

Single- or multistage regulation in complex life cycles: does it make a difference?

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Data on the different stages of complex life cycles are often rather unbalanced, especially those concerning the effects of density. How does this affect our understanding of a species' population dynamics? Two discrete three-stage models with overlapping generations and delayed maturation are constructed to address this question. They assume that survival or emigration in any life stage and/or reproduction can be density dependent. A typical pond-breeding amphibian species with a well-studied larval stage serves as an example. Numerical results show that the population dynamics resulting from density dependence at a single (e.g. the larval) stage can be decisively and unpredictably modified by density dependence in additional stages. Superposition of density-dependent processes could thus be one reason for the difficulties in identifying density dependence in the field. Moreover, in a simulated source-refuge system with habitat-specific density-dependent dispersal of juveniles density dependence in multiple stages can stabilize or destabilize the dynamics and produce misleading age structures. From an applied perspective this model shows that excluding multistage regulation prematurely clearly affects our ability to predict consequences of human impacts.

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Understanding how natural populations are regulated remains a challenge for ecologists and those concerned about the decline of biodiversity. A population is regulated if its fluctuations in size are bounded, with the limitation resulting from potentially stabilizing density-dependent processes (Berryman 1991, Murdoch 1994). Unfortunately, detecting density dependence and regulation in the field poses problems, such as finding the appropriate spatial and temporal scale (Turchin 1990, Pechmann and Wilbur 1994, Ray and Hastings 1996) and identifying the relevant physiological or life cycle stage(s) at which it occurs (Wilbur 1980, Metz and Diekmann 1986). It is unclear whether regulation is typically achieved by stabilizing mechanisms within a single population or through metapopulation dynamics (Murdoch 1994), how important delayed as opposed to direct density dependence is (Turchin 1990), and whether single- or multistage regulation is more preva-

lent. Multistage regulation here means multistage density dependence where density-dependent processes in more than one life stage *decisively* influence the population growth curve, e.g. the bounds between which it fluctuates and the type of dynamics that results.

Species with several life stages are excellent subjects for investigating population regulation (Wilbur 1980, Smith 1983) as their complex life cycle often consists of two or more temporally and spatially distinct phases adapted to growth, dispersal or reproduction. Consequently, the question of when regulation occurs is well defined. However, data on the different stages of animals with complex life cycles are often rather unbalanced, especially those concerning the effects of density (e.g. Ray and Hastings 1996). Pond-breeding amphibians are a good example illustrating this point. An aquatic herbivorous larval stage with rapid growth and high mortality is followed by an insectivorous or car-

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nivorous terrestrial phase adapted to dispersal (mostly juveniles) and reproduction. Dispersal ranges are restricted and terrestrial individuals can be marked individually. Nevertheless, extensive field studies on juveniles and adults are still remarkably scarce (but see e.g. Smith 1987, Berven 1990, Berven and Grudzien 1990). Existing time series are usually short (see Meyer et al. 1998), survival estimates are often unreliable (e.g. Riis 1991) and experimental studies after metamorphosis have either investigated behaviour or physiology in the laboratory or addressed questions on breeding activity, reproductive performance, homing and orientation. On the other hand, Semlitsch et al. (1996) cite "several excellent field studies [that] have clearly demonstrated the primacy of density-dependent growth and survival in larval amphibians". These results are supported by a wealth of tank and laboratory experiments (e.g. Wilbur 1980 reviews earlier work) strongly suggesting that regulation occurs at the larval stage. The one existing experimental field study directly addressing both aquatic and terrestrial (up to first reproduction) density dependence finds effects of density in both phases in one of two salamander species (Pechmann 1994). This leaves open whether regulation occurs only in the larval phase, the terrestrial phase or both (Wilbur 1980, Semlitsch et al. 1996).

Unfortunately, unbalanced data on the effects of density on different stages of a complex life cycle seem to enforce a tendency to assume single-stage regulation. How does this affect our understanding of a species' population dynamics? To address this question I use mathematical models to compare the consequences of density dependence and regulation in one or several stages on population dynamics. I assume an organism with overlapping generations, delayed maturation, discrete breeding seasons and a life cycle in which it is important to distinguish three life stages instead of the usual two, e.g. larvae grow, juveniles disperse and adults reproduce. The resulting three-stage models belong to a large family of discrete-time stage-structured models with density dependence (see e.g. Caswell 1989 for an introductory review). The exponential form of density dependence relates this approach more specifically to the two-stage models, for instance, of Hassell and Comins (1976) for two competing species, of Rodriguez (1988 for *Drosophila*), Wilbur (1996 for pond-breeding amphibians) and Higgins et al. (1997 for Dungeness crabs) for competition within species, or to the single-stage model of Hastings (1993) with density-independent dispersal. In the present study the first model more generally studies the influence of density dependence and regulation at one or more life stage(s) on the dynamics of an isolated population. It is subjected to a systematic numerical investigation, while a variant of it is only used to exemplify possible consequences of multistage regulation in a more realistic setting with two connected habitats of different quality.

Although the examples refer to pond-breeding amphibians the conclusions can be generalized.

The models

The two discrete-time models describe the population dynamics of an organism with three life stages and discrete breeding seasons. The census is taken at the start of the breeding season (t). The sex ratio is assumed to be 1:1. Adults (A) breed yearly but only a proportion s_A survives until the next season ($t+1$). Juveniles have a two-year cycle: In the first year larvae hatch from eggs (H), undergo metamorphosis (L) and grow into first year juveniles (J). During the second year surviving juveniles of both sexes reach maturity and those that survive join the adult population in their third year (maturation delay). Breeding results in a fixed number c of hatchlings per female and season (c incorporates clutch size, fertilization rate and zygote survival). Female reproduction can be affected by density (exponential term in eqs (1a) and (4a)). Survival after hatching is described by a constant rate for each life stage (s_L, s_{J1}, s_{J2}, s_A) which is multiplied by a density-dependent factor in case of intra-stage competition (exponential terms in eqs (1b)–(3) and (4b)–(6)). The coefficient β indicates the presence or absence of competition ($\beta = 1$ or 0), while K determines its strength. The effect of density is a reduction in population size resulting either from increased mortality or emigration or from reduced reproduction. Mathematically more tractable, but biologically less intuitive rescaled versions of model 1 (see Appendix) are used to study the dependence of the dynamics on the key parameter R which incorporates survival up to maturity and hatchling number per adult. All parameters are defined in Table 1.

