Aqua-BioScience Monographs, Vol. 4, No. 3, pp. 95–104 (2011) www.terrapub.co.jp/onlinemonographs/absm/

The Growth Rates of Population Projection Matrix Models in Random Environments

Tatsuro Akamine* and the late Maki Suda

National Research Institute of Fisheries Science, Fisheries Research Agency
Fukuura 2-12-4, Kanazawa, Yokohama 236-8648, Japan
e-mail: akabe@affrc.go.jp

Abstract

Population projection matrix models in random environments are random walk models. The growth rate of the mean population size, which is equal to the maximum eigenvalue of the mean matrix, is better than the average of the intrinsic rates of natural increase calculated by computer simulations, because the population size is more important than the growth rate. The arithmetic mean of the maximum eigenvalues of matrices for all permutations converges to the maximum eigenvalue of the mean matrix. The periodicity of environments is more important than the correlation between environments. Simple matrices and three numerical models are used as examples.

Received on June 1, 2011
Accepted on August 3, 2011
Online published on October 15, 2011

Keywords
- eigenvalue
- growth rate
- Lefkovitch
- Leslie
- permutation
- projection matrix

1. Introduction

Population projection matrix models, which are called the Leslie matrix model and the Lefkovitch matrix model, have been expanded for random environments (Caswell 2001). These models have already been used in fish population dynamics (Cohen *et al.* 1983; Quinn and Deriso 1999; Akamine 2009). However, there are two problems with these models. One is the method of estimating the population growth rate and the other is the negative correlation of the successive environmental states. In this paper, we will discuss these problems using simple models.

Akamine (2011) proved the theorem that the arithmetic mean of the maximum eigenvalues of matrices for all permutations of the random walk matrix model converges to the maximum eigenvalue of the mean matrix, which is defined as the population growth rate. Akamine (2010a, b) calculated the maximum eigenvalues of all permutations to estimate their distribution, which is more basic than random simulations generated by computers. We will also discuss these matters.

2. Scalar model

The basic model is

$$N(t+1) = N(t)\lambda(t), \tag{1}$$

where N is the population size, λ is the growth rate and t is discrete time. Thus, we obtain

$$N(t) = N(0)\prod_{i=0}^{t-1}\lambda(i). \tag{2}$$

Suppose the value of $\lambda(i)$ is α or β at random. The arithmetic mean of these is

$$\delta = \frac{1}{2}(\alpha+\beta). \tag{3}$$

The t-th power is

$$\delta^t = \frac{1}{2^t}(\alpha+\beta)^t. \tag{4}$$

The right-hand side has 2^t permutations of α and β and the left-hand side is an arithmetic mean of all permutations on the right-hand side. This is an exponential model and δ is the mean growth rate. When $\alpha = 2$, $\beta = 0.5$, we obtain $\delta = 1.25 > 1$. Thus, the mean population size will increase.

doi:10.5047/absm.2011.00403.0095

On the other hand, the logarithm of Eq. (1) is

$$\log N(t+1) = \log N(t) + r(t), \tag{5}$$

where $r = \log\lambda$ is the intrinsic rate of natural increase. We then obtain

$$\log N(t) = \log N(0) + \sum_{i=0}^{t-1} r(i). \tag{6}$$

This is a random walk model. In the above case, the mean logarithm of the population size will not increase because the arithmetic mean of $\log\alpha$ and $\log\beta$ is 0. When $t \to \infty$, the distribution of $\sum r$ approaches to the normal distribution. Thus, the distribution of $\prod\lambda$ in Eq. (2) approaches to the lognormal distribution.

The definition of the lognormal distribution is

$$\log X \approx \mathrm{Normal}\left(\mu, \sigma^2\right). \tag{7}$$

The following are well-established:

$$\mathrm{Mean}(X) = E(X) = \exp\left(\mu + \frac{\sigma^2}{2}\right), \tag{8}$$

$$\mathrm{Median}(X) = \exp\mu, \tag{9}$$

$$\mathrm{Mode}(X) = \exp\left(\mu - \sigma^2\right), \tag{10}$$

where $E(\cdots)$ is the expected value. Although Eq. (7) shows that the mean of $\log N$ is μ, Eq. (8) shows that the logarithm of $E(N)$ is $\mu + \sigma^2/2 > \mu$.

