

Dynamics of Age- and Size-Structured Populations in Fluctuating Environments: Applications of Stochastic Matrix Models to Natural Populations

Masahiro NAKAOKA¹⁾

Ocean Research Institute, University of Tokyo, Minamidai 1-15-1, Nakano, Tokyo 164, Japan

Abstract. Recent developments of the theory of stochastic matrix modeling have made it possible to estimate general properties of age- and size-structured populations in fluctuating environments. However, applications of the theory to natural populations are still few. The empirical studies which have used stochastic matrix models are reviewed here to examine whether predictions made by the theory can be generally found in wild populations. The organisms studied include terrestrial grasses and herbs, a seaweed, a fish, a reptile, a deer and some marine invertebrates. In all the studies, the stochastic population growth rate ($\ln \lambda_s$) was no greater than the deterministic population growth rate determined using average vital rates, suggesting that the model based only on average vital rates may overestimate growth rates of populations in fluctuating environments. Factors affecting $\ln \lambda_s$ include the magnitude of variation in vital rates, probability distribution of random environments, fluctuation in different types of vital rates, covariances between vital rates, and autocorrelation between successive environments. However, comprehensive rules were hardly found through the comparisons of the empirical studies. Based on shortcomings of previous studies, I address some important subjects which should be examined in future studies.

Key words: demography, matrix model, stochastic environment, population dynamics, natural populations, applications of the theory.

Introduction

It is not an exception but rather a rule that population sizes of wild animals and plants fluctuate widely in a complex manner. Factors affecting the dynamics of these populations include (1) intra- and inter-specific relationships such as density-dependence, competition and predator-prey interactions (Levin and Goodyear 1980; May 1981), (2) individual and/or genetic differences within a population (Wellington 1957; Iwao and Wellington 1970a, 1970b), (3) age- and size-structure of a population (Charlesworth 1980; Caswell 1989), (4) spatial structure of a population, and lateral movements of individuals (Roughgarden et al. 1985; Gilpin and Hanski 1991; Bascombe and Solé 1995), and (5) temporal variation in environments and demographic parameters (Turelli 1977; Tuljapurkar 1989). Among them, time-varying environments and resultant fluctuation in vital rates have been argued to

have significant effects not only on population dynamics, but also on the evolution of life histories (Murphy 1968; Schaffer 1974; Stearns 1976; Tuljapurkar 1990a; Yoshimura and Clark 1991, 1993; Yoshimura 1995). Most of the earliest works on this subject have been carried out using simple scalar models which can be applicable to organisms with simple life cycles (Levins 1969; Lewontin and Cohen 1969; May 1975; Roughgarden 1975).

Analysis of population dynamics of organisms with complex life cycles has been greatly facilitated by the development of matrix projection models, namely, the Leslie matrix model (Leslie 1945, 1948) for age-structured populations and the more general Lefkovich model (Lefkovich 1965, 1967) for stage- or size-structured populations. These models have been applied to a variety of natural populations (van Groenendael 1988; Caswell 1989). However, most of these studies are based on deterministic models which assume time-invariant, constant vital rates, even though effects of temporal variation are apparently

1) E-mail: nakaoka@ori.u-tokyo.ac.jp

significant in some cases (Huenneke and Marks 1987; Frazer et al. 1992; Grant and Grant 1992).

The theory of stochastic demography has been developed over the past two decades (Boyce 1977; Cohen 1976, 1977a, 1977b, 1979a, 1979b, 1979c; Tuljapurkar 1982a, 1982b, 1986, 1989; Tuljapurkar and Orzack 1980; see Cohen 1987; Caswell 1989; Tuljapurkar 1989, 1990b; Andersen 1994 for reviews), and has made it possible to examine the effects of stochastic variation in environments on the dynamics of age- and size-structured populations. The theory has been applied to natural populations for several cases (Bierzychudek 1982; Cohen et al. 1983; Heyde and Cohen 1985; Gotelli 1991; Silva et al. 1991; Åberg 1992b; Canales et al. 1994; Doak et al. 1994; Benton et al. 1995; Noda and Nakao 1996; Nakaoka 1996). However, no efforts have been made so far to obtain general properties of the population dynamics by comparing the results. Such attempts are worthwhile, especially when one faces increasing demands for the development of stochastic models in conservation biology, as represented by population viability analyses (Gilpin and Soulé 1986; Lande 1988; Lande and Orzack 1988; Armbruster and Lande 1993).

In the present paper, I review the empirical studies which applied stochastic matrix models to explain the dynamics of age- and size-structured populations in natural environments. After a brief introduction to the theory, I compare the methods and results of these studies, and examine (1) how the estimates of population growth rate differ between models with and without the assumptions of environmental fluctuations, and (2) which factors of fluctuating environments and vital rates have stronger effects on the estimates of stochastic population growth rate. Based on these examinations, I address prospects for future studies on population fluctuation in natural environments.

Theory

The theory of matrix models under fluctuating, stochastic environments is reviewed by Cohen (1987), Tuljapurkar (1989, 1990b) and Caswell (1989). In the present section, I introduce the theory according mainly to Caswell (1989, Chapter 8).

The general format for a time-varying matrix model is given by:

$$\begin{aligned} \mathbf{n}(t+1) &= \mathbf{A}_t \mathbf{n}(t) \\ &= \mathbf{A}_t \mathbf{A}_{t-1} \mathbf{A}_{t-2} \dots \mathbf{A}_0 \mathbf{n}(0) \end{aligned} \quad (1)$$

where $\mathbf{A}_0, \mathbf{A}_1, \dots, \mathbf{A}_t$ represents a series of projection matrices, each varied according to environmental fluctuations. The methods of analysis and underlying theorems vary depending on patterns of environmental variability.

