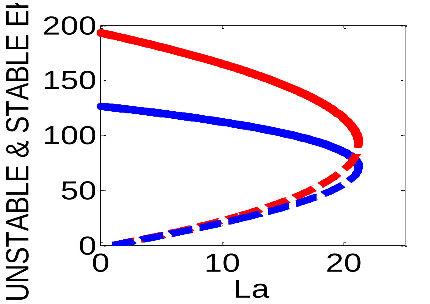
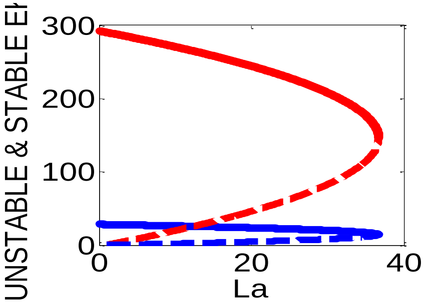
case	m=0.01	m=0.1	m=1	m=10
A **L_a=0**				
A **log y**				
B **L_j=0**				

Figure 3.II: ***CASE C1:*** *Stable (solid line) and unstable (dashed line) density equilibria of juveniles (blue) and adults (red) for various values of parameters m, L_j and L_a. For other parameters see Table 2.2.1.*

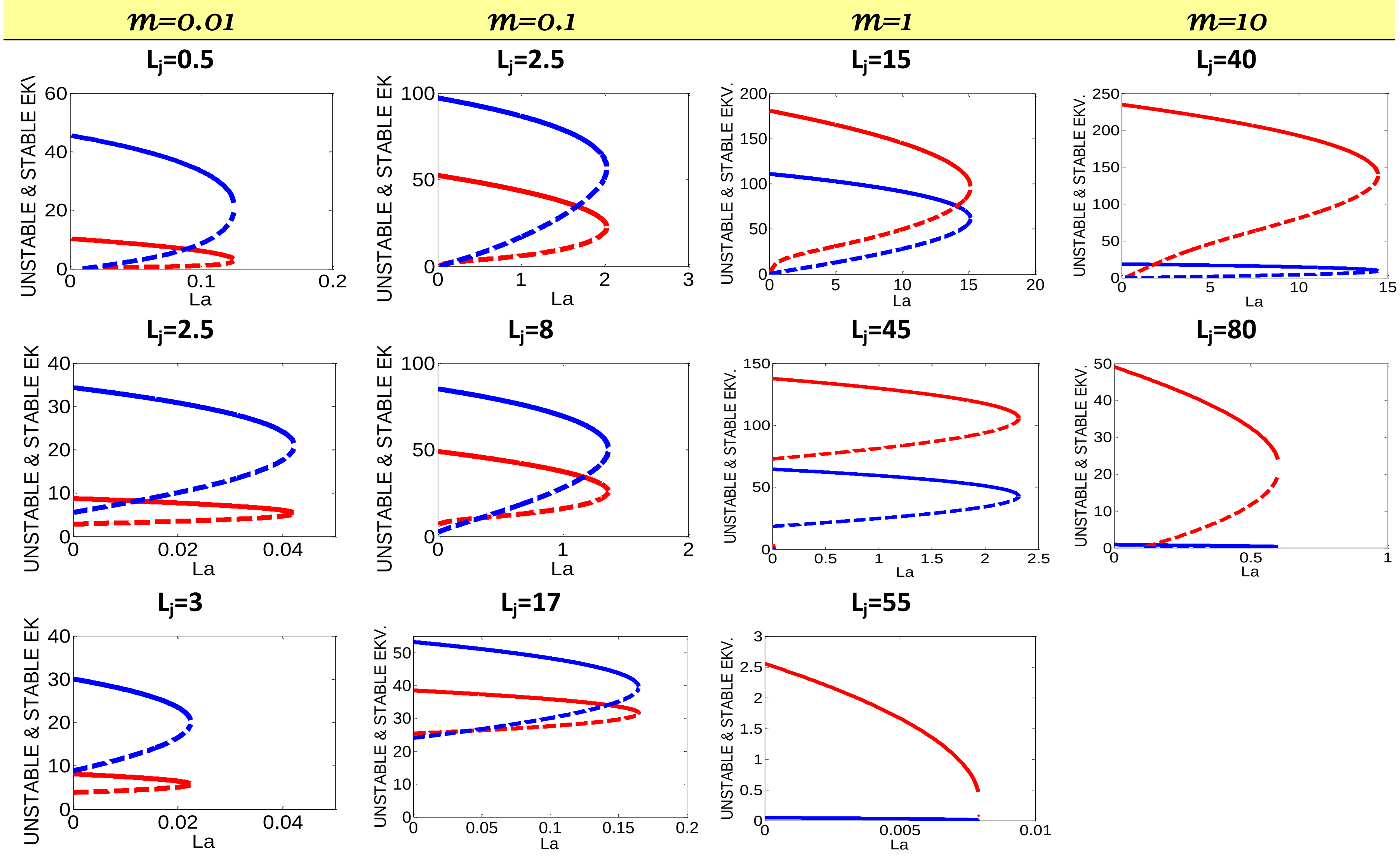


Fig. 3.III: ***CASE C2:*** *Stable (solid line) and unstable (dashed line) density equilibria of juveniles (blue) and adults (red) for various values of parameters m, L_j and L_a. For other parameters see Table 2.2.1.*

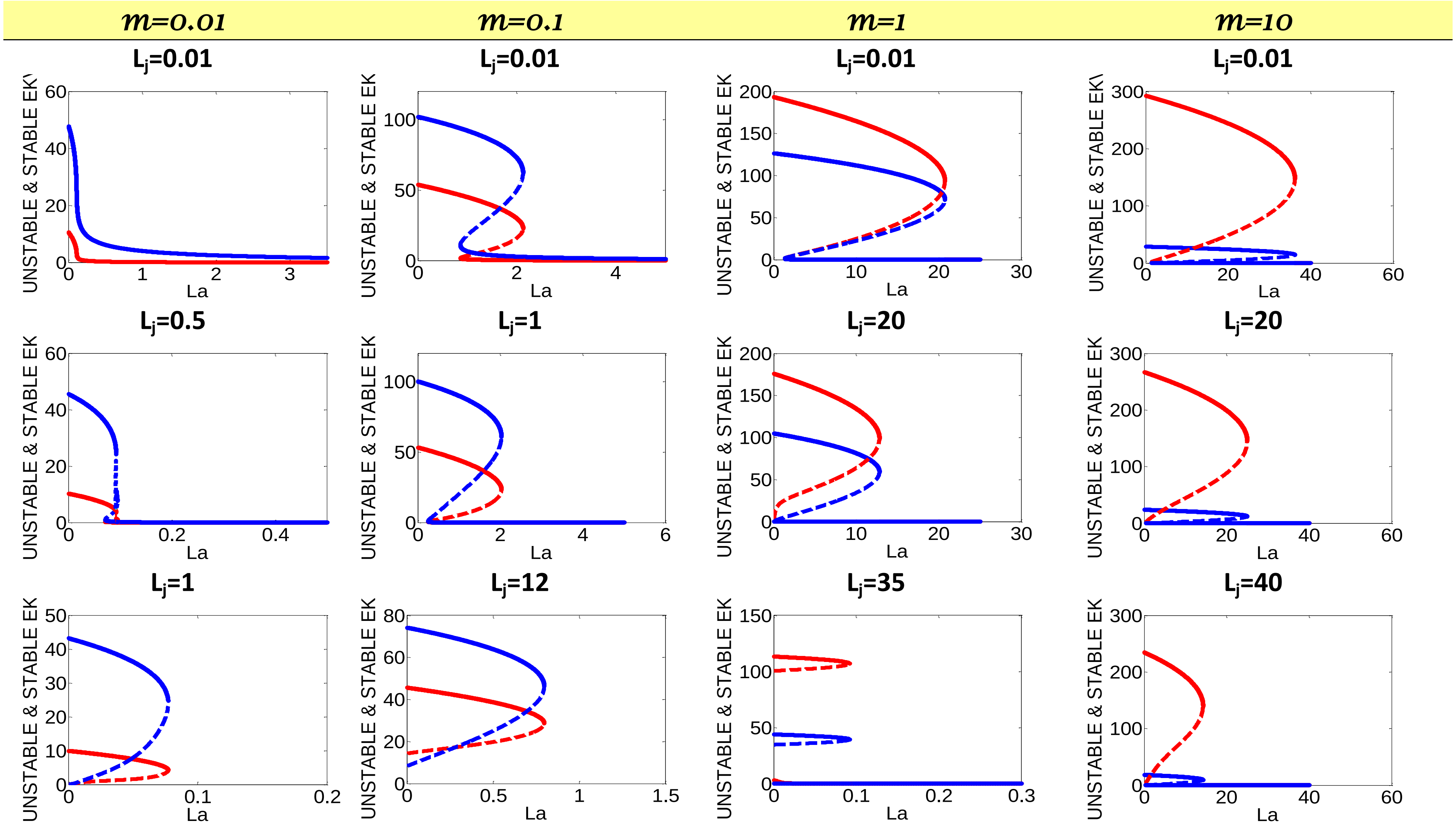


Figure 3.IV: ***CASE C2 LOG SCALE:*** *Stable (solid line) and unstable (dashed line) logarithmic density equilibria of juveniles (blue) and adults (red) for various values of parameters m, L_j and L_a. For other parameters see Table 2.2.1.*

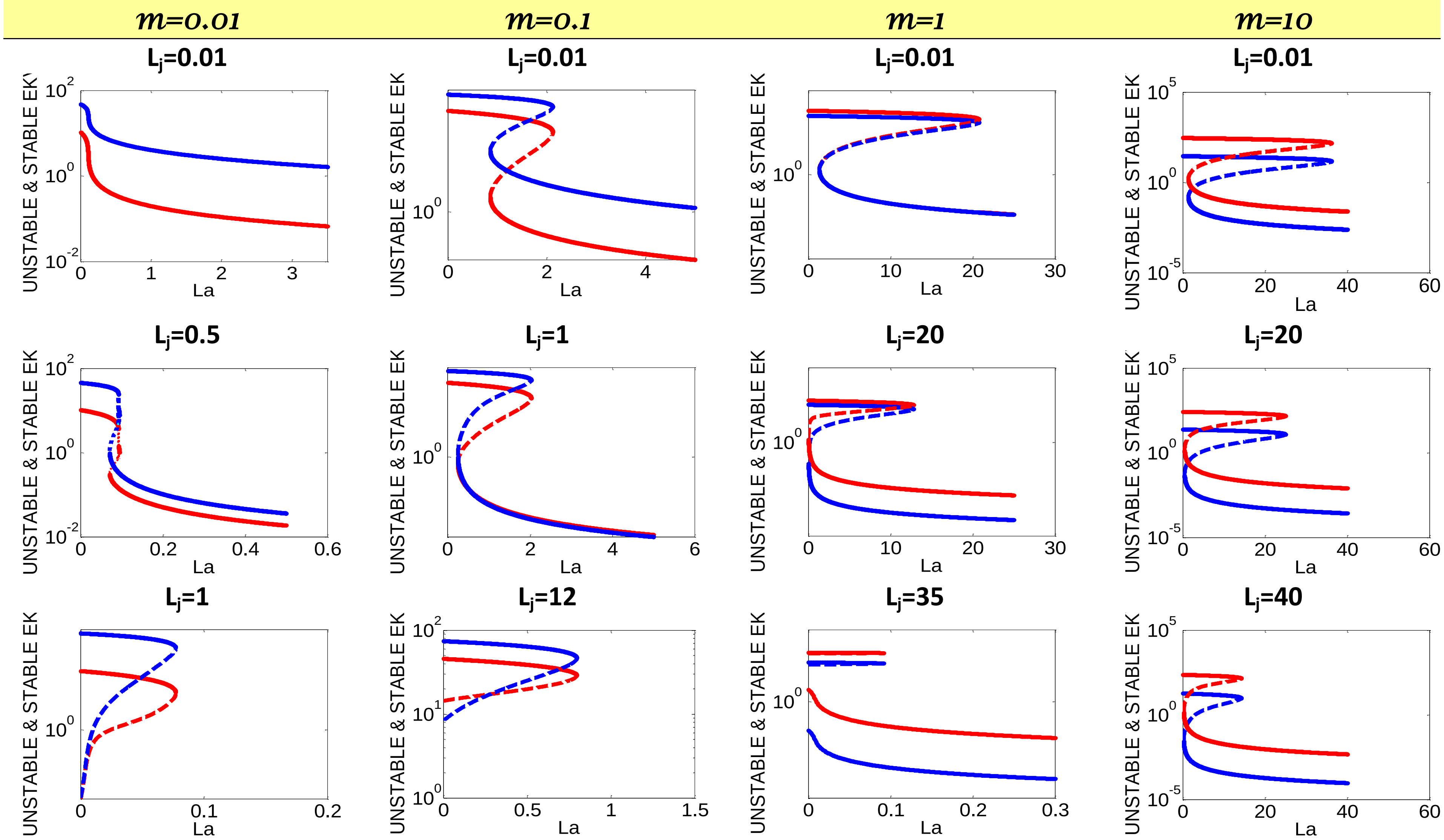


Figure 3.V: ***CASE C3:*** *Stable (solid line) and unstable (dashed line) density equilibria of juveniles (blue) and adults (red) for different m, L_j and L_a. For other parameters see Table 2.2.1.*