Model 1 for a single population

This model is used to study the influence of density dependence in different life stages on the dynamics of an isolated population (no immigration). It is a mathematical formulation of the above assumptions. For the ease of their accessibility I give a separate equation for each life stage instead of combining everything into a single difference equation for adults.

$$H(t+1) = c \exp \left[-\beta_B \frac{A(t)}{K_B} \right] \frac{A(t)}{2} \quad (1a)$$

larvae hatching = hatchlings per clutch \times competition effect on reproduction \times females

$$L(t+1) = s_L \exp \left[-\beta_L \frac{H(t+1)}{K_L} \right] H(t+1) \quad (1b)$$

metamorphs = larval survival \times effect of larval competition \times larvae

$$J(t+1) = s_{J1} \exp \left[-\beta_J \frac{L(t+1)}{K_J} \right] L(t+1) \quad (2)$$

1st-year juveniles = 1st-year survival \times effect of metamorphic competition \times metamorphs

$$A(t+1) = s_A \exp \left[-\beta_A \frac{A(t)}{K_A} \right] A(t) + s_{J2} J(t) \quad (3)$$

adults = adult survival \times effect of adult competition \times adults + 2nd-year survival \times mature 2nd-year juveniles

Notice that due to delayed maturation last year juveniles are added to the adult population ($J(t)$ not $J(t+1)$ in (3)).

Model 2 for two habitats of different quality

This extension of model 1 is used to exemplify the consequences of multistage regulation in a more realistic setting. Two habitats differ with respect to density dependence in larval survival, in dispersal of first- and second-year juveniles (replacing density-dependent juvenile survival) and in reproduction of females. They lie within the dispersal range of juveniles. First-year juveniles disperse to avoid competition, e.g. for resources or hibernation sites, while mature juveniles evade breeding competition (β_B) with their own cohort and other adults. A fraction σ_J of the dispersers survives (cost of dispersal). Adults do not disperse and their survival is assumed to be density independent.

Table 1. List of model parameters.

A	adult population [initial size = 100]
J	first-year juveniles
L	metamorphs
H	hatched larvae (tadpoles)
c	number of hatchlings per female per season
s_L, s_{J1}, s_{J2}, s_A	survival rates of larvae, first- and second-year juveniles and adults
$R = \frac{s_{J2}s_{J1}s_Lc}{2}$	dynamic key parameter (rescaled model in Appendix)
$\beta_L, \beta_J, \beta_A, \beta_B$	indicator of intra-stage competition in larvae, juveniles, adults and breeding females [$\beta = 1$ with competition, $= 0$ without]
K_L, K_J, K_A, K_B	carrying capacity for larvae, juveniles, adults and breeding females
k_{BL}, k_{LJ}, k_{AL}	capacity ratios (rescaled model)
	$k_{BL} = \frac{cK_B}{2K_L}, k_{LJ} = \frac{s_LK_L}{K_J}, k_{AL} = \frac{cK_A}{2K_L}$
σ_J	survival during juvenile dispersal

With 'i' and 'n' indicating the two habitats (if $i = 1$ then $n = 2$ and vice versa), the system of difference equations has the following form:

$$H_i(t+1) = c \exp \left[-\beta_B \frac{A(t)}{K_B} \right] \frac{A(t)}{2} \quad \text{larvae hatching in habitat } i \quad (4a)$$

$$L_i(t+1) = s_{Li} \exp \left[-\beta_{Li} \frac{H_i(t+1)}{K_{Li}} \right] H_i(t+1) \quad \text{metamorphs in habitat } i \quad (4b)$$

$$J_i(t+1) = s_{J1i} \exp \left[-\beta_{Ji} \frac{L_i(t+1)}{K_{Ji}} \right] L_i(t+1) + \sigma_J s_{J1n} \left(1 - \exp \left[-\beta_{Jn} \frac{L_n(t+1)}{K_{Jn}} \right] \right) L_n(t+1) \quad (5)$$

1st-year juveniles in habitat i = 1st-year survival \times fraction staying despite competition \times metamorphs in habitat i + dispersal survival \times 1st-year survival \times competition avoidance \times metamorphs in habitat n

$$A_i(t+1) = s_{Ai} A_i(t) + s_{J2} \left[\exp \left[-\beta_{Bi} \frac{s_{J2} J_i(t) + A_i(t)}{K_{Bi}} \right] J_i(t) + \sigma_J \left(1 - \exp \left[-\beta_{Bn} \frac{s_{J2} J_n(t) + A_n(t)}{K_{Bn}} \right] \right) J_n(t) \right] \quad (6)$$

adults in habitat i = adult survival \times adults in habitat i + 2nd-year survival \times [fraction staying despite breeding competition \times matures in habitat i + survival during dispersal \times avoidance of breeding competition \times matures in habitat n]

Numerical solutions for both models were obtained with the software package RAMSES2.2 © 1994 A. Fischlin (Fischlin 1991).

Numerical results

Density dependence at one or more life stage(s) in a single population (model 1)

Single-stage regulation is possible in any stage, namely if either survival/emigration of larvae or juveniles or female reproduction is density dependent. It results in different types of dynamics (see below). However, population growth cannot be controlled with density-de-

pendent survival of adults: the population either grows exponentially or dies out (see Appendix). To study multistage regulation I take density dependence in the larval stage for granted (see Introduction) and combine it with density dependence in other stages. This additional density dependence modifies the single-stage population growth curve by shifting the mean and by changing the amplitude and/or regularity of the fluctuations. While Fig. 1 gives explicit examples for the types of possible growth curves, Figs 2–4 show the general dynamic patterns depending on the key parameter R , density-independent adult survival (s_A) and the capacity ratios (k_{BL} , k_{LJ} , k_{AL} , see Table 1).