The sequences of projection matrices may be constant ($\mathbf{A}_t = \mathbf{A}$) or periodic ($\mathbf{A}_k = \mathbf{A}_{2k} = \mathbf{A}_{3k} = \dots$ for some period k) in the case of deterministic environments. In stochastic environments, the sequence of matrices is generated by a stochastic process, which is normally assumed to be a first-order finite state ergodic Markov chain. The stochastic environments are further classified into homogeneous and inhomogeneous environments. If the transition probabilities that govern the changes in the environment are time-invariant, it is called homogeneous. The environment is said to be inhomogeneous if the transition probabilities change over time (Caswell 1989). Environments are also classified by the presence or absence of autocorrelation between successive environments (autocorrelated or independent environments). Homogeneous, independent environments have been assumed in most of the empirical studies.

One of the important issues in the study of variable environments is ergodicity. A population is said to be ergodic if its long-term dynamics becomes independent of its initial state. In the case of stochastic environments, the strong and weak stochastic ergodic theorems promise "liberation from history" (Caswell 1989) for homogeneous and inhomogeneous environments, respectively. Ergodicity can be understood by considering two hypothetical populations $\mathbf{m}(t)$ and $\mathbf{n}(t)$ which start from different initial population structures $\mathbf{m}(0)$ and $\mathbf{n}(0)$:

$$\begin{aligned} \mathbf{m}(t) &= \mathbf{A}_t \mathbf{A}_{t-1} \mathbf{A}_{t-2} \dots \mathbf{A}_0 \mathbf{m}(0) \\ \mathbf{n}(t) &= \mathbf{B}_t \mathbf{B}_{t-1} \mathbf{B}_{t-2} \dots \mathbf{B}_0 \mathbf{n}(0) \end{aligned} \quad (2)$$

where $\mathbf{A}_t \mathbf{A}_{t-1} \mathbf{A}_{t-2} \dots \mathbf{A}_0$ and $\mathbf{B}_t \mathbf{B}_{t-1} \mathbf{B}_{t-2} \dots \mathbf{B}_0$ represent two independent paths of stochastic environments taken from a single probability distribution. The stochastic ergodic theorems state that "the probability distributions of $\mathbf{m}(t)$ and $\mathbf{n}(t)$ eventually converge to a stationary distribution, and thus forget their past" (Caswell 1989). The independence from initial conditions enables us to analyze the general properties of population dynamics in stochastic environments.

Population size $N(t)$ is a random variable in stochastic environments, and its probability distribution becomes lognormal asymptotically. Assuming that the strong stochastic ergodic theorem holds, population growth rate can be expressed by two measures: 1) the average growth rate $\ln \lambda_s$, defined as:

$$\ln \lambda_s = \lim_{t \rightarrow \infty} E[\ln N(t)]/t, \quad (3)$$

which is obtained by calculating the asymptotic growth rate for each population and averaging the results; 2) the growth rate of average population size $\ln \mu$ is defined as:

$$\ln \mu = \lim_{t \rightarrow \infty} \ln E[N(t)]/t, \quad (4)$$

which is obtained by averaging population size at each

time t and calculating its growth rate over time. The former is the most probable growth rate and it is always true that $\ln \lambda_s \leq \ln \mu$.

Calculation of $\ln \mu$ is analytically possible (see Caswell 1989 for detail). In particular, $\ln \mu$ is identical to the dominant eigenvalue of the average projection matrix when environments are independent (no autocorrelation). It is therefore equivalent to the population growth rate in a deterministic model ($\ln \lambda_1$) obtained by averaging time-varying vital rates.

Analytical calculation of $\ln \lambda_s$, on the other hand, is difficult. Two alternative approaches have been considered, i.e., numerical calculation and perturbation approach. Numerical methods can be applicable both to models and to field data. In a homogeneous environment, the estimate of $\ln \lambda_s$ ($\widehat{\ln \lambda_s}$) is given by:

$$\widehat{\ln \lambda_s} = [\ln N(T) - \ln N(1)] / (T - 1) \quad (5)$$

where $N(i)$ is the population size at time i ($i = 1, 2, \dots, T$). It is equivalent to obtaining a number of one step estimates of $\ln \lambda_s$ [$\ln \lambda_s(i)$] and averaging them over time. Thus,

$$\ln \lambda_s(i) = \ln N(i+1) - \ln N(i), \quad (6)$$

$$\widehat{\ln \lambda_s} = \sum_i \ln \lambda_s(i) / (T - 1). \quad (7)$$

Heyde and Cohen (1985) considered how to estimate the confidence interval of $\widehat{\ln \lambda_s}$. An approximate 95% confidence interval of $\widehat{\ln \lambda_s}$ is given by $\widehat{\ln \lambda_s} \pm 1.96 \sqrt{V[\ln \lambda_s(i)]/m}$, where $V[\ln \lambda_s(i)]$ is the variance of $\ln \lambda_s(i)$, and m , the number of iterations.

A perturbation approach, developed by Tuljapurkar (1982b), can be used when environmental variability is small (see also Caswell 1989 for detail). This approach, however, has applied to empirical data so far only on one occasion (Benton et al. 1995).

