Parity Law for Population Dynamics of N-Species with Cyclic Advantage Competitions

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Summary

We study population dynamics on lattice space with N species ($N = 3$, 4, 5, and 6) with cyclic competitive advantage, having both a weaker species and a stronger one. The steady state with equal population densities is the globally stable fixed point. For the biased-rate cyclic advantage population, we can observe the different features of the steady states and their stabilities for even N and for odd N, and we call it as "parity law." We obtain the following results on the parity law; (i) for odd number N all the species can coexist following the biased rate and we have the counterintuition for the change of equilibrium densities, (ii) for even N all the species cannot always coexist and it coincides with our intuition. We also analyzed mean-field approximation. It is revealed that most of the results of Monte Carlo simulation can be understood by mean-field approximation dynamics. However, equilibrium densities cannot be always predicted by mean-field approximation because of the spatial fixation.

1. Introduction

May & Leonard (1975) reveal that Lotka-Volterra competition model with three species shows the heteroclinic dynamics and concluded that coexistence of multiple species is difficult. As a competition between three species in nature, we can examplify that the stock abundance of pelagic fishes usually fluctuates and species replacement occurs forever. Spatial structure might help them to coexist in a homogeneous habitat. This cyclic advantage relationship was modeled by Matsuda et al. (1991, 1992), Takeuchi et al. (1992) and Takeuchi (1996). They tell us that only the introduction of refuges cannot avoid the extinction of some species.

Population dynamics with explicit spatial structure can be usefully studied by lattice models, and have been adopted for many systems, such as lattice logistic model (Matsuda et al., 1992), competition model with long dispersal distances (Durrett & Levin, 1994), population dynamics of perennials capable of vegetative propagation (Harada & Iwasa, 1994), social interaction dynamics with positive or negative neighboring effect (Harada et al., 1995), formation and closure of canopy gaps (Kubo et al., 1996), predator-prey dynamics (Satulovsky & Tomé, 1994; Tainaka, 1988, 1994a, 1994b), host-pathogen dynamics (Sato et al., 1994; Rand et al., 1995; Rhodes & Anderson, 1996) and host-parasitoid dynamics (Hassell et al., 1991), as well as spatially explicit evolutionary games (Boerlijst, 1994; Nakamaru et al., 1997). One feature of lattice models is that we can trace the population dynamics by each individual behavior with the clearly defined birth and death rules. However, there are mathematical difficulties in analyses of lattice models, and it is hard to study the complicated ecological systems with many species by lattice models.

Silvertown et al. (1992) introduced a lattice model for competitive interaction of five grass species, in which every species interacts each other and the replacement probabilities are assumed by the field data. Durrett & Levin (1998) analysed mathematically this model for the case of infinitely large dispersal range and they conclude that only the strongest species can survive in the equilibrium. They also investigate 3-species cyclic competitive model with generalized parameter sets by the mean-field dynamics in comparison with May & Leonard (1975).

The 3-species cyclic advantage model with equal transition rates for any species in two dimension was first studied by Tainaka (1988) by Monte Carlo simulations. He reported that the two-dimensional 3-species cyclic advantage model approaches the internal fixed point (i.e. three species coexist with equal population densities) regardless of initial conditions. On the other hand, the mean-field theory, which never considers the spatial correlation between lattice sites, reveals that 3-species cyclic advantage model in any dimension has a neutrally stable center; the population densities of each species oscillates around the fixed points, where the trajectories depend on the initial condition (see Itoh 1973, 1975, 1979). Moreover Tainaka (1994b) showed the fixed point for the dynamics of pair-approximation, which considers only nearest neighboring correlations in the dynamics, becomes unstable. Recently Tainaka & Yamasaki (1996) considered the case $N = 4$ with equal transition rates for any species in two and three dimensions by using Monte Carlo simulations. Furthermore concerning N-species cyclic advantage model ($N \geq 3$) with equal transition rates for any species in one dimension, Bramson & Griffeath (1989) mathematically studied the results on spatial fixation.

In this paper we study N-species cyclic advantage models ($N = 3, 4, 5$ and 6) on two-dimensional square lattice space by Monte Carlo simulation and mean-field approximation, especially the change of the dynamical properties when only one transition rate becomes large or small. We can observe the different features of the steady states and their stabilities for even N and for odd N, and we call it as "parity law."

2. N-Species Cyclic Advantage Competitive Model

N-species cyclic advantage model on lattice includes the following processes:
(1) The whole lattice has infinitely large population each of which sits on each site of lattice space. In this paper we mainly assume two-dimensional square lattice. The space offers the homogeneous environments to individuals for competitions.
(2) Each individual can be replaced by the stronger competitor as the result of competition. We define the competitive strength among species as follows: the species $i + 1$ is stronger than the species i expressed by the strength $\alpha_{i,i+1}$, then the species $i - 1$ is weaker than the species i, where the index of species is labeled by modulus the total number of species N. Now we consider the population dynamics on the lattice-structured space, so this interaction corresponds to the process that a pair of adjacent two individuals compete and the weaker should be replaced by the stronger stochastically following the strenth parameter α_{ij} (Fig.1). The rates of these processes are proportional to the number of stronger species in the nearest neighbors z (in the case of two-dimensional square lattice $z = 4$), and are defined by the expected number of events of Poisson process in unit time interval.

When we regard our model as the continuous time Markov chain, we can describe this model by the following master equations:

$$\frac{d\rho_t(i)}{dt} = \alpha_{i-1,i}\rho_t(i-1,i) - \alpha_{i,i+1}\rho_t(i,i+1), \tag{1}$$

$$\frac{d\rho_t(i,i)}{dt} = \frac{2\alpha_{2,0}}{z}\rho_t(i-1,i) + 2\sum_{y\in\mathcal{N}^-}\left[\frac{\alpha_{2,0}}{z}\rho_t(i,i-1,\underline{i}) - \frac{\alpha_{0,1}}{z}\rho_t(i,i,\underline{i+1})\right], \tag{2}$$

$$\frac{d\rho_t(i,i+1)}{dt} = -\frac{\alpha_{i,i+1}}{z}\rho_t(i,i+1)$$
$$+ \sum_{y\in\mathcal{N}^-}\left[\frac{\alpha_{i,i+1}}{z}\rho_t(i,i,\underline{i+1}) + \frac{\alpha_{i-1,i}}{z}\rho_t(\underline{i},i-1,i+1)\right.$$
$$\left. -\frac{\alpha_{i+1,i+2}}{z}\rho_t(i,i+1,\underline{i+2}) - \frac{\alpha_{i,i+1}}{z}\rho_t(\underline{i+1},i,i+1)\right], \tag{3}$$

$$\frac{d\rho_t(i,j)}{dt} = \sum_{y\in\mathcal{N}^-}\left[\frac{\alpha_{j-1,j}}{z}\rho_t(i,j-1,\underline{j}) + \frac{\alpha_{i-1,i}}{z}\rho_t(\underline{i},i-1,j)\right.$$
$$\left. -\frac{\alpha_{j,j+1}}{z}\rho_t(i,j,\underline{j+1}) - \frac{\alpha_{i,i+1}}{z}\rho_t(\underline{i+1},i,j)\right] \quad \text{for } |i-j| > 1. \tag{4}$$

