[NOTE: The paper was published in 1990 (see below for citation), and was Chapter 4 of J. Wu's dissertation (1991). The following is excerpted from the dissertation.]

Modelling patchy ecological systems using the System Dynamics approach

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Introduction

Patchiness has been increasingly recognized by ecologists as a ubiquitous phenomenon in nature. Therefore, substantial research has been directed at modeling the dynamics of metapopulations in patchy habitat settings (e.g., den Boer, 1968; Levins, 1969, 1970; Levins and Culver, 1971; Roff, 1974a,b; Levin, 1976b, 1978; Hastings, 1982, 1991; Hanski, 1983, 1985, 1991; Fahrig and Merriam, 1985; DeAngelis and Waterhouse, 1987; Lawton, 1987; Fahrig, 1988a,b; Hastings and Wolin, 1989; Shorrocks and Swingland, 1990; Taylor, 1990, 1991; Gilpin, 1991; Hanski and Gilpin, 1991; Hansson, 1991; Merriam et al., 1991; Sabelis et al., 1991). Because traditional modeling paradigms in ecology usually assume a spatially uniform environment, incorporation of spatial heterogeneity may revolutionize many of the current ecological theories derived from homogeneous models. In fact, the current understanding of the dynamics and persistence of metapopulation systems has been based primarily on such modeling studies.

An ultimate goal of studying these patchy systems is to understand dynamic mechanisms so as to predict their behavior and thereby manage them for persistence (Smith and Peacock, 1990). There are two traditional approaches to modeling population dynamics in heterogeneous environments. The first, "the patch-occupancy approach", describes the dynamics of populations in terms of changing proportions of patches of different kinds (e.g., predator-occupied, prey-

occupied, or empty patches). Although models of this type have been important in investigating the significance of dispersal as a stabilizing factor in species persistence, they ignore the within-patch dynamics of populations and the dependence of colonization and extinction processes on population size (Hastings and Wolin, 1989). While interpatch immigration is one of the most crucial aspects of metapopulation dynamics (Gilpin, 1987), within-patch population dynamics may have significant influences on the process.

In contrast, the second approach to modeling population dynamics in heterogeneous environments utilizes diffusion-reaction equations as its modeling framework and has the ability, in principle, to incorporate parameters reflecting differences in particular biological situations (e.g., variations of species habitats in space and time). Therefore, this approach has been widely adopted in recent mathematical modeling studies on population dynamics in varying environments (e.g., Levin, 1976b; Okubo, 1980). As a recent example, DeAngelis et al. (1979, 1986) employed the theory of positive linear systems with this modeling methodology in their study on persistence and stability of tree species in a system of forest islands. However, the assumption of randomness in dispersal and movement of organisms in the diffusion-reaction models has been questioned (e.g., Moffatt, 1989), and the complex mathematics involved have substantially limited the applicability and popularity of this approach in ecology. In addition, the minimum viable population (MVP) size characterizing many species population dynamics has been generally ignored in previous metapopulation models. Incorporating of the MVP concept into such models has the potential to advance study of the dynamics and stability of patchy population systems.

I have developed a one-species-two-patch model using the System Dynamics modeling approach to simulate the local (within-patch) and regional (over-all-patch) dynamics of populations (see Chapter 1 and Wu and Vankat, 1989). Following such an approach, impacts of dispersal on species persistence in a patchy system are examined through computer simulations. While the two approaches mentioned above have been carried out by analytical models, this modeling scheme may present a new perspective on developing realistic, comprehensive simulation models of population dynamics in patchy environments. Given the assumptions and model structure, the model applies primarily to plant populations whose dispersals do not directly decrease the size of the source patch populations.

Model description

Model Structure

Many plant species have populations occupying discrete habitat patches or islands, especially in human-dominated landscapes (e.g., habitat remnants, nature reserves, wildlife refuges). The term metapopulation has been used to denote several interacting subpopulations of a species distributed over such a patchy area (see Chapter 1). I have developed a one-species-two-patch model to investigate the dynamics of a metapopulation which is composed of two subpopulations. The two habitat patches are assumed identical and the major state variables are population sizes in the patches (Population-1 and Population-2). The within-patch (local) dynamics of each population is regulated by density-dependent mechanisms, which is essentially the same as described in Chapter 3. A regulatory delay is incorporated so that the crowding effect on the local net growth (recruitment) rate takes place after a time delay.

Each local population has its carrying capacity for the species in question which is in turn determined by the patch area. It is also assumed that there exists a threshold population size, the minimum viable population (cf. Shaffer, 1981; Soule, 1987). The MVP size is usually defined and determined in a probabilistic sense, implying that a population would take a great risk of extinction when smaller than this critical size. In this study and in Chapter 5, I assume that a completely isolated population will decline and eventually go extinct if its size is below MVP.

The overall dynamics of this metapopulation is determined by both local and regional processes. Interpatch colonization is affected by the species' colonizing ability, interpatch distance, population size of the source patch, and habitat availability in the target patch. The interpatch colonization loop, in its most general version, involves a third-order time delay. These regional processes along with the local density-dependent regulating mechanisms constitute the overall feedback loop structure of the model (Fig. 4.1). A STELLA version structural diagram that depicts the relationships among the model variables is presented in Fig. 4.2.

Model Formulation

As discussed in Chapter 2, the most critical and usually most challenging task is to determine the rate equations in System Dynamics modeling in particular and mathematical modeling in general. While the levels (state vaviables) and rates are of most interest, auxiliaries assist to specify the relationships in the model and to elaborate the mathematical formulation of the rates. The parameterization of this model is based primarily on literature (also see Chapter 3), with an emphasis on qualititive rather than exact numerical relationships between variables. All model equations, as well as constants and the numerical values for the graphical functions, are provided in the STELLA program listing (Table 4.1). The explicit graphical

presentation of relationships among variables in the structural diagram and the English-like STELLA language make it unnecessary to explain every individual equation.

The effect of crowding (expressed by the ratio of population to carrying capacity) on the local recruitment rate is presented graphically in Fig. 4.3a. Adopting a MVP value of 50 in this model (and in the animal population dynamics model in Chapter 5) does not mean or even imply that 50 is a generally acceptable "Magic Number" for all species. This figure assumes an MVP value of 50 and a carrying capacity of 500. Of course, these values should and can be easily changed for consideration of a particular species in a given habitat.

The effect of crowding on habitat availability (which in turn influences the regional colonization rates) is also graphically modelled (Fig. 4.3b). This graph assumes a carrying capacity of 500. Because the purpose here is to examine general properties of dynamics of patchy plant populations, the choice of the numerical values for these parameters and graphical functions is primarily arbitrary.

Model simulation and analysis of results

Population Dynamics without Interpatch Colonization

For the purposes of testing and verification of the basic model structure and functions, I first simulated the model without consideration of interpatch colonization. In this case, the populations in the two patches behave identically, exhibiting a MVP of 50 and a carrying capacity of 500 (Fig. 4.4). MVP is a unstable equilibrium point whereas carrying capacity is a stable one. The populations go extinct when they start below MVP, reach a steady state at the carrying capacity level when from above MVP, and remain unchanged when initially at MVP (Fig. 4.4).

The time delay engaged in the density-dependent regulating mechanisms may effect population oscillations. While a moderate delay time (for example, 5) generates damping oscillatory behavior, an extremely large delay time (e.g., 99,999) essentially breaks down the density-dependent regulatory feedback loops so that the exponential growth pattern emerges (Fig. 4.4). The above patterns and more detailed discussion on effects of population regulatory time delay on population dynamics can be found in Wu and Barlas (1989).

Dynamics of the Population System with Interpatch Colonization

In order to investigate the effects of different colonization intensities with varying initial population sizes on the dynamics of the metapopulational system, I designed three simulation scenarios. The first examines the system behavior when one of the two subpopulations is below MVP and the other larger than or equal to MVP. The second scenario focuses on analyzing the species persistence when both subpopulations start with below-MVP sizes, which is ecologically a more intriguing case. In both of the above two scenarios, the delay in interpatch colonization loop is assumed to be non-existent. The third scenario provides an initial examination of the effects of interpatch time delays on dynamics of the population system and thereby presents an introduction to further study.

<u>One subpopulation below the minimum viable population size</u>

While the source patch population, target patch habitat availability, and interpatch distance all affect the overall fluxes of colonists, percent colonization rate (PCR) in my model characterizes the biological colonizing ability of a species. In the case where one subpopulation is below MVP, different PCR values are examined and compared in different simulation runs. When PCR is larger than 0.004, both populations always reach the carrying capacity. This exemplified by the extreme case where one population starts with zero with the other being equal to the MVP (Fig.4.5a,b).

When PCR is smaller than 0.004, the outcome varies with different initial population sizes in the two patches. Interestingly, there occurs a new stable equilibrium at low population densities when a PCR between 0.002 and 0.004 is used. For a PCR of 0.003, the new equilibrium is 12 (rounded from 12.43). It is achieved when one population starts with 12 or below and the other between 50 and 500 (Fig. 4.6a), or when one population begins with 37 or below and the other stays at 500 (Fig. 4.6b), or when one is between 38 and 48 and the other is at or slightly larger than MVP (Fig. 4.6c,d). For a PCR of 0.002, a new stable point of 7 (rounded from 7.30) is found; it is approached when one population is lower than 7 and the other larger than MVP (Fig. 4.7a) or when one is smaller than 43 (42.79 to be exact) and the other stays at 500 (Fig. 4.7b).