Application of the stochastic matrix model to natural populations

As mentioned earlier, studies applying the stochastic matrix to empirical data on natural populations are still few. In addition, to fulfill their specific purposes (ranging from general predictions of population dynamics to risk assessment of endangered species), each study applied stochastic theory differently, and provided different sets of data, which precludes us from comparing many population characteristics in detail. In this section, I review empirical studies that estimated (or gave enough information to estimate) $\ln \lambda_s$, the most basic population parameter obtained by the stochastic matrix model.

Jack-in-the-pulpit

One of the earliest applications of the stochastic matrix model to field data was carried out by Bierzychudek (1982) for wild populations of a perennial herb, Jack-in-the-pulpit (*Arisaema triphyllum*). It is a common herb in the eastern half of North America, found in the forest understory in a wide variety of moisture and soil conditions. She studied its population dynamics at two sites: "wet" and "dry" forests around Ithaca, New York. Based on 2-yr data of unmanipulated populations, she constructed size-classified projection matrices which consisted of 7 size classes.

It was found that growth rates and mortality rates of the plant differed greatly between sites and years, leading to large variation between the matrices. Actual size distributions at each site differed from stable size distributions predicted by a deterministic model. The classical deterministic models for calculating population growth rate were therefore rejected, and an alternative method using a stochastic matrix model was employed for predicting a long-term growth rate. It is assumed that each of two matrices for the different years (1977-78 and 1978-79) occurs stochastically with an equal frequency of 0.5, so that "good" and "bad" years occur randomly at the same frequency. Beginning with the observed size distribution, changes in population size were simulated for 10 different hypothetical populations. Instead of calculating $\ln \lambda_s$, however, she calculated mean population size at each time step, and then regressed it against time to obtain a long-term growth rate. This procedure is equivalent to calculating $\ln \mu$ (see above), and therefore, obtained estimates were very close to $\ln \mu$ calculated analytically as a dominant eigenvalue of an average matrix.

Caswell (1989) re-analyzed Bierzychudek's data, and calculated $\widehat{\ln \lambda_s}$ and its confidence intervals based on 3000 iterations following an initial 1000 iterations to eliminate transient effects (Table 1). He also examined how many iterations are needed to gain reliable estimates of $\ln \lambda_s$, and found that 3000 iterations are not always too many to obtain precise estimates.

Although Bierzychudek's analyses are limited and based only on 2-yr data, this study is one of the earliest empirical studies which included the effects of temporal variation in environments into demographic analysis. In her discussion, she pointed out the limitation of demographic analyses that assume stable environments, and stressed the necessity of a long-term approach in demographic studies.

Striped bass

The striped bass (*Morone saxatilis*) is an important sport and commercial fish along the Atlantic coast of North

Table 1. Summary of empirical studies applying the stochastic matrix model to wild populations.

Species (References)	Type of matrix (no. of classes)	Time scale	No. of environments	Distribution pattern of environments	Vital rates subject to fluctuation	No. of numerical iterations	Stochastic growth rate $\ln \lambda_s$ ($\pm 95\%$ CI)	Deterministic growth rate $\ln \lambda$	Remarks
Jack-in-the-pulpit (Caswell 1989)	size (7)	year	2	discrete	all	3000	0.025669 (± 0.00119) -0.10765 (± 0.00322)	0.2566 -0.1049	Fall Creek Brooktondale
Striped bass (Heyde & Cohen 1985)	age (15)	year	13	discrete	first-year survivorship	1000	-0.083 (± 0.007)	-0.076	
Savanna grass <i>Andropogon semiberbis</i> (Silva et al. 1991)	size (4)	year	2	discrete	all	3000	0 (± 0.025)	0	at fire frequency of 0.85
<i>A. brevifolius</i> (Canales et al. 1994)	age (6)	month	6	discrete	all	3000	0	0	at fire frequency of 0.29
Marine gorgonian coral (Gotelli 1991)	size (5)	month	23	discrete	recruitment, growth and survivorship	5000	0.00743 (± 0.00363)	0.00917	
Seaweed (Åberg 1992a, 1992b)	size (5)	year	3	discrete	all	10000	-0.174 -0.274	-0.117 -0.198	Tjärnö Göteborg
Desert tortoise (Doak et al. 1994)	size (8)	year	2 to 4	continuous (β distribution)	growth and survivorship	25 (100 runs)	-0.053 to -0.043 ^a	-0.043	medium-high production rate
Red deer (Benton et al. 1995)	age (19)	year	21	discrete	survivorship and reproduction	250 (1500 runs)	0.05837 (± 0.00019)	0.05871	1971–1991
Marine gastropod (Noda & Nakao 1996)	age (6)	year	8	discrete	recruitment	4800	0.075	0.149	
Marine bivalve (Nakaoka 1996)	size (10)	year	18	continuous (lognormal)	recruitment	3000	-0.0137 (± 0.0299)	-0.0122	variation in recruitment
			9	continuous (normal)	individual growth	3000	-0.0264 (± 0.0026)	-0.0238	variation in individual growth

^a The estimates are not regarded as $\ln \lambda_s$ because of too small number of iterations.

America. Based on long-term data on fisheries records, its population dynamics have been studied intensively using a variety of population models (Van Winkle et al. 1979; Goodyear 1980; Cohen et al. 1983; Heyde and Cohen 1985; Goodyear et al. 1985). Most notably, 28-yr data by the Maryland Department of Natural Resources showed that average catch of young-of-year (fingerling, or 1-yr juvenile) of the Potomac River population varies greatly (ca. 150-fold) from year to year, reflecting variation in environmental factors such as freshwater discharge and water temperature (Cohen et al. 1983). Using these data, Cohen et al. (1983) analyzed its population dynamics by constructing an age-classified stochastic model.