Which is better for fish population dynamics, Eq. (1) or Eq. (5)? We think Eq. (1) is better than Eq. (5). This problem will be discussed again in Section 8. Therefore, in matrix models, it is better to choose the maximum eigenvalue of the mean matrix for the population growth rate, not the average of the population growth rate. These are described in the following section.

3. Matrix model

The population projection matrix model in quadratic form is defined as follows:

$$\begin{pmatrix} n_0(t+1) \\ n_1(t+1) \end{pmatrix} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} n_0(t) \\ n_1(t) \end{pmatrix}, \tag{11}$$

or

$$\mathbf{n}(t+1) = \mathbf{Ln}(t), \tag{12}$$

where n_i is the number of individuals in age or category class of i, a and b are reproduction rates and c and d are survival rates. All constants are not negative. Thus, the projection matrix $\mathbf{L}$ is a non-negative matrix.

When this model is modified as

$$\mathbf{L} = \mathbf{S}\begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}\mathbf{S}^{-1}, \tag{13}$$

the t-th power is

$$\mathbf{L}^t = \mathbf{S}\begin{pmatrix} \lambda_1^t & 0 \\ 0 & \lambda_2^t \end{pmatrix}\mathbf{S}^{-1}, \tag{14}$$

where λ_1 and λ_2 are eigenvalues and $\mathbf{S}$ is a matrix of eigenvectors. Eigenvalues are roots of the eigenequation

$$\lambda^2 - (a+d)\lambda + (ad - bc) = 0. \tag{15}$$

When $\nu = |\lambda_2|/\lambda_1 < 1$, we obtain $\nu^t \to 0$ $(t \to \infty)$,

$$\mathbf{L}^t \approx \lambda_1^t \mathbf{S}\begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix}\mathbf{S}^{-1} \approx \lambda_1 \mathbf{L}^{t-1}. \tag{16}$$

Therefore, the maximum eigenvalue λ_1 is defined as the population growth rate. The rank of this matrix is

$$\lim_{t\to\infty} \mathrm{rank}\left(\mathbf{L}^t\right) = 1. \tag{17}$$

Basic model (12) is expanded in random environments as

$$\mathbf{n}(t+1) = \mathbf{L}(t)\mathbf{n}(t). \tag{18}$$

Caswell (2001) defined the population size as

$$N(t) = w_0 n_0(t) + w_1 n_1(t) = \begin{pmatrix} w_0 & w_1 \end{pmatrix}\begin{pmatrix} n_0(t) \\ n_1(t) \end{pmatrix}, \tag{19}$$

where w_0 and w_1 are weights. He also defined the average growth rate as

$$\log\lambda_s = \lim_{t\to\infty} \frac{1}{t}\log N(t). \tag{20}$$

This is expressed exactly as

doi:10.5047/absm.2011.00403.0095

$$\log \lambda_s = \lim_{t\to\infty} \frac{1}{t} E[\log N(t)]. \qquad (21)$$

It is not possible to obtain this value analytically, this is an average of computer simulations.

On the other hand, Cohen *et al*. (1983) defined the growth rate of the expected population size as

$$\log \Lambda = \lim_{t\to\infty} \frac{1}{t} \log E[N(t)]. \qquad (22)$$

This is equal to

$$\Lambda = \lim_{t\to\infty} \left(E[N(t)]\right)^{1/t}. \qquad (23)$$

They used a general model

$$\mathbf{L}(t) = \begin{pmatrix} 0 & b \\ c(t) & 0 \end{pmatrix}, \qquad (24)$$

where $c(t)$ is a random variable. They also showed the following equation

$$E[\mathbf{L}(t-1)\mathbf{L}(t-2)\cdots\mathbf{L}(0)] = \left(E[\mathbf{L}(0)]\right)^t \qquad (25)$$

and proved

$$\Lambda = \lambda_1(\mathbf{R}), \qquad (26)$$

where the right-hand side is the maximum eigenvalue of the mean matrix. Akamine (2011) proved this theorem by using eigenvalues for the random walk matrix model, which is explained in the following section.

