Modelling Patchy Ecological Systems Using the System Dynamics Approach

Jianguo Wu[1], Yaman Barlas[2], and John L. Vankat[1]

Department of Botany[1]
and
Department of Systems Analysis[2]
Miami University
Oxford, OH 45056

Abstract

A System Dynamics model of an ecological system consisting of two patchily distributed populations is constructed to study the effects of inter-patch colonization on the persistence of the species. The model structure is primarily composed of the negative feedback loops dominant in local (within-patch) population regulation and a regional positive feedback loop coupled with two negative loops which regulate the inter-patch species colonization.

The simulation results show that with colonization the population system always persists if at least one of the populations is larger than a minimum viable population size (MVP). If the species has sufficiently large colonizing ability, the populations are always able to reach the carrying capacity. Otherwise, the population with below-MVP initial size may reach a new stable equilibrium at a low population density. When both populations are below MVP, there are two possibilities depending on the magnitude of species colonization ability: (1) both stabilize at the carrying capacity level and (2) both go extinct. The simulations also demonstrate that delays in colonization and population regulation may have distinctive impacts on species persistence and dynamics of the population system. The study may provide useful information for species conservation and design of nature reserves.

Introduction

Patchiness has been increasingly recognized by ecologists as a ubiquitous phenomenon in nature. For instance, species populations occur in spatially varying continuous environments or in discrete patches. Modelling the dynamics of populations in such patchy habitat settings is of great importance to gain understanding of ecological systems and has drawn a great deal of research endeavor recently (e.g., Levin 1976; 1978; DeAngelis and Waterhouse 1987; Lawton 1987; Hastings and

Wolin 1989). Because traditional modelling 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.

There are two predominant approaches in modelling the dynamics of pachily distributed populations. The first, "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 to 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). In contrast, the second approach utilizes diffusion-reaction equations as its modelling 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 modelling studies on population dynamics in varying environments (e.g., Levin 1976; Okubo 1980).

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 has substantially limited the applicability and popularity of this approach in ecology. DeAngelis et al. (1979; 1986) have made new headway by employing the theory of positive linear systems with this modelling methodology in their study on persistence and stability of tree species in a patchy environment.

Based on the framework put forward by Wu and Vankat (1989), we have developed a one-species-two-patch model using System Dynamics modelling approach to simulate the local (within-patch) and regional (over-all-patch) dynamics of populations. Impacts of dispersal on species persistence in such a patchy system are examined through simulations. While the two approaches mentioned above have been predominated by analytical models, our modelling scheme (also see Wu and Vankat 1989) may shed new lights on developing realistic, comprehensive simulation models of population dynamics in patchy environments.

Model Description

Model Structure

Many species have populations occupying discrete habitat patches or islands, especially, in human-dominated landscapes (e.g., mountain tops, habitat remnants, nature reserves). The term metapopulation has been used to denote several interacting subpopulations of a species distributed over such a patchy area (Levins 1970; Wilcox 1986). We develop a one-species-two-patch model to investigate the dynamics of a metapopulation which is composed of two subpopulations. The two patches are assumed identical and the major state variables are population sizes in the patches (Population-1 and Population-2). The within-patch or local dynamics of each population is regulated by density-dependent mechanisms, which is essentially the same as described in Wu and Barlas (1989). Each local population has its carrying capacity for the species in question which is in turn determined by the patch area. We also assume that there exists a threshold population size below which the population cannot recover (Allee effect, see Lande 1988) which has been called minimum viable population (MVP, cf. Shaffer 1981; Soule 1987). Finally, a regulatory delay is incorporated so that the crowding effect on the local net growth (recruitment) rate takes place after a time delay.

The overall dynamics of this metapopulation is determined by both local and regional processes. Inter-patch colonization is affected by the species' colonizing ability, inter-patch distance, population size of the source patch, and habitat availability in the target patch. The inter-patch 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. 1). A STELLA version structural diagram that depicts the relationships among the model variables is presented in Fig. 2.

Model Formulation

Due to space limitation, we will not discuss the individual model equations. All model equations, constants and graphical values are provided in the STELLA program listing (Table 1). We briefly describe how two crucial ecological concepts are modelled. First, the effect of crowding (expressed by the ratio of population to carrying capacity) on the local recruitment rate is presented graphically in Figure 3a. This figure assumes an MVP value of 50 (a number suggested by some population studies, cf. Lande 1988) and a carrying capacity of 500. Second, the effect of crowding on habitat availability (which in turn influences the regional colonization rates) is also graphically modelled (Fig. 3b). This graph, too, assumes a carrying capacity of 500.

Model Simulation and Analysis of Results

POPULATION DYNAMICS WITHOUT INTER-PATCH COLONIZATION

For the purposes of testing and verification of the basic model structure and functions, we have first simulated the model without consideration of inter-patch 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). 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).

However, the time delay engaged in the density-dependent regulating mechanisms may effect population oscillations. While a moderate delaytime (for example, 5) generates damping oscillatory behavior, a large enough delaytime (e.g., 99,999) can essentially break down the density-dependent regulatory feedback loops so that the exponential growth pattern emerges (Fig. 4). The above patterns and more detailed discussion on effects of population regulatory timedelay on population dynamics can be found in Wu and Barlas (1989).