$\rho_t(i), \rho_t(ij), \rho_t(ijk)$ for $i, j, k \in \{0, 1, \ldots, N-1\}$ are called as singlet densities, doublet densities and triplet densities, respectively, which are defined as the probabilities of randomly chosen one site of the species i, randomly chosen one pair of nearest neighboring sites of the species i-j and randomly chosen one triplet sequence of neighboring sites of the species i-j-k, respectively (see Matsuda et al., 1992). $\mathcal{N}^-$ in the summation of triplets is the set of $z - 1$ nearest neighboring sites except the site in the pair and y is the site which has the species indicated by the underline in the triplets. Therefore more accurate expressions for these densities become $\rho_t(i|0), \rho_t(ij|0e_1), \rho_t(ij|e_10), \rho_t(ij\underline{k}|0e_1y), \rho_t(\underline{i}jk|ye_10)$ with the species $i, j, k \in \{0, 1, \ldots, N-1\}$ and the corresponding sites $0 = (0,0), e_1 = (1,0), y \in \mathcal{N}^-$ where $0, e_1, y$ indicate the location of transition, the nearest neighbor, the next nearest neighbor, respectively.

In eq.(1) the first term corresponds to the birth process, and the second to the death. For the occurence of the birth process the nearest neighboring site should have the weaker species, so the site of the species i needs the nearest neighboring site of the $i - 1$. On the other hand, when the nearest neighboring site is the stronger species this site is replaced to that stronger; the site of the

i changes by the effect of the nearest neighboring site of the $i + 1$. The model assumes the spatial symmetry of the interactions, so it means $\rho_t(ij) = \rho_t(ji)$.

Similarly eqs.(2)-(4) includes birth and death terms, and we should consider all the cases for two individuals in doublets. There are triplet densities in these equations, and notice that the third site can give the different configurations for these triplets on two-dimensional square lattice space, so we must consider the sum of possible configurations given by the third site $y \in \mathcal{N}^-$.

3. Monte Carlo Simulation

In the previous section we obtain the mean-field dynamics of the model and we can easily know the non-trivial steady states or their stability. Unfortunately, however, it seems to be difficult to prove the existence of non-trivial steady state solution of the original spatially explicit model. So we investigate the dynamical properties by Monte Carlo simulations of the model for the odd number of species and the even ones respectively. In order to know the effect of the change in the transition rate, we fix the parameter $\alpha_{i,i+1} = 1$ except for $i = 0$ and we define $\alpha_{0,1} = \alpha$. The properties of the steady states and their stabilities are very different whether the total number of states N is odd or even, which we call "parity law." As the initial condition we set the spatial pattern at random with equal densities for all species.

3.1 The Case of Odd Number of Total Species N

Monte Carlo simulations for 3-species model show the asymptotic behavior to the steady states of coexistence with all species, which coincides with the expected value by mean-field approximation stated in the next section (Fig.2). In the case of $\alpha = 1$ all species can coexist with equal densities, $\rho^*(0) = \rho^*(1) = \rho^*(2) = 1/3$, in the equilibrium, which is shown by Tainaka (1988) and Durrett & Levin (1998). Notice that both $\rho^*(0)$ and $\rho^*(1)$ decrease (increase) and $\rho^*(2)$ increases (decreases) when α increases (decreases).

In the case of 5-species model the densities by Monte Carlo simulation closely approach to the expected densities by the mean-field approximation (Fig.3), but spatially fixed patterns, which depends on initial conditions, cause the disagreement between mean-field approximation and one example of the simulation as the sample path of the processes. $\rho^*(0), \rho^*(1)$ and $\rho^*(3)$ decrease (increase) and $\rho^*(2)$ and $\rho^*(4)$ increase (decrease) when α increases (decreases).

Perhaps it seems to be difficult by our intuition that the densities of species "0" and "1" increase (decrease) in the equilibrium when the biased rate $\alpha < 1$ ($\alpha > 1$), which indicates that the transition is increased (decreased) for the species "0" and decreased (increased) for "1". However, for the short period in the beginning the density of the species "0" follows the expectation by the biased transition rate α, i.e. "0" increases and "1" decreases. So we observe both the direct effect in the short term and the indirect effect after the long run on the population dynamics. The densities of other species may naturally be explained by the increases (decreases) of "0" and "1" as the result of competition, i.e. "2" decreases because the stronger competitor "0" increases when $\alpha < 1$, and it does not contradict the increase of "1".

3.2 The Case of Even Number of Total Species N

All species can coexist with equal densities in the case of 4-species for $\alpha = 1$ by Monte Carlo

simulation. However, only two species can coexist when one species has the different competitive parameter $\alpha \neq 1$ (Fig.4). Also in the case of 6-species model the coexistence of all species is suggested by Monte Carlo simulation when $\alpha = 1$. Note that only three species can coexist when $\alpha \neq 1$ (Fig.5).

We can evaluate the equilibrium densities for 4- and 6-species models by mean-field approximation for the biased transition rate $\alpha \neq 1$. However, in the case of 6-species model the spatial fixations offer the possibility of coexistence of all species, which produces the slight differences from the expectation by the mean-field approximation (Fig.5).

Notice that in the case of even N there does not appear the contradiction between short-term effect and long-term effect, so the effect of α on population dynamics coincides with our intuition; "0","2",...,"$N - 1$" increase (decrease) and "1","3",...,"$N - 2$" decrease (increase) when $\alpha < 1$ ($\alpha > 1$).