4. Theorem

Two environments expressed as **P** or **Q** occur at random. The mean matrix of these is

$$\mathbf{R} = \frac{1}{2}(\mathbf{P} + \mathbf{Q}) \qquad (27)$$

and the t-th power is

$$\mathbf{R}^t = \frac{1}{2^t}(\mathbf{P} + \mathbf{Q})^t = \frac{1}{2^t}\sum_i \mathrm{Perm}(\mathbf{P}, \mathbf{Q}, t, i), \qquad (28)$$

where Perm(**P**, **Q**, t, i) is a permutation of **P** and **Q** whose length is t (for example, **PPQPQQQPP** when $t = 9$) and $\sum$ means the sum of all permutations. This equation can be rewritten as

$$\mathbf{R}^t = E[\mathrm{Perm}(\mathbf{P}, \mathbf{Q}, t)], \qquad (29)$$

or

$$\mathbf{R} = \left[\frac{1}{2^t}\sum_i \mathrm{Perm}(\mathbf{P}, \mathbf{Q}, t, i)\right]^{1/t}. \qquad (30)$$

Akamine (2011) proved the equation

$$\lim_{t\to\infty}\left[\frac{1}{2^t}\sum_i \lambda_1\left(\mathrm{Perm}(\mathbf{P}, \mathbf{Q}, t, i)\right)\right]^{1/t} = \lambda_1(\mathbf{R}), \qquad (31)$$

which means that the arithmetic mean of the maximum eigenvalues of matrices for all permutations on the random walk matrix model converges to the maximum eigenvalue of the mean matrix.

5. Proof

(Lemma)

The general theory of eigenvalues is as follows: Let

$$\mathbf{W} = \mathbf{U} + \mathbf{V}. \qquad (32)$$

Then

$$\mathrm{trace}\mathbf{W} = \mathrm{trace}\mathbf{U} + \mathrm{trace}\mathbf{V}. \qquad (33)$$

This equation implies

$$\sum_k \lambda_k(\mathbf{W}) = \sum_k \lambda_k(\mathbf{U}) + \sum_k \lambda_k(\mathbf{V}). \qquad (34)$$

(Proof)

In Eq. (28), the following equations hold:

$$\lim_{t\to\infty} \mathrm{rank}\left(\mathbf{P}^t\right) = 1,\ \lim_{t\to\infty} \mathrm{rank}\left(\mathbf{Q}^t\right) = 1,\ \lim_{t\to\infty} \mathrm{rank}\left(\mathbf{R}^t\right) = 1. \qquad (35)$$

When the following equation holds,

$$\lim_{t\to\infty} \mathrm{rank}[\mathrm{Perm}(\mathbf{P}, \mathbf{Q}, t, i)] = 1, \qquad (36)$$

Eq. (31) will hold because of the above lemma. The linear mapping of **P** or **Q** in Eq. (11) projects the basic vectors of the x- and y-axes

$$\mathbf{e}_1 = \begin{pmatrix} 1 \\ 0 \end{pmatrix},\ \mathbf{e}_2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}, \qquad (37)$$

doi:10.5047/absm.2011.00403.0095

to

$$\mathbf{e}_1' = \begin{pmatrix} a & b \\ c & d \end{pmatrix}\begin{pmatrix} 1 \\ 0 \end{pmatrix} = \begin{pmatrix} a \\ c \end{pmatrix}, \ \mathbf{e}_2' = \begin{pmatrix} a & b \\ c & d \end{pmatrix}\begin{pmatrix} 0 \\ 1 \end{pmatrix} = \begin{pmatrix} b \\ d \end{pmatrix}. \quad (38)$$

The inner product of these vectors is

$$\mathbf{e}_1' \cdot \mathbf{e}_2' = ab + cd = \sqrt{a^2 + c^2}\sqrt{b^2 + d^2}\cos\theta. \quad (39)$$

Thus, when $ab + cd \neq 0$, the cosine of these vectors is

$$0 < \cos\theta = \frac{ab + cd}{\sqrt{a^2 + c^2}\sqrt{b^2 + d^2}} \quad (40)$$

and the angle of these vectors is $|\theta| < \pi/2$. When $t \to \infty$, these projected vectors will overlap with each other, because Perm(**P**, **Q**, $2t$, i) involves **P** or **Q** over or equal to t times. Thus, for any Perm(**P**, **Q**, t, i), rank[Perm(**P**, **Q**, t, i)] $\to 1$ ($t \to \infty$). (Q.E.D.) It is easy to expand this proof for the m-dimensional matrix.