They assumed that the variation in young-of-year reflects random fluctuation in recruitment rate $s_0(t)$, i.e., survivorship during the first year from egg release. They also assumed constant survivorship after the first year and time-invariant age-specific fecundity, and estimated $s_0(t)$ for 13 years. Since $s_0(t)$ is not correlated with time, its variation is regarded as homogeneous. There was no evidence for density-dependence in $s_0(t)$, nor for autocorrelation between successive estimates of $s_0(t)$. The distribution of $s_0(t)$ was found to fit the lognormal distribution better than the normal distribution.

The stochastic analysis was conducted using 13 Leslie matrices, each of which used 15 age classes and whose first-

year survival corresponded to one of 13 estimates of $s_0(t)$. Calculation of $\ln \mu$ was carried out analytically, while $\ln \lambda_s$ was estimated by numerical iterations (Table 1). The iteration was started from an arbitrary initial age structure that consisted of one individual in each age class. At each time step, one of 13 matrices was randomly chosen with a probability of 1/13. The change in population size was followed for 1000 time steps to obtain $\ln \lambda_s$, following 100 iterations to eliminate transient effects.

Heyde and Cohen (1985) developed a method to estimate variation of $\ln \lambda_s$, and calculated its 95% confidence interval for the striped bass population using the same set of data (Table 1).

Savanna grasses

Plant communities in tropical savanna are greatly affected by fire occurring naturally or anthropogenically. Effects of fire frequency on plant population dynamics were studied in Venezuelan savannas for a perennial grass *Andropogon semiberbis* (Silva et al. 1991) and an annual grass *A. brevifolius* (Canales et al. 1994).

The two studies were undertaken at different localities, but used similar methodology. Data on survivorship, growth and fecundity were recorded at an annually-burnt area and a protected (unburnt) area, and projection

matrices were constructed for each environment. Matrices for the perennial species consisted of 4 size classes, while those for the annual made up of 6 monthly age classes. In both species, deterministic population growth rate λ_1 was higher at burnt areas than at unburnt ones.

For each species, a stochastic analysis was carried out by assuming that burnt and unburnt environments occur at the arbitrary probabilities of p and $1-p$, respectively. The stochastic growth rate $\ln \lambda_s$ was numerically obtained using the Markov model to generate a sequence of 3000 matrices. The results showed that $\ln \lambda_s$ increases linearly with p , and the populations were predicted to be stable at the fire frequencies of 0.85 for *A. semiberbis* and 0.29 for *A. brevifolius*. Both studies have also examined the effect of autocorrelation (see below).

Gorgonian coral

The gorgonian *Leptogorgia virgulata* is a dioecious coral that colonizes on hard substrata in shallow waters along the Atlantic coast and in the northern Gulf of Mexico. Gotelli (1991) studied its demography at a shallow subtidal area of Florida by monthly census for 2 years. By measuring recruitment rate, growth and survivorship of individually-distinguished colonies, he constructed 23 monthly projection matrices which consisted of 5 size classes.

He estimated population growth rates both by a deterministic model using an average matrix and by a stochastic model assuming 23 matrices occur randomly at the same frequency. The estimate of $\ln \lambda_s$ was obtained numerically based on the population track for 5000 iterations after removing transient effects with 1000 iterations. The field measurements showed that recruitment, growth and survivorship varied greatly from month to month. To see the separate effect of variation in these vital rates on population growth rate, he ran several simulations which assumed random variation in some vital rates while keeping others constant. The comparison of simulations showed that the variation in recruitment, growth and survivorship has a different contribution to $\ln \lambda_s$ (see below).

Seaweed

The perennial seaweed *Ascophyllum nodosum* inhabits the intertidal zone of northern Atlantic rocky shores. Åberg (1992a, 1992b) studied the demography of two populations along the Swedish coast. Using a deterministic model, he found that vital rates of the seaweed varied between years with or without ice and that the frequency of ice differed between the two study sites (Åberg 1992a). He developed a stochastic model using the same data to examine the effects of ice frequency on its population dynamics (Åberg 1992b).

Size-specific annual growth and survivorship were measured for 5 size classes in 3 different years, i.e., normal year, ice year and extreme ice year. Stochastic analyses were carried out assuming homogeneous, independent environments. The growth rate of average population size $\ln \mu$ was calculated analytically, while stochastic growth rate $\ln \lambda_s$ was estimated by numerical iteration for 10000 time steps. At each time step, one of three matrices representing vital rates in different ice conditions was chosen randomly at the frequency of ice years given in ice-statistics at the two sites. Since it was impossible to obtain fertility estimates (rate of sexual reproduction), two types of matrices were used: (1) matrices without the information on fertility, and (2) those with arbitrarily-scaled fertility resulting in a growth rate of $\ln \lambda_s = 0$.

The results of the analyses showed that $\ln \lambda_s$ for matrices without the fertility elements was higher at the site with less frequent ice years, demonstrating that this site needed lower fertility to achieve stable population size ($\ln \lambda_s = 0$).

Åberg (1992b) also estimated the elasticity (proportional sensitivity) of λ_s to changes in elements in the matrices. The elasticity he used was not the same as that used in a deterministic model, and was expressed as the percentage changes in λ_s before and after one matrix element is reduced by 25%. To obtain the elasticity, λ_s was obtained firstly by a simulation for 5000 years, and then a new estimate of λ_s was calculated with the same sample path but with a 25% reduction in one element. It was revealed that λ_s was more sensitive to changes in matrix elements of larger size classes.