4. Mean-Field Approximation

We show the mean-field approximation in this section, which neglects the spatial correlation between nearest neighboring sites, to support the results of simulation in the previous section. The dynamics of mean-field approximation can be obtained by the replacement of doublet densities to the product of singlet densities, i.e. $\rho_t(ij) = \rho_t(i)\rho_t(j)$, in eq.(1):

$$\frac{d\rho_t(i)}{dt} = \rho_t(i)\left[\alpha_{i-1,i}\rho_t(i-1) - \alpha_{i,i+1}\rho_t(i+1)\right] \quad \text{for any } i \in \{0, 1, \ldots, N-1\}. \tag{5}$$

In equilibrium we get the peripheral solutions: $\rho^*(k) = 0$, or $\rho^*(k-1) = \rho^*(k+1) = 0$ if $\rho^*(k) \neq 0$, with the constraint $\sum_k \rho^*(k) = 1$. Furthermore we can get the steady state solutions with all the species coexistence depending on whether the total number of species N is even or odd (see Appendix).

In the following we consider the N-species cyclic advantage models, $N = 3, 4, 5$ and 6. We put the same transition rates between any two nearest neighboring species except species "0" and "1" to investigate the effect of the change of the transition rate, i.e. $\alpha_{0,1} = \alpha, \alpha_{1,2} = \alpha_{2,3} = \cdots = \alpha_{N-1,0} = 1$.

4.1 The Case of Odd Number of Total Species N

Concerning the stationary density for the 3-species model, we get the following steady states (for the case of the internal equilibrium, put $N = 3$ and $\alpha_{0,1} = \alpha, \alpha_{1,2} = \alpha_{2,0} = 1$ in Appendix).

$$(\rho^*(0), \rho^*(1), \rho^*(2)) = (1, 0, 0), (0, 1, 0), (0, 0, 1), \left(\frac{1}{\alpha+2}, \frac{1}{\alpha+2}, \frac{\alpha}{\alpha+2}\right).$$

For 5-species model mean-field approximation suggests the following statement (see Appendix for the internal equilibrium),

$$\begin{aligned}
(\rho^*(0), \rho^*(1), \rho^*(2), \rho^*(3), \rho^*(4)) =& (1,0,0,0,0), (0,1,0,0,0), (0,0,1,0,0), (0,0,0,1,0), (0,0,0,0,1), \\
& (\rho^*(0), 0, 1 - \rho^*(0), 0, 0), (\rho^*(0), 0, 0, 1 - \rho^*(0), 0), \\
& (0, \rho^*(1), 0, 1 - \rho^*(1), 0), (0, \rho^*(1), 0, 0, 1 - \rho^*(1)), \\
& (0, 0, \rho^*(2), 0, 1 - \rho^*(2)), \\
& \left(\frac{1}{2\alpha+3}, \frac{1}{2\alpha+3}, \frac{\alpha}{2\alpha+3}, \frac{1}{2\alpha+3}, \frac{\alpha}{2\alpha+3}\right).
\end{aligned}$$

At a glance it seems that when α is larger, then the density of "1" becomes larger in the case of 3- and 5-species models, and it is correct in the beginning (we call it "direct effect") but is the opposit in the equilibrium ("indirect effect"). Notice that we start at a random configuration as the initial condition, the time evolution of $\rho_t(0)$ and $\rho_t(1)$ can be evaluated in the beginning: when $\alpha > 1(\alpha < 1)$, $d\rho_t(0)/dt = \rho_t(0)\left[\rho_t(N-1) - \alpha\rho_t(1)\right] < 0$ and $d\rho_t(1)/dt = \rho_t(1)\left[\alpha\rho_t(0) - \rho_t(2)\right] > 0$, so $\rho_t(0)$ decreases (increases) and $\rho_t(1)$ increases (decreases). For the equilibrium we can understand by the above internal mean-field equlibrium densities that both $\rho_t(0)$ and $\rho_t(1)$ decrease (increase) when $\alpha > 1\ (\alpha < 1)$.

4.2 The Case of Even Number of Total Species N

The results on stationary densities for 4-species model obtained by the mean-field approximation when $\alpha \neq 1$:

$$(\rho^*(0), \rho^*(1), \rho^*(2), \rho^*(3)) = (1,0,0,0), (0,1,0,0), (0,0,1,0), (0,0,0,1),$$
$$(\rho^*(0), 0, 1 - \rho^*(0), 0), (0, \rho^*(1), 0, 1 - \rho^*(1)).$$

Besides that all species can remain only when $\alpha = 1$ (by Appendix for the interanal equilibrium):

$$(\rho^*(0), \rho^*(1), \rho^*(2), \rho^*(3)) = \left(\rho^*(0), \frac{1}{2} - \rho^*(0), \rho(0)^*, \frac{1}{2} - \rho^*(0)\right).$$

Next we examine the effect of the change of α. When α is larger, then the density of "1" becomes larger and "0" is smaller. As a result we can expect that $\rho^*(1) + \rho^*(3) = 1$ because the transition from 0 to 1 enhances further. Monte Carlo simulation also supports it (Fig.4).

By mean-field approximation we get the following for 6-species model for $\alpha \neq 1$ by Appendix,

$$(\rho^*(0), \rho^*(1), \rho^*(2), \rho^*(3), \rho^*(4), \rho^*(5))$$
$$=(1,0,0,0,0,0), (0,1,0,0,0,0), (0,0,1,0,0,0), (0,0,0,1,0,0), (0,0,0,0,1,0), (0,0,0,0,0,1),$$
$$(\rho^*(0), 0, 1 - \rho^*(0), 0, 0, 0), (\rho^*(0), 0, 0, 1 - \rho^*(0), 0, 0), (\rho^*(0), 0, 0, 0, 1 - \rho^*(0), 0),$$
$$(0, \rho^*(1), 0, 1 - \rho^*(1), 0, 0), (0, \rho^*(1), 0, 0, 1 - \rho^*(1), 0), (0, \rho^*(1), 0, 0, 0, 1 - \rho^*(1)),$$
$$(0, 0, \rho^*(2), 0, 1 - \rho^*(2), 0), (0, 0, \rho^*(2), 0, 0, 1 - \rho^*(2)), (0, 0, 0, \rho^*(3), 0, 1 - \rho^*(3)),$$
$$(\rho^*(0), 0, \rho^*(2), 0, 1 - \rho^*(0) - \rho^*(2), 0), (0, \rho^*(1), 0, \rho^*(3), 0, 1 - \rho^*(1) - \rho^*(3)).$$

Besides that only when $\alpha = 1$ all states can remain as follows (by Appendix for the internal equilibrium):

$$(\rho^*(0), \rho^*(1), \rho^*(2), \rho^*(3), \rho^*(4), \rho^*(5)) = \left(\rho^*(0), \frac{1}{3} - \rho^*(0), \rho(0)^*, \frac{1}{3} - \rho^*(0), \rho(0)^*, \frac{1}{3} - \rho^*(0)\right).$$

When the values of α change, there is no contradiction on our intuition as in the case of 4-species model and Monte Carlo simulation also supports it (Fig.5).