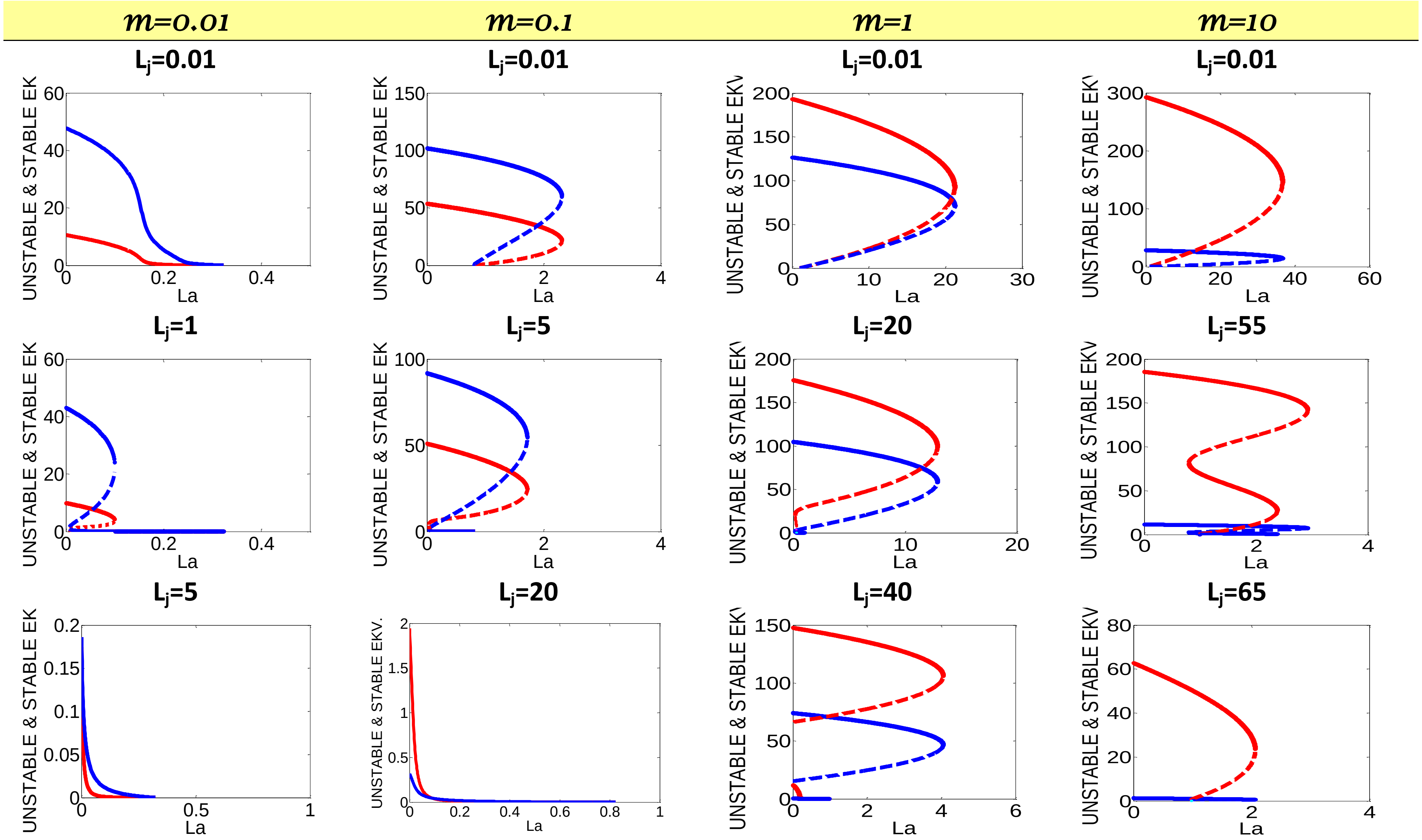
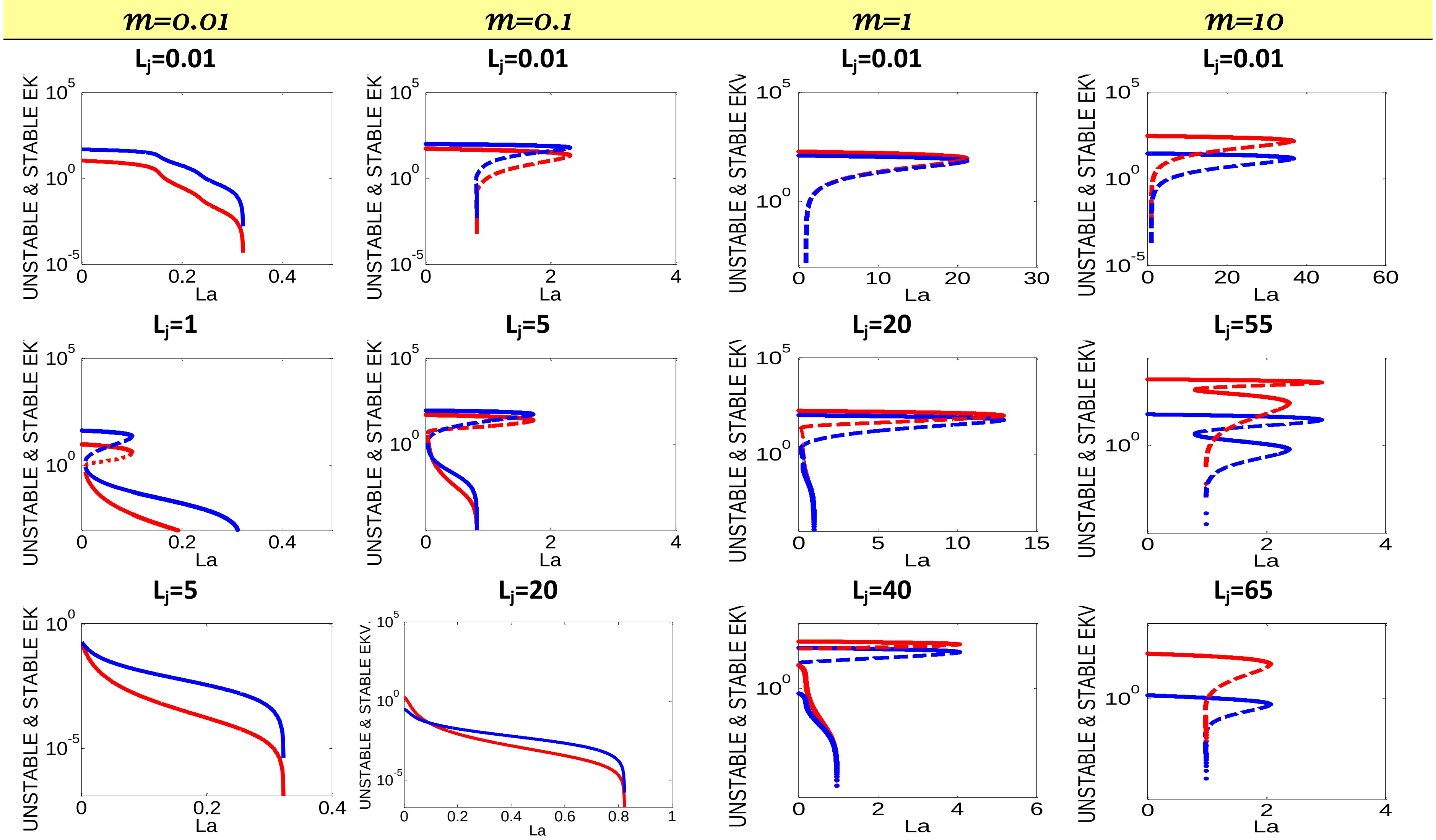


Figure 3.VI: ***CASE C3 LOG SCALE:*** *Stable (solid line) and unstable (dashed line) logarithmic density equilibria of juveniles (blue) and adults (red) for various values of parameters m,* L_j *and* L_a*. For other parameters see Table 2.2.1.*



Case A (Fig. 3.I)

In case A where there is only predation on juveniles and the predator exhibits a saturation foraging behaviour (i.e. a Holling type II functional response), we can clearly see that when maturation of young is slow (m = 0.01) then at some high enough value of L_j the Allee effect develops (Fig. 3.I). However, no such Allee effect occurs if the maturation is very fast (m = 10). This is because juveniles escape the danger of predation swiftly and enjoy a safe life as adults and reproduce, which allows the exploited pool of juveniles to replenish. At an intermediate maturation rate, a low level of predation induces an Allee-effect-free population, whereas an intermediate level of predation allows an alternative, low-density stable equilibrium to appear. This finding is of particular importance because to our best knowledge, this phenomenon was until now described in predator-prey interactions only as a product of a type III functional response of a generalist predator applied to an unstructured, logistically growing population of prey (May 1977). Figure 3.I also shows that the higher is the maturation rate, the wider is the range of predation pressure under which the prey population is able to persist; note different x-axis scales.

Figure 3.2 shows ranges of maturation rates for which we can expect different numbers of stable and unstable equilibria. As there exist two limit points for approximately $0.01 < m < 10$, this is the area of the “predator pit” occurrence. For $m \geq 10$ there are no limit points, implying just one branch of stable equilibria. For very small m, only one curve of limit points is observed, which signals the demographic Allee effect.

Case B (Fig. 3.I)

If only prey adults suffer from predation, the Allee effect was also observed but almost no multiple positive stable states have been detected (this is discussed further in this section). This time, contrary to the case A, if the maturation rate is very low, there is no Allee effect and the values of stable juvenile density are above those of adult density. This is due to the fact that the slow maturation allows the pool of adults, diminished by predators, to recover only very slowly. In addition, the overall predation pressure must be comparatively small in order to allow the prey population persistence. With faster maturation, higher predation pressure is plausible. At a strong enough predation, a branch of unstable equilibria arises. If the maturation is very fast the stable juvenile density is at very low values as the young tend to quickly leave their class. The stable juvenile density is very close to the unstable one and low in absolute values. However, the ecological stability of the population cannot be assessed easily as the range of stability of adults is much wider, and, roughly speaking, only the suppression of both age classes below respective unstable values drives the population extinct. Overall, we can detect the trend of stability decrease with an increasing strength of predation. A higher maturation rate naturally allows for a stronger predation on adults.

Again, Fig. 3.2 shows ranges of maturation rates for which we can expect different qualitative behaviour of the model. This time, mostly only one limit point exists across all values of m, suggesting an Allee effect. An exception is here the interval $0.01 < m < 0.1$ within which there is a very small area with one more limit point, suggesting occurrence of two positive stable equilibria. These are not shown in Fig. 3.I as this scenario is here rather marginal.

Stability decline – consume juveniles or adults?

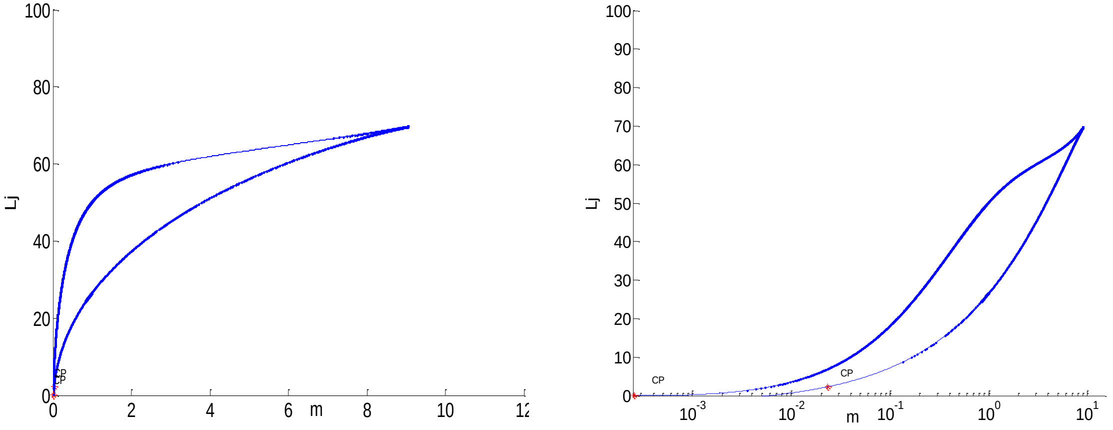
Figure 3.3 shows the decline of stability of prey population in the cases A and B in response to predation. This decrease is calculated as follows:

$$stability\ decrease\ (\%)\ =\ 100\ (1–\ (AS+JS)_i/\ (AS+JS)_0)$$

where $(AS+JS)_0$ is the sum of stable equilibria of adults and juveniles without predation (case A: $L_j = 0$, case B: $L_a=0$) and $(AS+JS)_i$ is the sum of stable equilibria of adults and juveniles with predation (case A: $L_j \neq 0$, case B: $L_a \neq 0$); 100% stability decrease means the prey population extinction.