Desert tortoise

The desert tortoise *Gopherus agassizii* lives in the desert of the American Southwest. It is decreasing rapidly in number and is listed as a threatened species. Doak et al. (1994) analyzed the dynamics of the population in the Western Mojave desert, California, to understand its current status as well as to evaluate effective strategies for its conservation.

They constructed a matrix model with 8 size classes. Field data for the model were taken at 10 sites for the period of 2–4 years. They found that variation in vital rates is correlated with each other and with environmental factors such as rainfall. Stochastic analyses were carried out by randomly varying growth and survivorship according to beta distributions, assuming different levels of variation in these parameters (full or half of observed variation), and with or without correlation between vital rates. Unlike other studies, they did not estimate the asymptotic stochastic growth rate $\ln \lambda_s$, but calculated an average growth rate by short-term numerical simulations. Each simulation was run for 50 years, starting with the stable size distribution obtained by a deterministic model.

Population trajectory between years 25 and 50 was used for the calculation of the population growth rate. One hundred independent simulations were carried out to obtain a 95% confidence interval of population size. They found that the variation and correlations in vital rates have significant effects on the estimate of the population growth rate (see below).

Red deer

A population of red deer *Cervus elephas* on the island of Rum off the west coast of Scotland has been intensively studied for more than 25 years (Clutton-Brock and Albon 1989). The weather is variable, and in particular, the variation in rainfall is highly correlated with adult mortality and population size (Benton et al. 1995). The birth and death, as well as reproductive success of all individuals in the population has been recorded by continuous monitoring, which made it possible to investigate the effects of varying environments on population growth rate and life-history evolution of this long-lived mammal.

Based on long-term data for 21 years, Benton et al. (1995) developed a Leslie matrix model consisting of 19 age classes, and compared several measures of population growth rates: i.e., deterministic population growth rate ($\ln \lambda_1$) assuming a constant environment, stochastic population growth rate ($\ln \lambda_s$) calculated by the perturbation method of Tuljapurkar (1982b), and $\ln \lambda_1$ and $\ln \lambda_s$ with both obtained by numerical simulations based on 1500 independent runs of 250 iterations each.

They also estimated sensitivity and elasticity of both deterministic and stochastic population growth rates to changes in age-specific survivorship and fecundity. By comparing the results of the models between those assuming independent change in each vital rates and those incorporating trade-offs between current fecundity and survivorship or future fecundity, they examined how cost of reproduction acts as the selective pressure on life-history evolution in deterministic and stochastic environments.

Marine molluscs

It is generally known that most marine benthic invertebrates with free-swimming larvae show large temporal variation in recruitment (Vahl 1982; Bachelet 1986; Nakaoka 1993). The effects of year-to-year variation in recruitment on population dynamics were studied for two molluscan species living in shallow soft-bottom around the northeastern Japanese coast; the gastropod *Umbonium costatum* (Noda and Nakao 1996) in Hakodate Bay and the bivalve *Yoldia notabilis* in Otsuchi Bay (Nakaoka 1996).

Eight years of study by Noda and Nakao (1996) revealed that recruitment density of *U. costatum* was highly

variable from year to year (85-fold difference between minimum and maximum). Recruitment rate calculated from the recruitment density, adult density and fecundity also showed large annual variation, characterized by an extremely high estimate in one of 8 years (1982).

Based on quantitative data on recruitment rate, age-specific survivorship and fecundity, they built 8 age-classified projection matrices for the gastropod which consisted of 6 age classes. The recruitment rate of each matrix corresponds to one of 8 estimates, while all the other vital rates (age-specific survivorship and fecundity) were kept constant. They first calculated $\ln \lambda_s$ using all the matrices, assuming each of them occurs randomly at the same frequency (1/8). Then, they calculated $\ln \lambda_s$ by removing the matrix with the largest recruitment rate (the value in 1982), and compared the results to see the effect of the occasional mass recruitment on population growth.

A *Y. notabilis* population in Otsuchi Bay shows large annual variation not only in recruitment rate (Nakaoka 1993), but also in individual growth rate (Nakaoka and Matsui 1994). Nakaoka (1996) studied the relative importance of the variation in these parameters by constructing a stochastic matrix model whose matrix consisted of 10 size classes.

Estimates of $\ln \lambda_s$ were based on 3000 iterations, starting from initial size distributions observed in the field and following initial 1000 iterations to eliminate transient effects. The same 3000 matrices were used to calculate the corresponding $\ln \mu$. Eighteen years of data on recruitment were fitted with normal or lognormal probability distributions, and 9 years of data on individual growth rate were fitted with normal distributions. At each time step of iteration, recruitment rate and/or individual growth rate were randomly chosen from the fitted distributions. Several simulations were run with different assumptions on probability distributions (lognormal or normal), and on the types of vital rates subject to vary (recruitment rate or individual growth rate). He also examined the effect of the variation in these vital rates by arbitrarily changing the magnitude of variation.

General properties

By comparison with the empirical studies, I examine some important properties of the stochastic matrix model found by theoretical studies. I will first discuss the differences in population growth rates with and without the assumption of environmental fluctuations, and then on some factors affecting the stochastic population growth rate $\ln \lambda_s$ and its confidence interval, namely: a) magnitude of variation in vital rates; b) probability distribution of random environments; c) fluctuation in different types of vital rates; d) covariances between vital rates; and e) autocorrelation

between successive environments.