In the example (Fig. 1) parameter values are chosen as follows: The survival constants (s) are set to reasonable values for frogs (see e.g. Wilbur 1980, Berven 1990). In case of competition they are increased to compensate for the additional density-dependent mortality, e.g. larval survival from $s_L = 0.07$ to $s_L = 0.3$. The carrying capacities (K) are chosen to achieve mean population sizes between 900 and 1000 adults with density dependence in a single stage. For studying multistage regulation the parameters used for the respective single stages are just combined. Then single-stage regulation (Fig. 1a) as well as all two-stage combinations (density dependence in larvae and juveniles, larvae and female reproduction, larvae and adults-not shown) produce irregular fluctuations. Three-stage density dependence of tadpole, juvenile and adult survival results in periodic cycles, while an equilibrium is reached when density-dependent reproduction replaces density-dependent adult survival (Fig. 1b).

Note that the same dynamic pattern can be achieved in different ways: e.g. equilibrium population sizes can result from density dependence in a single stage (black bars in Figs 2a, 3a), in two stages, combining an equilibrium in one stage with irregular fluctuations in the other (not shown), or in three stages, combining three times irregular dynamics (Fig. 1b).

Figs 2–4 more generally show how adult population dynamics depends on R , on density-independent adult survival (s_A) and on the capacity ratios ($k_{BL} = cK_B/2K_L$; $k_{LJ} = s_L K_L/K_J$; $k_{AL} = cK_A/2K_L$), when density affects more than one stage. According to their definition these capacity ratios compare the maximum outcome of one stage (numerator) with the capacity of a later stage (denominator). Therefore a capacity ratio of one is always given as a reference, while the other capacity ratios are chosen to be the same as in Fig. 1. In Figs 2 and 3 survival/emigration of larvae and juveniles and/or female reproduction are density dependent; in Fig. 4 adult survival or emigration instead of reproduction is density dependent. The situation shown in Fig. 2 differs from that in Fig. 3 by representing the population dynamics without a maturation delay, implying that there is no additional time lag above that inherent in

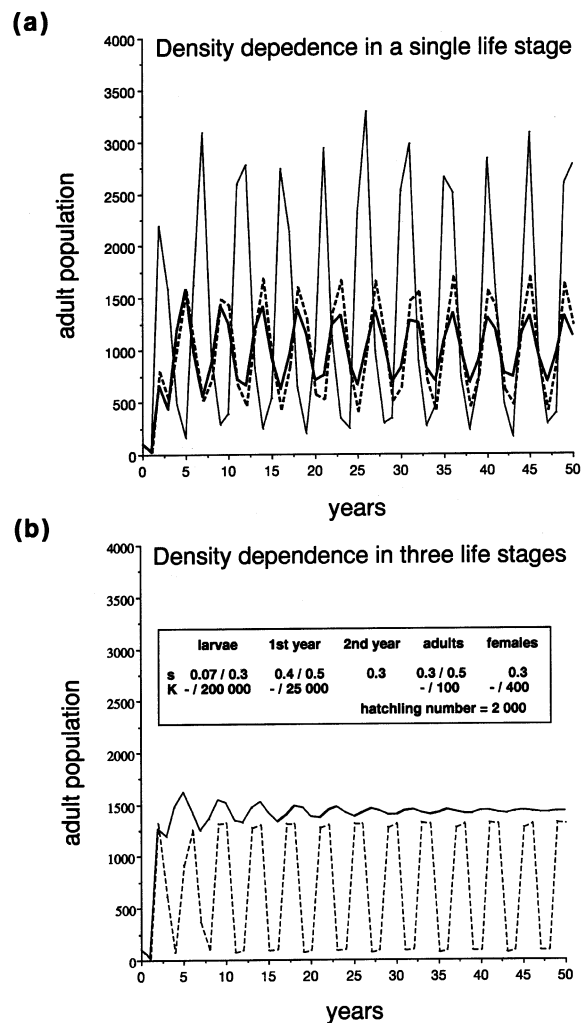


Fig. 1. Influence of density dependence (d-d) in one or more life stages on the dynamics of an isolated (frog) population (model 1). Lines and parameters for resealed model (see Appendix): (a) Single-stage density dependence in larval survival (thin solid; $R = 36$), juvenile survival (dashed; $R = 45$) or female reproduction (thick solid; $R = 8.4$). All three population growth curves fluctuate irregularly, but within bounds and therefore are regulated. (b) Three-stage density dependence ($R = 45$, capacity ratio $k_{LJ} = 2.4$): d-d in larval and juvenile survival combined with d-d in reproduction (solid; $k_{BL} = 2$) or adult survival (dashed; $k_{AL} = 0.5$). The non-equilibrium curve is cyclic. Both populations are regulated but they fluctuate within different bounds and show different dynamics than the single-stage curves. They are examples of multistage regulation as defined in the text. Legend: density-independent survival ' s '; carrying capacity ' K '; for the choice of values see text.

discrete-time models. The major effect of the time lag is to increase the dynamic complexity. As a consequence the difference between density dependence in one or several stages is more pronounced with a time lag.