The above simulation results show in the scenario of one population below MVP that both populations stabilize at the carrying capacity level when PCR is sufficiently large (i.e., >0.004 in this particular model). When the value of PCR is rather small (e.g., 0.002-0.004), the population that starts from below MVP may end up with a new stable equilibrium which is much lower than the carrying capacity. However, the persistence of populations with such small sizes depends heavily on interpatch colonist influxes because of stochastic events in nature. A

value for PCR smaller than 0.002 will result in an even lower new equilibrium and it eventually approaches zero when the value of PCR is sufficiently small. When this occurs, the colonization feedback loops have effectively collapsed and, therefore, a subpopulation below its MVP would become extinct regardless of the size of the other subpopulation.

<u>Both subpopulations below the minimum viable population size</u>

Can the system persist with interpatch colonization when each of its subpopulations is below MVP? How do different PCR values affect the species persistence in such a patchy environment? I address these questions by simulating the model for different PCRs and varying initial population sizes. When PCR is equal to 0.2, both populations eventually reach the carrying capacity if at least one of them starts larger than zero (Fig. 4.8a). When the value of PCR is reduced to 0.1 and the two populations start with the same number, they both rise to the carrying capacity only when the initial population size is larger than a critical threshold (19, rounded from 18.9), below which both of them go extinct (Fig. 4.8b).

When the two populations are different in initial size, the results are diverse. For a PCR of 0.1, if extinction occurs to one of the populations, the other must have a size of at least 33 to restore the empty patch and for both to ultimately stabilize at the carrying capacity (Fig. 4.9a). To achieve the same result, one population has to be larger than 22 if the other is 15 (Fig. 4.9b). In fact, for a given size of population-1, there always exists a minimum size of population-2 for their persistence, and this size decreases with the increase in the size of population-1, or vice versa (Fig. 4.10a). The phase-plane diagram illustrates that both populations persist (eventually reach the carrying capacity) when they start from the "persistence isocline" or go extinct when from below it. The key reason for species persistence in such situations is that the fluxes of colonists are large enough to offset the negative local net recruitment. This is revealed by comparing the combined percent net local recruitment rate (Comb-PNRR) versus crowding curve (Fig. 4.10b) with the previous PNRR-Crowding curve (the first half of Fig. 4.3a). Comb-PNRR is defined as the sum of the percent local net recruitment rate and percent colonization rate from the other patch (see Table 4.1).

For a PCR of 0.02, the populations reach the carrying capacity when they both start with 44 or above or they go to extinction when both start below 44 (Fig. 4.11a). If one population has an initial size of 48, the other has to be at least 21 for both of them to attain the carrying capacity (Fig. 4.11b). For a PCR of 0.005, in the case of the two populations being equal, both reach the carrying capacity only when they are larger than 48 and otherwise both become extinct (Fig. 4.11c). However, if

one population is 49, the persistence of both populations is guaranteed if the other is larger than 40 (Fig. 4.11d). For a PCR of 0.004, the two populations eventually stabilize at the carrying capacity when they both start with 49, but both go extinct when starting with the same initial size and a smaller PCR (0.003, Fig. 4.12a,b).

Effects of time delays on metapopulation dynamics

How do the time delays involved in regional colonization and local density-dependent regulatory processes affect the dynamics of population systems and thus species persistence? As a preliminary attempt, I approached this problem by examining the effects of delays for a PCR of 0.1 and a colonization delay time of 30 (Fig. 4.13a-d) without including the local regulatory delay. This time delay induces an earlier arrival to the carrying capacity when one population starts with 32 and the other is zero (Fig. 4.13a, in contrast with Fig. 4.9a). However, the time for both of the populations to reach the carrying capacity is postponed by the colonization delay when they start with 15 and 25 (Fig. 4.13b, compare with Fig. 4.9b). While the former can be attributed to the prolonged high colonist flux from population-2 to population-1 at the beginning and the reinforced interactions between the populations afterwards, the latter may result from prolonged low colonist fluxes. In addition, a colonization delay of this size is able to cause the populations to overshoot the carrying capacity (Fig. 4.13a,b).

The delay in local population regulation introduces fluctuations to the system (Fig.4.4 and 14a). When the colonization delay time is 30 and the regulation delay time is 4, a damping fluctuation in population size occurs (Fig. 4.14a). Associated with this, the combined percent net recruitment rate exhibits a distinctive pattern with increasing populations (Fig. 4.14b). The combination of the two types of delays with different magnitude may have rather different effects on the overall dynamics of metapopulations. These questions are topics for future studies.

Discussion and conclusions

Simulations of the 2-patch plant metapopulation model have demonstrated that a metapopulation may persist only with colonization whose intensity is large enough to overcome the declining tendency of small populations. The intensity of overall fluxes of colonists depends on the interactions among the biological ability of the species (PCR), the initial population sizes, and the target patch habitat availability (see Table 4.1). When one of the two subpopulations is larger than the minimum viable population the metapopulation system always persists (i.e., at least one subpopulation is persistent). For a species with colonization ability sufficiently large (PCR>0.004 in this case), both populations stabilize at the carrying capacity. But

with small colonizing ability (PCR<0.004 in the model), the population below MVP will, instead, either reach a new lower equilibrium or approach zero. Considering the stochasticities in population demography, genetics, and environment, populations at such low density equilibria would be subject to frequent local extinctions (Shaffer, 1987; Wu, 1991a).

In a patchy system consisting of two subpopulations below MVP, depending on the colonization ability of species and the initial population sizes, they either stabilize at the carrying capacity or both go extinct. Therefore, it seems that the combination of a large-sized and a small-sized population offers a better chance for persistence than the one of two medium-sized populations when both of them are smaller than MVP.

Assuming continuous fluxes of colonists, a time delay does not necessarily slow down the dynamic process of the population system and a single large population may play a more crucial role in such a situation. The effects of combination of local (population regulatory) and regional (colonization) delays can induce population fluctuations and further alter the overall dynamics of the metapopulational system. While these simulation results may have implications for species conservation and the design of nature reserves, virtually no direct field or experimental data are available to verify them.

As far as the colonization process is considered, the model is primarily appropriate for plants rather than animals because plant dispersal of propagules usually does not directly decrease the size of the source patch populations whereas animal dispersal usually does. The model may be used to conduct more comprehensive investigation on effects of delays and asymmetric colonization rates on metapopulation dynamics. The effects of spatial aspects (e.g., patch area and interpatch distance) and population demographic and environmental stochasticities on colonization and persistence of species can also be relatively easily included with STELLA. In addition, the current modeling framework can be extended to one-species-several-patch models. However, the general findings with the two-patch model seem unlikely to be changed by multi-patch models using the same modeling approach because the fundamental mechanisms determining the dynamics and persistence of such plant metapopulations will remain the same.

Table 4.1. A STELLA program listing of the two-patch plant metapopulation model

Population_1 = Population_1 + dt * (Net_Recruit_Rate_1 +

Act_Clnz_Rate_2to1)

INIT(Population_1) = 25

Net_Recruit_Rate_1 = Act_Pct_NRR_1*Population_1

Act_Clnz_Rate_2to1 = SMTH3(Indct_CR_2to1, 10)

Population_2 = Population_2 + dt * (Net_Recruit_Rate_2 + Act_Clnz_Rate_1to2)

INIT(Population_2) = 25

Net_Recruit_Rate_2 = Act_Pct_NRR_2*Population_2

Act_Clnz_Rate_1to2 = SMTH3(Indct_CR_1to2, 10)

Act_Pct_NRR_1 =SMTH3(Indicated_PNRR_1, 4)

Act_Pct_NRR_2 = SMTH3(Indicated_PNRR_2, 4)

Carrying_Cap_1 = CC_Per_Area*Patch_Area_1

Carrying_Cap_2 = CC_Per_Area*Patch_Area_2

CC_Per_Area = 50

Crowding_1 = Population_1/Carrying_Cap_1

Crowding_2 = Population_2/Carrying_Cap_2

Indct_CR_1to2 =
(Pct_Clnztn_R_2*Population_1)*Habitat_Avail_2*IP_Dist_Multplr

Indct_CR_2to1 =
(Pct_Clnztn_R_1*Population_2)*Habitat_Avail_1*IP_Dist_Multplr

InterPatch_Dist = 0

Patch_Area_1 = 10

Patch_Area_2 = 10

Pct_Clnztn_R_1 = 0.1

Pct_Clnztn_R_2 = 0.1

Rel_InterPatch_Dist = InterPatch_Dist/Sp_Disp_Dist

Sp_Disp_Dist = 100

Habitat_Avail_1 = graph(Crowding_1)
(0.0,1.00),(0.100,0.985),(0.200,0.965),(0.300, 0.930), (0.400,0.890), (0.500, 0.840), (0.600,0.765),(0.700,0.675),(0.800,0.555),(0.900,0.355),(1.00, 0.0)

Habitat_Avail_2 = graph(Crowding_2)
(0.0,1.00),(0.100,0.985),(0.200,0.965),(0.300,0.930),(0.400,0.890), (0.500, 0.840),(0.600,0.765),(0.700,0.675),(0.800,0.555),(0.900,0.355),(1.00, 0.0)

Indicated_PNRR_1 = graph(Crowding_1)
(0.0,-0.160),(0.100,0.0),(0.200,0.106),(0.300,0.154),(0.400,0.160),(0.500, 0.160),(0.600,0.150),(0.700,0.122),(0.800,0.0880),(0.900,0.0500),(1.00, 0.0),(1.10,-0.0420),(1.20,-0.0680),(1.30,-0.0880),(1.40,-0.100),(1.50,-0.114),(1.60,-0.124),(1.70,-0.132),(1.80,-0.136),(1.90,-0.138),(2.00,-0.140)