Figure 3.2: Limit points (the blue curve) of equlibria curves in cases A and B:

A	**A** **log m**	
B	**B** **log m**	**B log m** **log L_a**



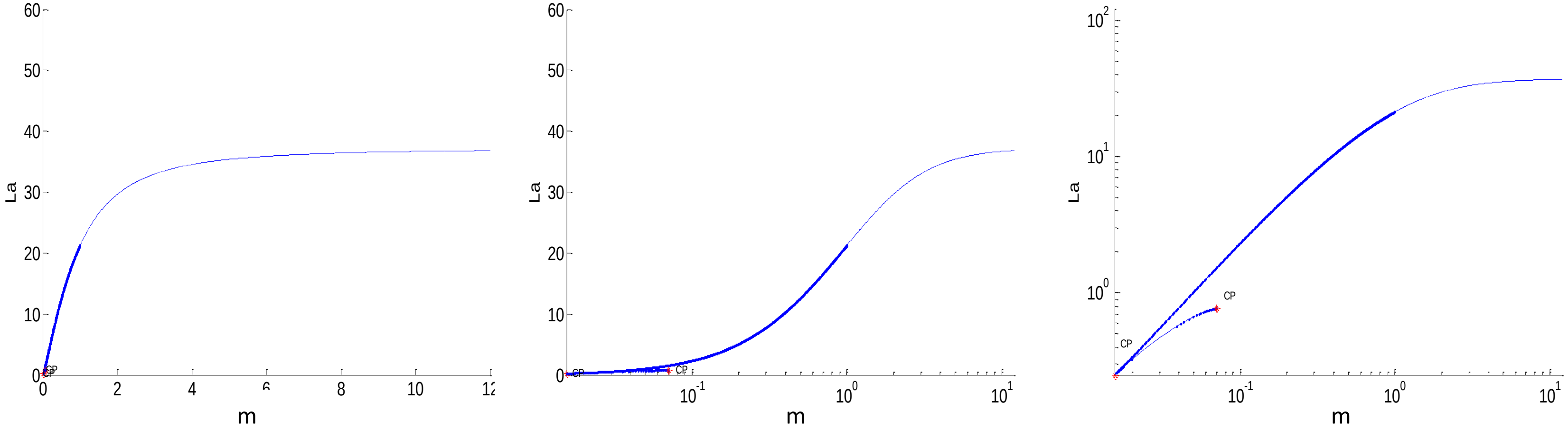
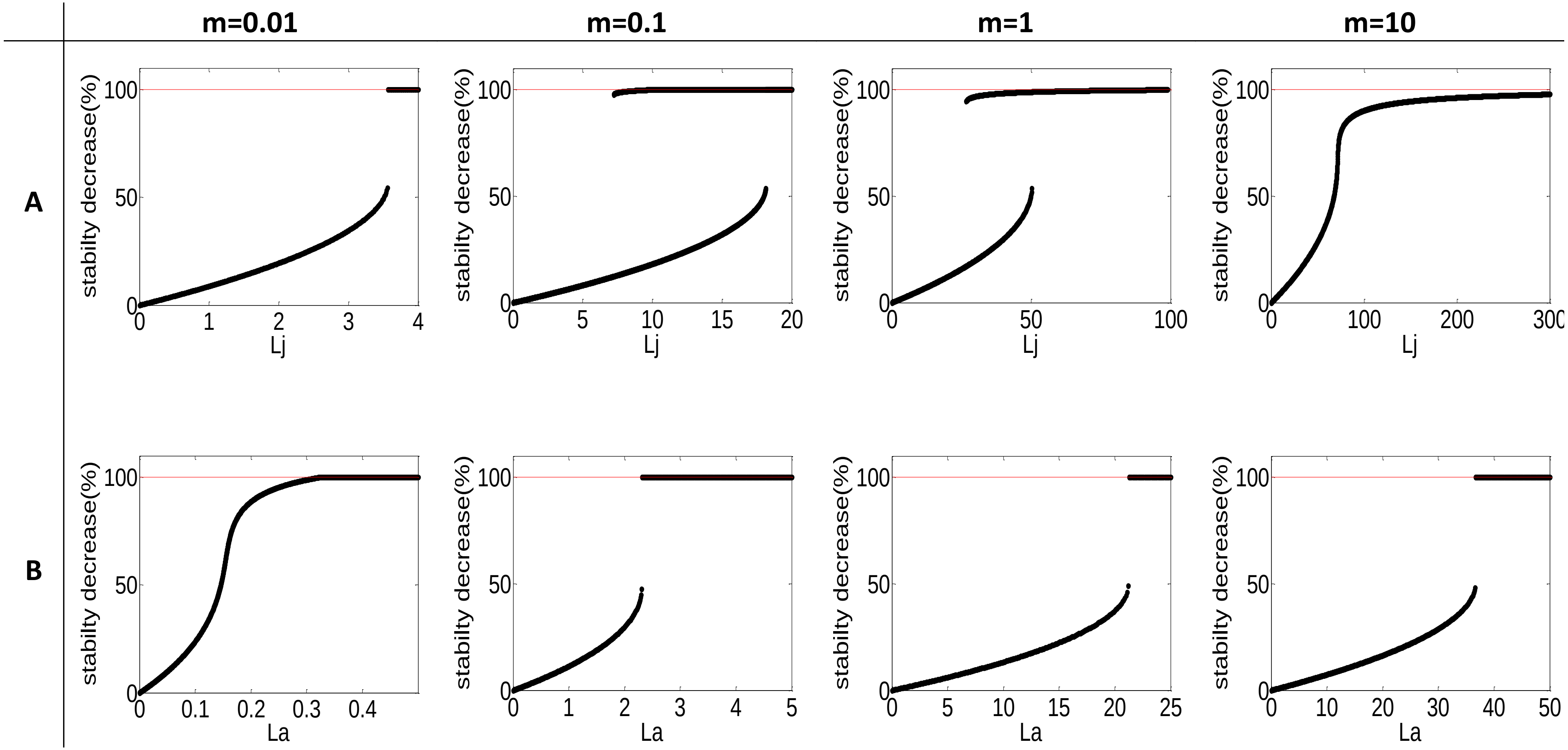


Figure 3.3: Stability decrease (%) of the overall population due to the predation pressure in case A(dependent on L_j) and B (dependent on L_a) for various values of maturation rate m. For other parameters see Table.2.2.1.



Here we can compare the different impact of predation on juveniles and adults on prey population stability. In populations with slow maturation it seems to be more efficient to apply predation to adults, if we intend to destabilize the pest population. For higher maturation rates, the quantitative difference is smaller; however, applying predation to juveniles might be advantageous thanks to the predator pit effect, if the low-density stable equilibrium lies below the economic threshold.

Case C1 (Fig. 3.II)

In this case, both juveniles and adults are decimated by predation via a Holling type II functional response. For the adopted parameter values, mostly one stable and one unstable equilibria develop, demonstrating an Allee effect, with the main differences in their absolute values. If the maturation of juveniles is slow (m = 0.01 or 0.1), the stable equilibrium densities of juveniles remain above those of adults. Increasing the predation level on juveniles leads to destabilization of the population as the stable equilibria move downwards on the vertical axes and the unstable equilibria upwards, keeping shorter distance in between them and thus making the population less resistant to disturbances. For the prey population to persist, only remarkably weak predation on adults is required if predation on juveniles is heavy. In short, predation on both juveniles and adults add to the instability of the system in synergy. If the maturation is very fast, then the predation on juveniles may be extensive, but the stable configuration would include a high density of adults and a very low density of juveniles. In this case, juveniles leave their class quite fast, but in comparison with the case A would not escape predation in this way as the adults are exploited as well and only a very weak predation on adults is bearable. Slowly maturating populations can stand only very weak predation on both classes as any positive equilibria cease to exist at very low predation levels.

Figures 3.4 and 3.5 show contours of surfaces of unstable equilibrium densities of juveniles and adults for different maturation rates. It can be seen that the values of unstable equilibria with higher predation on juveniles as well as higher predation on adults reach higher values as well, which has a destabilizing effect on the population. This naturally occurs for all values of m.

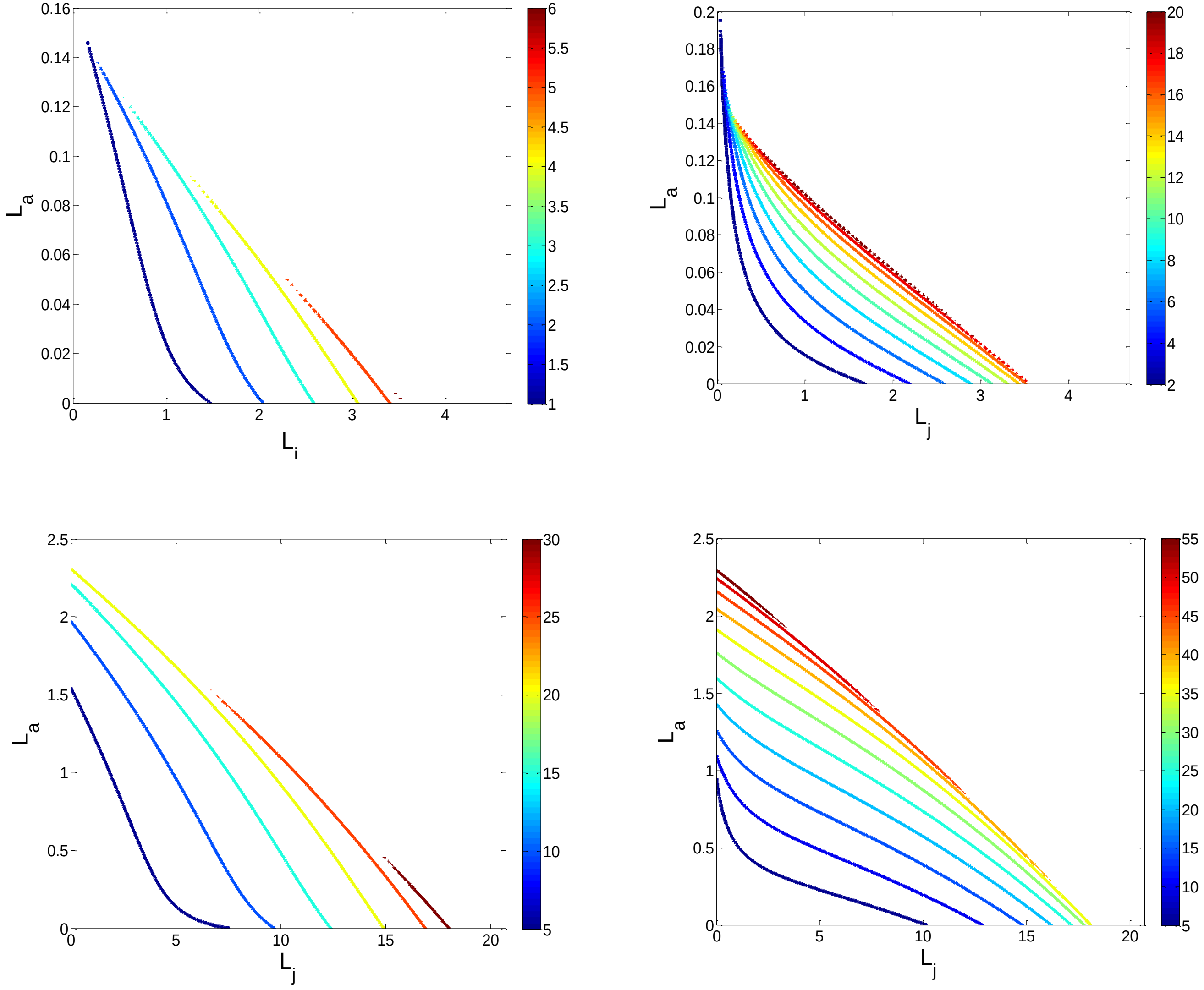


Figure 3.4.: Case C1, contours of surfaces of unstable equilibria of prey desity dependent on L_j and L_a:

AN	JN	m=0.01
AN	JN	m=0.1

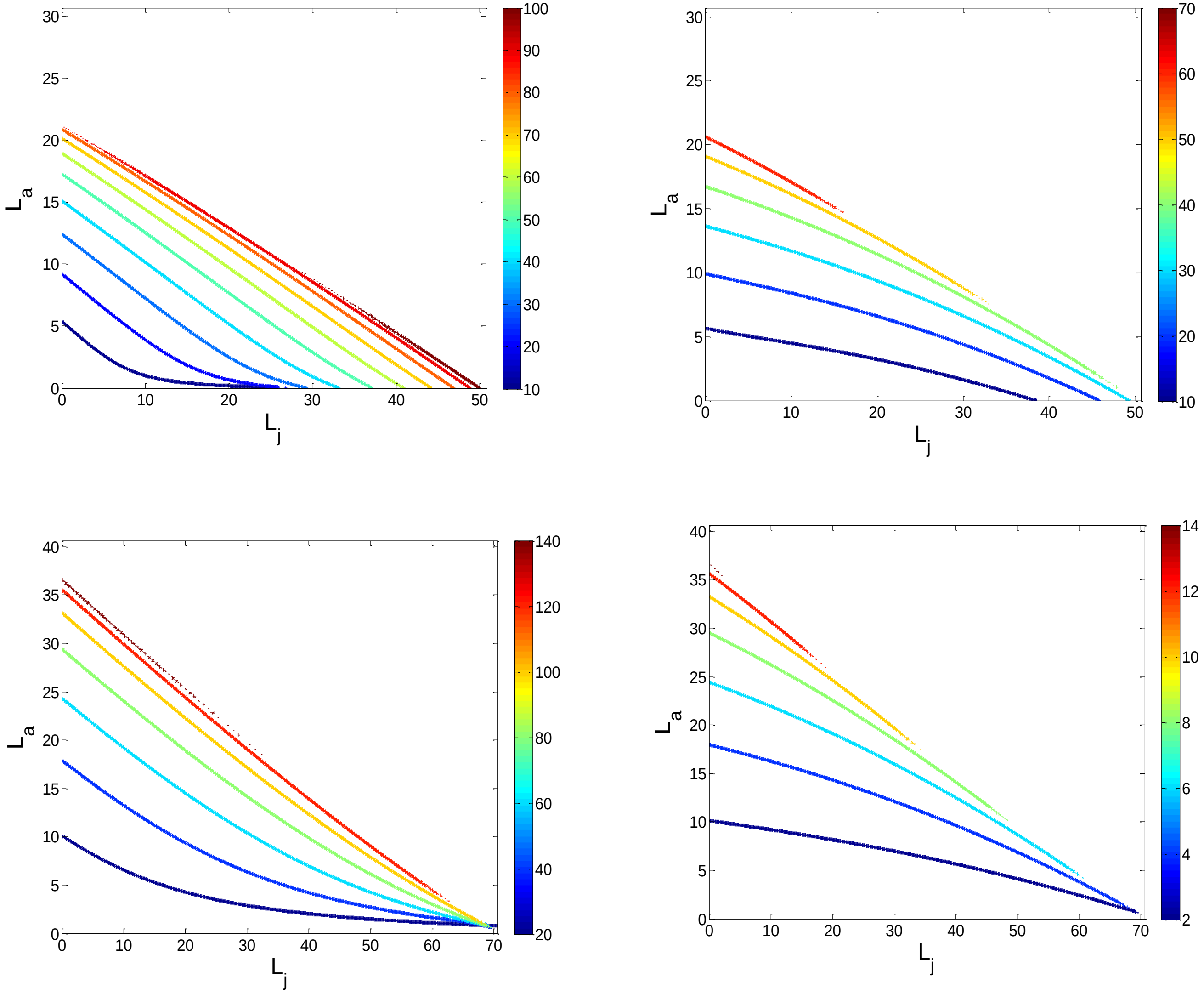


Figure 3.5.: Case C1, contours of surfaces of unstable equilibria of prey desity dependent on L_j and L_a:

AN	JN	*m*=1
AN	JN	*m*=10

Case C2 (Fig. 3.III, 3.IV)

In this case, the predator would exploit the adults only if abundant enough (type III functional response). The juveniles are killed in the saturating manner (type II functional response). The existence of two positive stable equilibria is here the most frequent pattern for the studied values of parameters, with the main differences in the shape and position of equilibrium curves. However, there still exists the scenario with only a branch of stable equilibria when both the maturation rate and the predation on juveniles are small. A high density of juveniles is beneficial for their survival, but a higher density of adults is less advantageous for them as the lower density forces predators to search for another type of prey. The Allee effect arises when the juveniles mature slowly and are heavily predated, in which case the type II response has a stronger influence on the prey population than the type III one. The faster the juveniles mature the higher values of the high-density stable state are exhibited and the heavier predation is necessary to reach the limit point at which the high-density equilibrium ceases to exist. For higher maturation rates, the low-density stable equilibria arise already at very low predation levels in both age stages.

Case C3 (Fig. 3.V, 3.VI)

Here the predator exhibits switching (type III response) on juveniles and saturation (type II response) on adult prey individuals. A population with slow maturation rate can lack multiple stable equilibria for the studied parameters if the predation on juveniles is very low. If predation on juveniles is moderate hysteresis again occurs; in addition, with high level of predation on juveniles only the lower branch of stable equilibria is left with Allee-effect-free dynamics albeit with very low population density. Demographic Allee effect arises quite often in this scenario, predominantly for higher maturation rates and low predation pressure on juveniles, and occurs much more frequently than in the scenario C2. Finally and quite interestingly, fast maturation combined with strong predation on juveniles may induce existence of three simultaneous stable states of which one is the extinction equilibrium (m = 10, L_j = 55).

Conclusions & some economical reflections

In conclusion, the age-structured predation on a logistically growing prey population with different functional responses offers three typical types of dynamics: a unique stable positive equilibrium, demographic Allee effect, and the predator-pit-like behaviour. The results are partly consistent with what has already been observed in predator-prey models of logistically growing, non-structured prey populations – demographic Allee effects were observed under operation of a type II functional response (Berec et al. 2007) while a predator pit was observed for a type III functional response (May 1977). All these three types of dynamics were observed also for the age-structured prey, in all the examined scenarios. Yet, we have also observed two quite unexpected results.

First, a predator-pit-like behaviour has been observed in the case A and found quite inspiring as there are quite many examples of species where only juveniles are predation-susceptible and are exploited by a functional response of type II. Quite intriguing has also been the triple stable state in case C3, of which one was the extinction equilibrium. This last outcome can be viewed as a combined operation of known impacts of type II and type III functional responses.

The occurrence of predator pit is usually explained by a predation refuge that is typical if the prey is sparse and the predator switches to another species of prey. In an intuitive way we can compare this situation to the adult class, which provides an escape from predation on juveniles while being the only reproductive power. This is no more important if maturation is very fast and therefore most juveniles become adult.

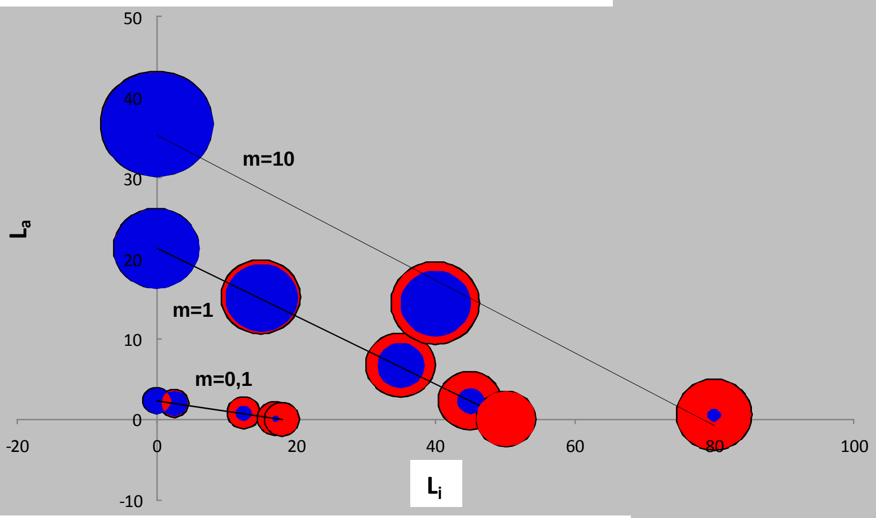
Besides of the qualitative effects of predation represented in our results, a quantitative effect in terms of costs of biocontrol can be taken into account as well. As can be seen in Fig. 3.3, if there exists predation only (or mainly) on adults, this leads to 100% stability decrease by smaller effort than if predation is on juveniles and no alternative stable states occur. Therefore, if two predators, the one killing adults and the other one killing juveniles, could be compared by the values of L_j and L_a (representing something like killing efficiency when predator density is fixed or the number of released predator individuals if killing efficiency is fixed), our results could give an advice on which predator to choose for more efficient control, considering per individual costs of each predator. Having a given budget to perform a biocontrol action or artificial removal and knowing the costs of predators or human workers (for example, in the *Acanthaster planci* the price of removing one individual can reach \$40 and the cost of preserving an 2-4 hectares area up to \$20.000-\$200.000 over 3 years (Lassig 1995)) we can assess what stability decrease may be achieved and how the finances may be allocated in order to get the best result, that is, which strategy to use.

To give an idea of the possible decision-making according to the costs of each biocontrol agent we present Fig. 3.6. In this very simple demonstration we assumed that predators used against adults and juveniles have given prices in currency “Units” per unit of L_a and L_j, respectively. We consider predation either on juveniles (case A), adults (case B) or on both classes (C1). The cost is either the same, 5:5, or biased, 5:1 or 1:5. In Fig. 3.6, the size of the disc represents the final budget to be paid for such a combination of predators to reach the limit point, that is, to make the prey population not persistent for any density (see Chapter 3, case A; the same could be done to find the optimal funding allocation to suppress the population bellow some economic threshold). Hence we can see that for example in the system with m = 10 *(the circles for each m are connected by the thin line)*, where prices of predators are the same (Fig. 3.6c) it is cheapest to buy predators only against adults. On the contrary, if juveniles are cheaper and the maturity rate m = 1 it might be cheaper to buy only predators against juveniles (Fig. 3.6a). If m = 0.01 and cost of 1 unit L_j = 1U and L_a = 5U the difference in overall costs is small. It is not difficult to count the proportion of costs of each predator in the financial budget and thus we could further on consider the predators that are naturally available in the environment and costs of them or their natural habitat preservation.

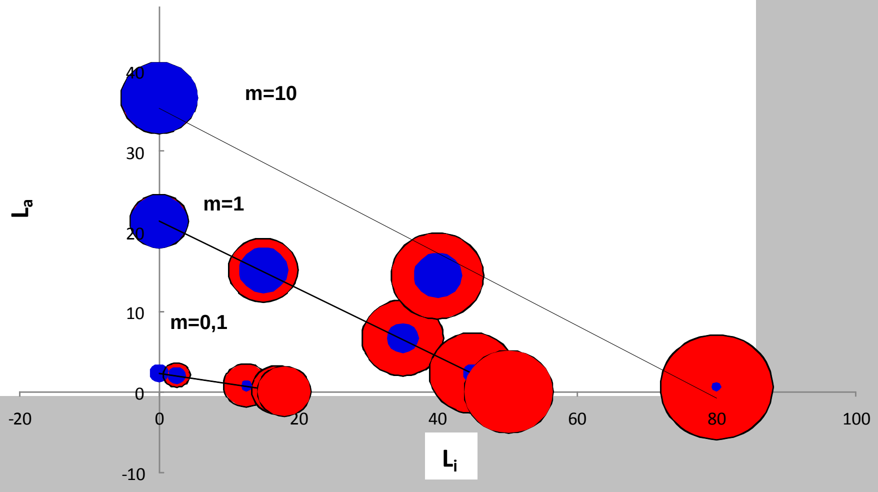
In contrast to Fig. 3.6, for which we assume the budget is unlimited and the question stands how much the final costs will be or how to find the cheapest solution, we now assume that we have a limited amount of money at disposal and ask how to optimally allocate this budget between adult- and juvenile-specific predators in order to achieve the highest control efficiency (Fig. 3.7). This analysis was conducted only for the system with m=1 and functional responses of type II. Figure 3.7a,c,e shows contours of stable equilibrium densities of the pest population for different combinations of L_j and L_a. The bold lines represent possible combinations of predation on juveniles and adults that can be purchased for our budget B = [5, 10, 15] given $B = L_a+xL_j$. The price of 1 unit of L_a is always 1U and the price of 1 unit of L_j is xU. We tested three price models, where x = [0.2, 1, 5]. Figure 3.7b,d,f shows the resulting stability decrease that can be achieved with a given budget (bold lines) as it depends L_j (thin lines; $L_a=B-xL_j$). Thus, we can see that if 1 unit of L_j is five times cheaper then 1 unit of L_a (Fig. 3.7b) and our budget is 10 (red line) we can achieve a 50% stability decrease when buying only predators against juveniles. On the other hand, if we did the opposite and bought only predators against adults we would achieve only about 13% stability decrease for the same price. Once the price of 1 unit L_j is the same as of 1 unit L_a (Fig. 3.7d) or even higher (Fig. 3.7f), it is advisable to purchase as high a proportion of predators against adults as possible, because then the achieved stability decrease will be higher. These results are consistent with those presented in Fig. 3.6.