5. Discussion

In this paper we analyse a model of N-species competitors with cyclic advantage relations. Coexistence of multiple species that engage in a cyclic competitive relationship may be exemplified by the succession in the forest, from the pioneer species, gradually changing to the climax

species and again entering this cycle from the beginning due to the local environmental changes. Although most examples if succession is controled strongly by external disturbances that create a high resource availability , it is an interesting theoretical theme whether an autonomous system for species interaction is able to maintain multiple species of competitors that have cyclic competitive advantage.

In the case of 3-species cyclic case ($N = 3$) our model coincides with the generalized cyclic model by Durrett & Levin (1998), i.e. all species interact with each other. When we consider more complex systems with the total number of species $N \geq 4$, however, not only the model descriptions but also the biological situations are completely different. Their models concern the interactions among all species, so only one dominant species, which has the largest probability of replacement to other species, must occupy the whole population eventually. On the other hand, our successional model indicates that all species can coexist even when the dominant species exists, but the population dynamics strongly depend on whether the total number of species is even or odd, i.e. parity law. Kobayashi & Tainaka (1997) discovers a similar parity law for another model.

Interacting particle systems have been studied for various kinds of models, but we cannot get enough mathematical results because of much difficulties. Even in one of the simplest models, basic contact processes, for example, critical values or critical exponents for phase transition are not known (e.g. Konno, 1994). In this paper we adopt mean-field approximation to evaluate equilibrium densities because even that approximation seems to give the correct values for 3-species model (Tainaka, 1988). We can easily construct mean-field dynamics for the system with the large number of species, and we can explain both equilibrium densities and the qualitative effect of the biased transition rates on the equilibrium densities by this approximation even if the result has the contradiction of our intuition; when the rate of the reproduction becomes larger we may expect the population size of that species increases (see another model; Kobayashi & Tainaka, 1997).

Parity law, which indicates the different dynamical properties whether the total number of species N is odd or even, appears when we change only one transition rate. Though we are confronted with our counterintuition, mean-field dynamics can explain it. The cause of our counterintuition occurs by the contradiction of the long term effect of the biased rate on the population dynamics only for the odd N. However, this type of parity law does not hold when the model includes the site-independent rate and that rate is changed (Kobayashi & Tainaka, 1997). As the future study we should determine the cause of parity law and specifies what kind of models show it.

Also for N-species models with $N \geq 7$, it is expected that mean-field dynamics can predict the values of steady state densities when we replicate many runs of Monte Carlo simuation and calculate the average. However, each sample path of Monte Carlo simulations may give the different densities from expected by the mean-field because the spatial fixation will frequently occur. Unlike Bramson & Griffeath (1989) with $\alpha = 1$, even for not so many-species models the spatial fixation seems to occur easily, especially for the strongly biased rate α; they prove that spatial fixation always occurs for more than 5-species on 1-dimension, and estimate by simulation that it occurs about 8-16 species on 2-dimension. We would like to investigate this effect on population extinction in the future study. The effect of escape for population extinction may occur when the spatial segregation makes a region with non-interactive neighbors each other as a refuge. In that case we can say that the biological system with spatial structure produces the stable steady world comprising large species diversity.

REFERENCES

BOERLIJST, M.C. (1994). "Selfstructuring: a substrate for evolution," Doctoral Thesis of Utrecht University.

BRAMSON, M. & GRIFFEATH, D. (1989). Flux and fixation in cyclic particle systems. *Ann. Probab.* **17**, 26-45.

DURRETT, R. (1988). "Lecture Notes on Particle Systems and Percolation," Wadsworth, Inc., California.

DURRETT, R. & LEVIN, S.A. (1994). Stochastic spatial models: a user's guide to ecological applications. *Phil. Trans. R. Soc. Lond.* **B343**, 329-350.

DURRETT, R. & LEVIN, S.A. (1998). Spatial aspects of interspecific competition. *Theor. Popul. Biol.* **53**, 30-43.

HARADA, Y. & IWASA, Y. (1994). Lattice population dynamics for plants with dispersing seeds and vegetative propagation. *Res. Pop. Ecol.* **36**, 237-249.

HARADA, Y., EZOE, H., IWASA, Y., MATSUDA, H. & SATO, K. (1995). Population persistence and spatially limited social interaction. *Theor. Popul. Biol.* **48**, 65-91.

HASSELL, M.P., COMINS, H.N. & MAY, R.M. (1991). Spatial structure and chaos in insect population dynamics. *Nature* **353**, 255-258.

ITOH, Y. (1973). On a ruin problem with interaction. *Ann. Inst. Statist. Math* **25**, 635-641.

ITOH, Y. (1975). An H-theorem for a system of a competing species. *Proc. Jpn. Acad.* **51**, 374-379.

ITOH, Y. (1979). Random collision models in oriented graphs. *J. Appl. Prob.* **16**, 36-44.

KOBAYASHI, K. & TAINAKA, K. (1997). Critical phenomena in cyclic ecosystems: parity law and selfstructuring extinction pattern. *J. Phys. Soc. Jpn.* **66**, 38-41.

KONNO, N. (1994). *Phase Transitions of Interacting Particle Systems,* World Scientific.

KUBO, T., IWASA, Y. & FURUMOTO, N. (1996). Forest spatial dynamics with gap expansions: total gap area and gap size distribution. *J. theor. Biol.* **180**, 229-246.

LIGGETT, T. M. (1985). "Interacting Particle Systems," Springer-Verlag, New York.

MATSUDA, H., OGITA, N., SASAKI, A. & SATO, K. (1992). Statistical mechanics of population: the Lotka-Volterra model. *Prog. Theor. Phys.* **88**, 1035-1049.

MATSUDA, H., WADA, T., TAKEUCHI, Y. & MATSUMIYA, Y. (1991). Alternative models for species replacement of pelagic fishes. *Res. Popul. Ecol.* **33**, 41-56.