Difference in the measures of population growth rate with and without environmental fluctuations

Some studies reviewed in the previous section analyzed population dynamics both by deterministic and stochastic matrix models using the same source of data (Gotelli 1991; Silva et al. 1991; Åberg 1992a, 1992b; Canales et al. 1994; Doak et al. 1994; Benton et al. 1995), while others concentrated on the stochastic model (Bierzychudek 1982; Cohen et al. 1983; Nakaoka 1996; Noda and Nakao 1996). Even in the latter 4 studies, the deterministic growth rate can be represented by $\ln \mu$, because in these studies, the series of random environments were chosen by an iid (independent, identically distributed) process, under which condition $\ln \mu$ is equivalent to the deterministic growth rate of a population ($\ln \lambda_1$) obtained as the largest eigenvalue of an average matrix (Caswell 1989; Tuljapurkar 1989). Therefore, it is possible to compare how the estimates of population growth rate change when one takes into account the random variation in environments.

The estimates of two measures of population growth rates are summarized in Table 1. The stochastic growth rate $\ln \lambda_s$ was no greater than the deterministic growth rate in all the studies. The difference between the two measures, however, varies greatly among studies. The stochastic and deterministic growth rates were almost the same in Jack-in-the-pulpit, the savanna grasses and the red deer, while the former was much smaller than the latter in the gorgonian, the seaweed, the marine gastropod and bivalve.

Factors causing the differences between stochastic and deterministic growth rates are not clear from the comparison of the empirical studies. The theoretical studies predict that the difference between $\ln \lambda_s$ and $\ln \mu$ increases with variation in matrix elements expressing fluctuating vital rates (Tuljapurkar 1982b; Caswell 1989). This trend, however, is not obvious by qualitative comparisons of the empirical studies. For example, the estimates of $\ln \lambda_s$ and $\ln \lambda_1$ are similar for *A. semiberbis* even though matrix elements vary 1.1 to 23 fold between the two environments (Silva et al. 1991). In contrast, $\ln \lambda_s$ is much smaller than $\ln \lambda_1$ for the seaweed with a similar degree of variation in matrix elements (1.0 to 19 fold, Åberg 1992b). The amount of difference between stochastic and deterministic growth rates seems neither related to other factors such as the number of environments, the type and size of matrices, nor the methods of numerical iteration.

Nevertheless, the fact that the population growth rate determined by stochastic matrix models always becomes no greater than that of corresponding deterministic model has a significant meaning for the application of population

models to empirical populations, especially when using them for conservation purposes. One needs to take precaution for the use of deterministic models in fluctuating environments, because in some cases, the models based solely on average vital rates and ignoring temporal fluctuation may overestimate the population growth rate in reality.

Factors affecting the estimates of $\ln \lambda_s$

a) Magnitude of variation in vital rates

As discussed earlier, degree of variance in vital rates affects estimates of $\ln \lambda_s$ and its confidence intervals. Two empirical studies examined this effect by assuming continuous probability distributions for some matrix elements and by changing their variances arbitrarily (Doak et al. 1994; Nakaoka 1996).

Doak et al. (1994) calculated the distribution of the short-term population growth rate (expressed as λ) by 100 independent simulations for the desert tortoise, and compared it between simulations which assumed the variances in vital rates observed in the field (full variation) and those assuming a half of the observation (half variation). Although the mean λ was relatively unaffected by the differences in variation, they had great effects on the distribution of λ . The range of λ with full variation ($0.89 < \lambda < 1.00$) was greater than that with half variation ($0.93 < \lambda < 1.00$). Accordingly, 95% confidence intervals of the predicted population size were about 1.5 times greater in the former. Broader confidence intervals in population size lead to a higher probability of extinction. Based on the result, they pointed out how important it is to include information on variability into population models for conservation purposes, by stating that "whereas population projections based solely on mean rates would predict substantial numbers of tortoises 100 yr into the future, the same mean rates combined with their estimated variation indicate a striking risk of population extinctions within decades" (Doak et al. 1994). It has been theoretically established that environmental stochasticity has significant effects on extinction rate (Leigh 1981; Goodman 1987). The analyses by Doak et al. (1994) demonstrated that this general rule is significant in a size-structured population in the field.

Nakaoka (1996) examined the effects of variation in recruitment rate and individual growth rate on $\ln \lambda_s$ for the marine bivalve by arbitrarily changing the variances of probability distributions fitted to the fluctuation in the vital rates. Confidence intervals of $\ln \lambda_s$ increased with the variance in both vital rates, but the variance in recruitment rate had more effects than that in individual growth rate, because the former was fitted by lognormal distribution with the latter by normal distribution. An interesting finding was that $\ln \lambda_s$ was significantly lower than 0 with

lower variation in recruitment rate, while it did not differ from 0 with larger variation because confidence intervals of $\ln \lambda_s$ got also broader. Therefore, the possibility of maintaining constant population size increased with variation.

A similar analysis was carried out by Noda and Nakao (1996) by assuming discrete random variation in recruitment rate for a marine gastropod. They compared $\ln \lambda_s$ between a model incorporating all of 8-yr estimates on recruitment rate, and one using the 7 lowest values. The stochastic growth rate obtained by the former model was positive, so that the population may persist, while it was negative in the latter model, suggesting a decrease in population size without the mass recruitment once in 8 years. In their case, since not only the variation but also the average of the recruitment rate was lower in the latter model, the change in $\ln \lambda_s$ is not solely ascribed to the difference in variance. Nevertheless, the studies by Nakaoka (1996) and Noda and Nakao (1996) demonstrated that the populations of these molluscs are maintained by occasional mass recruitment.

b) Probability distribution of random environments

More than half of the empirical studies reviewed here assumed a few different environments for stochastic analyses whose random variation occur in a discrete manner (e.g., good and bad years, burnt and unburnt environments, or normal and ice years occurring at fixed probabilities). However, fluctuations in environment and vital rates are normally expressed by continuous variables. Ideally, random variables in these parameters should be fitted to continuous probability distributions based on long-term data.