DYNAMICS OF THE POPULATION SYSTEM WITH INTER-PATCH COLONIZATION

In order to investigate the effects of different colonization intensities with varying initial population sizes on the dynamics of the metapopulational system, we designed three simulation scenarios. The first is to examine 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 an even more intriguing case in an ecological sense. In both of the above two scenarios, the delay in inter-patch colonization loop is assumed to be non-existent. The third scenario briefly examines effects of inter-patch time delays on dynamics of the population system and present an introduction to further study along the line.

Population Dynamics with One Subpopulation below MVP

While the source patch population, target patch habitat availability, and inter-patch distance all affect the overall fluxes of colonists, percent colonization rate (PCR) in our 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 the 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.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 - 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. 6a), or when one population begins with 37 or below and the other stays at 500 (Fig. 6b), or when one is between 38 and 48 and the other is near MVP from above (Fig. 6c,d). For a PCR of 0.002, a new stable point of 7 (rounded from 7.30) is found, which is approached when one population is lower than 7 and the other larger than MVP (Fig. 7a) or when one is smaller than 43 (42.79 to be exact) and the other stays at 500 (Fig. 7b).

The above simulation results show that, in the scenario of one population below MVP, 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 blow 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 have to rely heavily on inter-patch colonist influxes because of stochastic events in nature. It becomes foreseeable by now that 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 collapsed in effect and, therefore, a population below its MVP is bound to be extinct no matter how large the other one is in such a system.

Population Dynamics with both Subpopulations below MVP

Can the patch system persist with inter-patch colonization when each of its subpopulations approaches extinction alone? How different PCR values affect the species persistence in such a patchy environment? We address these questions by simulating the model for different PCRs along with varying initial population sizes. When PCR is equal to 0.2, both populations eventually reach the carrying capacity if at least one of them is larger than zero (Fig. 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. 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 stabilize at the carrying capacity ultimately (Fig. 9a). To achieve the same goals, one population has to be larger than 22 if the other is 15 (Fig. 9b). In fact, for a given size of population-1, there always exists a minimum size of population-2 for their persistence which decreases with the increase in the size of population-1, or vise versa (Fig. 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 can be clearly revealed by comparing the combined percent net local recruitment rate (Comb-PNRR) versus crowding curve (Fig. 10b) with the previous PNRR-Crowding curve (the first half of Fig. 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 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. 11a). If one population has an initial size of 48, the other has to be at least 21 for both of them to sustain at the carrying capacity (Fig. 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 disappear together otherwise (Fig. 11c). However, if one population is 49, the persistence of both populations is guaranteed if the other is larger than 40 (Fig. 11d). For a PCR of 0.004, the two populations eventually stabilize at the carrying capacity level when they both start with 49, but both go extinct when starting with the same initial size for a smaller PCR (0.003, Fig. 12a,b).

In summary, with colonization both of the constituent populations either stabilize at the carrying capacity level or go to extinction ultimately when they are both below MVP. The simulations have demonstrated that a metapopulational system can 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.

Effect of Time Delays on the Patchy Population System

How do the time delays involved in regional colonization and local density-dependent regulatory processes affect the dynamics of population systems and thus the species persistence? As a preliminary attempt, we approach this problem by examining the effects of delays for a PCR of 0.1 and a colonization delaytime of 30 (Fig. 13a-d) without including the local regulatory delay. 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. 13b, compare with Fig. 9b). However, the same delay induces an earlier arrival to the carrying capacity when one population starts with 32 and the other is zero (Fig. 13a, in contrast with Fig. 9a). While the former may result from prolonged low colonist fluxes, the latter 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. In addition, a colonization delay of this size is able to cause the populations to overshoot the carrying capacity (Fig. 13a,b).

The delay in local population regulation introduces fluctuations to the system (Fig.4 and 14a). When the colonization delaytime is 30 and the regulation delaytime is 4, a damping fluctuation in population size occur (Fig. 14a). Associated with this, the combined percent net recruitment rate exhibits a distinctive pattern with increasing population (Fig. 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 yet to be dealt with further in our future studies.

Conclusions and discussion

According to our model, when one of the two subpopulations is larger than the minimum viable population the metapopulational system always persists. 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 necessarily subject to frequent local extinctions. In a patchy system consisting of two below MVP populations, depending on the colonization ability of species and the initial population sizes, they either stabilize at the carrying capacity or both go to extinction. It seems that a system with a large-sized and a small-sized population has a better chance for persistence than one with two medium-sized populations.

Assuming continuous fluxes of colonists, the 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. These simulation results may have implications for species conservation and the design of nature reserves.

In our continuing study, a more comprehensive investigation on effects of the delays and asymmetric colonization rates on metapopulation dynamics will be conducted. Effects of spatial aspects (e.g., patch area, inter-patch distance) and stochasticities in population demography and environment on colonization and species persistence are to be included. In addition, the current one-species-two-patch model will be extended to one-species-many-patch models.

Acknowledgement

The study was supported by the Academic Challenge Grant from the Department of Botany, Miami University to Jianguo Wu.

References

DeAngelis, D. L., W. M. Post, and C. C. Travis. 1986. *Positive Feedback in Natural Systems.* Berlin: Springer-Verlag.

DeAngelis, D. L., C. C. Travis, and W. M. Post. 1979. Persistence and Stability of Seed-Dispersed Species in a Patchy Environment. *Theoretical Population Biology* 16:107-125.

DeAngelis, D. L., and J. C. Waterhouse. 1987. Equilibrium and Nonequilibrium Concepts in Ecological Models. *Ecological Monographs* 57:1-21.

Hastings, A., and C. L. Wolin. 1989. Within-patch Dynamics in a Metapopulation. *Ecology* 70:1261-1266.