When $ab + cd = 0$, we can show the exception (A-model, Akamine 2010a, b):

$$\mathbf{B} = \begin{pmatrix} 0 & b \\ 0 & 0 \end{pmatrix}, \ \mathbf{C} = \begin{pmatrix} 0 & 0 \\ c & 0 \end{pmatrix}. \quad (41)$$

The mean matrix of these is

$$\mathbf{D} = \frac{1}{2}(\mathbf{B} + \mathbf{C}) = \frac{1}{2}\begin{pmatrix} 0 & b \\ c & 0 \end{pmatrix}. \quad (42)$$

This matrix projects basic vectors to

$$\mathbf{e}_1' = \begin{pmatrix} 0 \\ c/2 \end{pmatrix}, \ \mathbf{e}_2' = \begin{pmatrix} b/2 \\ 0 \end{pmatrix}. \quad (43)$$

These vectors intersect orthogonally and the rank of matrix **D** is still 2 when $t \to \infty$.

6. Correlation and periodicity

In this section we will discuss the correlation and periodicity of successive environmental states. Let us consider the A-model (Eq. (41)). The squared matrix of **D** is

$$\mathbf{D}^2 = \frac{1}{4}(\mathbf{BC} + \mathbf{CB}) = \frac{bc}{4}\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}. \quad (44)$$

In this model, the correlation coefficient of two environmental states, **B** and **C** , is $\rho = -1$.

Let us consider the following matrices:

$$\mathbf{E} = \begin{pmatrix} 0 & 0 & e \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, \ \mathbf{F} = \begin{pmatrix} 0 & 0 & 0 \\ f & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, \ \mathbf{G} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & g & 0 \end{pmatrix}. \quad (45)$$

The mean matrix of these is

$$\mathbf{H} = \frac{1}{3}(\mathbf{E} + \mathbf{F} + \mathbf{G}) = \frac{1}{3}\begin{pmatrix} 0 & 0 & e \\ f & 0 & 0 \\ 0 & g & 0 \end{pmatrix}. \quad (46)$$

Thus, we obtain

$$\mathbf{H}^2 = \frac{1}{9}(\mathbf{FE} + \mathbf{GF} + \mathbf{EG}) = \frac{1}{9}\begin{pmatrix} 0 & ge & 0 \\ 0 & 0 & ef \\ fg & 0 & 0 \end{pmatrix}, \quad (47)$$

$$\mathbf{H}^3 = \frac{1}{27}(\mathbf{GFE} + \mathbf{EGF} + \mathbf{FEG}) = \frac{efg}{27}\begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}. \quad (48)$$

We think that the correlation coefficient is difficult to define for this model because there are three environmental states. For these multi-state models, the periodicity of environmental states is more important than the correlation of them.

7. Example

We show three examples for the distributions of eigenvalues as Matsuda and Iwasa (1993)'s M-model:

$$\mathbf{P} = \begin{pmatrix} 0 & 2 \\ 0.2 & 0.8 \end{pmatrix}, \ \mathbf{Q} = \begin{pmatrix} 0 & 0 \\ 0.2 & 0.8 \end{pmatrix}, \ \mathbf{R} = \begin{pmatrix} 0 & 1 \\ 0.2 & 0.8 \end{pmatrix}, \quad (49)$$

Tuljapurkar (1989)'s T-model:

$$\mathbf{P} = \begin{pmatrix} 0.25 & 2.8571 \\ 0.25 & 0 \end{pmatrix}, \ \mathbf{Q} = \begin{pmatrix} 0.8375 & 0.1525 \\ 1 & 0 \end{pmatrix},$$
$$\mathbf{R} = \begin{pmatrix} 0.54375 & 1.5048 \\ 0.625 & 0 \end{pmatrix} \quad (50)$$

and Caswell (2001)'s C-model:

$$\mathbf{P} = \begin{pmatrix} 0.1 & 3 \\ 0.2 & 0 \end{pmatrix}, \ \mathbf{Q} = \begin{pmatrix} 0.2 & 0.2 \\ 1 & 0 \end{pmatrix}, \ \mathbf{R} = \begin{pmatrix} 0.15 & 1.6 \\ 0.6 & 0 \end{pmatrix}. \quad (51)$$

doi:10.5047/absm.2011.00403.0095

Table 1. Maximum eigenvalues of matrices for permutations in the M-model. Modified from *Bull. Jpn. Soc. Fish. Oceanogr.*, **74**, Akamine, Mathematical study of matrix models for fish population dynamics in random environments, 208–213, © 2010, with permission from the Japanese Society of Fisheries Oceanography.