Year-to-year variation in recruitment rate of *Y. notabilis* is fitted better to lognormal distribution than normal distribution. Nakaoka (1996) fitted the data to both distributions and compared $\ln \lambda_s$ and its confidence intervals between them. The stochastic growth rate was much higher and its 95% confidence interval was much smaller with the normal distribution (0.0098 ± 0.0001) than with the lognormal distribution (-0.0137 ± 0.0299). It is therefore concluded that the prediction of population growth rate may be totally different according to the types of probability distribution fitted to the fluctuating environments.

c) Fluctuations in different matrix elements

A projection matrix is composed of elements expressing different types of vital rates, such as growth, survivorship and reproduction. Fluctuation in environments may have different effects on variation in these vital rates, and in turn, fluctuations in different types of vital rates may have different contributions to changes in population growth rate.

Gotelli (1991) found large monthly variation in recruitment, growth and survivorship of the gorgonian. To examine the relative contributions of the fluctuating vital rates, he ran several simulations by assuming random variation in some vital rates, while keeping others constant. The results showed that the predicted population size became significantly lower when the survivorship, or both survivorship and growth were subject to vary. The variation in recruitment, on the other hand, had little effects on the population statistics. He concluded that the contribution of the variation in recruitment was smaller than that in mortality.

Yoldia notabilis shows large year-to-year variation in both recruitment rate and individual growth rate. Nakaoka (1996) analyzed the effects of variation in these vital rates by comparing simulations that took into account the variation in (1) recruitment rate, (2) individual growth rate, and (3) both vital rates. The stochastic population growth rate $\ln \lambda_s$ and its 95% confidence intervals obtained by varying both vital rates were almost identical to those obtained by assuming fluctuation only in the recruitment rate. The variation in recruitment rate, therefore, has great effects on $\ln \lambda_s$, while that in individual growth rate has negligible effect.

It is interesting to know if the contributions of fluctuation in different matrix elements are related to the sensitivity or elasticity of population growth rate to changes in corresponding elements. The theoretical study by Tuljapurkar (1982a) showed that population dynamics are most sensitive to fluctuation in vital rates for which sensitivities is large. Two studies described above (Gotelli 1991; Nakaoka 1996) examined this problem by estimating sensitivities and elasticities for vital rates. In case of the gorgonian, elasticities for survivorship and growth were also larger than those for recruitment, and therefore, the effect of fluctuation in a vital rate on $\ln \lambda_s$ was positively related to its elasticity. In the case of the marine bivalve, however, the sensitivities were also higher for elements expressing growth and survivorship than those expressing recruitment, which lead to a negative relationship between elasticities and the effect of fluctuation on $\ln \lambda_s$. The relative contribution of fluctuating vital rates, thus, cannot be explained from the sensitivities. Since both studies on natural populations used sensitivities or elasticities in size-classified matrices, they may not follow Tuljapurkar's results based on sensitivities in age-classified matrix. In case of the bivalve, furthermore, the fluctuation in recruitment rate was fitted with a lognormal distribution, while that in individual growth rate with a normal distribution. It is therefore possible that the effects of different sensitivities were masked by those of different probability distributions discussed earlier.

Åberg (1992a, 1992b) and Benton et al. (1995) took different approaches and examined how the sensitivities

and elasticities of each element differ between deterministic and stochastic models. The elasticities of stochastic population growth rates for the seaweed, defined as the percentage changes of λ_s to the 25% decrease in matrix elements (Åberg 1992b) did not differ largely from those obtained by the deterministic model (Åberg 1992a). The stochastic sensitivity for vital rates of the red deer, defined as the rate of change in $\ln \lambda_s$ with changes in the matrix elements (Benton et al. 1995), was almost the same as the deterministic version of sensitivity. Based on the results, Benton et al. (1995) concluded that environmental variation may not directly affect selective pressures of life-history traits which are expressed by the relative amounts of sensitivity or elasticity.

d) Covariances between vital rates

Variation in some vital rates is often correlated with that in other vital rates. Theoretical studies have shown that one-period covariances between vital rates can have significant effects on dynamics of structured populations (Tuljapurkar 1982a; Caswell 1989).

Doak et al. (1994) found that growth and survivorship of some size classes of the desert tortoise are positively or negatively correlated with each other. They analyzed the effects of the observed correlations by comparing their estimates of population growth rate (λ) between simulations with and without the assumption of the correlation. The result showed that the addition of correlation leads to broader variation in λ and population size. Its effect, however, was not as large as that of variation in vital rates discussed earlier.

It is theoretically predicted that positive one-period covariances between matrix elements will increase the degree of population fluctuation (Tuljapurkar 1982a). In case of the tortoise, most of the correlations between vital rates are positive, so their effects are consistent with the theory. Negative covariances, on the other hand, will have a stabilizing effect on population fluctuation. No empirical studies, however, have examined this possible effect yet.

e) Autocorrelation between successive environments

The underlying theorems of stochastic matrix model analysis, as well as methods of estimating stochastic population growth rates are much influenced by the presence or absence of autocorrelation between environments. Most empirical studies listed here assumed independent environments for the stochastic analyses mainly because the data on environmental fluctuation were not long enough to detect any pattern of autocorrelation. Numerical experiments by Tuljapurkar and Orzack (1980) and an analytical study by Tuljapurkar (1982a) have shown that autocorrelation has only small effects on the estimates of $\ln \lambda_s$, while Matsuda and Iwasa (1993) describ-

ed a numerical example in which the effect of autocorrelation is important in predicting population dynamics.