Lande, R. 1988. Genetics and Demography in Biological Conservation. *Science* 241:1455-1460.

Lawton, J. H. 1987. Population Dynamics: Fluctuations in a patchy world. *Nature* 326:328-329.

Levin, S. A. 1976. Population Dynamic Models in Heterogeneous Environments. *Annual Reviews of Ecology and Systematics* 7:287-310.

———. 1978. Population Models and Community Structure in Heterogeneous Environments. In *Studies in Mathematical Biology, Part II: Populations and Communities*, ed. S. A. Levin, pp.439-476. The Mathematical Association of America.

Levins, R. 1970. Extinction. In *Some Mathematical Problems in biology*, ed. M. Gerstenhaber, pp.77-107. American Mathematical Society.

Moffatt, A. S. 1989. Invaded Ecosystems: Models and Theory for an Ecological Phenomenon. *MOSAIC* 20:4-15.

Okubo, A. 1980. *Diffusion and Ecological Problems: Mathematical Models.* Berlin:Springer-Verlag.

Shaffer, M. L. 1981. Minimum Population Sizes for Species Conservation. *BioScience* 31:131-134.

Soule, M. E. 1987. *Viable Populations for Conservation.* Cambridge: Cambridge University Press.

Wilcox, B. A. 1986. Extinction Models and Conservation. *Trends in Ecology and Evolution* 1:46-48.

Wu, J., and Y. Barlas. 1989. Simulating the Dynamics of Natural Populations Using the System Dynamics Approach. In *Proceedings of the SCS Western Multiconference* (San Diego, CA), ed. S. Spencer and G. Richardson, pp.6-11. San Diego, CA.: Simulation Councils, Inc.

Wu, J., and J. L. Vankat. 1989. A Framework for Studying Species Population Dynamics of Landscape Patches. In *Proceedings of the Fourth Annual Landscape Ecology Symposium* (Fort Collins, CO), pp.47. US-International Association for Landscape Ecology.