	Permutation	k[1)]	λ_1	λ_2	λ_2/λ_1
$n=1$	P	1	1.1483	–0.34833	–0.30334
	Q	1	0.8	0	0
	m[2)]		0.974166		
$n=2$	PP	1	1.3187	0.12134	0.09201
	PQ	2	1.04	0	0
	QQ	1	0.64	0	0
	m		1.009666		
	$\sqrt{m}$		1.004822		
$n=3$	PPP	1	1.5143	–0.04226	–0.02791
	PPQ	3	1.152	0	0
	PQQ	3	0.832	0	0
	QQQ	1	0.512	0	0
	m		0.997283		
	$\sqrt[3]{m}$		0.999094		
$n=4$	PPPP	1	1.7389	0.01472	0.00847
	PPPQ	4	1.3376	0	0
	PPQQ	4	0.9216	0	0
	PQPQ	2	1.0816	0	0
	PQQQ	4	0.6656	0	0
	QQQQ	1	0.4096	0	0
	m		1.00068		
	$\sqrt[4]{m}$		1.00017		
$n=5$	PPPPP	1	1.9968	–0.00513	–0.00257
	PPPPQ	5	1.5309	0	0
	PPPQQ	5	1.0701	0	0
	PPQPQ	5	1.1981	0	0
	PQPQQ	5	0.8653	0	0
	PPQQQ	5	0.7373	0	0
	PQQQQ	5	0.5325	0	0
	QQQQQ	1	0.3277	0	0
	m		0.99984		
	$\sqrt[5]{m}$		0.999968		
$n=6$	PPPPPP	1	2.293	0.00178	0.00078
	PPPPPQ	6	1.7597	0	0
	PPPPQQ	6	1.2247	0	0
	PPPQPQ	6	1.3911	0	0
	PPQPPQ	3	1.3271	0	0
	PPPQQQ	6	0.8561	0	0
	PPQPQQ	6	0.9585	0	0
	PQPQPQ	2	1.1249	0	0
	PPQQPQ	6	0.9585	0	0
	PQQPQQ	3	0.6922	0	0
	PQPQQQ	6	0.6922	0	0
	PPQQQQ	6	0.5898	0	0
	PQQQQQ	6	0.426	0	0
	QQQQQQ	1	0.2621	0	0
	m		1.000036		
	$\sqrt[6]{m}$		1.000006		

[1)]Number of permutations that have the same eigenvalues.
[2)]Arithmetic mean.

doi:10.5047/absm.2011.00403.0095

Table 2. Maximum eigenvalues of matrices for permutations in the T-model. Modified from *Bull. Jpn. Soc. Fish. Oceanogr.*, **74**, Akamine, Mathematical study of matrix models for fish population dynamics in random environments, 208–213, © 2010, with permission from the Japanese Society of Fisheries Oceanography.

	Permutation	k[1)]	λ_1	λ_2	λ_2/λ_1
$n=1$	P	1	0.9793	−0.72935	−0.74473
	Q	1	0.9913	−0.15383	−0.15518
	m[2)]		0.9853		
$n=2$	PP	1	0.9591	0.53195	0.55462
	PQ	2	3.0692	0.03549	0.01156
	QQ	1	0.9827	0.02367	0.02408
	m		2.02		
	$\sqrt{m}$		1.4213		
$n=3$	PPP	1	0.9393	−0.38798	−0.41304
	PPQ	3	1.4288	−0.05445	−0.03811
	PQQ	3	2.6445	−0.00628	−0.00238
	QQQ	1	0.9742	−0.00364	−0.00374
	m		1.7667		
	$\sqrt[3]{m}$		1.2089		
$n=4$	PPPP	1	0.9199	0.28297	0.30761
	PPPQ	4	2.5393	0.02189	0.00862
	PPQQ	4	1.3698	0.00866	0.00633
	PQPQ	2	9.4197	0.00126	0.00013
	PQQQ	4	2.6821	0.00094	0.00035
	QQQQ	1	0.9658	0.00056	0.00058
	m		2.9431		
	$\sqrt[4]{m}$		1.3098		
$n=5$	PPPPP	1	0.9009	−0.20638	−0.22908
	PPPPQ	5	1.6461	−0.02411	−0.01465
	PPPQQ	5	2.2329	−0.0038	−0.0017
	PPQPQ	5	4.2417	−0.002	−0.00047
	PQPQQ	5	8.0999	−0.00022	−0.00003
	PPQQQ	5	1.3654	−0.00132	−0.00097
	PQQQQ	5	2.6495	−0.00015	−0.00006
	QQQQQ	1	0.9574	−0.00009	−0.00009
	m		3.2199		
	$\sqrt[5]{m}$		1.2635		
$n=6$	PPPPPP	1	0.8823	0.15053	0.1706
	PPPPPQ	6	2.2222	0.01276	0.00574
	PPPPQQ	6	1.5379	0.00394	0.00256
	PPPQPQ	6	7.7884	0.00078	0.0001
	PPQPPQ	3	2.0416	0.00297	0.00145
	PPPQQQ	6	2.2569	0.00057	0.00025
	PPQPQQ	6	3.941	0.00033	0.00008
	PQPQPQ	2	28.9105	0.00004	0
	PPQQPQ	6	3.941	0.00033	0.00008
	PQQPQQ	3	6.9936	0.00004	0.00001
	PQPQQQ	6	8.2201	0.00003	0
	PPQQQQ	6	1.3524	0.0002	0.00015
	PQQQQQ	6	2.628	0.00002	0.00001
	QQQQQQ	1	0.9491	0.00002	0.00002
	m		4.5326		
	$\sqrt[6]{m}$		1.2864		