Fig.: 3.6: Total costs expressed by disc area necessary to suppress the pest population to the limit point of equilibria existence using various combinations of predation on juveniles and adults (only type II. f. response) under different price models. Red disc – total costs, blue disc– cost of predator against adults. Discs for different maturation rates are interconnected by lines.

a) Cost 1 unit L_j = 1 U, 1 unit L_a = 5 U



b) Cost 1 unit L_j = 5 U, 1 unit L_a = 5 U



c) Cost 1 unit L_j = 5 U, 1 unit L_a = 1 U

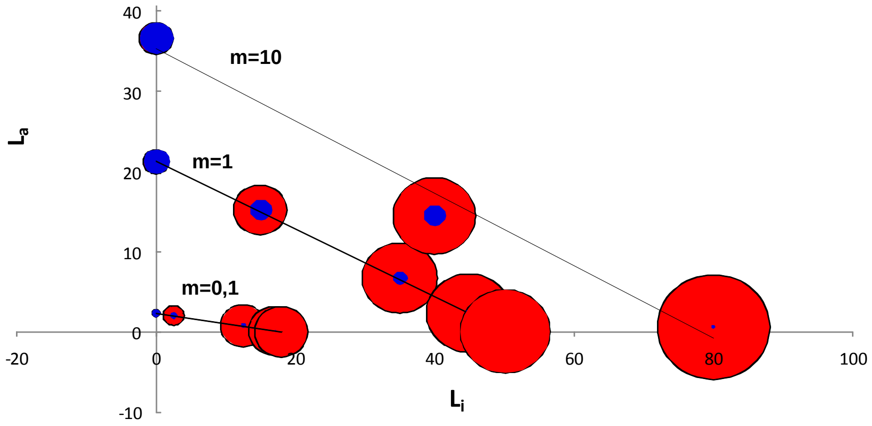
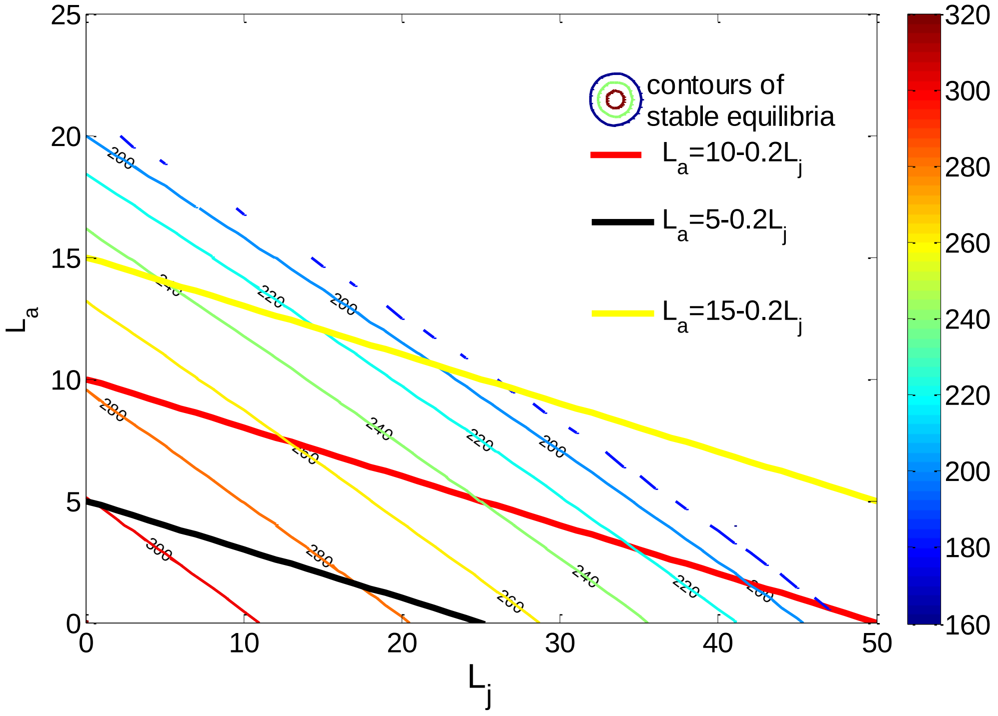
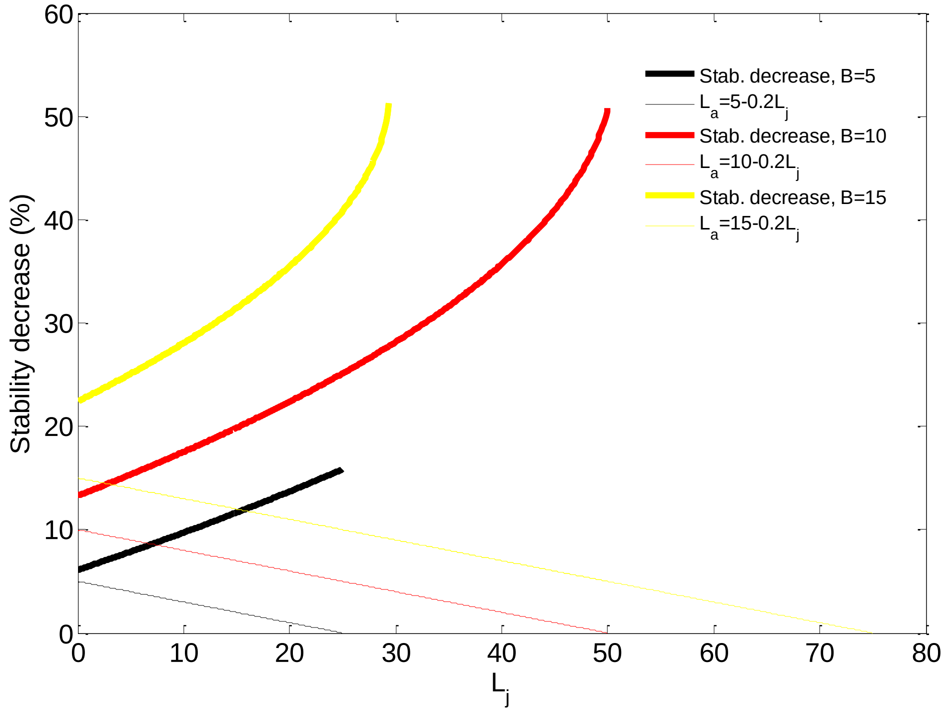


Fig. 3.7: Stability decrease that can be achieved by using various combinations of predation (type II functional response, CASE C1) on juveniles and adults for different values of budget, m=1.

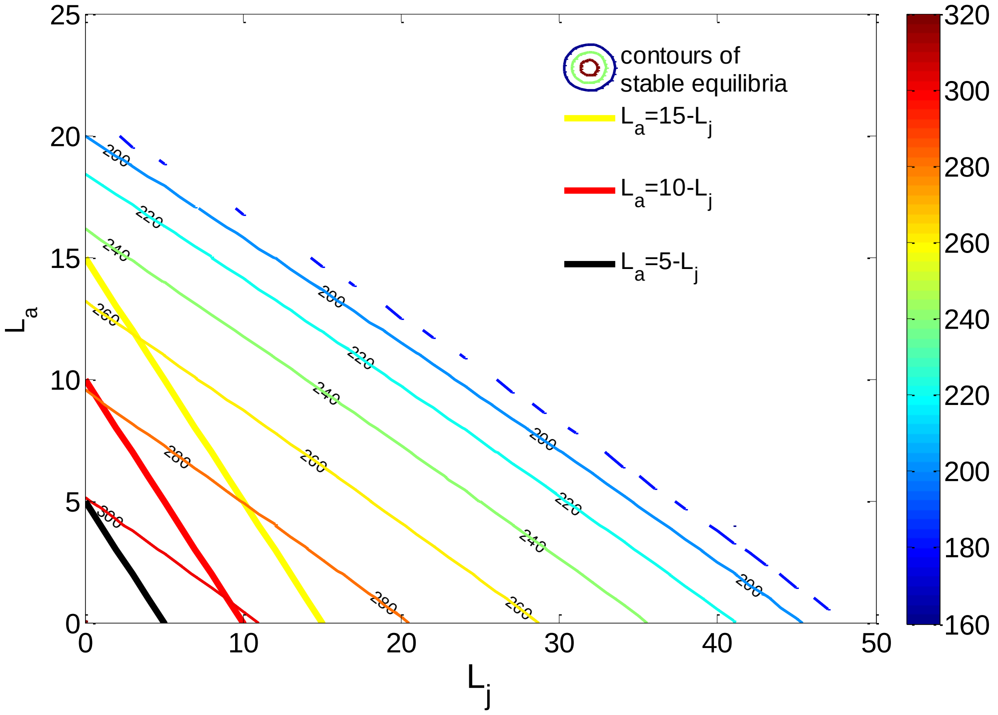
a) Contours of stable equilibria for different L_j and L_a and lines L_a= B-xL_j, x=0.2, m=1, budget B = [5(black),10(red),15(yellow)]



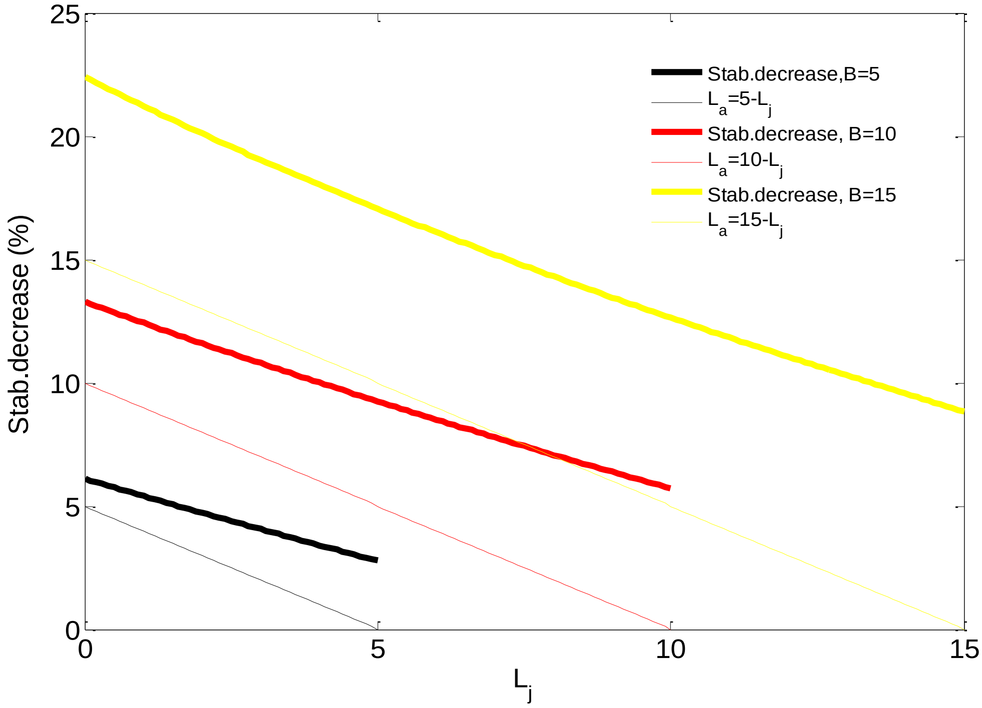
b) Stability decrease (%, bold lines) for budget B=[5,10,15] dependent on L_j, where L_a= B-xL_j (thin lines); cost of 1 unit L_a=1U,1 unit Lj=0.2U



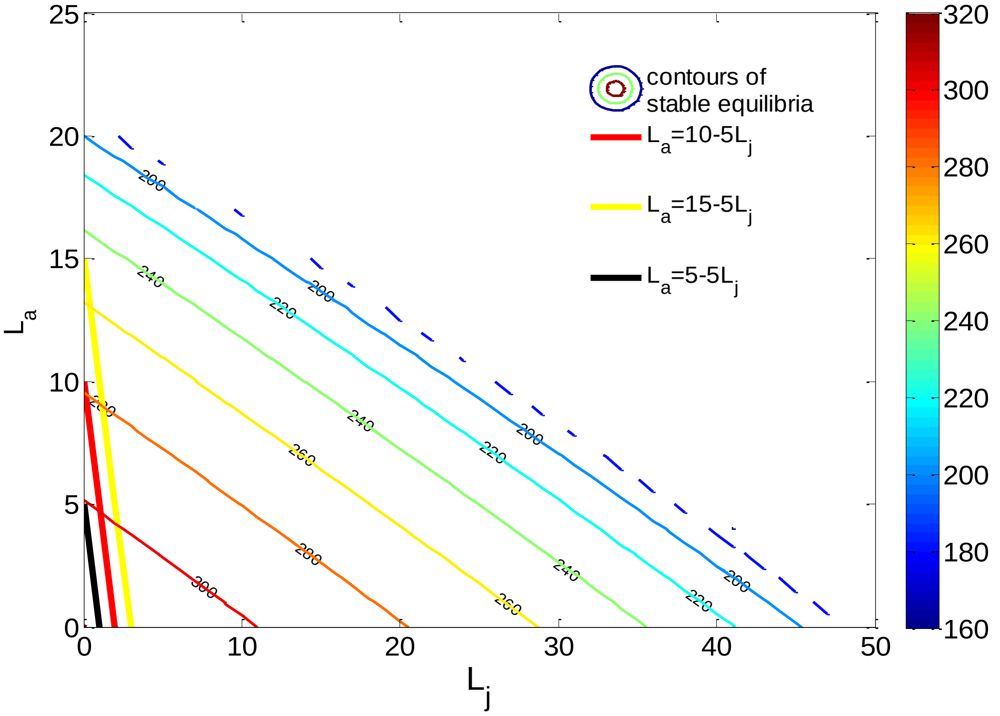
c) Contours of stable equilibria for different L_j and L_a and lines L_a= B-xL_j, x=1, m=1, budget B = [5 (black),10(red),15(yellow)]