The effects of autocorrelation were examined in the two studies on savanna grasses by hypothetically assuming positive or negative correlations between burnt and unburnt environments (Silva et al. 1991; Canales et al. 1994). Negative autocorrelation indicates that burnt and unburnt years tend to occur alternately, while positive autocorrelation indicates that one environment tends to continue for long-term. The estimates of $\ln \lambda_s$ was almost the same among simulations with positive and negative autocorrelations ($\rho=0.5$ and -0.5 , respectively) and that without autocorrelation ($\rho=0$). Autocorrelation, therefore, has little effects on the population dynamics of these grasses.

Prospect for future research

Since papers applying stochastic matrix models to natural populations are still rather small in number, it is premature to conclude that some trends discussed in the previous section will always be true for any structured populations in natural environments. Based on the shortcomings of the available information, I point out some important problems which should be tested in future studies.

First of all, the effects of time-varying environments on population dynamics should be further investigated by collecting long-term field data on environmental fluctuations. It has already been shown that $\ln \lambda_s$ is greatly affected by the types of probability distribution of environments, magnitude of variation in vital rates, and possibly by the presence of autocorrelation. In most empirical studies, however, information on environmental fluctuation was over too short a time scale to examine these effects. Estimates of $\ln \lambda_s$ calculated from a small number of observations on fluctuating environments should be interpreted with caution, because they may largely deviate from reality if the observations do not represent the nature of fluctuating pattern in environments. It is, of course, not easy to collect long-term data in the field, especially for organisms with long lifespans, and in addition, there are always financial and other practical limitations for carrying out long-term research. In such cases, one of the alternative approaches is to find correlations between variation in vital rates and long-term environmental records such as meteorological and oceanographic data, and to use the latter for stochastic analyses (e.g., Chapter 7 in Caughley and Gunn 1996).

Secondly, the effects of fluctuation in different matrix elements should be studied in more detail, because it may result in some fundamental differences between scalar and structured populations. In deterministic models, sensitivity and elasticity analyses are now frequently used for ex-

amining the relative importance of each matrix element on population growth rate. However, the equivalent methods have rarely been applied to the stochastic models. Two studies calculated both deterministic and stochastic sensitivities (or elasticities), and they did not find differences between them (Åberg 1992a, 1992b; Benton et al. 1995). However, analyses by Gotelli (1991) and Nakaoka (1996) have shown contrasting results about the relationship between relative contribution of fluctuation in matrix elements and sensitivity or elasticity of corresponding elements. More empirical studies are necessary to find general trends on this relationship.

Thirdly, all the studies reviewed here assume homogeneous environments, i.e., the pattern of stochastic variation does not change with time. Prediction of population dynamics, however, may be different when the environment is inhomogeneous, i.e., the pattern of fluctuation changes with time. Such irreversible changes in environments are likely to occur especially when they are related to human activities, such as alteration of local habitats, discharge of waste materials, and the global warming of the atmosphere. One must therefore pay special attention to this point when applying stochastic models to conservation biology problems. It is interesting to carry out theoretical and empirical studies testing how population dynamics differs between homogeneous and inhomogeneous environments.

Fourthly, the effects of density-dependence must be taken into account in stochastic models in future studies. All the studies reviewed here assumed density-independent vital rates, without any evidence for density-dependence. In fluctuating environments, the relative importance of density-dependence may also fluctuate. For example, a significant density effect may be found in years with good recruitment, while it may be negligible in years with poor recruitment (Hancock 1973; Goshima 1982).

When density-dependence is included in the model, it is no longer possible to obtain deduced general properties such as $\ln \lambda_s$ (Caswell 1989). Some empirical studies have incorporated effects of both density-dependence and fluctuating environments into matrix models; e.g., Burgman and Gerard (1990) for predicting population structure of the giant kelp (*Macrocystis pyrifera*), and Armbruster and Lande (1993) for calculating extinction probability of a population of African elephant (*Loxodonta africana*). Their results suggest that the fluctuating environments have significant effects on population structure and extinction probabilities of the organisms studied. However, interacting effects of density-dependence and environmental fluctuation are unknown.

Finally, the extension of the stochastic matrix model for analyzing the effects of spatial structure is another step to be overcome. Temporal variation in one site may be buffered or escalated by lateral movements of individuals

between sites. Gotelli (1991) built an expanded matrix model which took dynamics at two sites into consideration, though his brief description of methodology precludes us from distinguishing whether his results are based on the deterministic or the stochastic model. It is expected that spatial structure will have little effect on population dynamics if the temporal variation occurs synchronously across areas, while it may have stabilizing effects if the variation is spatially asynchronous (Harrison and Quinn 1989; Akçakaja and Ginzburg 1991).

In conclusion, applications of stochastic matrix models to empirical populations have given some insights on how the dynamics of natural populations with age or size structure behave in time-varying environments. However, they highlight more important questions which need to be solved in future studies. The combined approach of developing theoretical models and testing them against empirical populations will be promising not only for more precise prediction of population dynamics of specific populations, but also for a better understanding of the dynamics of structured populations in general.

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