Table 1. A STELLA Program Listing of the One-Species-Two-Patch 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),(0.500,0.160),
        (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)
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)
```

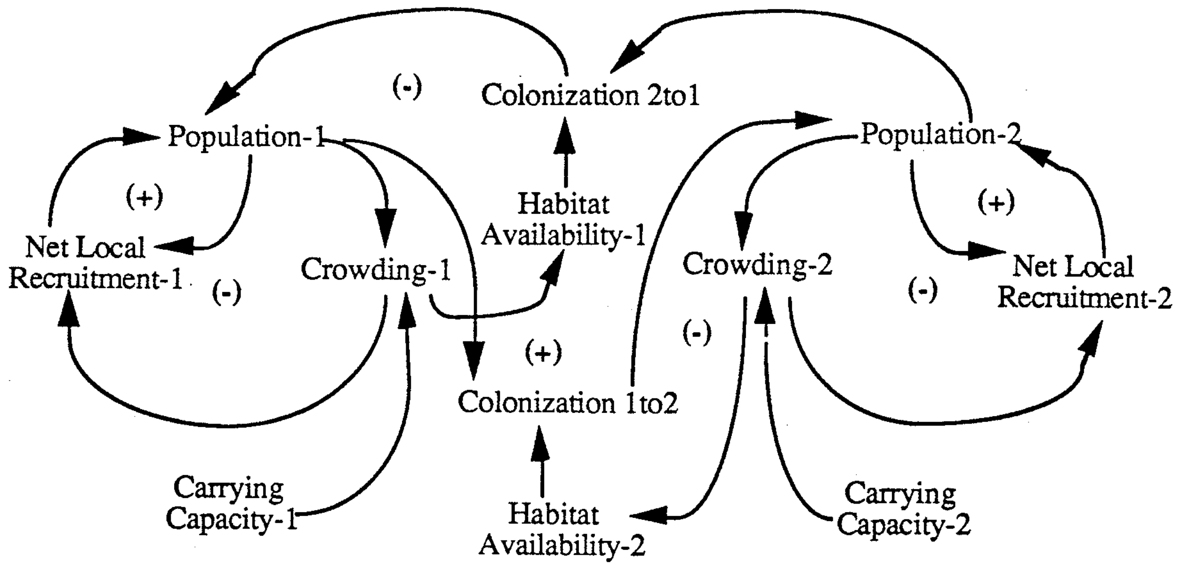


Fig. 1. Causal-loop diagram of the feedback structure of the one-species-two-patch model.

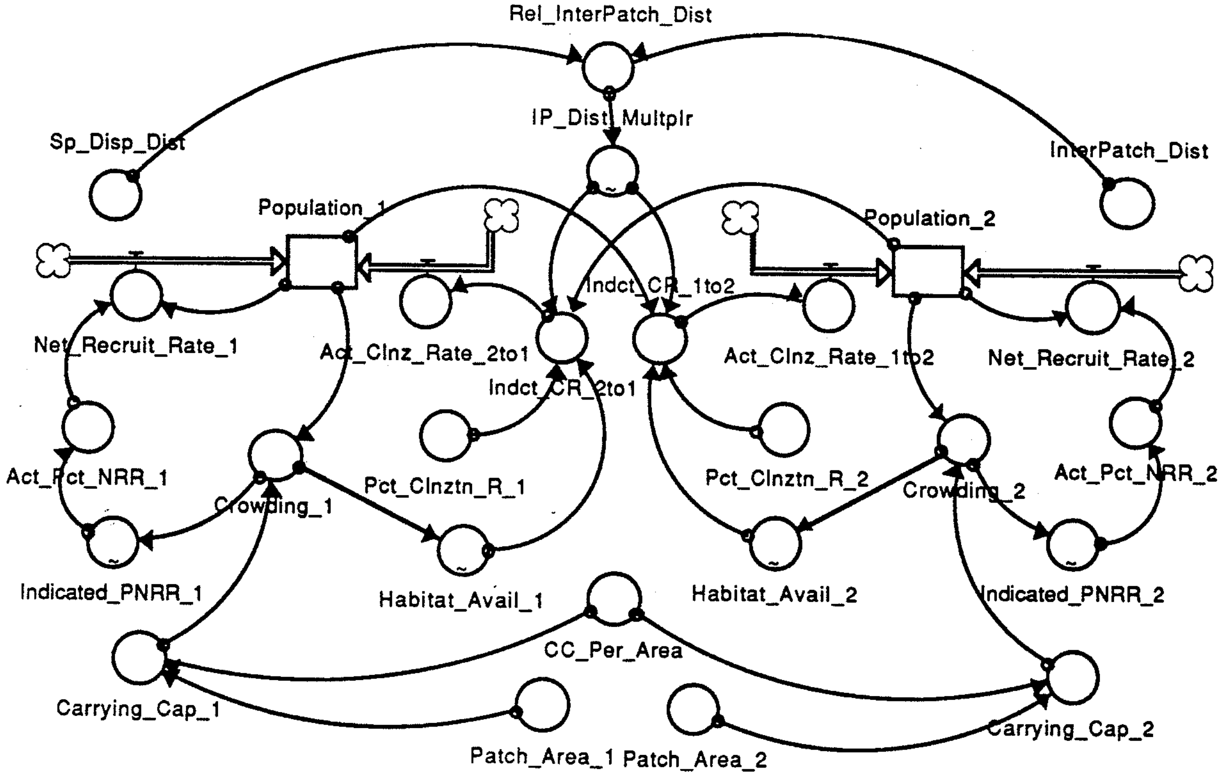
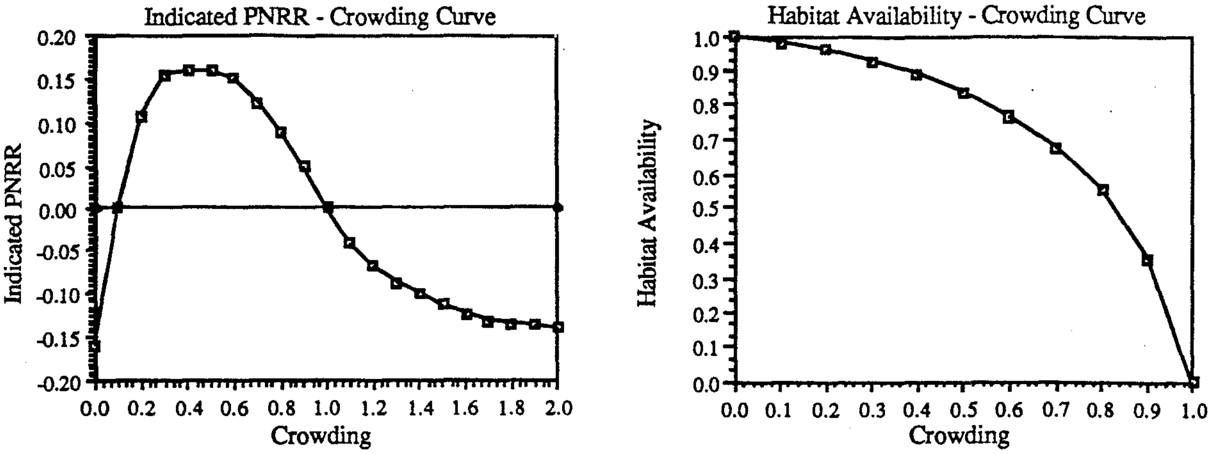


Fig. 2. Structural diagram of the one-species-two-patch model.



(a) (b)

Fig. 3. (a) Relationship between crowding and indicated (without delay) percent net recruitment rate. (b) relationship between crowding and habitat availability for colonization.