Indicated_PNRR_2 = graph(Crowding_2)
(0.0,0.160),(0.100,0.0),(0.200,0.106),(0.300,0.154),(0.400,0.160),(0.500,0.16 0),(0.600,0.150),(0.700,0.122),(0.800,0.0880),(0.900,0.0500),(1.00, 0.0),(1.10,-0.0420),(1.20,-0.0680),(1.30,-0.0880),(1.40,-0.100),(1.50,-0.114),(1.60,-0.124),(1.70,-0.132),(1.80,-0.136),(1.90,-0.138),(2.00,-0.140)

IP_Dist_Multplr = graph(Rel_InterPatch_Dist)
(0.0,1.00),(0.300,0.650),(0.600,0.395),(0.900,0.210),(1.20,0.125),(1.50, 0.0850),(1.80,0.0600),(2.10,0.0350),(2.40,0.0200),(2.70,0.0100),(3.00, 0.0)
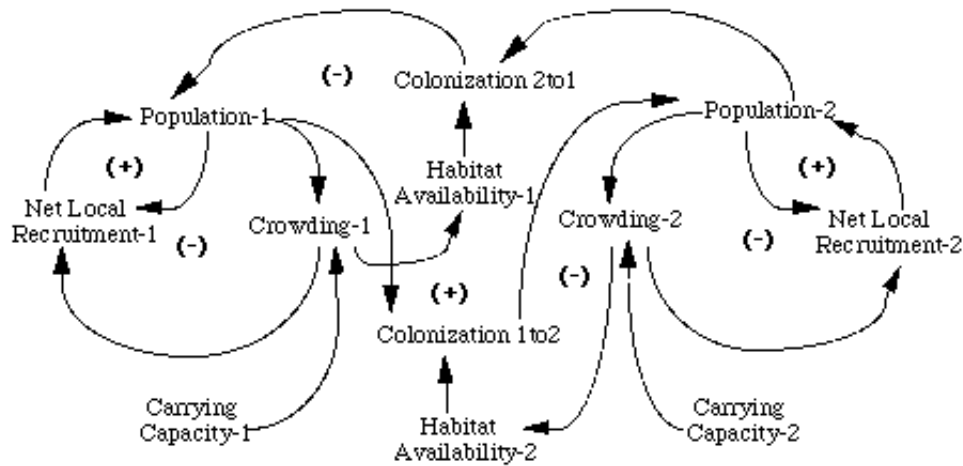
Fig. 4.1. Causal-loop diagram of the feedback structure of the two-patch plant metapopulation model.
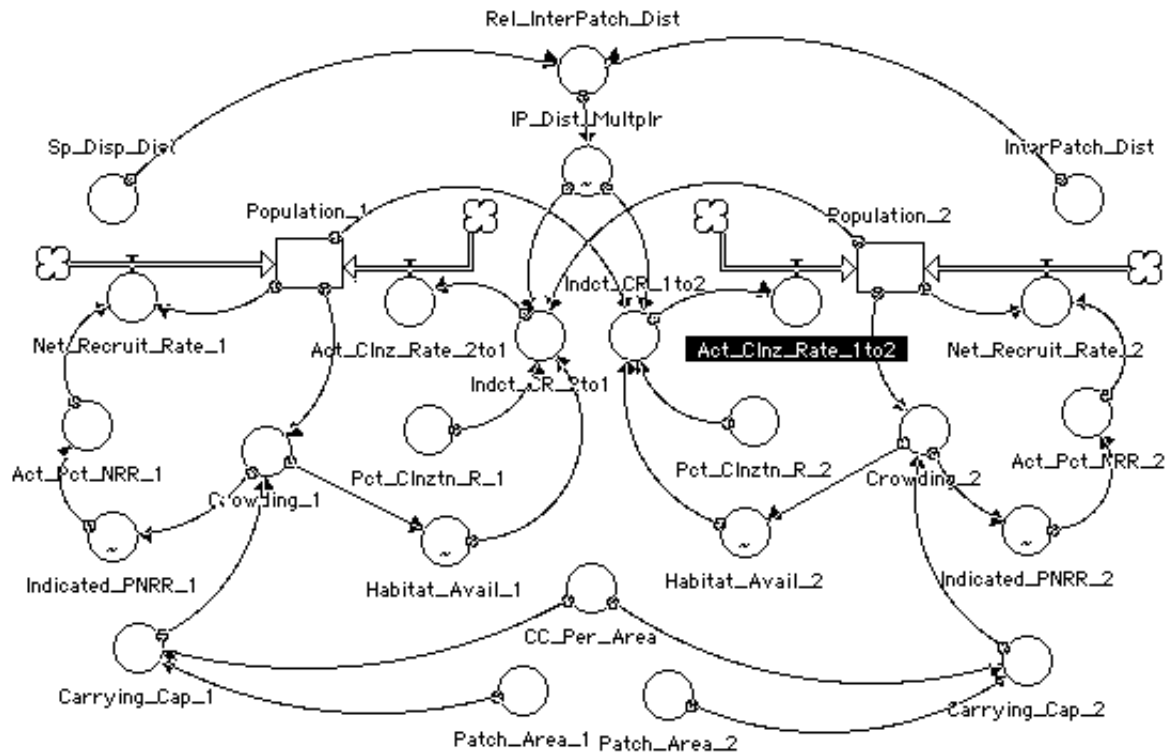
Fig. 4.2. Structural diagram of the two-patch plant metapopulation model.
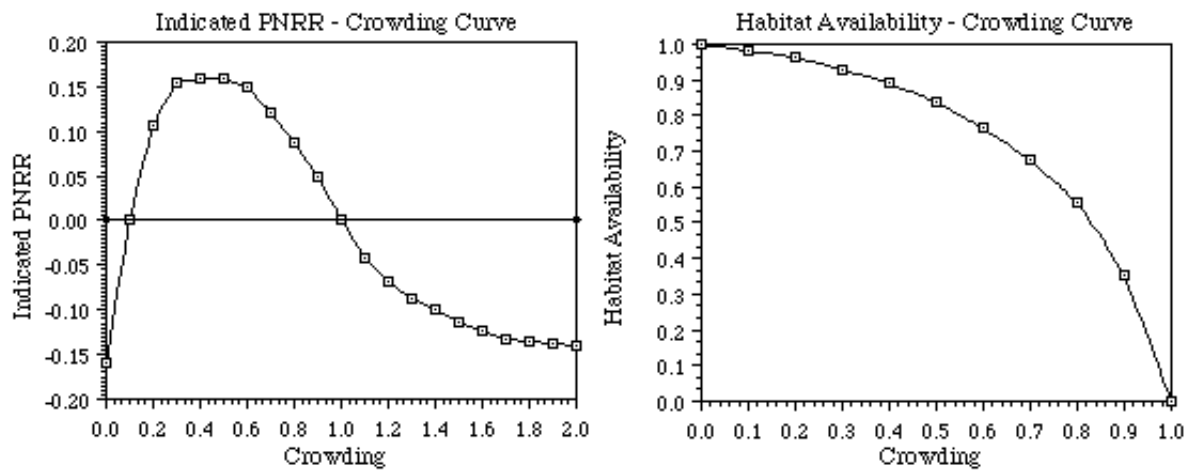
Fig. 4.3. (a) Relationship between crowding and indicated (without delay) percent net recruitment rate. (b) relationship between crowding and habitat availability for colonization.