[1)]Number of permutations that have the same eigenvalues.
[2)]Arithmetic mean.

doi:10.5047/absm.2011.00403.0095

Table 3. Maximum eigenvalues of matrices for permutations in the C-model. Modified from *Bull. Jpn. Soc. Fish. Oceanogr.*, **74**, Akamine, Mathematical study of matrix models for fish population dynamics in random environments, 208–213, © 2010, with permission from the Japanese Society of Fisheries Oceanography.

	Permutation	k[1]	λ_1	λ_2	λ_2/λ_1
$n=1$	P	1	0.8262	−0.72621	−0.87897
	Q	1	0.5583	−0.35826	−0.64174
	m[2]		0.6922		
$n=2$	PP	1	0.6826	0.52738	0.77258
	PQ	2	3.0203	0.03973	0.01316
	QQ	1	0.3117	0.12835	0.41183
	m		1.7587		
	$\sqrt{m}$		1.3262		
$n=3$	PPP	1	0.564	−0.38299	−0.67907
	PPQ	3	0.5556	−0.12959	−0.23325
	PQQ	3	0.6679	−0.03593	−0.0538
	QQQ	1	0.174	−0.04598	−0.26429
	m		0.5511		
	$\sqrt[3]{m}$		0.8199		
$n=4$	PPPP	1	0.466	0.27813	0.59688
	PPPQ	4	1.8553	0.02329	0.01255
	PPQQ	4	0.2748	0.0524	0.19069
	PQPQ	2	9.122	0.00158	0.00017
	PQQQ	4	0.7318	0.00656	0.00896
	QQQQ	1	0.0971	0.01647	0.16961
	m		1.8909		
	$\sqrt[4]{m}$		1.1727		
$n=5$	PPPPP	1	0.385	−0.20198	−0.52464
	PPPPQ	5	0.4957	−0.05229	−0.10547
	PPPQQ	5	0.4319	−0.02	−0.04631
	PPQPQ	5	1.2982	−0.00666	−0.00513
	PQPQQ	5	1.9114	−0.00151	−0.00079
	PPQQQ	5	0.1678	−0.01716	−0.10228
	PQQQQ	5	0.2775	−0.00346	−0.01246
	QQQQQ	1	0.0542	−0.0059	−0.10884
	m		0.7298		
	$\sqrt[5]{m}$		0.9389		
$n=6$	PPPPPP	1	0.3181	0.14668	0.46114
	PPPPPQ	6	1.1581	0.01343	0.0116
	PPPPQQ	6	0.2132	0.02432	0.11405
	PPPQPQ	6	5.6024	0.00093	0.00017
	PPQPPQ	3	0.3087	0.0168	0.05441
	PPPQQQ	6	0.4543	0.0038	0.00837
	PPQPQQ	6	0.6313	0.00274	0.00433
	PQPQPQ	2	27.551	0.00006	0
	PPQQPQ	6	0.6313	0.00274	0.00433
	PQQPQQ	3	0.4461	0.00129	0.00289
	PQPQQQ	6	2.2064	0.00026	0.00012
	PPQQQQ	6	0.0891	0.00647	0.07256
	PQQQQQ	6	0.2015	0.00096	0.00474
	QQQQQQ	1	0.0303	0.00211	0.06979
	m		1.9506		
	$\sqrt[6]{m}$		1.1178		

[1]Number of permutations that have the same eigenvalues.
[2]Arithmetic mean.