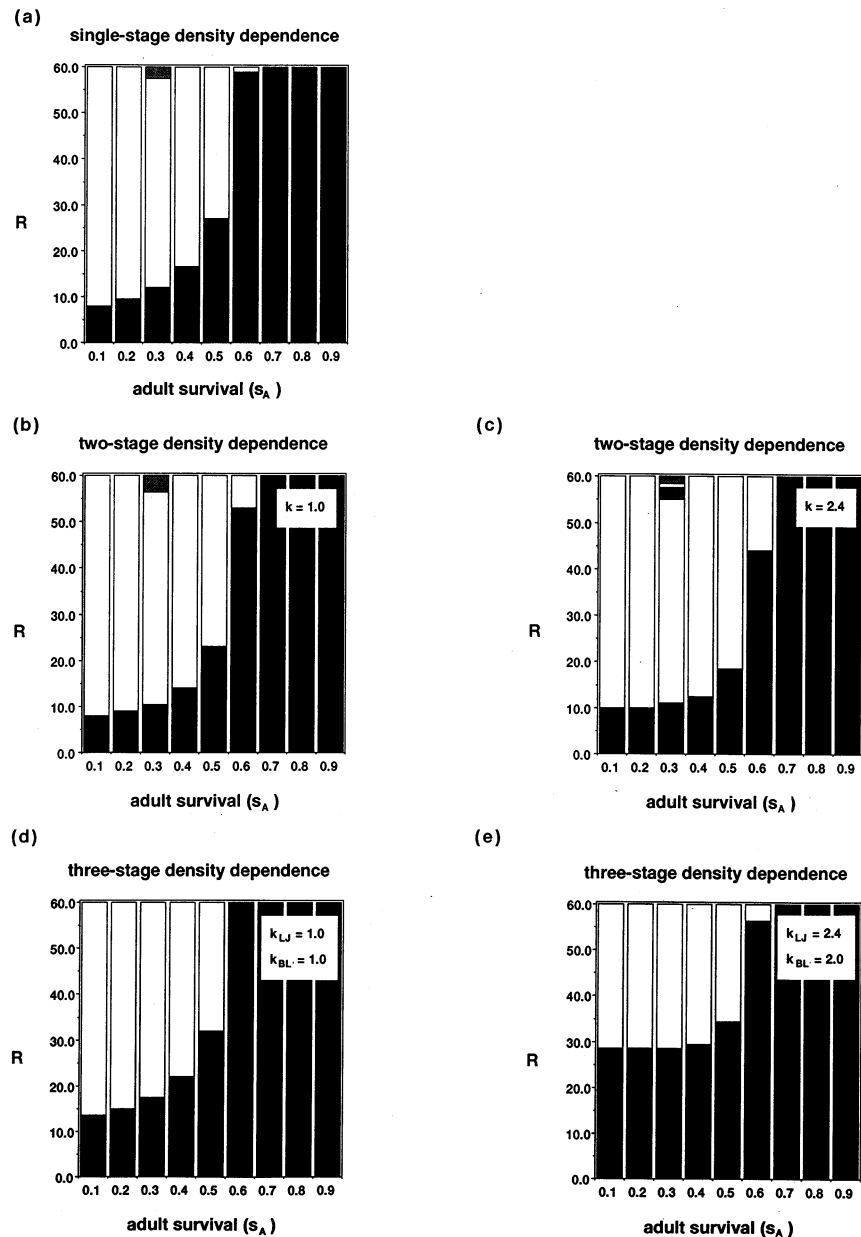
With a time lag there seems to be a general tendency for less irregular dynamics with density dependence in

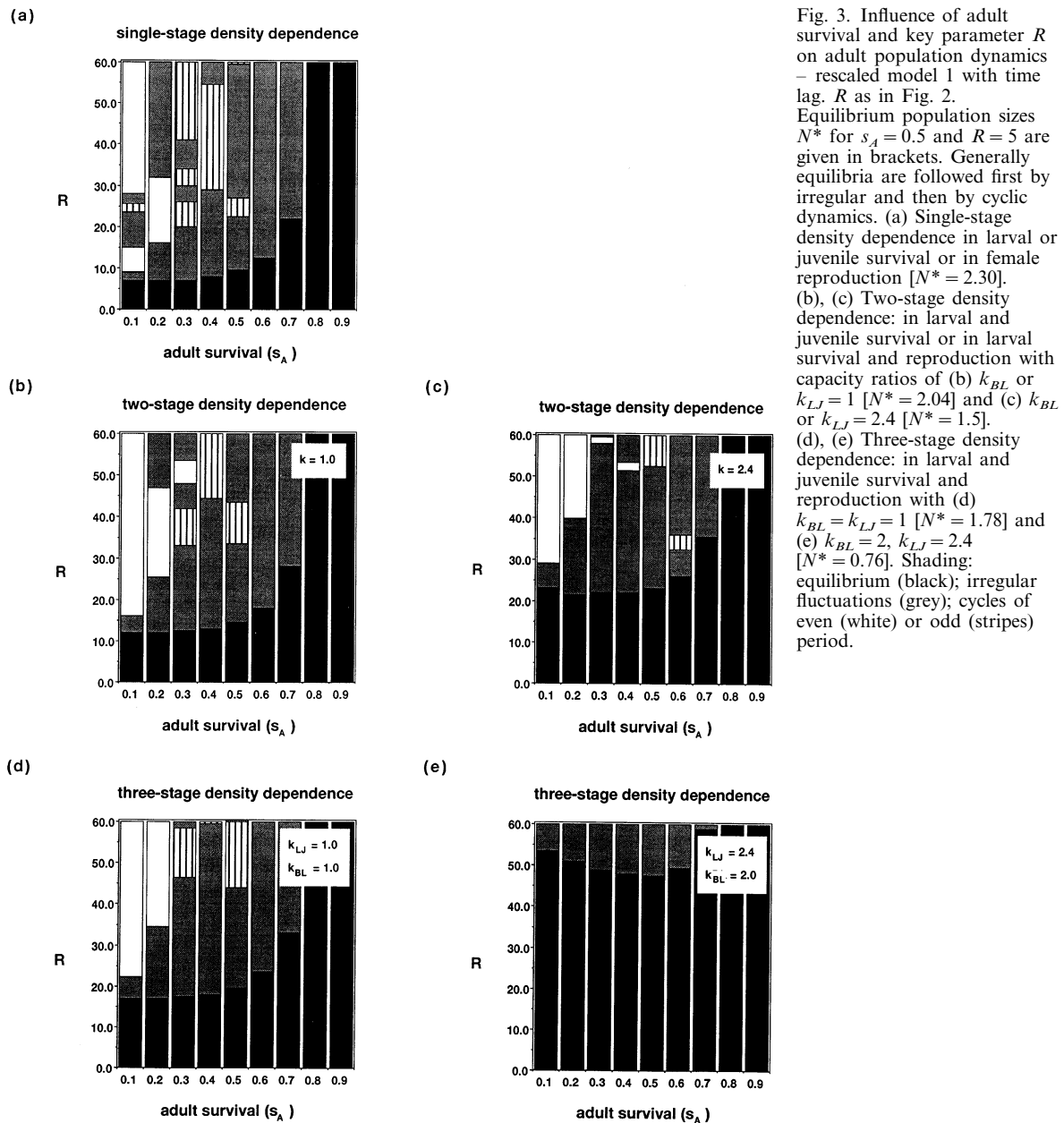
several stages (Figs 3, 4). This effect is more pronounced at extreme values of density-independent adult survival if larvae, juveniles and/or reproduction are affected by density (Fig. 3). High adult survival ($s_A > 0.7$) leads to equilibrium population sizes over a large range of R values independent of a time lag and the number of stages involved (Figs 2, 3). Low adult survival ($s_A < 0.3$) implies equilibria and cyclic dynamics over large ranges of R (Fig. 3). When adults are affected by density the picture is completely different: density-independent adult survival has no influence on the range of R values leading to population equilibria (Fig. 4). Here mainly the number of stages involved and