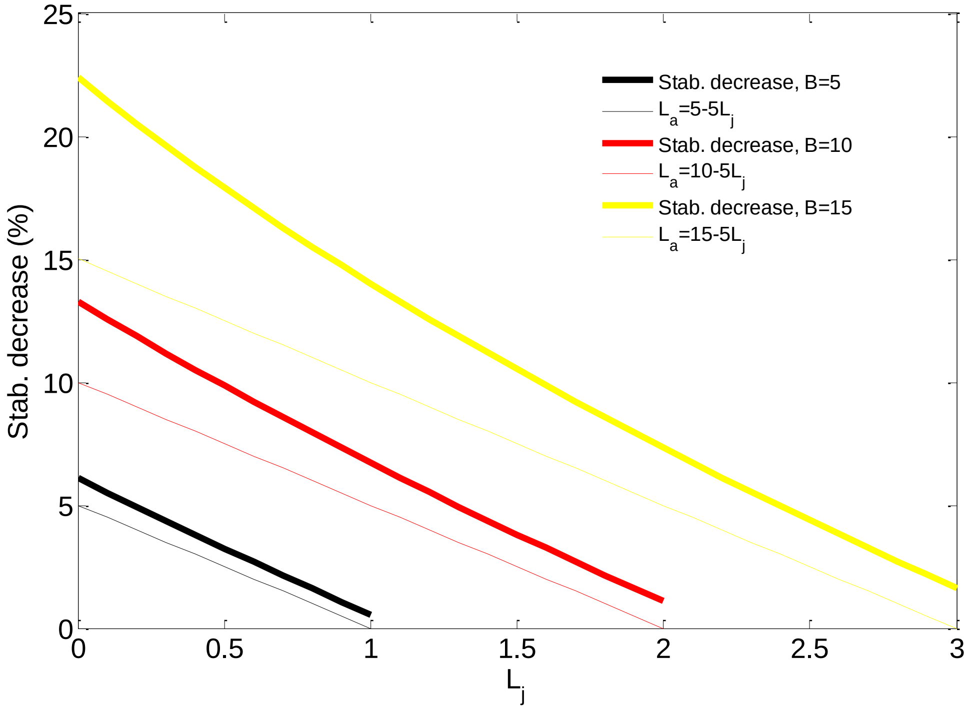
d) Stability decrease (%, bold lines) for budget B=[5,10,15] dependent on L_j, where L_a= B-xL_j (thin lines); cost of 1 unit L_a=1U,1 unit Lj=1U



e) Contours of stable equilibria for different L_j and L_a and lines L_a= B-xL_j, x=5, m=1, budget B = [5 (black),10(red),15(yellow)]



f) Stability decrease (%, bold lines) for budget B=[5,10,15] dependent on L_j, where L_a= B-xL_j (thin lines); cost of 1 unit L_a=1U,1 unit Lj=5U



Using models for comparative studies of plausible biocontrol agents has become recently more popular than the former approach of deriving the optimal features for the “best predator” from the results of modelling (Murdoch & Briggs 1996). Further on, optimization of decisions according to the financial matters and the ecological features of target species based on modelling have been well demonstrated by Taylor & Hastings (2004). Depending on the yearly budget available they are able to predict which strategy to use to control an invasive grass *Spartina alterniflora* in order to achieve the best results possible with the given finances. We carry on a similar analysis for our predator-prey system.

4 The Resource-Prey-Predator (R-P-P) model

4.1 Outbreaking populations and possible control by predation

As already mentioned in the introduction, predation on one of the age classes of prey may have a crucial effect on the whole population dynamics. Raymond et al. (2002) suspected that the “escape” from predation of winter moth pupae (*Operophtera brumata*) might be the reason for the tendency of this species to outbreak.

As an inspiration to our R-P-P model served the well-known outbreaking behaviour of populations of the Crown of Thorns Starfish *(Acanthaster planci)* that feeds on coral reefs. Its outbreaks are a serious threat to coral reef ecosystems but, even after several decades of intensive research, remain poorly understood (Kenchington & Kelleher 1992). Among the numerous hypotheses that tried to explain population explosions in the past decades, predation has been considered a possible regulating agent in several studies. For example, juvenile Crown of Thorns Starfish are consumed by some species of fish (e.g. *Lethrinus spp*.), as tested by Sweatman (1994). However, he found it unlikely that just fish predation could be a regulating factor strong enough to control this species. In addition, there are predators of other taxa (Annelids, Crustaceans and other epibenthic fauna) that feed on this starfish and are believed to be an important factor in the mostly juvenile mortality (Keesing & Halford 1992; Keesing et al. 1996). Adult starfish are less prone to predation due to their morphology. Still, several predators do feed on them. It has been discussed whether the extirpation of the Giant Triton mollusc *(Charonia tritonis)* that feeds on starfish adults and is frequently hunted in tropical waters because of its shell could have caused the outbreaks (Pearson & Endean 1969).

The Crown of Thorns Starfish has already induced a number of modelling studies, from simple to complex and using diverse modelling approaches (McCallum 1987; Antonelli & Krivan 1993; Crimp & Braddock 1993; Scandol 1999). We note that by developing our model we do not intend to explain the outbreaks of this particular species. Rather, we aim to demonstrate possibilities of control of a population with a strong connection to its food source by generalist predators given selective predation on juvenile and adult individuals of the prey species. We have not found any study on oscillating systems or outbreaking populations that would combine a tri-trophic interaction with an age structure in the prey (or consumer).

In this thesis, we generally want to prevent large fluctuations in resource density by driving the prey either extinct or to low densities. It is not necessary to bring the system to stable coexistence equilibrium. Oscillations are not necessarily harmful as long as the pest population remains below the economic threshold (Section 1.7). Our aim to preserve the resource can also be interpreted in the terms of biocontrol of pests that reduce crops yields.

In our model the role of the predatory species can also be replaced by human harvesting. For example, in the case of Crown of Thorns Starfish, its outbreaks cause, besides environmental degradation, economic losses to tourist operators. In order to save the diversity of the reefs and keep tourists coming some projects were developed to control the starfish population by their removal or killing or using fences (Johnson et al. 1990, Lassig 1995). The manual treatment consists mostly of injecting the starfish with some poisoning agent, causing death to the animal (Johnson et al. 1990, Lassig 1995). The usefulness of actions like these remains a question as little is known about factors inducing an outbreak, its role in the natural ecosystem and, last but not least, the costs and efficiency of such a conservation effort (Johnson et al. 1990; Kenchington & Kelleher 1992). For example, even though it is difficult to suppress an outbreak after it has started, the Great Barrier Reef management wants to avoid actions if the starfish density is sufficiently low as the starfish is a natural element of the ecosystem (Lassig 1995). We believe that exploring further theoretical background of involved ecological mechanisms can contribute to the successful decision-making in certain cases.

Not only can the human harvesting (or the organized removal of animals) be here well comparable to predation by generalist predators, but also the Holling type II functional response might be here well expected to model harvesting, as the manipulation requires some "handling" time. Thus, we may ask if it is more efficient to focus on juveniles that may be more difficult to find (Johnson et al. 1992), on adults, or rather if both classes should be removed in order to obtain the best result with minimum effort, or if there are further studies necessary on possible combination of anthropogenic removal and natural predation.

Another model species that could suit our system is the bark beetle. It is usually considered to be bottom-up controlled by the resource (Hunter & Price 1992). However according to Reeve (1997), some species of Clerid beetles feed on both the brood and adult bark beetles. Reeve suggested that predation may be in some species of bark beetles of big importance to their population dynamics, for example the predator *Thanasimus dubius* might control the outbreaks of the bark beetle *Dendroctonus frontalis*.

4.2 Model development

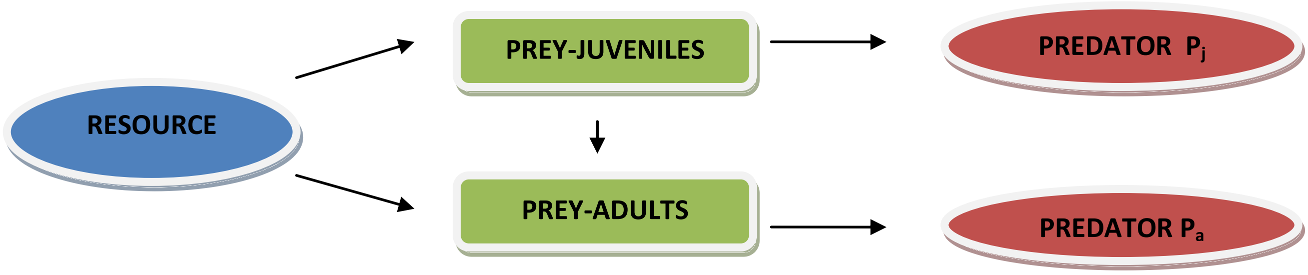


Figure 4.2.1: The R-P-P model scheme

The R-P-P system to be modelled is schematically depicted in Fig. 4.2.1. We assume there is a resource with logistic growth that supplies both the juveniles and adults of the prey species. Both age classes of prey are assumed to exhibit a Holling type II functional response ($f_J(N)$, $f_A(N)$) with respect to the resource. Either juveniles or adults or both age classes of prey are exploited by generalist predators with a Holling type II functional response (P_a, P_j). In this model, we will refer to the two classes of adults (A) and juveniles (J) as the prey species, and their food as the resource (N). *(In many species their ecological role is dependent on the context of interactions in which they participate. For example, in lemmings the question occurred if they rather should be perceived as predators or prey (Turchin et al. 2000). In more complicated trophic cascades the bottom-up versus the top-down control of a population is thus a rather complicated matter.)* Here we speak of predators only in connection with the predators that consume the age-structured prey. Predator or predators are generalists, their population dynamics is not considered and we do not take into question whether they are of one or more species. The functional responses are of type II with zero or positive searching rate, with the main difference lying in the values of searching rates of predators for adult and juvenile prey. The system therefore consists of three ordinary differential equations:

$$\frac{dJ}{dt} = e_a f_a(N)A - d_j J\left(1 + \frac{J}{K_j}\right) - mJ\frac{e_j f_j(N)}{e_j f_j(N)+1} - P_j \tag{2}$$

$$\frac{dA}{dt} = mJ\frac{e_j f_j(N)}{e_j f_j(N)+1} - d_a A\left(1 + \frac{A}{K_a}\right) - P_a \tag{3}$$

$$\frac{dN}{dt} = rN\left(1 + \frac{N}{K_n}\right) - f_a(N)A - f_j(N)J \tag{4}$$

where

$$f_a(N) = \frac{\lambda_a N}{1+Nh_a\lambda_a} \quad , \; f_j(N) = \frac{\lambda_j N}{1+Nh_j\lambda_j}, \;\; P_j = \frac{L_j J}{1+B_j J} \;, \; P_a = \frac{L_a A}{1+B_a A}$$

4.3 Parameters

In the **R-P-P model** we are again interested in the impact of age-selective predation and hence our focal parameters are L_a and L_j, the maximum attack rates of predator on adult and juvenile prey, respectively, at low prey densities. Also, we again observe differences in populations with various maturation rates m (see Section 4.4 for further description). All the other parameters are assumed fixed at values for which consumption of resource by prey species, in the absence of predation, gives rise to outbreaks in the density of both (Table 4.3.1). Still, in these parameters basic assumptions about their comparative values were reflected ($K_j > K_a$, $d_j > d_a$ etc.). The parameters B_j and B_a have already been discussed in Section 2.1. Initial densities (i.e. densities at time t = 0) were as follows: adult prey A = 2, juvenile prey J = 2, resource N = 5.

Table 4.3.1: Parameter values

Parameter	Meaning	Value
b	per capita birth rate in prey	0.5
d_j	per capita mortality rate of juveniles	0.2
d_a	per capita mortality rate of adults	0.1
K_j	parameter scaling carrying capacity – juveniles	20

K_a	parameter scaling carrying capacity – adults	10
λ_a	prey food searching rate – adults	3
λ_j	prey food searching rate – juveniles	3
h_j	prey food handling time – juveniles	0.5
h_a	prey food handling time – adults	0.25
e_j	scaling parameter of energy transformation – juveniles	0.8
e_a	scaling parameter of energy transformation – adults	1
B_j	behavioural response to predators – juvenile	0.5
B_a	behavioural response to predators – adult	0.5
r	resource growth rate	0.4
K_n	parameter scaling carrying capacity – resource	8

4.4 Maturation rate as population characteristic, parameter or variable?

Unlike the P-P model where the proportion of juveniles that mature was expressed by the linear term *mJ,* this time juvenile outflow to the adult class is a function of resource density. The maturation rate is still a parameter and this time we have chosen three values of *m* across three orders of magnitude, *m* = (0.1, 1, 10), which we have found in the pre-tests to be sufficient in order to describe the possible behaviour of the model.

The actual rate at which juveniles join the adult class is now given *as*

$$mJ\frac{e_j f_j(N)}{e_j f_j(N)+1}$$

where there is included the influence of food density and the rate of consumption of the resource on juvenile maturation.

In this thesis, we thus model maturation as a function of food availability, a mechanism observed in many natural systems. For example, Moorhouse et al. (2008) have found that in water voles the time taken by the young to reach maturity was greater in higher-density populations because of the reduction in the forage available per individual, which caused slower individual growth rates. The experiments of Plaistow et al. (2004) discovered that mites reared in poor growth conditions took up to five times longer to develop compared to the mites that were reared under good growth conditions. The echinoderms are known to exhibit positive correlations between growth rate and food availability. A lower growth rate in the Crown of Thorns Starfish described in Section 4.1 was documented in response to reduced food quality (Lucas 1984).

Food availability can also influence the female fecundity as has been shown for example in amphipods by Sundelin et al. (2008). This dependence is reflected in our model through the term:

$$e_a f_a(N) A$$

Also survival in each category and the environmental carrying capacity can be reduced by missing feeding opportunities, but these further interactions go beyond the scope of this thesis.