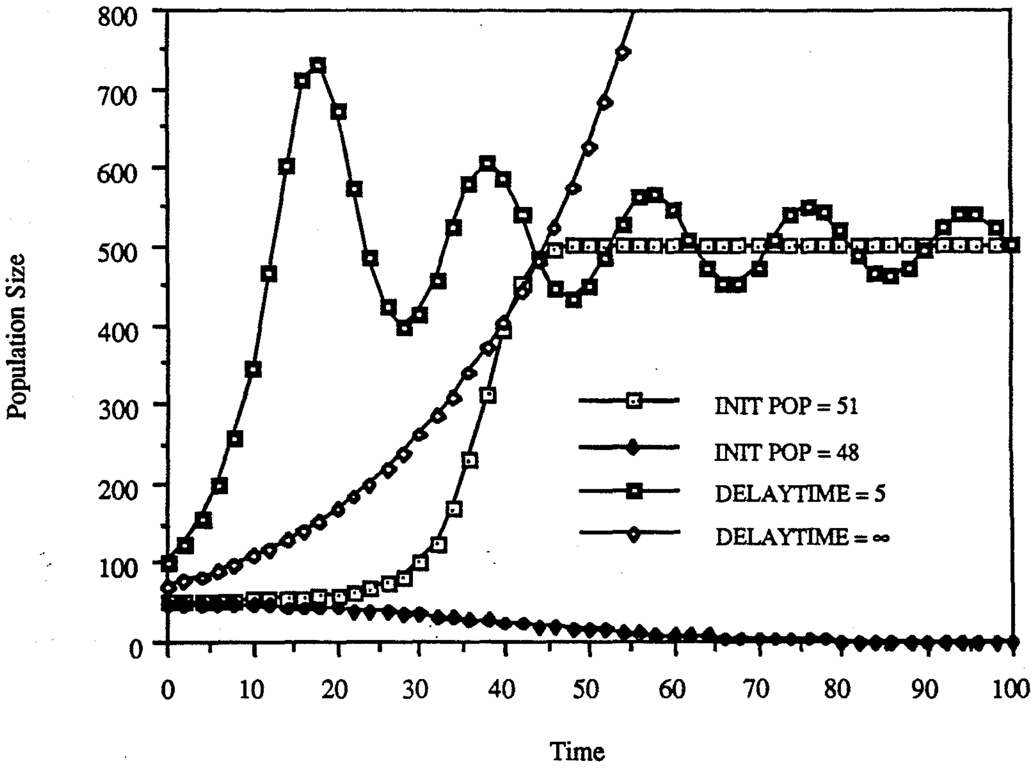
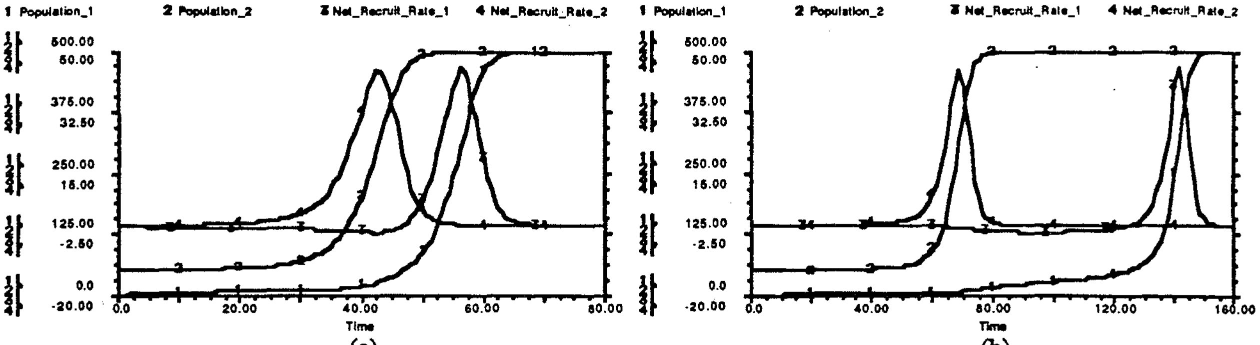
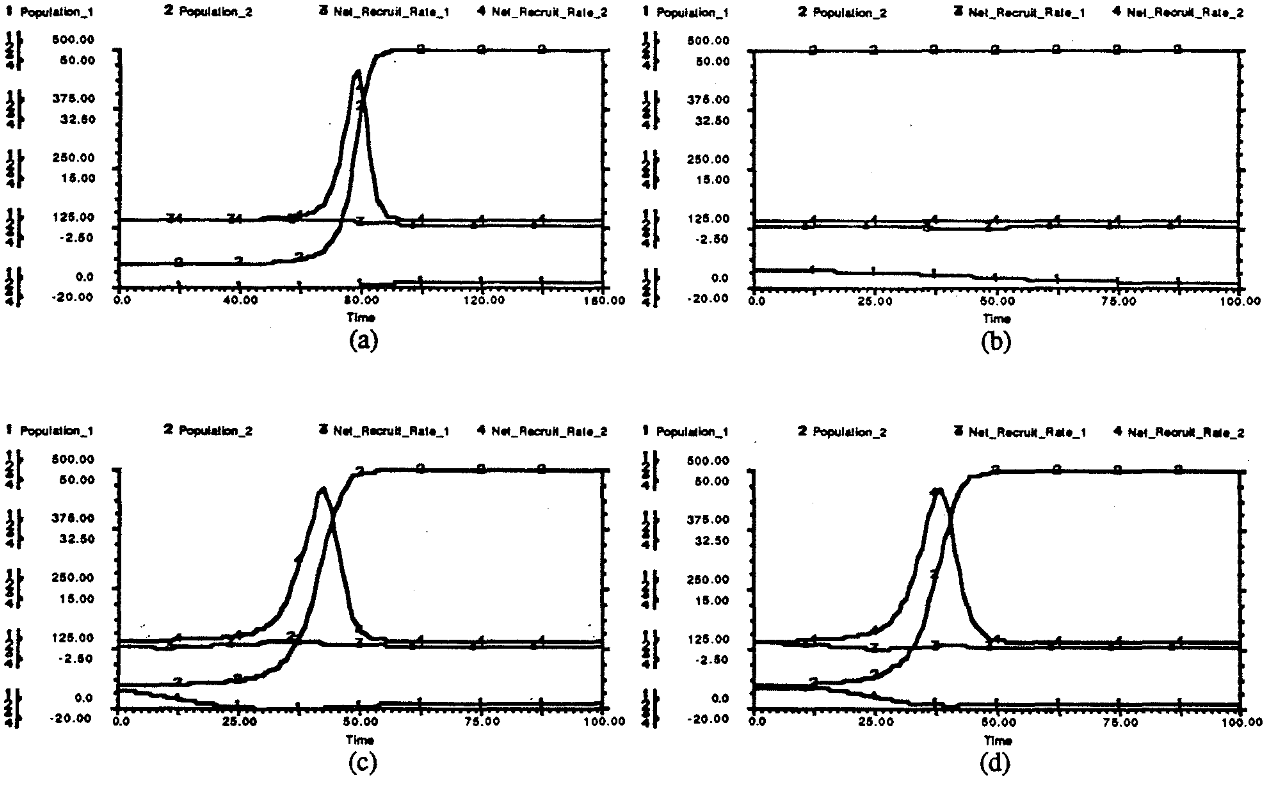


Fig. 4. Dynamics of the population system without inter-patch colonization, illustrating a MVP of 50 and a carrying capacity of 500. A moderate delaytime produces oscillatory behavior and a large enough delaytime eventually generates an exponential growth pattern.



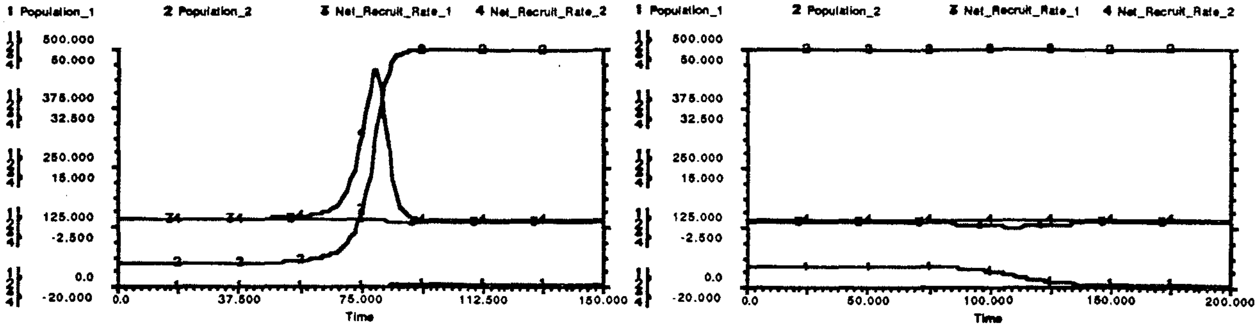
(a) (b)

Fig. 5. Dynamics of the population system when one subpopulation is below and the other 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, for a PCR of 0.005.



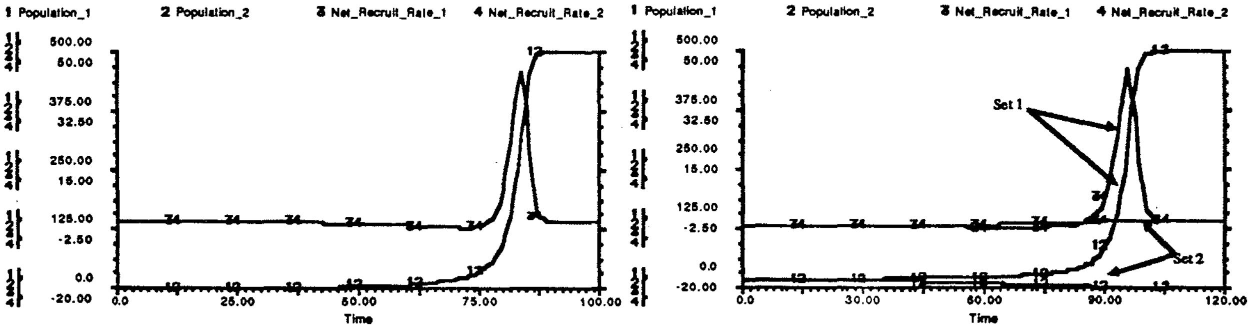
(a) (b) (c) (d)