(a)   (b)
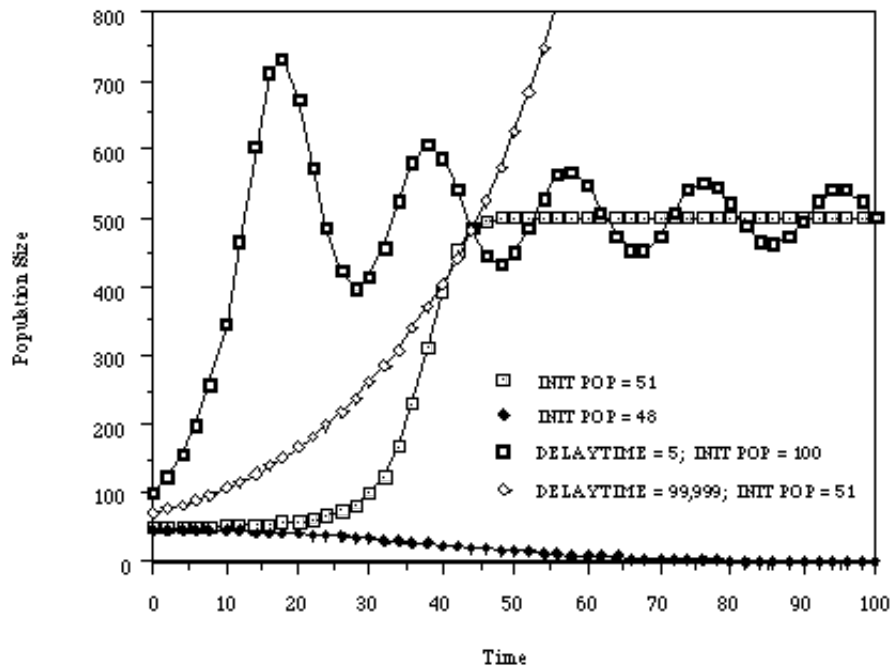
Fig. 4.4. Dynamics of the population system without interpatch colonization, illustrating a MVP of 50 and a carrying capacity of 500. Oscillatory behavior occurs when a moderate delaytime is used and exponential growth pattern may eventually be approached when an extremely large delaytime is used.
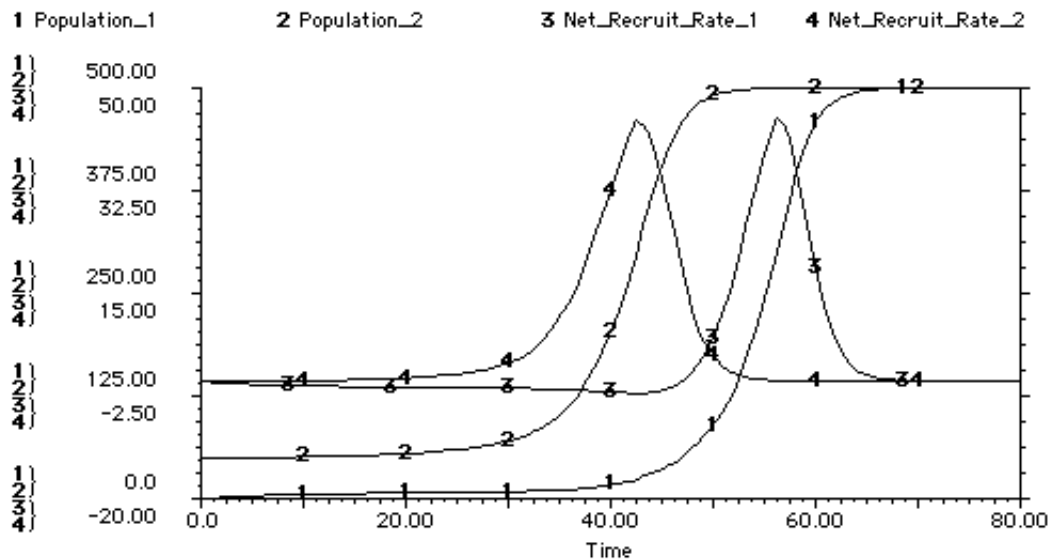
(a)
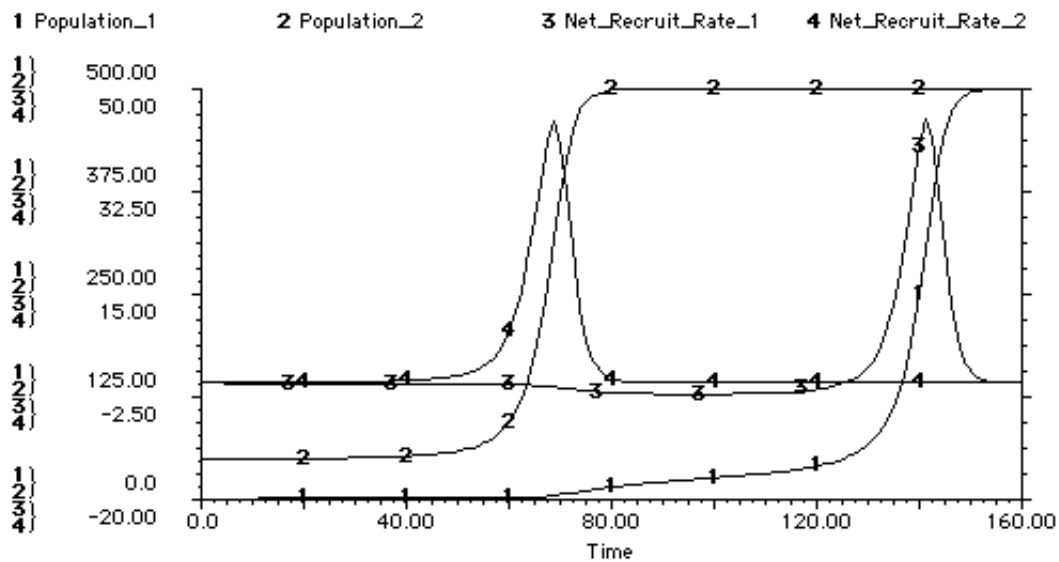
(b)

Fig. 4.5. Dynamics of the population system when one subpopulation is below and the other at or above MVP for PCRs larger than 0.004. (a) The populations start with 0 and 50, respectively, with a PCR of 0.02. (b) The two populations start with 0 and 50, respectively, with a PCR of 0.005.

(a)

(b)
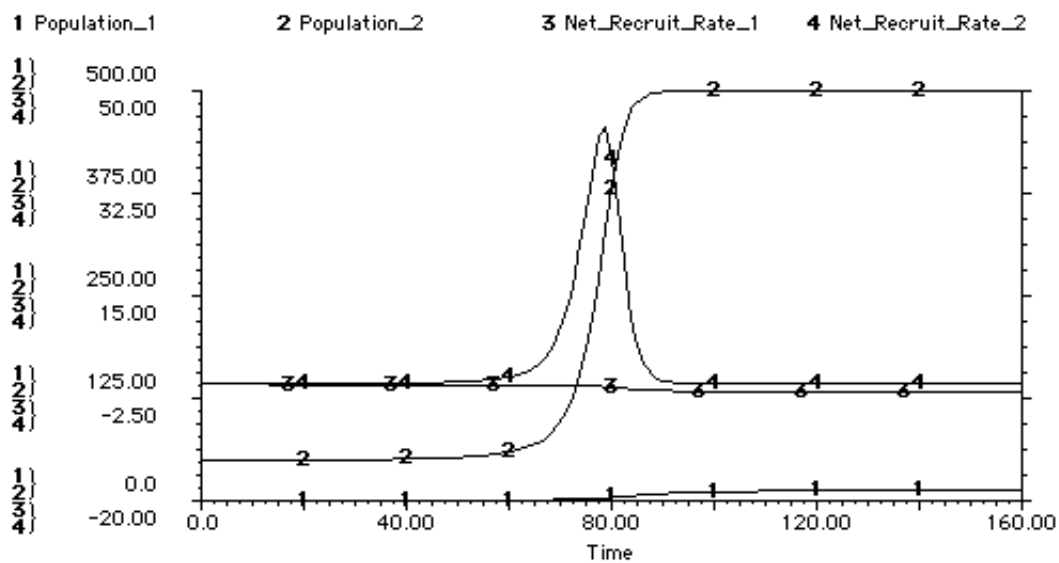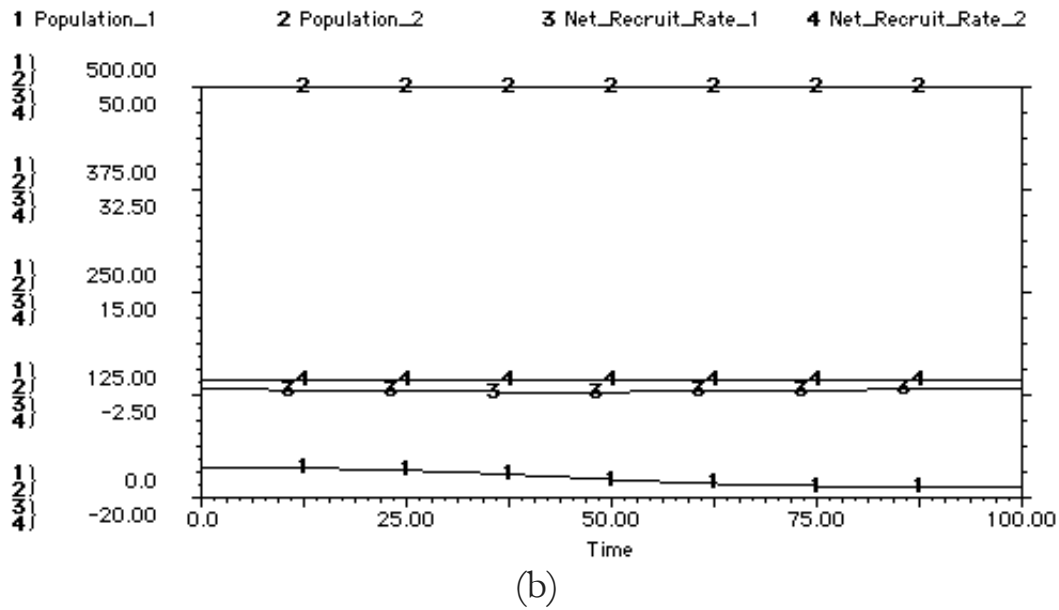
Fig. 4.6. A new stable equilibrium for population-1 is discovered when population-1 starts below and population-2 starts at or above MVP using a PCR of 0.003. The initial population sizes for the two populations are (a) 0 and 50 and (b) 37 and 500, respectively.
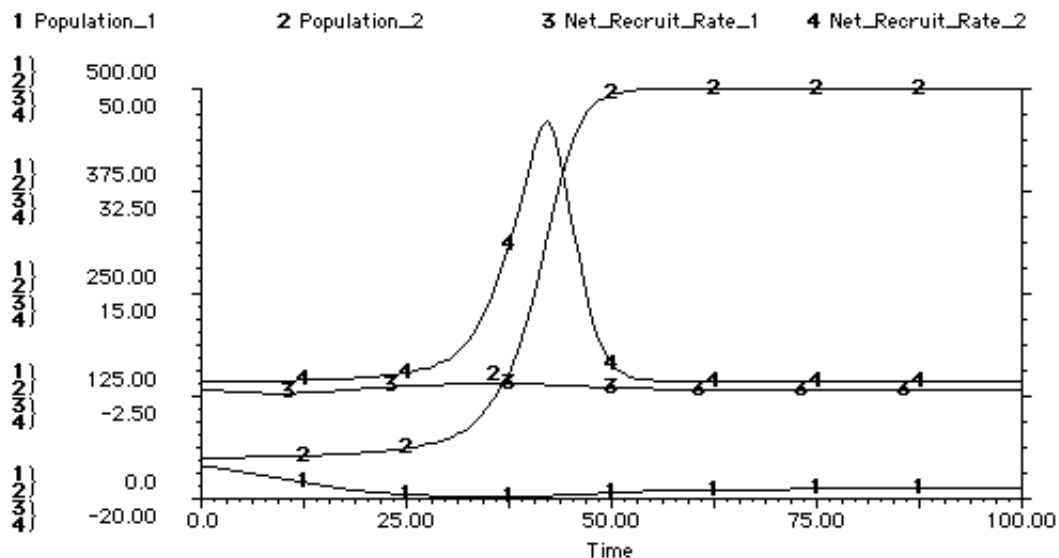
(c)
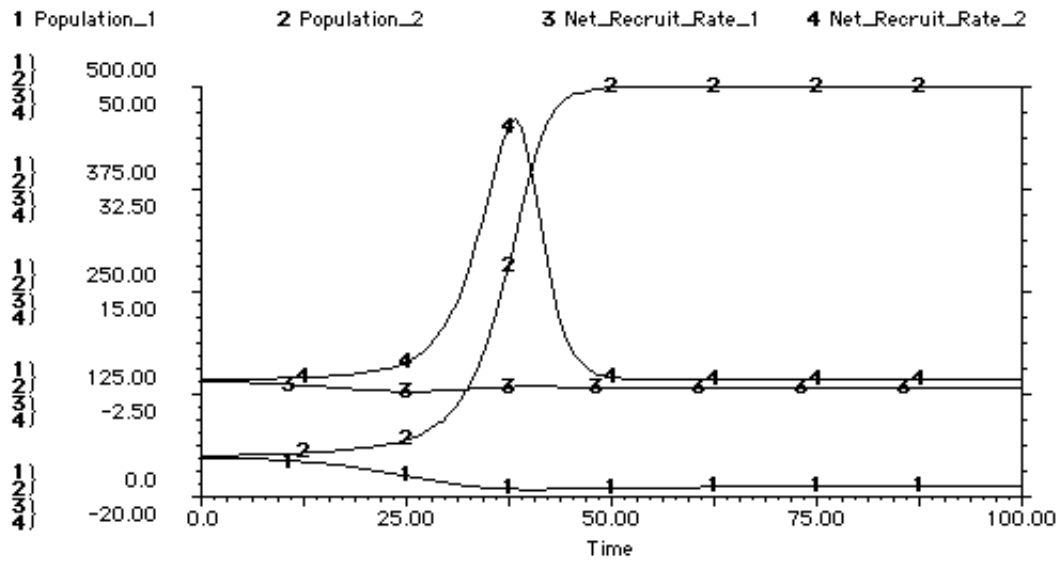
(d)