MATSUDA, H., WADA, T., TAKEUCHI, Y. & MATSUMIYA, Y. (1992). Model analysis of the effect of environmental fluctuation on the species replacement pattern of pelagic fishes under interspecific competition. *Res. Popul. Ecol.* **34**, 309-319.

MAY, R.M. & LEONARD, W. (1975). Nonlinear aspects of competition between three species. *SIAM J. Appl. Math.* **29**, 243-252.

NAKAMARU, M., MATSUDA, H. & IWASA, Y. (1997). The evolution of cooperation in a lattice-structured poopulation. *J. theor. Biol.* **184**, 65-81.

RAND, D.A., KEELING, M. & WILSON, H.B. (1995). Invasion stability and evolution to criticality in spatially extended, artificial host-pathogen ecologies. *Proc. R. Soc. Lond.* **B259**, 55-63.

RHODES, C.J. & ANDERSON, R.M. (1996). Persistence and dynamics in lattice models of epidemic spread. *J. theor. Biol.* **180**, 125-133.

SATO, K., KONNO, N. & YAMAGUCHI, T. (1997). Paper-scissors-stone game on trees. *Mem. Muroran Inst. Tech.* **47**, 109-114.

SATO, K., MATSUDA, H. & SASAKI, A. (1994). Pathogen invasion and host extinction in lattice structured population. *J. Math. Biol.* **32**, 251-268.

SATULOVSKY, J.E. & TOMÉ, T. (1994). Stochastic lattice gas model for a predator-prey system. *Phys. Rev. E* **49**, 5073-5079.

SILVERTOWN, J., HOLTIER, S., JOHNSON, J. & DALE, P. (1992). Cellular automaton models of interspecific competition for space – the effect of pattern on process. *J. Ecol.* **80**, 527-534.

TAINAKA, K. (1988). Lattice model for the Lotka-Volterra system. *J.Phys.Soc.Jpn.* **57**, 2588-2590.

TAINAKA, K. (1993). Paradoxical effect in a three-candidate voter model. *Phys.Lett.A* **176**, 303-306.

TAINAKA, K. (1994a). Intrinsic uncertainty in ecological catastrophe. *J.theor.Biol.* **166**, 91-99.

TAINAKA, K. (1994b). Vortices and strings in a model ecosystem. *Phys. Rev. E* **50**, 3401-3409.

TAINAKA, K. & YAMASAKI, M. (1996). Interaction between vortices in the first and second excited states. *J. Phys. Soc. Jpn.* **65**, 643-644.

TAKEUCHI, Y. (1996). Global dynamical properties of Lotka-Volterra systems, World Scientific.

TAKEUCHI, Y., OSHIME, Y. & MATSUDA, H. (1992). Persistence and periodic orbits of a three-competitor model with refuges. *Math. Biosci.* **108**, 105-125.

APPENDIX
Internal Equilibrium Densities by Mean-Field Approximation

We can obtain the internal equilibrium densities from eq.(5). The results are different depending that N is even or odd in the following.

(i) The Case of Odd N

Eq.(5) gives the equilibrium densities when we put $d\rho_t(i)/dt = 0$. To get the internal solutions $\rho^*(i) > 0$ for any i, so we can conclude that $\rho^*(i+1) = \beta_i \rho^*(i-1)$ where $\beta_i = \alpha_{i-1,i}/\alpha_{i,i+1}$. When N is odd, i.e. $N = 2k + 1$, the following relations hold:

$$\rho^*(1) = \beta_0 \rho^*(2k),$$
$$\rho^*(2) = \beta_1 \rho^*(0),$$
$$\cdots$$
$$\rho^*(2k - 1) = \beta_{2k-2} \rho^*(2k - 3),$$
$$\rho^*(2k) = \beta_{2k-1} \rho^*(2k - 2),$$
$$\rho^*(0) = \beta_{2k} \rho^*(2k - 1).$$

Using all relations we can show that

$$\rho^*(0) = \beta_0 \beta_1 \cdots \beta_{2k-1} \beta_{2k} \rho^*(0)$$

where $\beta_0 \beta_1 \cdots \beta_{2k-1} \beta_{2k} = 1$ is always true as defined. Finally we should check the constrained condition $\sum_{i=0}^{N-1} \rho^*(i) = 1$. For the sum of even indices of species

$$\rho^*(0) + \rho^*(2) + \cdots + \rho^*(2k) = (1 + \beta_1 + \cdots + \beta_1 \beta_3 \cdots \beta_{2k-1})\rho^*(0).$$

On the other hand for the sum of odd indices of species

$$\rho^*(1) + \rho^*(3) + \cdots + \rho^*(2k - 1) = (\beta_0 + \beta_0 \beta_2 + \cdots + \beta_0 \beta_2 \cdots \beta_{2k-2})\beta_1 \beta_3 \cdots \beta_{2k-1}\rho^*(0).$$

Then we summarize for the case of odd N as follows:

$$(\rho^*(0), \rho^*(1), \ldots, \rho^*(N-1))$$
$$= \left(\frac{1}{Z}, \frac{Y}{Z}, \frac{\beta_1}{Z}, \frac{\beta_2 Y}{Z}, \frac{\beta_1\beta_3}{Z}, \frac{\beta_2\beta_4 Y}{Z}, \ldots, \frac{\beta_2\beta_4\cdots\beta_{N-3}Y}{Z}, \frac{\beta_1\beta_3\cdots\beta_{N-2}}{Z}\right),$$

where

$$Y = \beta_0\beta_1\beta_3\cdots\beta_{N-2},$$
$$Z = 1 + \beta_1 + \beta_1\beta_3 + \cdots + \beta_1\beta_3\cdots\beta_{N-2} + (1 + \beta_2 + \beta_2\beta_4 + \cdots + \beta_2\beta_4\cdots\beta_{N-3})Y.$$

(ii) The Case of Even N

As in the case of odd N, we put $d\rho_t(i)/dt = 0$ in eq.(5) and assume $\rho^*(i) > 0$ for any i to obtain the internal equilibrium. When N is even, i.e. $N = 2k$, the following relations hold:

$$\rho^*(1) = \beta_0\rho^*(2k-1),$$
$$\rho^*(2) = \beta_1\rho^*(0),$$
$$\ldots$$
$$\rho^*(2k-1) = \beta_{2k-2}\rho^*(2k-3),$$
$$\rho^*(0) = \beta_{2k-1}\rho^*(2k-2).$$