Fig. 6. A new stable equilibrium for population-1 is discovered when population-1 starts below and population-2 starts above MVP using a PCR of 0.003. The initial population sizes for the two populations are (a) 0 and 50, (b) 37 and 500, (c) 40 and 50, and (d) 48 and 50, respectively..



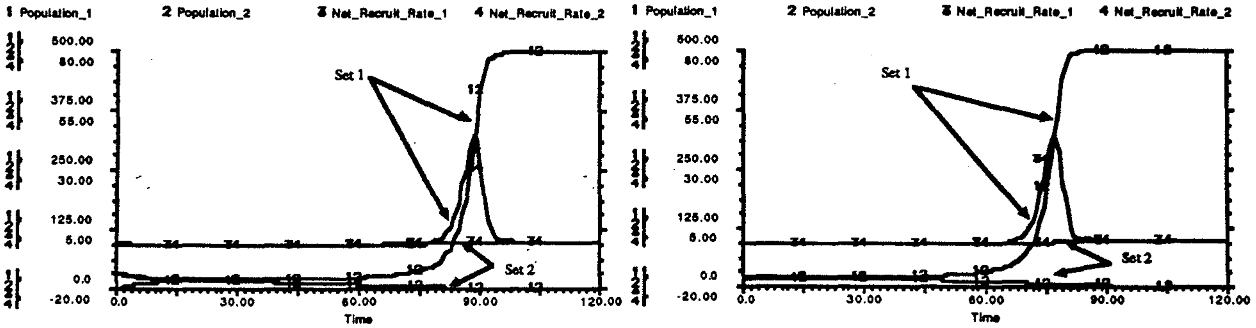
(a) (b)

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



(a) (b)

Fig. 8. Dynamics of the population system when both the 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, set 1: both the populations start with 19 and set 2: both the populations start with 18.



(a) (b)