4.5 Model analysis

Because the system (2)-(4) consists of three non-linear differential equations with numerous parameters and is quite complicated, we explore its behaviour via simulations in MATLAB, using the ode45 solver.

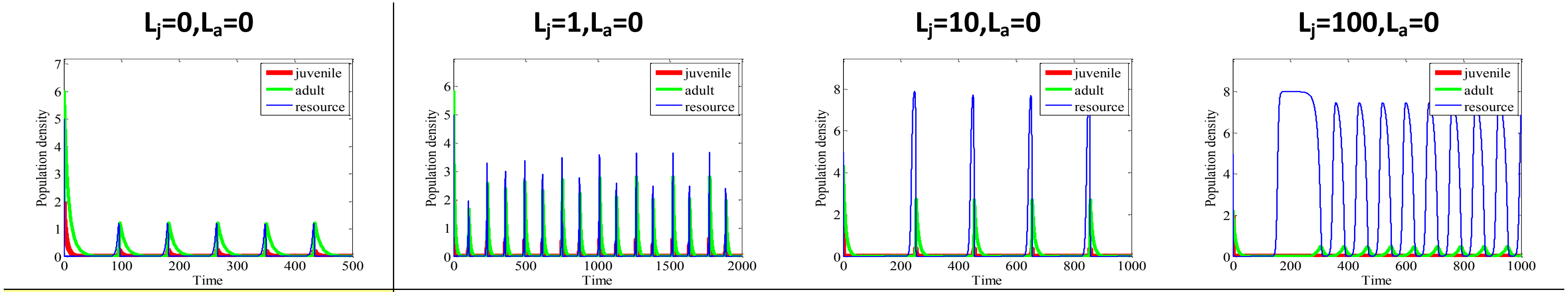
5 Results

The results are presented in Figs. 5.I, 5.II, and 5.III. As can be seen, the maturation rate in a system without predation influences the amplitude of the resource and prey cycles: a very fast maturation leads to low amplitudes, whereas slow maturation allows the resource to grow to much higher densities and it takes longer time before the resource collapse occurs. The frequency of oscillations changes with the maturation rate only very slightly. It is not surprising that for slowly maturating prey the juvenile density exceeds the adult density and for the rapidly maturating prey we observe the opposite result.

When testing the impact of predation in the **rapidly maturating prey (m = 10, Fig. 5.I)** we can generally observe an increase of resource amplitude with predation as well as an increase in the amplitude of adults of prey species. Naturally, a further increase in predation causes prey species eradication (L_j=0 & L_a=3). Some lower values of predation on juveniles (L_j = 1) cause bicyclical oscillations, a dynamic behaviour that does not occur if there is predation only on adults. Thanks to the fast maturation, the prey population is very resistant to predation on juveniles (L_j=100 & L_a=0). As for the predation efficiency, predation on adults is far more efficient as regards prey population suppression than predation on juveniles.

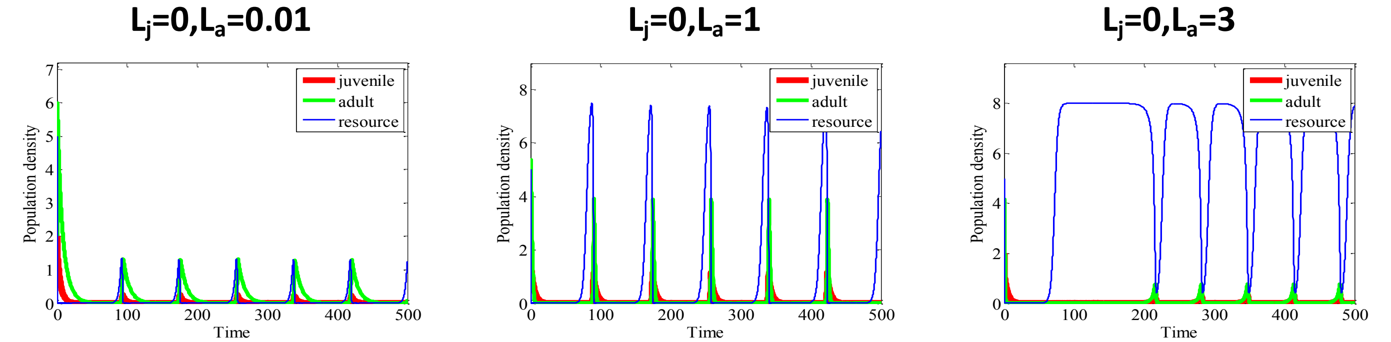
Slowly maturating juveniles (m = 0.1, Fig. 5.II) in the prey population allow high amplitudes of resource density. Predation on juveniles causes faster resource recovery after collapses. However, the resource reaches lower peaks than with no predation (L_j=1 & L_a=0). There is only moderate difference in the impact of predation on the prey population suppression, but still predation on adults is more efficient than on juveniles and again the most efficient strategy Is to combine predation on both age classes.

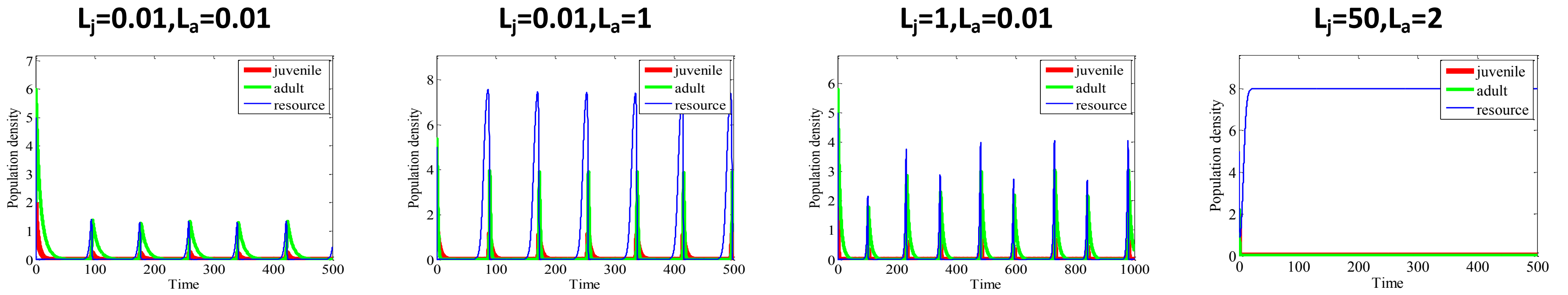
If the **maturation rate is somewhere in between (m = 1, Fig.5.III),** again the predation is more efficient when applied to adults, with the combined predation pressure being the most efficient. Weaker predation on juveniles (L_j = 1) causes higher amplitude in resource density and a lower frequency of oscillations. This time no bicyclical oscillations were detected, but in some cases resource and prey coexist via regular oscillations (L_j = 15 & L_a = 0) or in a stable equilibrium (L_j = 0 &L_a = 2.2).

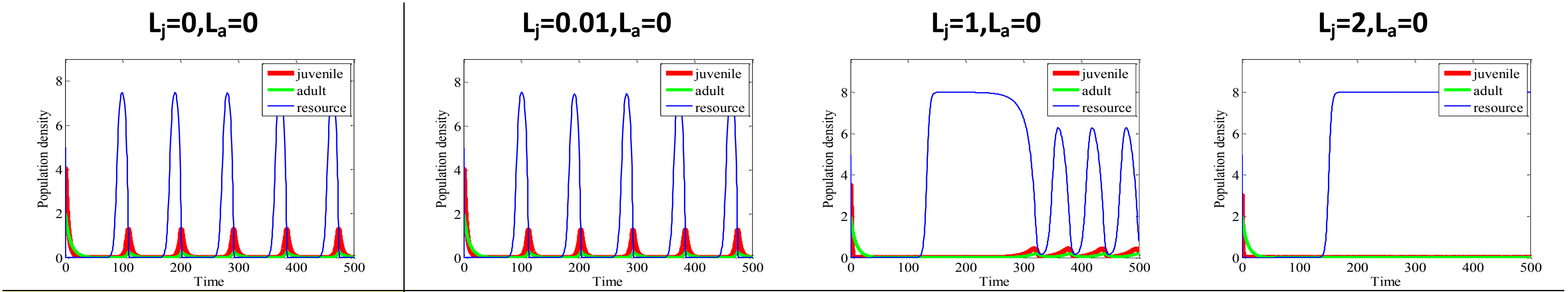


$m = 10$

Fig. 5.I: Population density of resource (blue) and adults (green) and juveniles (red) of prey for m=1, for other parameters see Table 4.3.1.

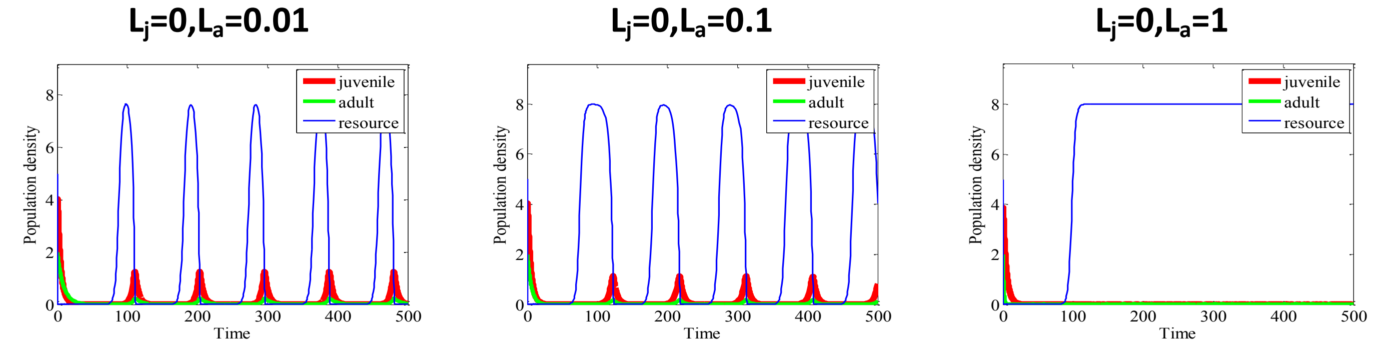


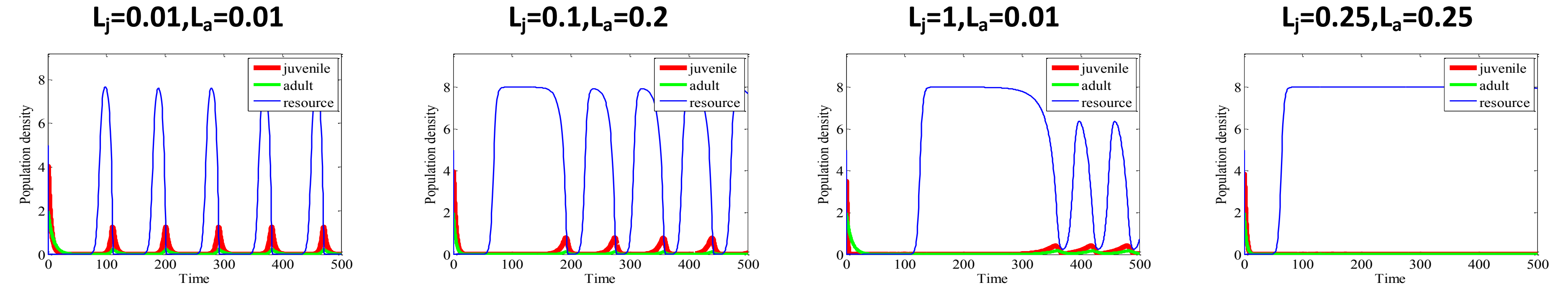




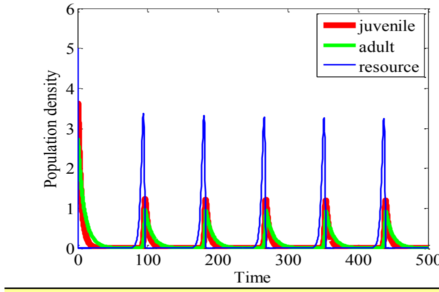
m = 0.1

Figure 5.II: Population density of resource (blue) and adults (green) and juveniles (red) of prey for m=0.1, for other parameters see Table 4.3.1.