Then we have for the even indices of sepcies

$$\rho^*(2) = \beta_1\rho^*(0),$$
$$\rho^*(4) = \beta_1\beta_3\rho^*(0),$$
$$\ldots$$
$$\rho^*(2k-2) = \beta_1\beta_3\cdots\beta_{2k-3}\rho^*(0),$$
$$\rho^*(0) = \beta_1\beta_3\cdots\beta_{2k-3}\beta_{2k-1}\rho^*(0).$$

The last relation is meaningful only when $\beta_1\beta_3\cdots\beta_{2k-3}\beta_{2k-1} = 1$.
Similarly for the odd indices of species

$$\rho^*(3) = \beta_2\rho^*(1),$$
$$\rho^*(5) = \beta_2\beta_4\rho^*(1),$$
$$\ldots$$
$$\rho^*(2k-3) = \beta_2\beta_4\cdots\beta_{2k-4}\rho^*(1),$$
$$\rho^*(2k-1) = \beta_2\beta_4\cdots\beta_{2k-4}\beta_{2k-2}\rho^*(1).$$

Notice that there is a restricted condition $\sum_{i=0}^{N-1}\rho^*(i) = 1$, so we can summarize the steady state solution as follows:

$$(\rho^*(0), \rho^*(1), \ldots, \rho^*(N-1))$$
$$= (\rho^*(0), \rho^*(1), \beta_1\rho(0)^*, \beta_2\rho^*(1), \beta_1\beta_3\rho^*(0), \beta_2\beta_4\rho^*(1),$$
$$\ldots, \beta_1\beta_3\cdots\beta_{N-3}\rho^*(0), \beta_2\beta_4\cdots\beta_{N-2}\rho^*(1)),$$

with

$$A\rho^*(0) + B\rho^*(1) = 1,$$

where

$$A = 1 + \beta_1 + \beta_1\beta_3 + \cdots + \beta_1\beta_3\cdots\beta_{N-3},$$
$$B = 1 + \beta_2 + \beta_2\beta_4 + \cdots + \beta_2\beta_4\cdots\beta_{N-2},$$
$$\beta_i = \frac{\alpha_{i-1,i}}{\alpha_{i,i+1}}$$

with the condition

$$\beta_1\beta_3\cdots\beta_{N-1} = 1.$$

Figure Legends

Fig.1. N-species cyclic advantage model.

Transition rate from the species "i" to "j" is denoted by α_{ij}. Notice that transitions are restricted between nearest neighboring species in our model.

Fig.2. Population size in the steady state of 3-species cyclic advantage model for various α.

Horizontal axis indicates the transition rate α from 0 to 1. When α is smaller than 1, the population of "0" and "1" decrease and "1" increases. On the other hand, when α is larger than 1, the situation reverses.

Fig.3. Population size in the steady state of 5-species cyclic advantage model for various α.

In similar to Fig.2 the superiors for $\alpha > 1$ turn to be the inferiors for $\alpha < 1$.

Fig.4. Population size in the steady state of 4-species cyclic advantage model for various α.

When α is smaller than 1, the population of "0" and "2" can survive, and "1" and "3" go extinct. On the other hand, when α is larger than 1, the situation reverses.

Fig.5. Population size in the steady state of 6-species cyclic advantage model for various α.