Fig. 9. Dynamics of the population system when both the subpopulations are below MVP with a PCR of 0.1. (a) The initial size of population one is 0 (for both sets) while the initial size of population two is 33 for set 1 and 32 for set 2. (b) The initial size of population one is 15 (for both sets) while the initial size of population two is 23 for set 1 and 22 for set 2.

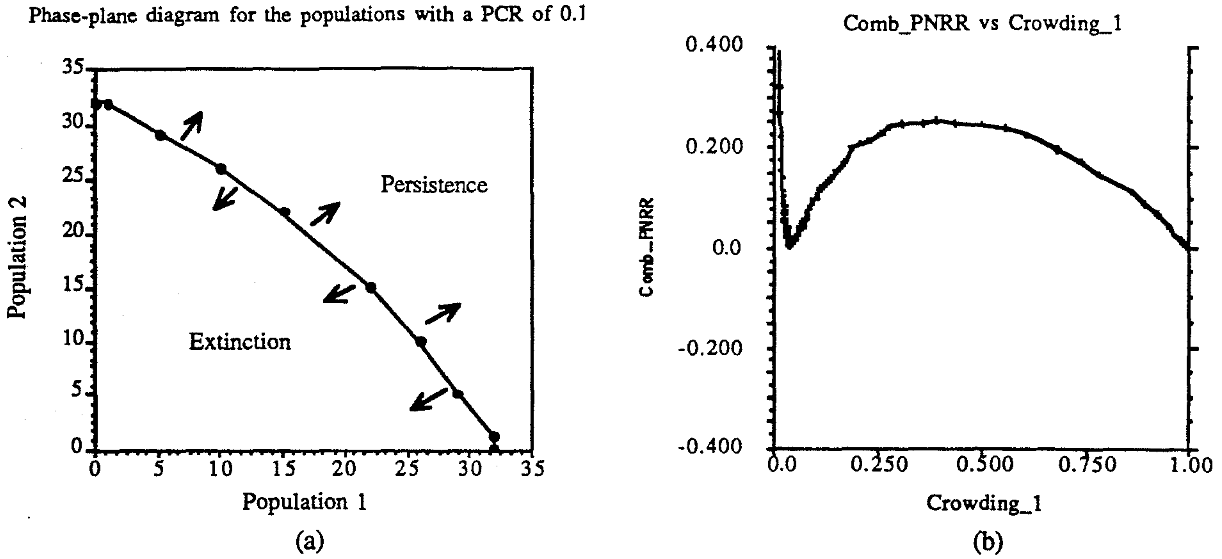


Fig. 10. (a) A phase-plane diagram for the populations both below MVP with a PCR of 0.1. (b) A combined percent net recruitment rate versus crowding curve generated by simulation with initial size of 0 and 33 for the two populations.

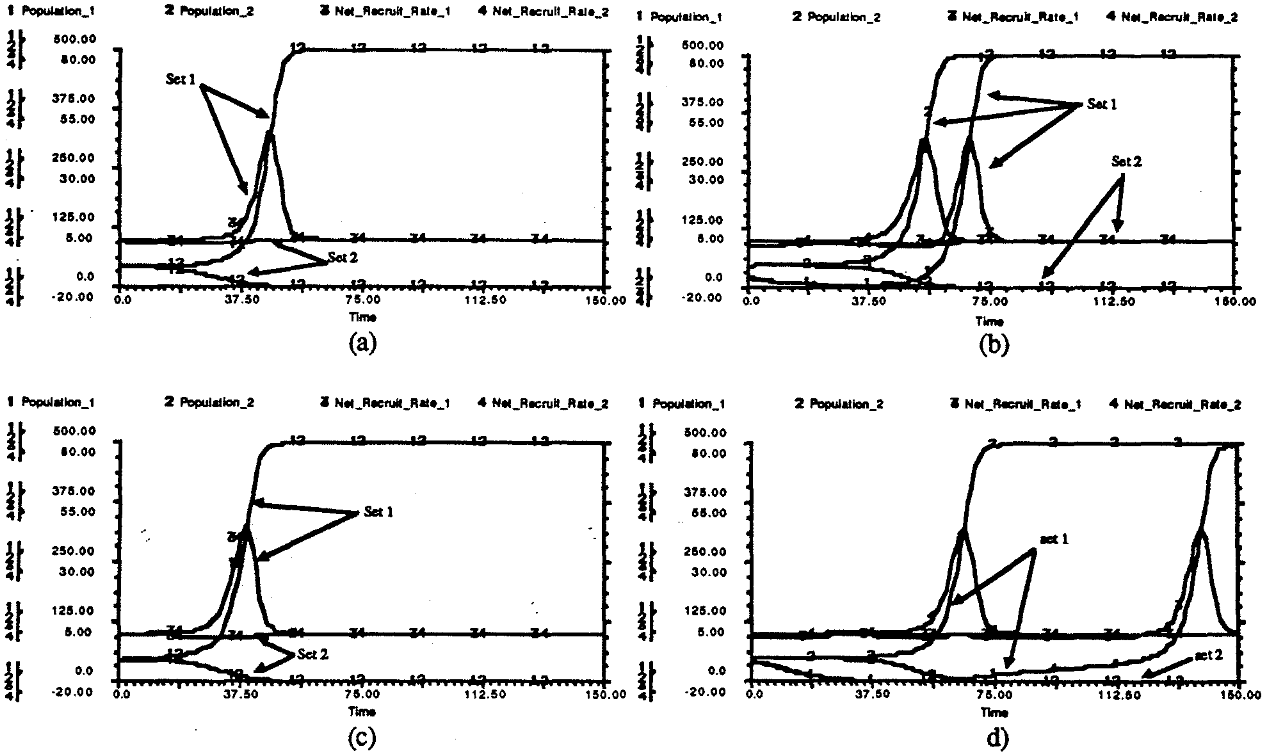
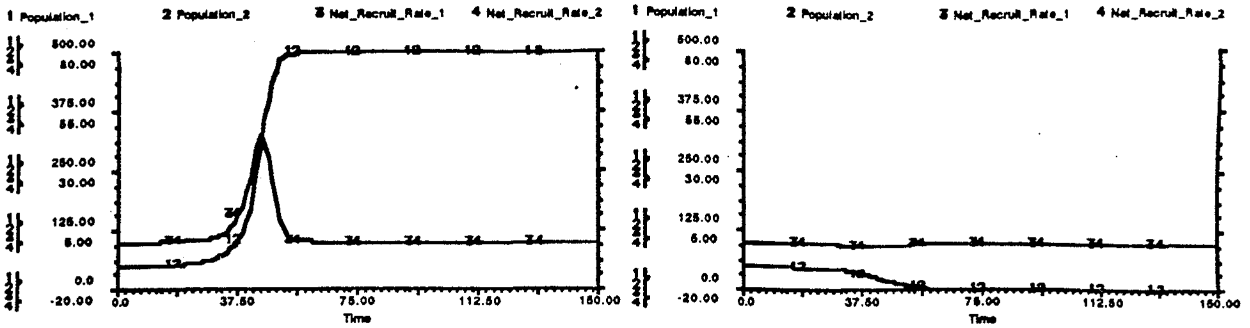
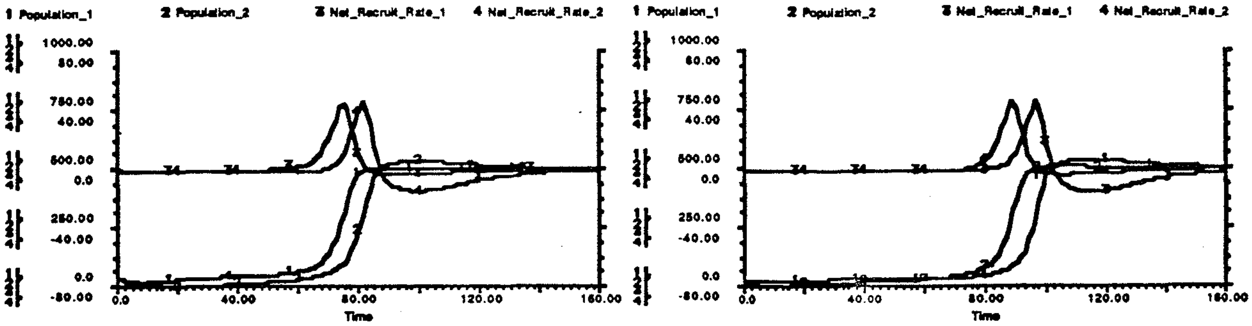