Fig. 4.6 (Continued). A new stable equilibrium for population-1 is discovered when population-1 starts below and population-2 starts at or above MVP using a PCR of 0.003. The initial population sizes for the two populations are (c) 40 and 50 and (d) 48 and 50, respectively.
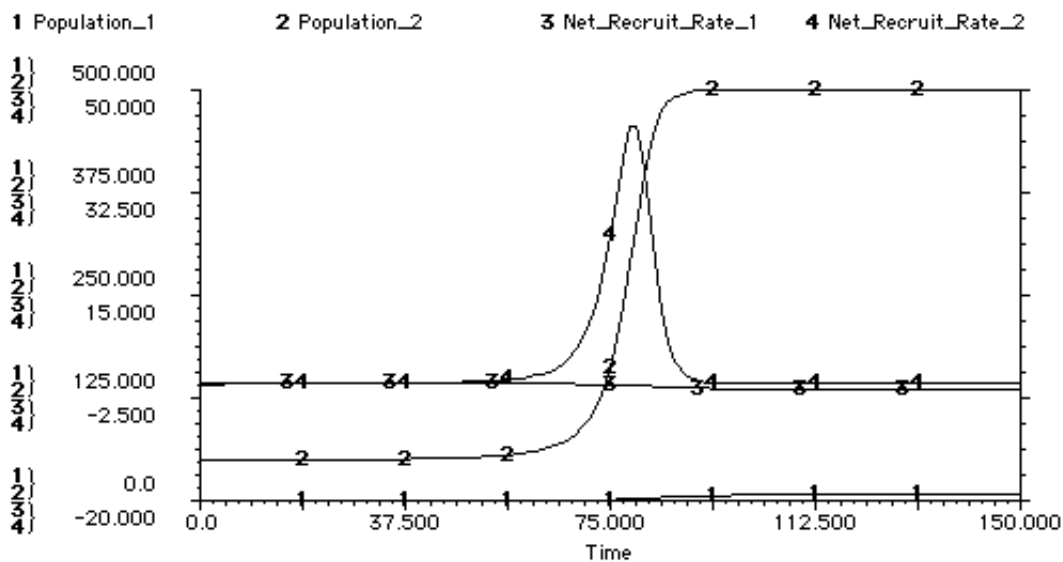
(a)
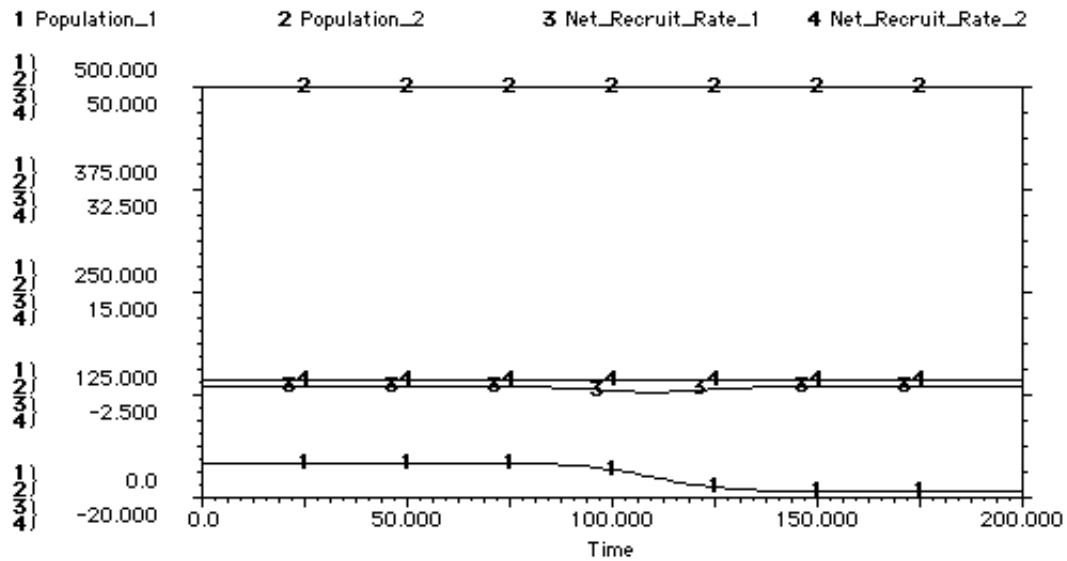
(b)

Fig. 4.7. A new stable equilibrium (7) for population-1 is reached when it starts below MVP and population-2 starts at or above MVP for a PCR of 0.002. The respective populations start with: (a) 1 and 50 and (b) 42 and 500.
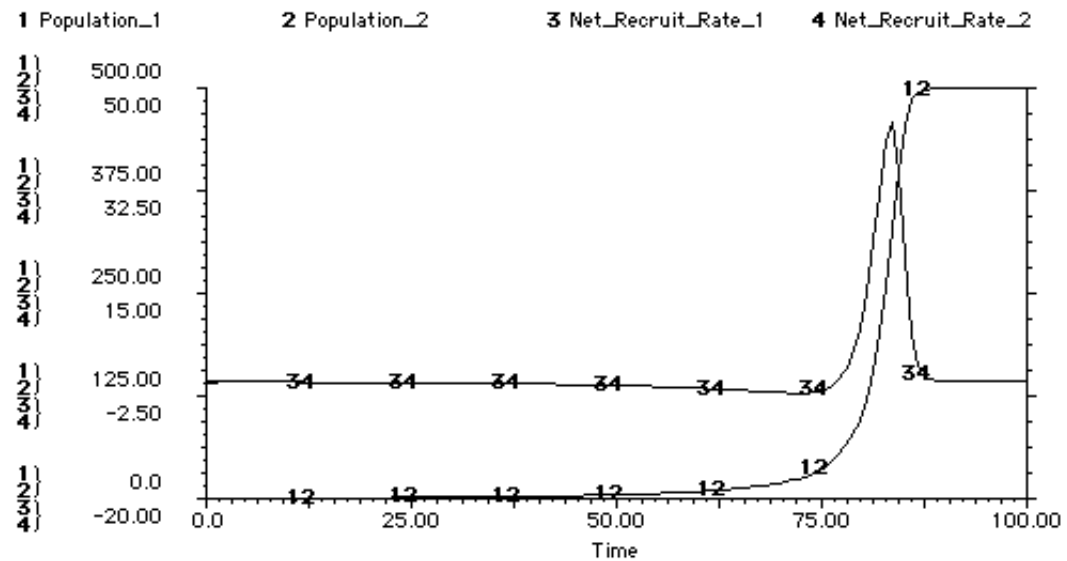
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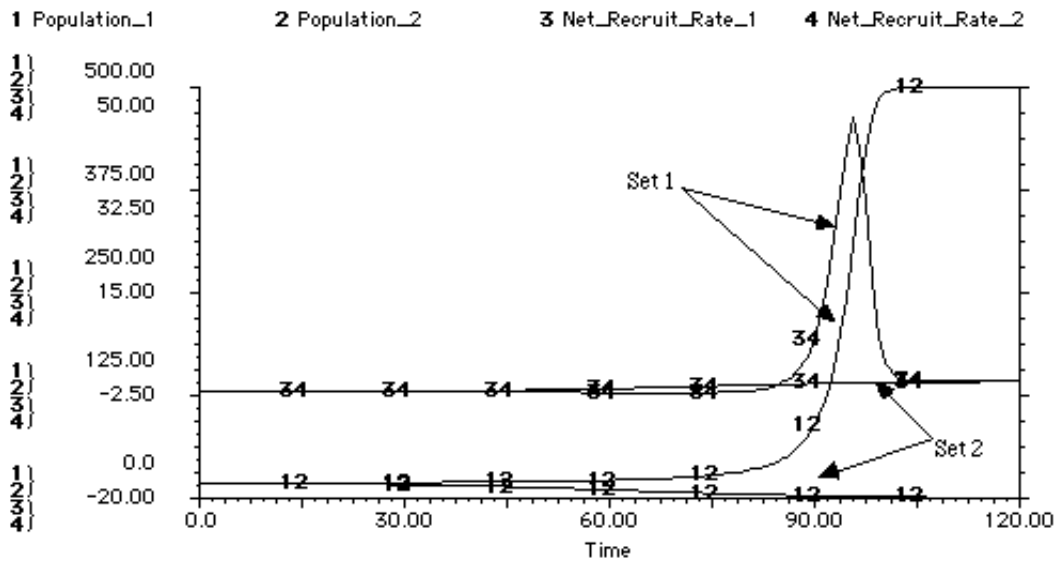
(b)