the capacity ratios determine the dynamics; except that again low adult survival ($s_A < 0.3$) implies equilibria and cyclic dynamics over large ranges of R (compare Fig. 3). Low values of R generally result in equilibrium population sizes. In Figs 2–4 this range for R is increased by density dependence in several stages at least for moderate to high adult survival rates and, depending on the capacity ratios, also for low adult survival.

The equilibrium population size generally increases with increasing density-independent adult survival, although much less so when adults are affected by density (Fig. 4), and it is higher for capacity ratios less than one. Equilibrium population size decreases with the

Fig. 2. Influence of adult survival and key parameter R on adult population dynamics – rescaled model 1 but without time lag. This case serves as a point of reference to distinguish between the effects of the time lag and of density dependence in additional life stages. R incorporates survival up to maturity and hatchlings per adult. Equilibrium population sizes N^* for $s_A = 0.5$ and $R = 5$ are given in brackets. Generally equilibria are followed by cyclic dynamics. (a) Single-stage density dependence in larval or juvenile survival or in female reproduction [$N^* = 2.30$]. (b), (c) Two-stage density dependence: in larval and juvenile survival or in larval survival and reproduction with capacity ratios of (b) k_{BL} or $k_{LJ} = 1$ [$N^* = 2.04$] and (c) k_{BL} or $k_{LJ} = 2.4$ [$N^* = 1.5$]. (d), (e) Three-stage density dependence: in larval and juvenile survival and reproduction with (d) $k_{BL} = k_{LJ} = 1$ [$N^* = 1.78$] and (e) $k_{BL} = 2$, $k_{LJ} = 2.4$ [$N^* = 0.76$] (as in Fig. 1b). Shading: equilibrium (black); irregular fluctuations, i.e. quasiperiodic cycles or chaos, (grey); cycles of even period (white).





number of stages at which density dependence occurs, especially with capacity ratios greater than one. This effect again is less pronounced with density dependence in adult survival/emigration.

Example for multistage regulation in two habitats of different quality (model 2)

Two extremely different habitat types are chosen (Fig. 5): Habitat H1 is characterized by high larval competition ($K_{L1} = 1200$) and breeding competition resulting in

dispersal of second year juveniles ($K_{B1} = 600$), while first year juveniles and adults are unaffected by density ($\beta_{J1} = \beta_{A1} = 0$). Habitat H2 has less larval competition ($K_{L2} = 120000$) and competition between first year juveniles ($K_{J2} = 15000$), but second year juveniles and adults are unaffected by density ($\beta_{B2} = \beta_{A2} = 0$). I also look for additional effects of density-dependent reproduction in H2 ($K_{B2} = 600$; see arrows in Fig. 5).

Without dispersal ($\sigma_{Ji} = 0$ in eqs (5), (6)), population 1 fluctuates around very low numbers, while population 2 reaches a considerably larger equilibrium size (H1: $\sim 15 / \sim 30$, H2: 856/2595 adults/juveniles; Fig. 5a).

With additional density dependence of female reproduction in H2 the equilibria in this habitat increase (1146/3477 adults/juveniles; see arrows).

If first and second year juveniles can leave the respective unfavourable sites the dynamics change. With 30% survival during dispersal the population sizes in both habitats show damped oscillations finally reaching equilibria (H1: 128/418, H2: 866/2560 adults/juveniles; Fig. 5b). Dispersal stabilizes the dynamics of population 1 and its size increases by more than tenfold (adults plus juveniles), while population 2 decreases slightly. With density-dependent reproduction in H2 the equilibria are higher (H1: 212/1308, H2: 1257/3441; see arrows). Survival during dispersal of 50% results in fluctuating dynamics in both habitats (H1: $\sim 149/\sim 932$, H2: $\sim 900/\sim 2370$ means for adults/juveniles; Fig. 5c). Dispersal destabilizes the dynamics of population 2. In H1 juvenile numbers are large compared to adult numbers (factor 6.3; H2: 2.6). With density-dependent reproduction in H2 equilibria are reached at both sites (H1: 219/1868, H2: 1441/3352; see arrows).