This system has the even number of species, and the states "0"-"2"-"4" or "1"-"3"-"5" behave in a similar way respectively such as 4-species model. However, sometimes a small fraction of popuation remains because of the spatial fixation which occurs for almost extinct small population surrounded by the non-interactive species.
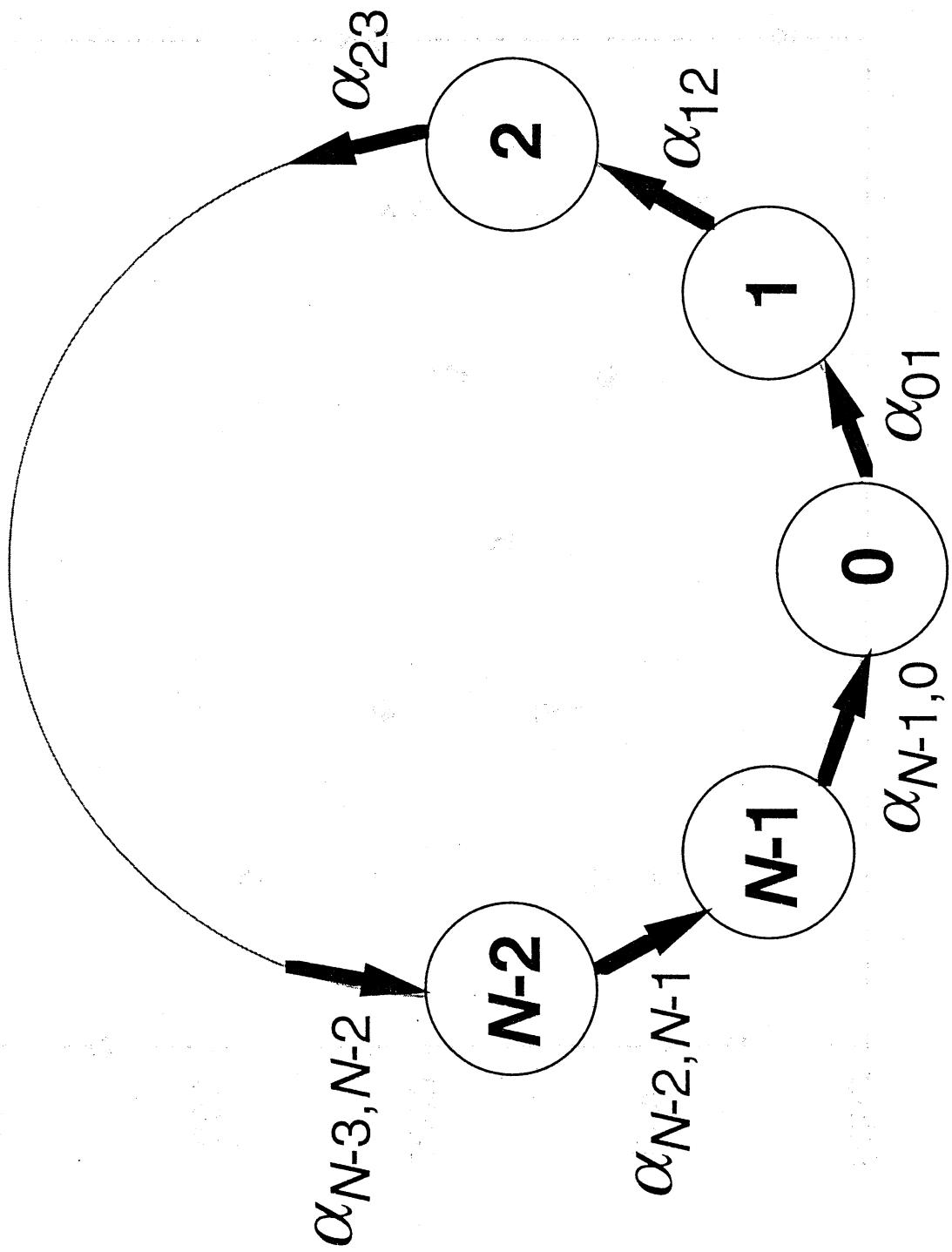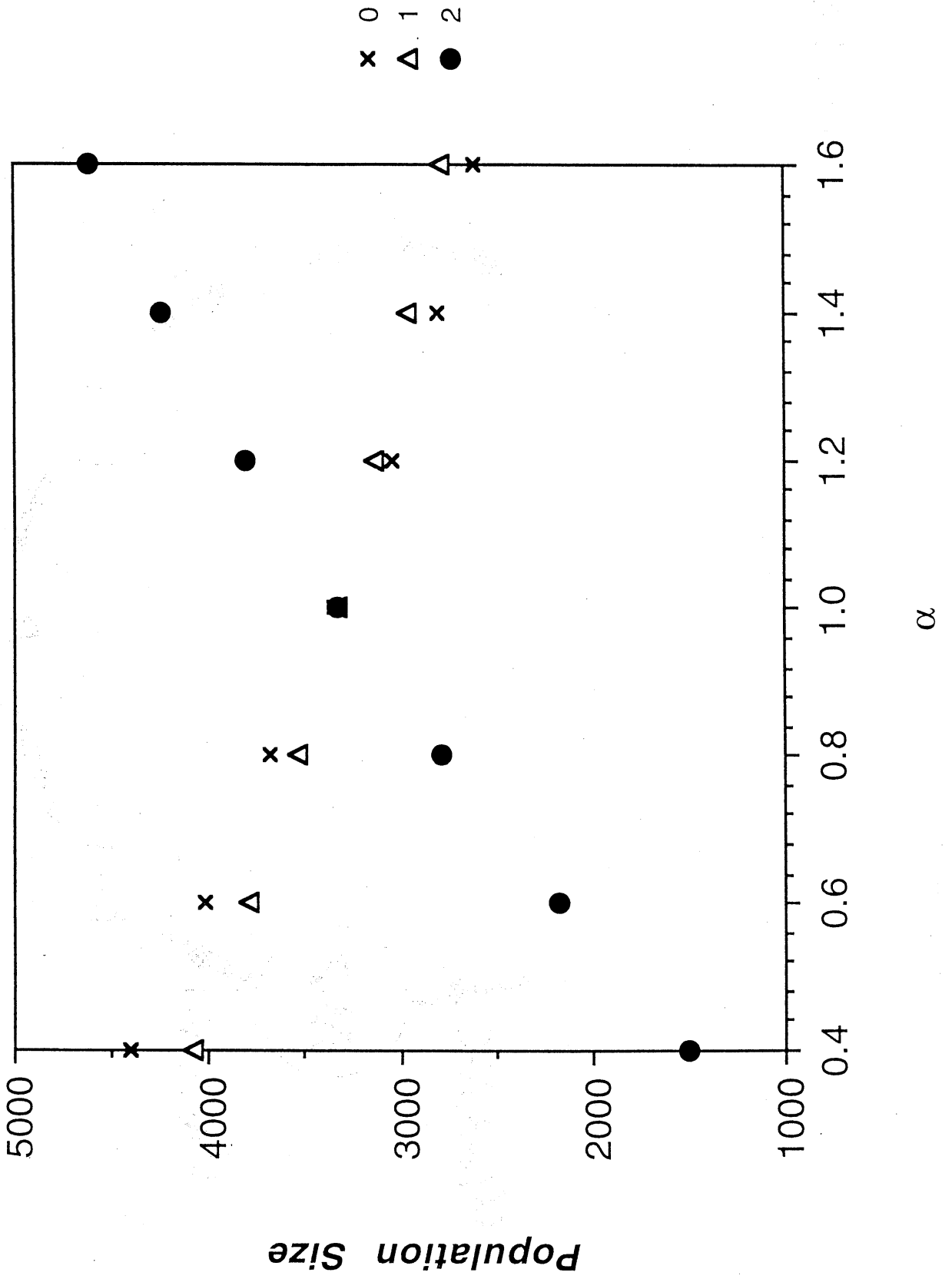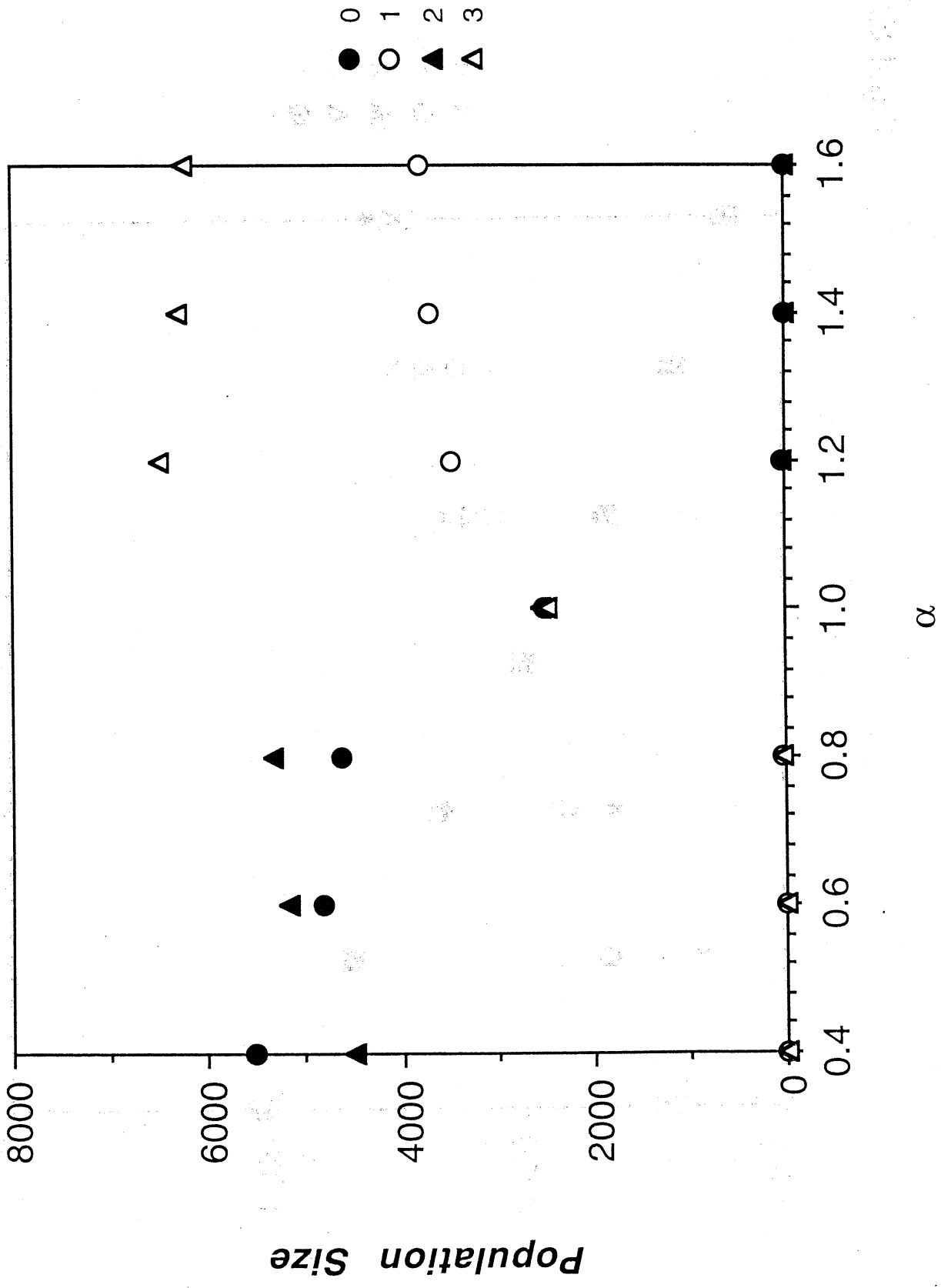
Fig.1 Sato *et al.*
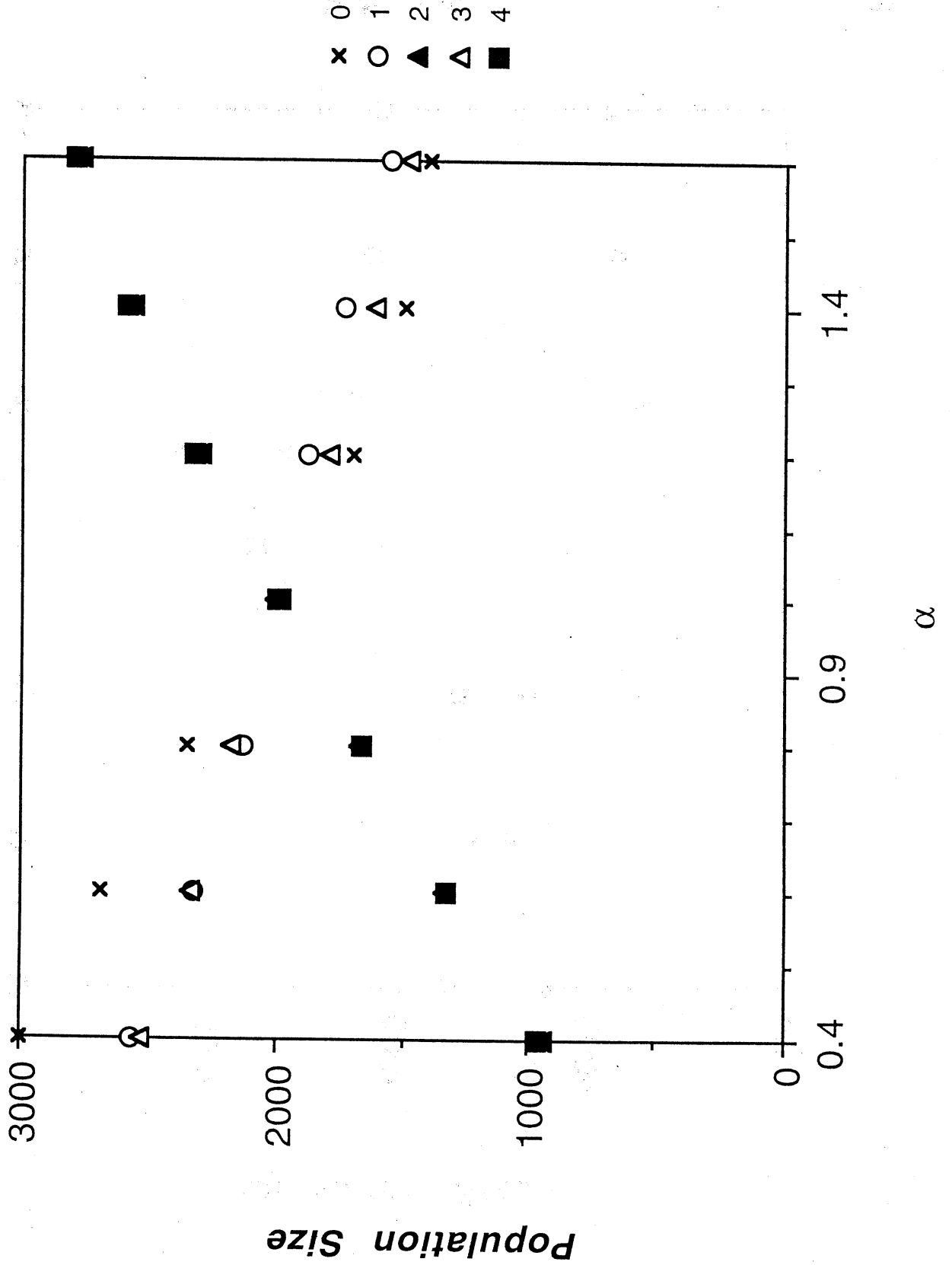
Fig.2 Sato et al.

Fig.3 Sato et al

Fig.4 Sato et al.

Fig.5 Sato et al.