doi:10.5047/absm.2011.00403.0095

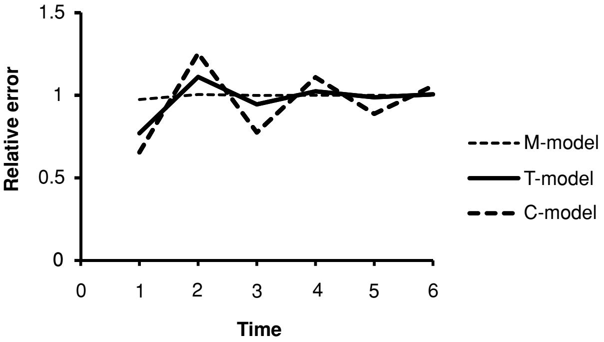

Fig. 1. Convergence of arithmetic means of the maximum eigenvalues of matrices for all permutations to the maximum eigenvalue of the mean matrix. Relative error is $\sqrt[t]{m}$ / $\lambda_1(\mathbf{R})$. Modified from *Bull. Jpn. Soc. Fish. Oceanogr.*, **74**, Akamine, Mathematical study of matrix models for fish population dynamics in random environments, 208–213, © 2010, with permission from the Japanese Society of Fisheries Oceanography.

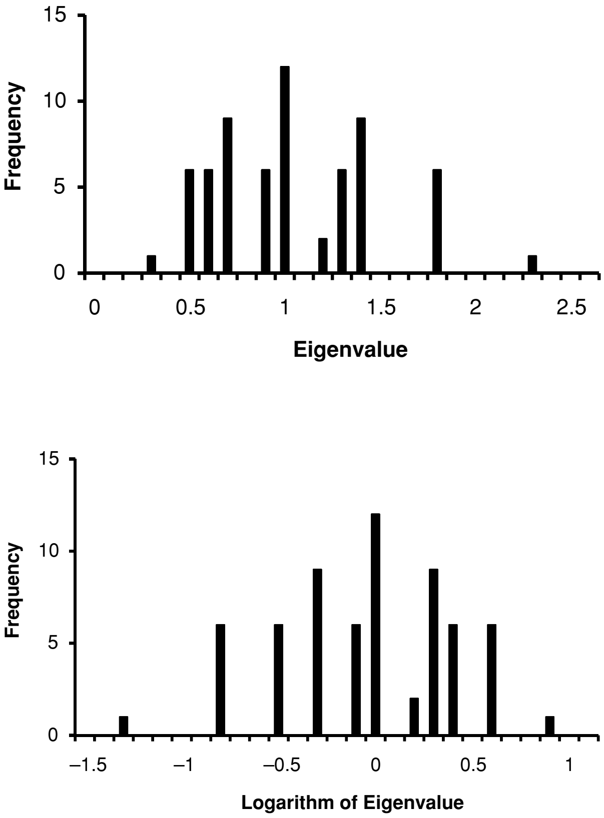

Fig. 2. Distribution of the maximum eigenvalues of matrices for all permutations and their logarithms in the M-model when $t = 6$. Modified from *Bull. Jpn. Soc. Fish. Oceanogr.*, **74**, Akamine, Mathematical study of matrix models for fish population dynamics in random environments, 208–213, © 2010, with permission from the Japanese Society of Fisheries Oceanography.