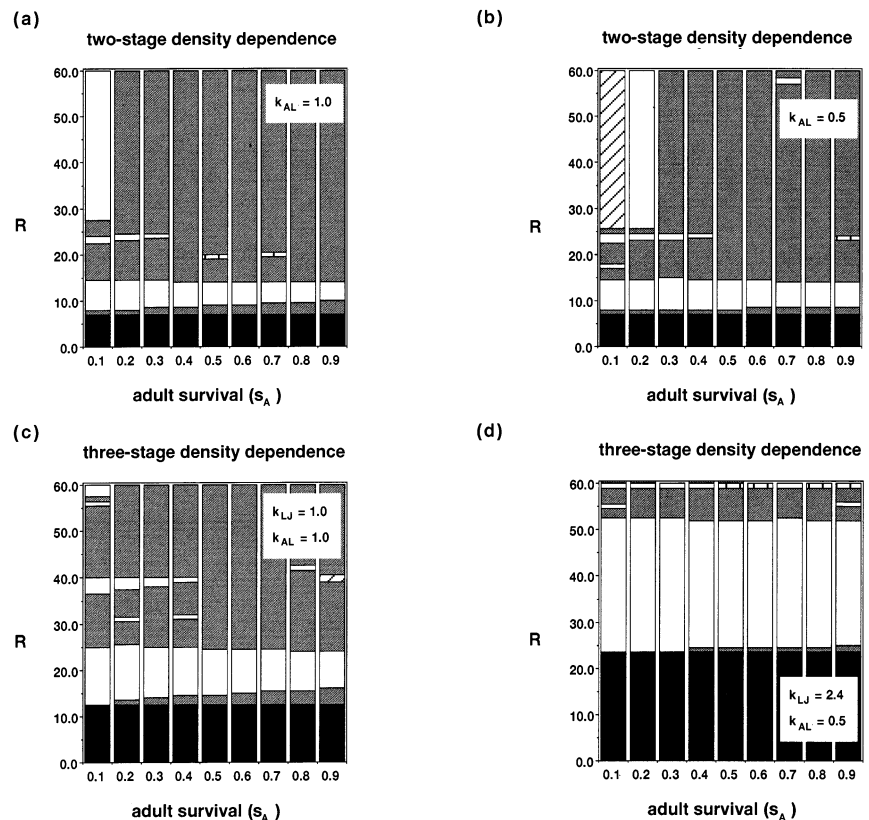
Discussion

In the light of unbalanced data on the effects of density on different stages of complex life cycles I use mathe-

matical models (1) to study the influence of density dependence at one or more life stages on the population dynamics and (2) to exemplify possible practical implications of multistage regulation in a heterogeneous environment. Here density can affect the main events of a three-stage cycle with delayed maturation: survival or emigration in any stage and/or reproduction of females.

Regulation is possible at any single stage: either through density-dependent larval or juvenile survival/emigration or through density-dependent reproduction of females. However, due to the fact that density dependence occurs after breeding, exclusive regulation through density-dependent survival or emigration of adults is impossible. Single-stage regulation results in different types of dynamics: (1) in case of low to moderate density-independent adult survival, equilibria for low values of R are followed by a succession of irregular fluctuations (quasiperiodic cycles or chaos) and periodic cycles for moderate to high R values; (2) with higher adult survival equilibria are (mainly) followed by irregular fluctuations. With density dependence in multiple stages the dynamics also depends on the ratios between the stage-specific carrying capacities. When density affects survival or emigration of larvae and juveniles and/or reproduction there is a tendency towards smaller ranges of R producing irregular fluctuations, at least for low (more equilibria and periodic

Fig. 4. Influence of adult survival and key parameter R on adult population dynamics – rescaled model 1 with time lag (see Appendix). R as in Fig. 2. Equilibrium population sizes N^* for $s_A = 0.5$ and $R = 5$ are given in brackets. Single-stage regulation at the adult level is not possible (see text). Two-stage density dependence in larval and adult survival with capacity ratios of (a) $k_{AL} = 1$ [$N^* = 1.70$] and (b) $k_{AL} = 0.5$ [$N^* = 3.26$]. Three-stage density dependence in survival of larvae, juveniles and adults with (c) $k_{LJ} = k_{AL} = 1$ [$N^* = 1.40$] and (d) $k_{LJ} = 2.4$, $k_{AL} = 0.5$ [$N^* = 1.68$]. Shading: equilibrium (black); irregular fluctuations (grey); cycles of even (white), odd (stripes) or mixed (hatched) period.



cycles) and high density-independent adult survival rates (more equilibria). Without a maturation delay the dynamics are much more regular (compare Higgins et al. 1997) and thus the effects are less pronounced. A partly different picture arises when survival or emigration of adults instead of reproduction is density dependent.