Fig. 11. Dynamics of the population system: (a) PCR=0.02, the initial populations are 44 for set 1 and 43 for set 2; (b) PCR=0.02, the initial populations are 21 and 48 for set 1, 20 and 48 for set 2; (c) PCR=0.005, the initial populations are 49 for set 1 and 48 for set 2; and (d) PCR=0.005, the initial populations are 41 and 49 for set 1, 40 and 49 for set 2.



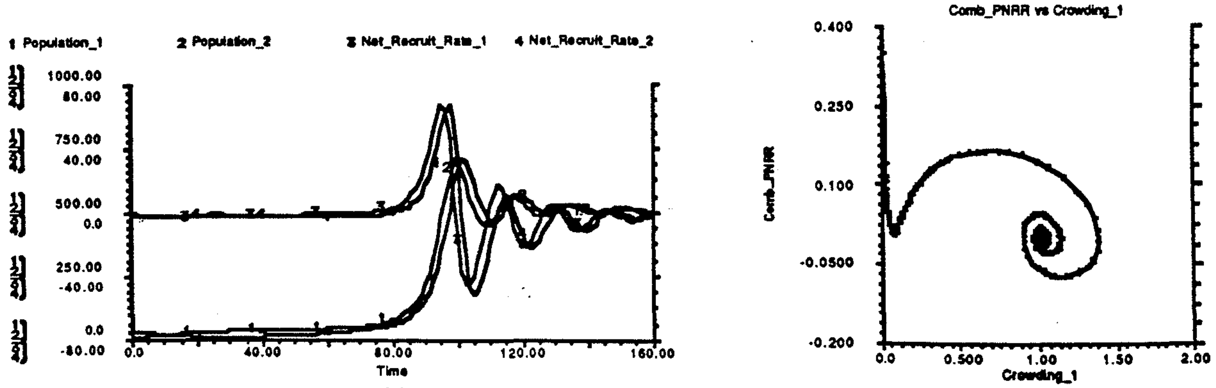
(a) (b)

Fig. 12. Dynamics of the population system: (a) PCR=0.004, the initial populations are 49 and (b) PCR=0.003, the initial populations are 49 again.



(a) (b)

Fig. 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. 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.