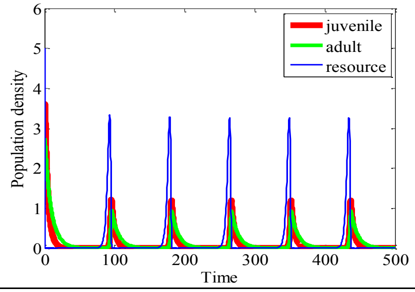




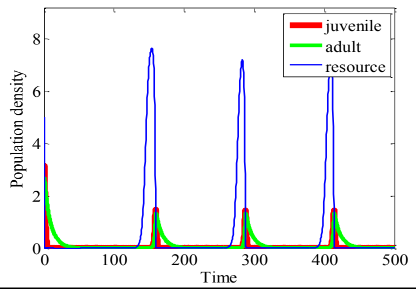
$L_j=0, L_a=0$



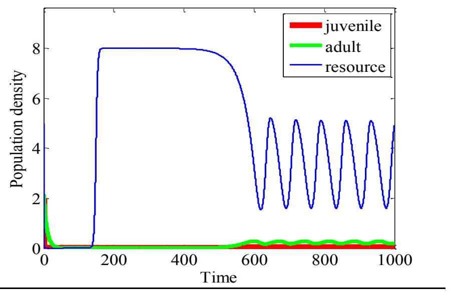
$L_j=0.01, L_a=0$



$L_j=1, L_a=0$



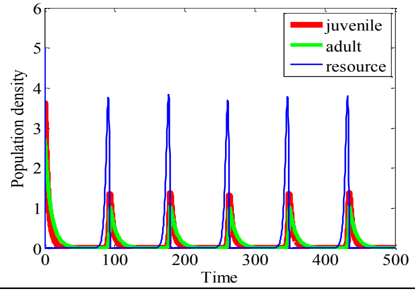
$L_j=15, L_a=0$



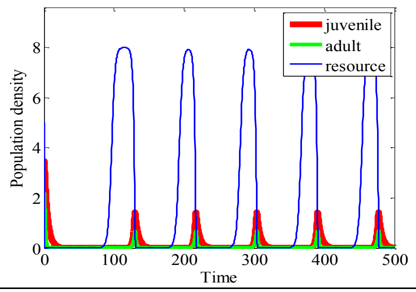
$m = 1$

Figure 5.III: Population density of resource (blue) and adults (green) and juveniles (red) of prey for m=1, for other parameters see Table 4.3.1.

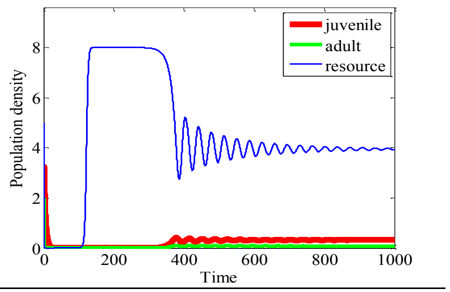
$L_j=0, L_a=0.01$



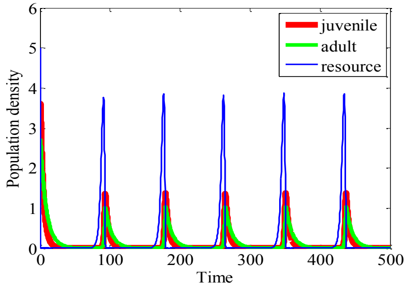
$L_j=0, L_a=1$



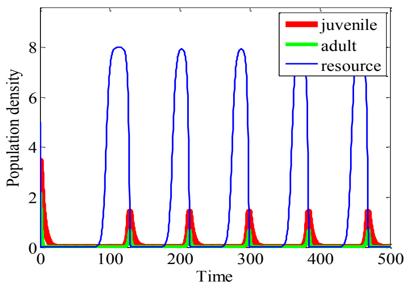
$L_j=0, L_a=2.2$



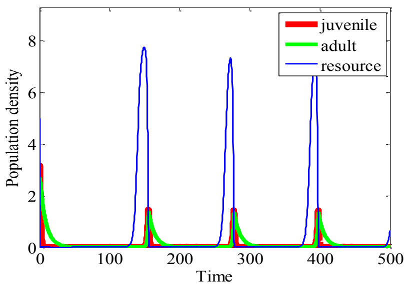
$L_j=0.01, L_a=0.01$



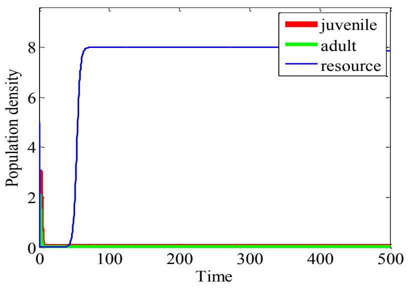
$L_j=0.01, L_a=1$



$L_j=1, L_a=0.01$



$L_j=1, L_a=1$



In conclusion, predation in an oscillating resource-prey system can have the following impacts: suppressing the population density of prey so that oscillations still occur but the resource reaches higher amplitudes, coexistence of resource and prey at stable equilibrium or as stable and regular oscillations, resource survival with complete prey extinction or resource survival with very low densities of prey.

6 Discussion

In this thesis, we developed two mathematical models in order to study possibilities of control of an age-structured prey population by age-specific predators. We perceived the “prey” rather as a harmful species even though the results may be applicable for endangered species protection as well, for example for predictions of population viability of indigenous animal species in areas where there is a non-native or newly introduced predator. Another application in the sense of preserving the prey species may be considering the predator’s impact for reintroduction or biocontrol projects, where the successful establishment of the biocontrol agent (which would be the “prey” in our model) may be dependent on the battery and feeding preferences of potential predators in the area. The modelled predation can also be linked to harvesting of economically important species by humans, reminding us that harvesting of more age classes at the same time or harvesting of only one age class combined with naturally occurring predation on another one might destabilize the entire population. Detailed studies of predator-prey relationships in the environment are therefore highly needed in all these cases.

We partly focused on the comparison of the predation impacts in populations with different inner dynamicity (expressed by the maturation rate). The interaction of age-selective predation pressure and the rate by which the individuals move from juvenile to adult class creates the final outcome of the trials. Presumably in the **P-P model** in case A the results show how the influence of the maturation rate can be crucial to the viability of the population when exposed to predation. Although we defined the values of the maturation rate in the **P-P model** in a heuristic way, in field experiments the maturation rate belongs to parameters that are possible to measure. In this thesis, we compared values that differ in orders of magnitude, which would rather correspond to comparisons of species of different families or orders than of closely related species. In order to give the comparison a more solid frame it would be very useful to conduct a further study to categorize different taxons by their characteristic or "expected" maturation rates and life histories. For example, Arendth (1997) attempted to find rules that regulate growth rates (not maturity rate or age) in different groups of organisms. Nonetheless, although we provide results for more or less intuitive categories (fast, slow or intermediate maturation) it is evident that different maturation rate is able to induce very different scenarios in the population viability analysis and therefore it provides useful information for ecosystem managers.

In the **R-P-P** model the maturation rate was a function of resource availability and the parameter *m* had rather a scaling role and it is no longer simple to discriminate its qualitative influence. As already mentioned in Section 4.4, the maturation rate may be a plastic feature dependent on many other environmental conditions or population density and it might even be different for both sexes (as was documented for example by Chen & Harvey in 1994), a feature that we did not consider here as our models were unstructured with respect to prey sexes.

Last but not least, the maturation rate is one of the population features that is believed to be subject to evolutionary processes in respect to environmental conditions, predation or even harvesting (Ernande et al. 2004). Selective predation on juveniles might favour rapidly maturating juveniles making the maturation rate an even more complicated parameter; evolutionary processes were likewise not studied in this thesis.

In the **P-P model** we mainly tested the influence of different foraging behaviour of predators on juveniles and adults. As we have demonstrated, the outcome for population viability may differ in response to the functional response of the predator and maturation rate. One of the most surprising findings of the **P-P model** is the occurrence of the predator pit phenomenon in the case where only juveniles are consumed via a Holling type II functional response. This finding could be consistent with the possible population regulation mechanisms of moose suggested by Messier (1994). Besides the possible regulation of the population by the predation of wolfs, which is the main topic in that study, Messier gives an idea that a predator pit (that is, a low-density equilibrium) in the moose population may be induced by the predation of bears on the calves – the first year age class. This could happen if the bears always remove a constant proportion of calves. A predator pit has also been suggested in zebra by Grange et al. (2004). Using long-term data and modelling they discovered that the zebra population might be limited by a very low foal survival, yet the exact reason for this is still unknown (predation, diseases, hunting?). Anyway, there is a high predation on adults by lions and hyenas, which together with the juvenile mortality might also correspond to cases C2, C3 of the **P-P model** where the predator pit occurs as well.

These studies on mammals give an example of how age-selective predation might mediate prey species persistence at a low equilibrium, which is the desirable state in biocontrol as a complete eradication of most pests is rather unlikely. However, our further findings on frequent occurrence of a demographic Allee effect, presumably in cases B and C1 (but also in all other cases under some conditions) give the idea of a possibility that total eradication is not out of question. These facts might contribute to biocontrol science as well. Interestingly, a study on predation regulation of *A. planci* by McCallum (1987), where there is no resource and no age-structure, but only one category – the starfish and a separate equation for a generalist predator with Holling type II functional response suggested under some conditions the existence of an Allee effect as well; this case is similar to our cases B and C1. However, if the parameters of predator behaviour for different categories differ (as shown in C1) it can have important influence on population stability in quantitative terms. That the importance of the age class that is preyed upon should not be overlooked because of the impacts on population structure has also been suggested by Zink & Rosenheim (2008) in their study on *Lygus hesperus*. The excessive predation of *Geocoris spp*. on eggs and larvae induced a shift in population structure towards higher density of adult *Lygus hesperus* in field. The use of age-selective predation in pest control has however further implications: it is common to focus the regulation directly on the age class or instar that causes the most serious damage on crops as in the cited case of cotton.

Feeding preferences of various biocontrol agents are diverse and as we have shown this might influence the viability of the pest population and hence the success of biocontrol action. It is often the immature stages that are preferred: *Galendromus helveolus* Acari in the trials conducted by Chen et al. (2006) clearly preferred juvenile stages of *Brevipalpus californicus* Acari, *Amphibolus venator* (Klug) was able to consume all stages of *Tribolium confusum*, yet preferred larvae (Nishi et al. 2004). Some parasitoids select only one instar of the target species: for example, the parasitoid *Aphidius matriae* attacks preferentially the third instar nymphs of *Aphis fabae* (Tahriri et al. 2007). Contrary to that, Tanhuanpaa et al. (2003) tested in their rare study predation on adult individuals of the moth *Epirrita autumnata* using a tethering method developed by Sharov (1995) and found out that ants and harvestmen are important predators of the adult individuals in this species. According to that study, predation on adult females may result in a lower number of eggs laid and thus considerably reduce the number of larvae in the next generation. Even though they did not find any difference in adult mortality in outbreaking and non-outbreaking populations, predation on adults is discussed as a contributing factor, together with predation on other age classes, to regulation of the population of this Lepidopteran species. Regulation of insect populations by predation on adults has received little attention and in agreement with that study we have found that studies on predation on adult stages of insects compared to those on eggs, larvae or pupae are very rare to none, presumably because of the technical difficulty of such studies. But the regulating effect might be strong. As the most recent example of its unknown impact might serve the fear of mosquito and crop damaging insect outbreaks that has risen in the media in connection with the new mysterious White Nose Syndrome in bats. This disease severely threatens bat populations in North America (FoxNews.com 4. 2. 2009; White-Nose Syndrome Threatens the Survival of Hibernating Bats in North America http://www.fort.usgs.gov/WNS/). The bias in the number of studies of predation on juveniles versus adults might have a negative effect on the assessments of the impact of predation on the population level and it should be considered in biocontrol (of arthropod species) assessments as well, just like the possible bias towards the studies on adults with a lack of studies on juveniles in other taxa (for example the above mentioned zebras), when addressing population regulation for whatever reason.

In the **R-P-P model** we have verified that under some conditions predation can lead to stable coexistence of the resource and prey. Except of the rapidly maturating prey with m = 10, where predation must be very heavy, predation on either juveniles or adults is able to suppress the prey population successfully by some quite low values of L_j or L_a. Thus, it is advisable to control a rapidly maturating species by removing adults. Taken from another perspective, in a species that is as an adult not a popular food source, tendency to fast maturation can ecologically and evolutionarily be a powerful strategy. An example where the size might work as a predation refuge has been partly demonstrated in a study by Keesing et al. (1996). They compared the mortality of juveniles of two starfish species, *A. planci* and *Nardoa novaecaledoniae*, which have contrasting strategies in investments in reproduction. *A. planci* produces huge numbers of small eggs and the post-settlement size of juveniles is very small (0.5-0.7 mm), *N. noveacaledoniae* produces a small number of larger eggs resulting into bigger (1.2-1.6 mm) post-settlement size. In the experiment, *A. planci* suffered from far heavier mortality due to predation than the larger *N. noveacaledoniae.* By a simple illustrative calculation, Keesing gave an idea that by observed mortality and predation rates of 1000 individuals of each species 78 *Acanthaster* relative to 635 *Nardoa* would survive, which might have further impacts on population size. Thus exploring further relations between maturation rate (growth rate), predation refuge in adulthood (size) and trade-offs that have to be faced might bring quite interesting new insights in predator-prey relationships.

The very slowly maturating system is on the other hand very sensitive to predation on both stages, which might be rather important in the conservation effort of the prey species.

The selection of an optimal biocontrol agent is crucial if a biocontrol action is to be successful. However, it is at the same time far from simple predominantly due to complexity of many studied systems (van Klinken & Raghu 2006). Our models are very simplistic and therefore the information cannot be used directly for making any predictions in any particular system. We are aware that an optimal biocontrol agent has to be suitable in a range of other features and its efficiency must be assessed in respect to those (taxonomic compatibility, climatic matching, risks to the environment, etc.; Hoelmer & Kirk 2005) in order to obtain an optimal and economically friendly performance. In this thesis, we presented some mechanisms affecting predator-prey dynamics that can work well towards the best biocontrol agent selection if reflected or reduce the success of the action if neglected and that certainly occur in natural ecosystems as well.

7 References

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