Fig. 4.8. Dynamics of the population system when both subpopulations are below MVP. (a) For a PCR of 0.2, one population starts with 0 and the other with 1. (b) For a PCR of 0.1, where both the populations start with 19 for set 1 and both the populations start with 18 for set 2.

(a)

(b)
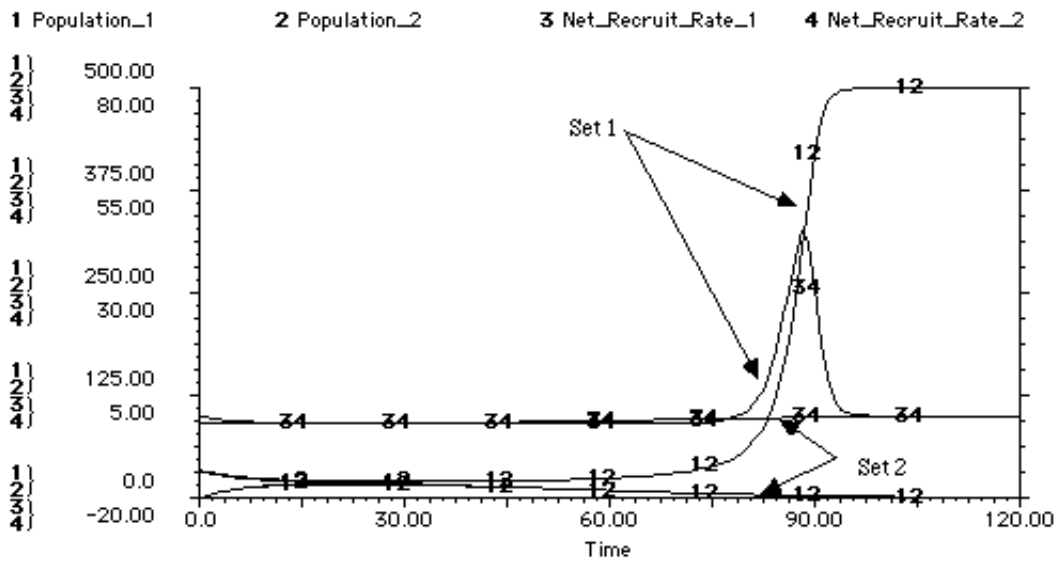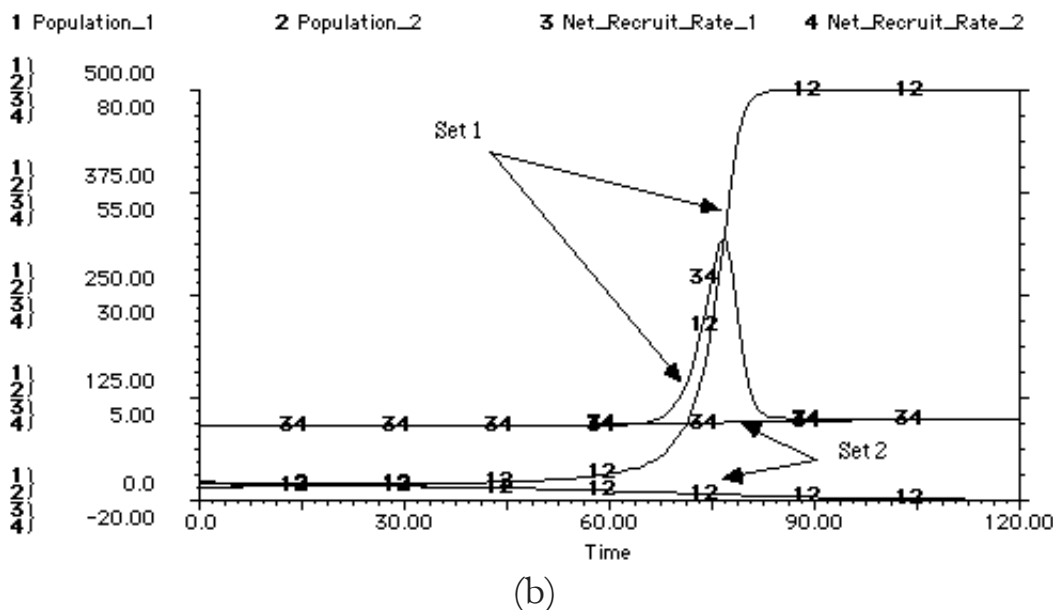
Fig. 4.9. Dynamics of the population system when both subpopulations are below MVP with a PCR of 0.1. (a) The initial size of population-1 is 0 (for both sets) while the initial size of population-2 is 33 for set 1 and 32 for set 2. (b) The initial size of population-1 is 15 (for both sets) while the initial size of population-2 is 23 for set 1 and 22 for set 2.

(a)

(b)
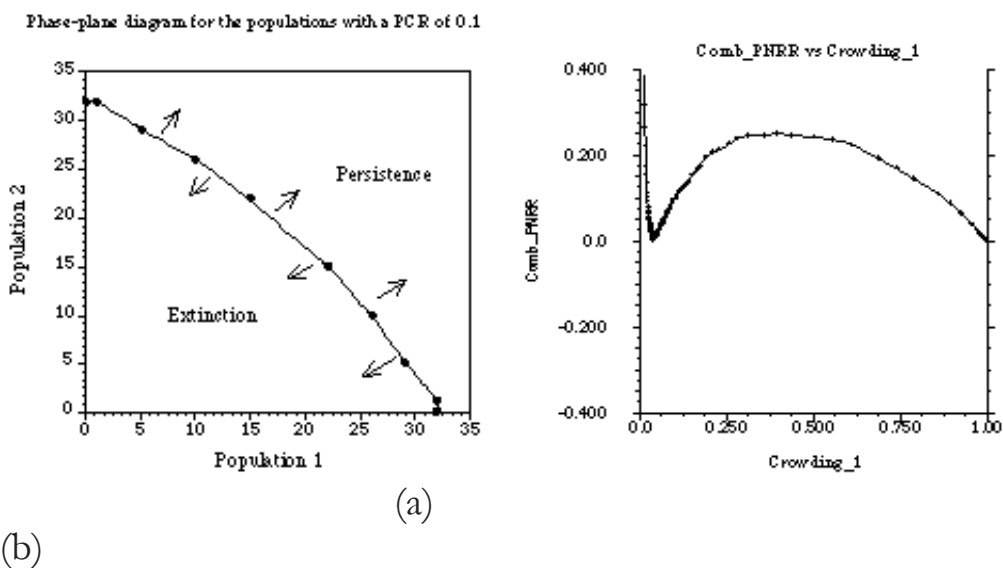
Fig. 4.10. (a) A phase-plane diagram for the populations both below MVP with a PCR of 0.1. (b) A combined percent net recruitment rate versus crowding curve generated by simulation with initial size of 0 and 33 for the two populations.
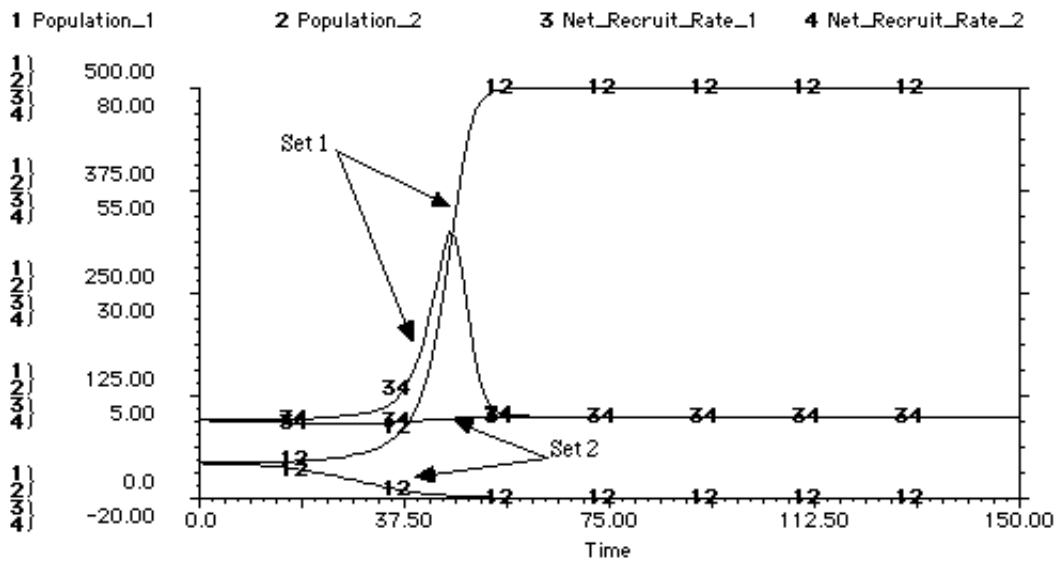
(a)
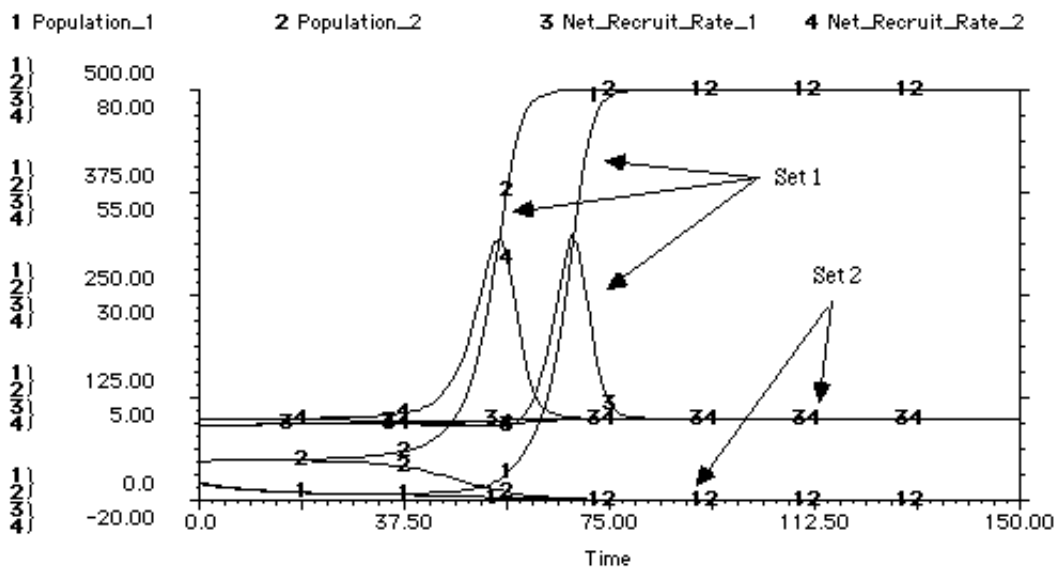
(b)