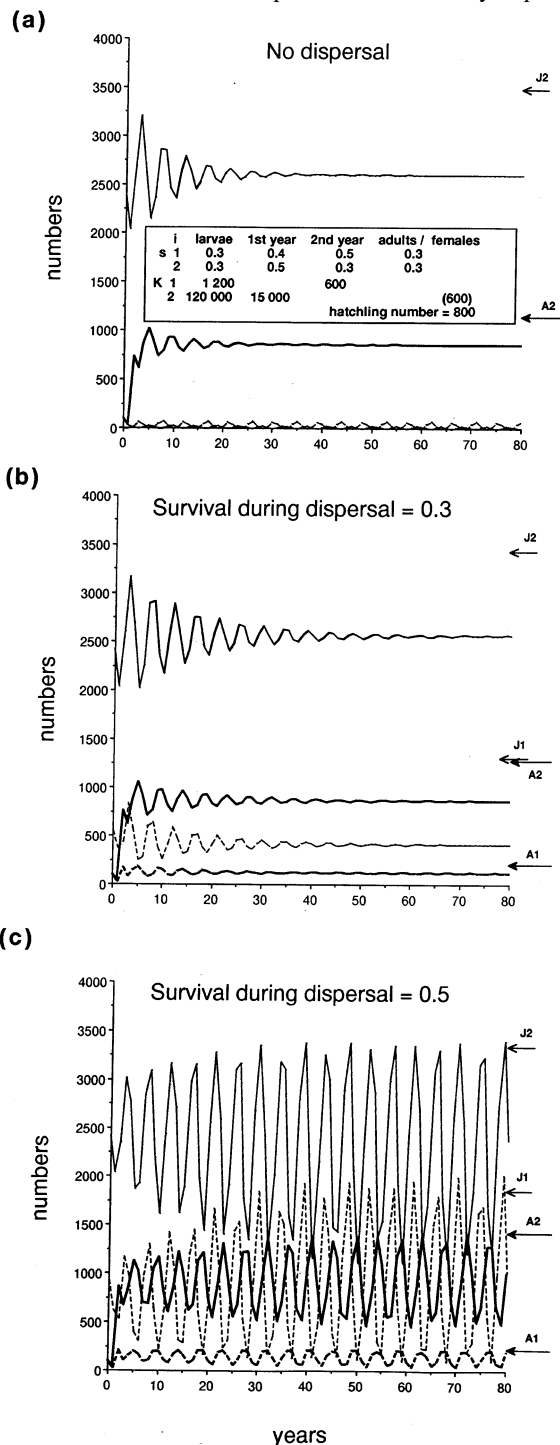


Fig. 5.

In this case mainly the number of stages involved and the capacity ratios determine the dynamics. In general, the equilibrium population size increases with density-independent adult survival and (slightly) with R and it decreases with the number of stages at which density dependence occurs. In case of fluctuations the variability in population size, that is highest divided by lowest observed density, increases with R and decreases with the number of density-dependent stages. That is, density dependence in additional life stages generally changes at least the equilibrium or mean population sizes, their variability and the time course of the population growth curves compared to single-stage density dependence. As long as these changes are small to moderate it might still be possible to identify the one stage where most of the regulation occurs. It then would be single-stage regulation with the additional density dependence in other stages acting as modifiers. However, when density dependence in multiple stages results in a completely different dynamic pattern of population growth curves compared to any of the single-stage curves, multistage regulation would prevail. Curves generated by multistage regulation therefore cannot even qualitatively be predicted assuming density dependence at a single (e.g. the larval) stage.

One reason for the general difficulties in identifying density-dependent processes in the field might therefore be that multistage regulation is more prevalent than we generally assume and that the observed changes in population size result from the superposition of density-dependent processes at several levels. Moreover to identify the ecological mechanisms explaining population fluctuations it is important to know which stages and processes are affected by density (Turchin 1999). In this model the decisive difference occurs in the adult stage between density dependence in reproduction and survival or emigration. Results from a data-based simulation model describing seven life stages of the codling moth (*Laspeyresia pomonella*) are most sensitive to density dependence in fecundity and first-instar survival (Brown et al. 1978). Åström et al. (1996) show that even the relative temporal order of sequential density-dependent events has profound effects on the resulting dynamics if three or more of them occur within the same year/time step. Although due to the maturation

Fig. 5. Influence of multistage regulation including density-dependent dispersal on the dynamics of juvenile and adult frogs (model 2). Habitat H1 is suitable for first year juveniles, but not for breeding because of high larval competition ($R = 24$), while habitat H2 is a good breeding site, but unsuitable for first year juveniles ($R = 18$, $k_{BL} = 2$, $k_{LJ} = 2.4$; compare Fig. 3e). Shown are the resulting population sizes (a) without and (b), (c) with dispersal. In (b) 30% of the dispersers survive, in (c) 50%. — Lines: H1 (dashed), H2 (solid); all juveniles (thin), adults (thick). Arrows: equilibria in case of density-dependent reproduction in H2: all juveniles (J), adults (A); numbers indicate habitats. Legend: density-independent survival 's'; carrying capacity 'K'.

delay this precondition is not met here, their results emphasize as well the importance of knowing the number and type of processes that are density dependent. Currently available tests for statistically significant density dependence (e.g. Dennis and Taper 1994) require long time series of population estimates (at least 20 to 30 years) and do not indicate at which stage(s) regulation occurs or provide information on demographic rates. Leirs et al. (1997) use a 24-month series of capture-mark-recapture data on rodents for estimating survival probabilities from statistical models with and without density dependence. These estimates are then combined into a two-stage population model. According to the results here the success of their approach in predicting population dynamics critically depends on the adequate choice of stages and processes (e.g. survival, maturation, reproduction) to be included into the model. The relationship between age at maturity and the age at which a sharp reduction in adult survivorship occurs might be another factor that should be accounted for (Higgins et al. 1997).

The example studied by the second model is meant to illustrate possible implications of multistage regulation. It accounts for the fact that dispersal is an important feature of many complex life cycles. The results show that multistage regulation including habitat-specific density-dependent dispersal of juveniles can have considerable influence on the dynamics of adjacent populations. The practical consequences – e.g. in terms of site removal and habitat fragmentation – become very striking if we take the time series of Fig. 5b, c as real data. Unaware of the underlying processes and assuming density effects on larvae only, we would assume two independent populations regulated at the larval stage, whereas, in fact, we have two tightly coupled subpopulations: a source emitting immature juveniles to a 'refuge' from which they partly return after maturation. This feedback nature intensifies the coupling and distinguishes this example from a classical source/sink constellation (Pulliam 1988, Dias 1996). Here, depending on survival during dispersal, the fluctuating dynamics in the refuge either destabilizes the stable source population or is stabilized through it (for more detailed work on the dynamic consequences of dispersal see e.g. Davis and Howe 1992, Gyllenberg et al. 1993, Hastings 1993, Doebeli 1995). Moreover, interpreting the age structure at just one site would also mislead us here. Low adult and relatively high juvenile numbers in the refuge are not indicating a young and growing population (Fig. 5c). That is, without following both populations simultaneously for at least two years (maturation delay) and monitoring dispersal, we would have great difficulties to find out 'the reality'. Unfortunately, many studies on amphibians (and maybe other organisms with complex life cycles) do not account adequately for delayed maturation and interconnectedness of populations.