Fig. 4.11. Dynamics of the population system: (a) PCR=0.02, the initial populations are 44 for set 1 and 43 for set 2 and (b) PCR=0.02, the initial populations are 21 and 48 for set 1 and 20 and 48 for set 2.
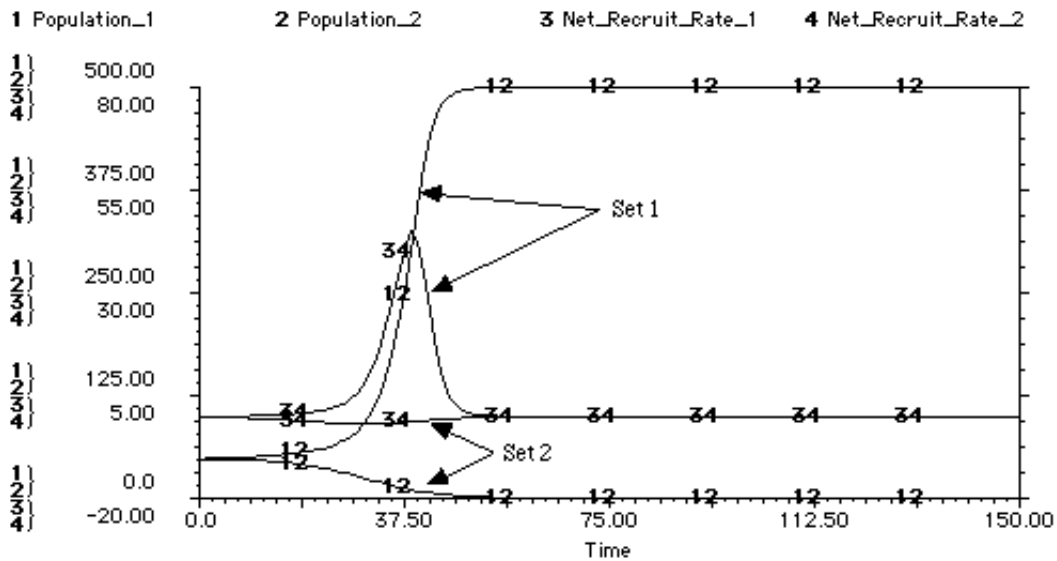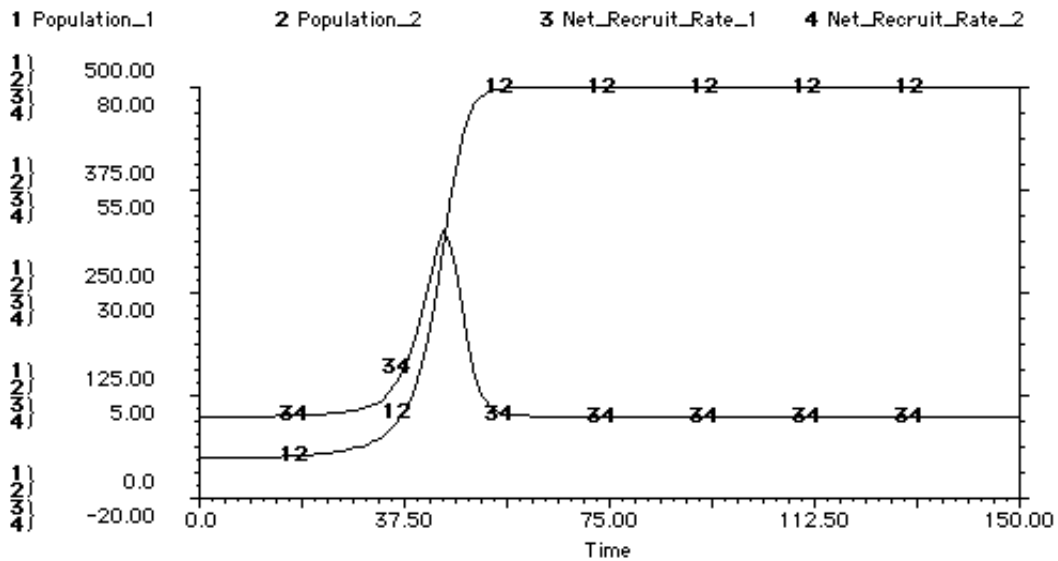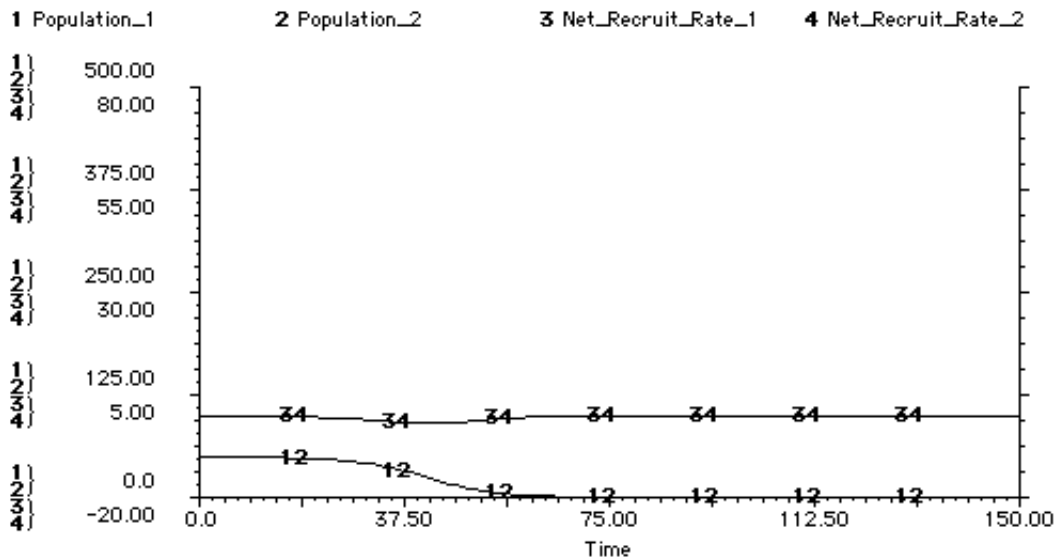
(c)
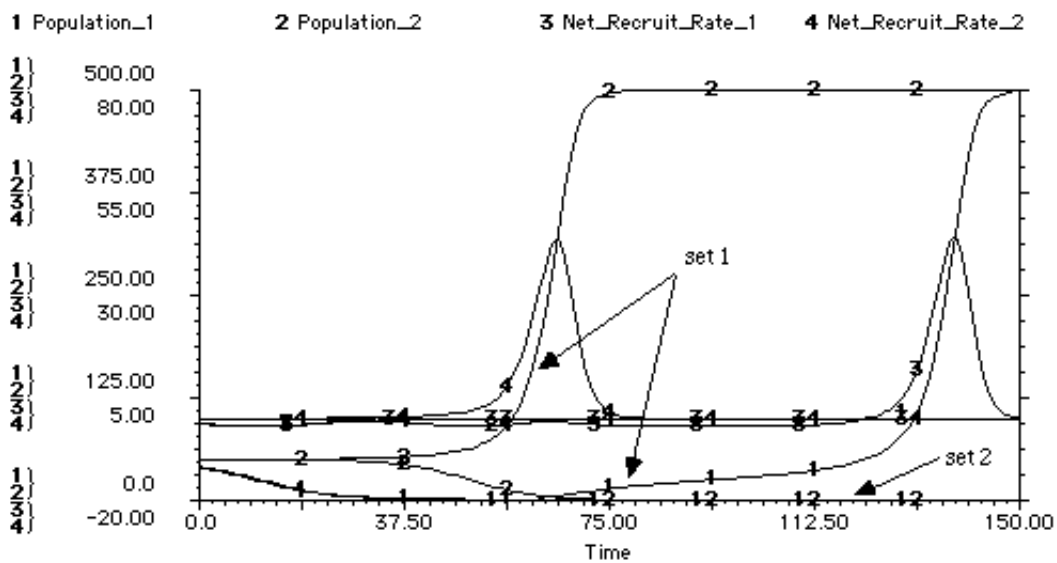
(d)

Fig. 4.11 (Continued). Dynamics of the population system: (c) PCR=0.005, the initial populations are 49 for set 1 and 48 for set 2 and (d) PCR=0.005, the initial populations are 41 and 49 for set 1 and 40 and 49 for set 2.
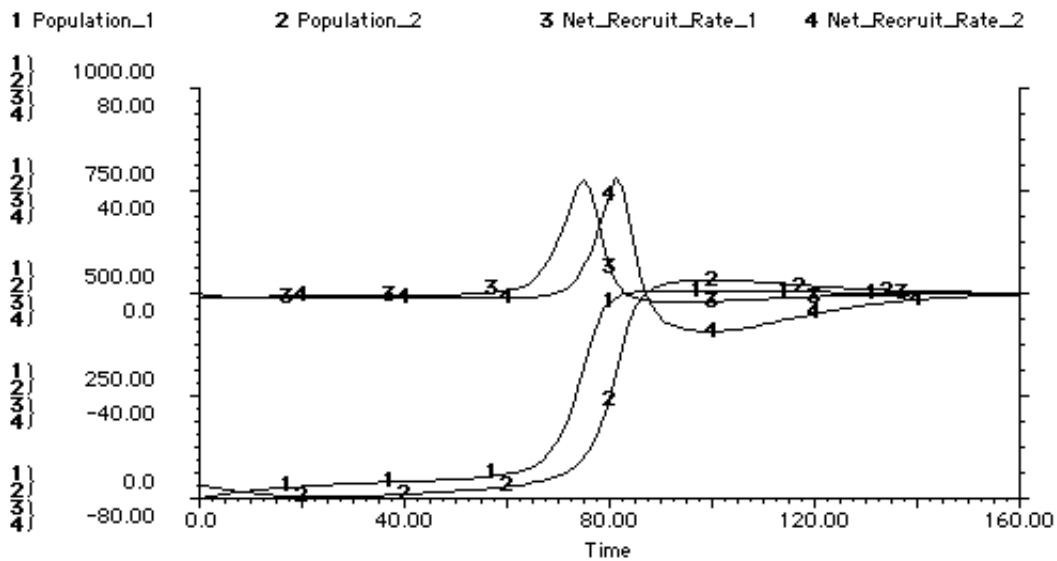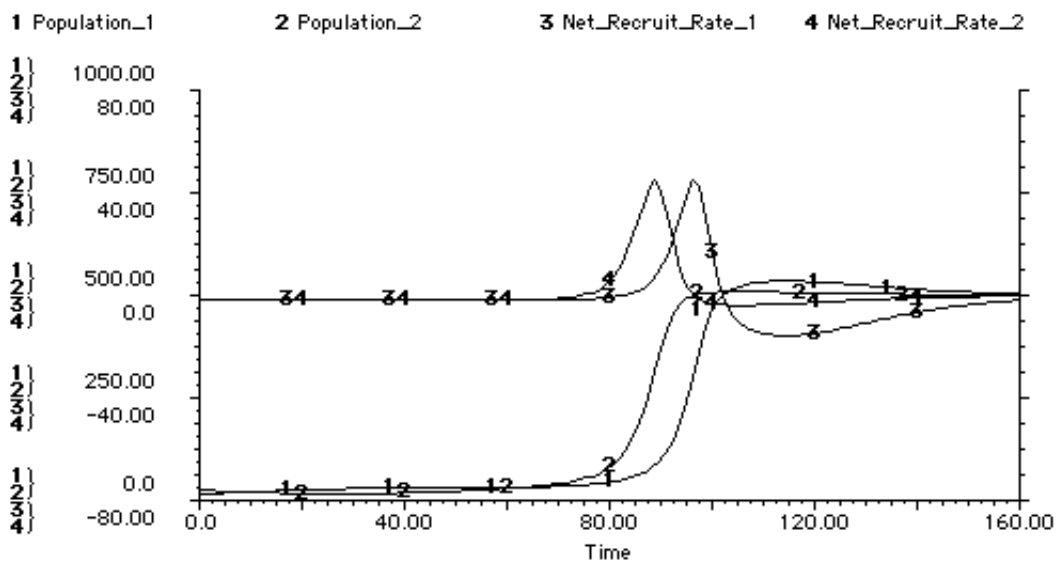
(a)

(b)

Fig. 4.12. Dynamics of the population system when the initial populations are 49: (a) PCR=0.004 and (b) PCR=0.003.
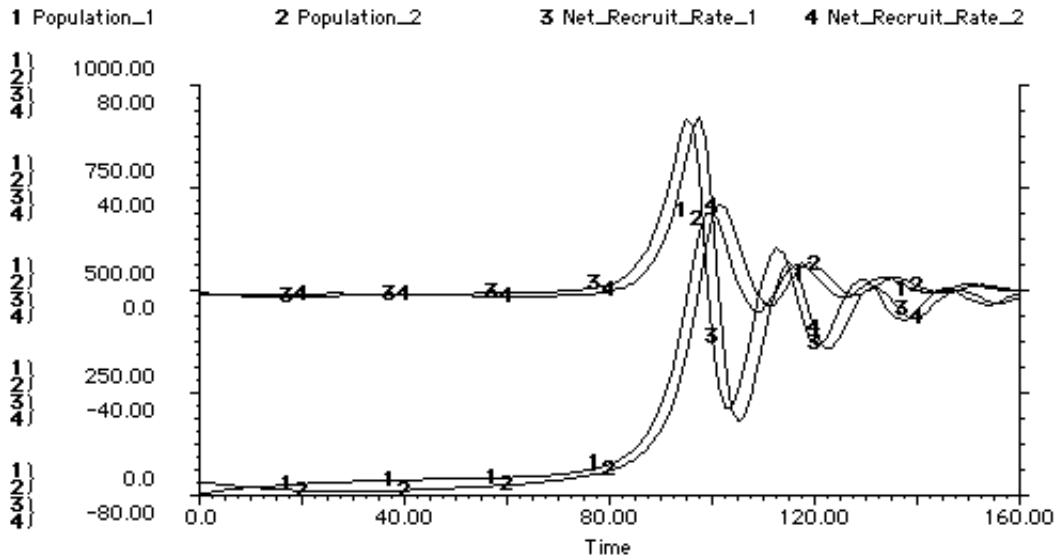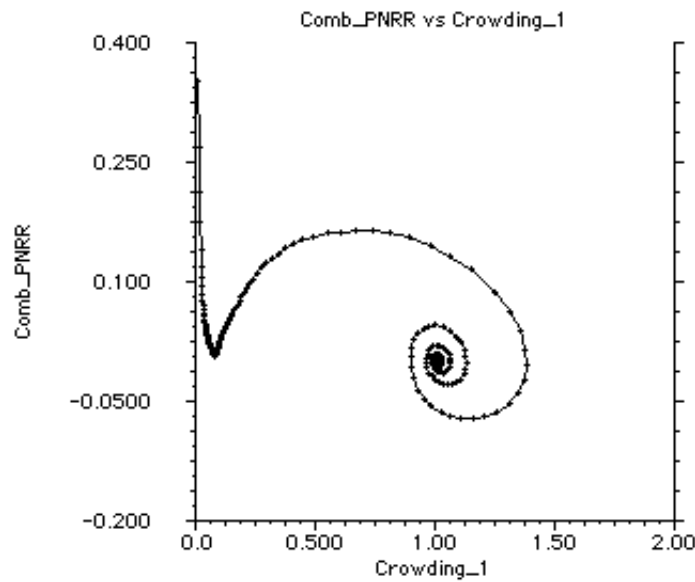
(a)

(b)

Fig. 4.13. Dynamics of the population system with a timedelay in colonization: (a) delaytime=30, the initial populations are 0 and 32, respectively, and (b) delaytime=30, the initial populations are 15 and 25, respectively.

(a)

(b)

Fig. 4.14. Dynamics of the population system with respective delaytimes of 30 and 4 for colonization and density-dependent regulation: (a) temporal change in population size and net recruitment rates with initial populations being 5 and 32 and (b) the percent net recruitment rate versus crowding curve whose altered trajectory reflects the effects of the delays.