The results of this study clearly show the difference it makes whether density dependence and population regulation occur at one or more life stages; the effects are more pronounced if maturation is delayed. Even if regulation predominantly occurs in a specific stage, the time course and range of population fluctuations might be decisively and unpredictably modified by density-dependent processes at other stages. If in one stage habitat-specific dispersal is density dependent, the modifications or even regulation itself might mainly result from the densities and dynamics at neighbouring sites. Prematurely excluding multistage regulation should therefore affect our ability to predict consequences of habitat fragmentation and thereby constrain realistic actions to be taken in species conservation. Thus, to better understand the population dynamics of species with complex life cycles, for control of pest populations and to resolve discussions about human impacts on species decline (for amphibians see e.g. Blaustein 1994, Pechmann and Wilbur 1994) we need to know more about how density affects different life stages. We urgently need good time series of population estimates, which means either long(er) series (see Meyer et al., 1998) or shorter series at the appropriate spatial scale (Ray and Hastings 1996), and manipulative field experiments directly addressing density relationships in each life stage.

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Appendix

Rescaled form of model 1

The aim is to reduce the number of parameters for the numerical investigations. Roughly speaking survival up to maturity and hatchling number per adult are combined into the dynamic key parameter R , population sizes are scaled by the carrying capacities for the stage(s) of interest and the carrying capacities themselves are combined into capacity ratios (for details see below).

(1) Single-stage density dependence

(a) in larval or juvenile survival/emigration or in female reproduction

$$N(t+1) = s_A N(t) + R \exp[-N(t-1)] N(t-1) \quad (\text{A1})$$

$$\text{with } R := \frac{s_{J2} s_{J1} s_L c}{2}$$

The non-zero equilibrium is

$$N^* = \ln \left[\frac{R}{1 - s_A} \right] \quad (\text{A2})$$

with $N := cA/2K_L$ in case of larval, $N := s_L cA/2K_J$ of juvenile and $N := A/K_B$ of reproductive density dependence. The ranking of the carrying capacities does not necessarily imply the same ranking for the equilibria, e.g. in Fig. 1 $K_B < K_J < K_L$ but $N_J^* = K_B^* < K_L^*$. Everything else being equal the three equilibria are identical if $K_J = s_L K_L$ and $K_B = (2/c) K_L$. The restriction on adult survival resulting from (A2) is easily fulfilled: $s_A < 1$.

(b) in adult survival

$$N(t+1) = s_A \exp[-N(t)] N(t) + R N(t-1) \quad (\text{A3})$$

$$\text{with } N := \frac{A}{K_A}$$

The non-zero equilibrium is

$$N^* = \ln \left[\frac{s_A}{1 - R} \right] \quad (\text{A4})$$

The inequality $R = s_{J2} s_{J1} s_L c / 2 < 1$ resulting from (A4) implies either unrealistically low survival rates up to maturity which compensate for larger hatchling numbers per female, or, conversely, a very small number of hatchlings compensating for higher survival rates. Otherwise the population grows exponentially due to the second term of the sum in (A3).

(2) Two-stage density dependence

(a) in larval and juvenile survival/emigration or in larval survival/emigration and female reproduction

$$X(t+1) = k_x \exp[-N(t)] N(t) \quad \text{with } k_x = k_{LJ} \text{ or } k_{BL}$$

$$N(t+1) = s_A N(t) + \frac{R}{k_x} \exp[-X(t)] X(t)$$

and (i) for larvae and juveniles

$$X := \frac{L}{K_J}, \quad N := \frac{cA}{2K_L}, \quad k_{LJ} = \frac{s_L K_L}{K_J},$$

(ii) for larvae and females

$$X := \frac{H}{K_L}, \quad N := \frac{A}{K_B}, \quad k_{BL} = \frac{cK_B}{2K_L}.$$

The non-zero equilibria are implicitly given through

$$-N^* + \ln \left[\frac{R}{1-s_A} \right] = k_x N^* \exp[-N^*]$$

(b) in larval and adult survival/emigration

$$X(t+1) = k_{AT} N(t) \quad \text{with } k_{AL} = \frac{cK_A}{2K_L}$$

$$N(t+1) = s_A \exp[-N(t)] N(t) + \frac{R}{k_{AL}} \exp[-X(t)] X(t)$$

$$\text{and } X := \frac{H}{K_L}, \quad N := \frac{A}{K_A}.$$

The non-zero equilibria are implicitly given through

$$-s_A + \exp[N^*] = R \exp[(1-k_{AL})N^*]$$

(3) *Three-stage density dependence*

(a) in survival/emigration of larvae and juveniles and in female reproduction

$$L'(t+1) = k_{BL} \exp[-A'(t)] A'(t) \quad \text{with } k_{BL} = \frac{cK_B}{2K_L}$$

$$J'(t+1) = k_{LJ} \exp[-L'(t+1)] L'(t+1)$$

$$\text{with } k_{LJ} = \frac{s_L K_L}{K_J}$$

$$A'(t+1) = s_A A'(t) + \frac{R}{k_{LJ} k_{BL}} \exp[-J'(t)] J'(t)$$

$$\text{and } L' := \frac{H}{K_L}, \quad J' := \frac{L}{K_J} \quad \text{and} \quad A' := \frac{A}{K_B}.$$

(b) in larval, juvenile and adult survival

$$L'(t+1) = k_{AL} A'(t) \quad \text{with } k_{AL} = \frac{cK_A}{2K_L}$$

$$J'(t+1) = k_{LJ} \exp[-L'(t+1)] L'(t+1)$$

$$A'(t+1) = s_A \exp[-A'(t)] A'(t) + \frac{R}{k_{LJ} k_{AL}} \exp[-J'(t)] J'(t)$$