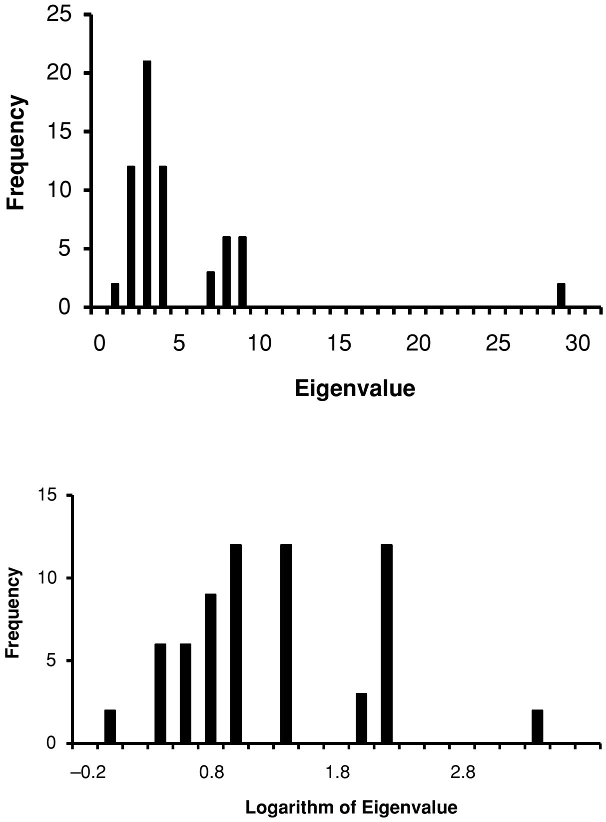

Fig. 3. Distribution of the maximum eigenvalues of matrices for all permutations and their logarithms in the T-model when $t = 6$. Modified from *Bull. Jpn. Soc. Fish. Oceanogr.*, **74**, Akamine, Mathematical study of matrix models for fish population dynamics in random environments, 208–213, © 2010, with permission from the Japanese Society of Fisheries Oceanography.

Tables 1–3 show λ_1, λ_2 and λ_2/λ_1 when $t = 1, ..., 6$ for each model. Figure 1 shows the convergence of the arithmetic mean of the eigenvalues and Figs. 2–4 show the distribution of the eigenvalues and their logarithms when $t = 6$.

In these calculations, the following formula is used

$$\lambda_i(\mathbf{PQ}) = \lambda_i(\mathbf{QP}). \tag{52}$$

This is proved easily as follows (Yano 1974): The left-hand side is

$$\mathbf{PQx} = \lambda_i \mathbf{x}. \tag{53}$$

Thus, we can obtain

$$(\mathbf{QP})\mathbf{Qx} = \lambda_i \mathbf{Qx}. \tag{54}$$

This is the right-hand side of Eq. (52).

Tuljapurkar (1989) showed that $r_s = \log\lambda_s = 0.1954$

doi:10.5047/absm.2011.00403.0095

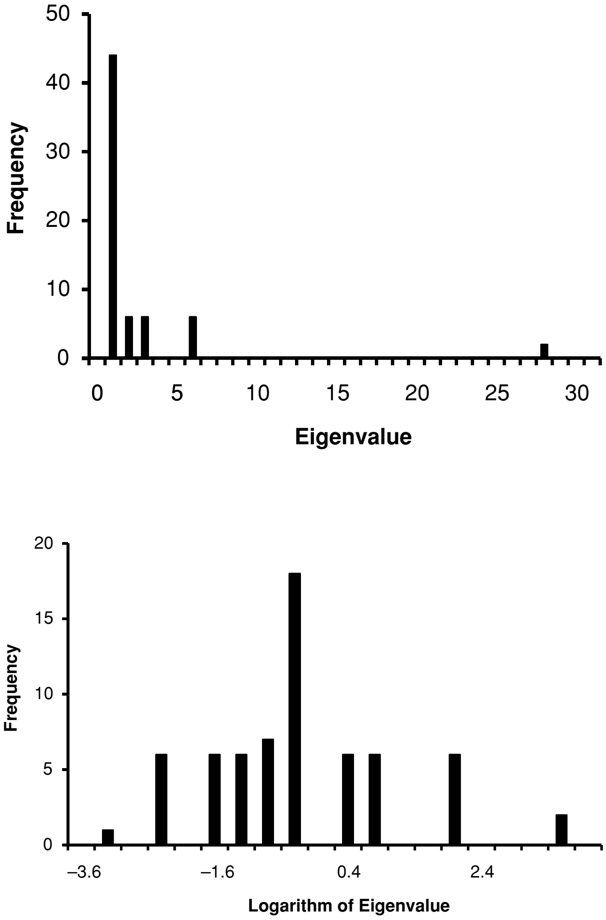

Fig. 4. Distribution of the maximum eigenvalues of matrices for all permutations and their logarithms in the C-model when $t = 6$. Modified from *Bull. Jpn. Soc. Fish. Oceanogr.*, **74**, Akamine, Mathematical study of matrix models for fish population dynamics in random environments, 208–213, © 2010, with permission from the Japanese Society of Fisheries Oceanography.

calculated by computer simulations for the T-model. **Table 2** gives us the arithmetic mean of $\log\lambda_1$, which is 0.1974 when $t = 6$. This is evidence that the distribution of $\log\lambda_1$ approaches to the normal distribution when $t \to \infty$. The T- and C-models are approximately equal to the A-model, which is the reason why they are cautionary (Caswell 2001).

8. Discussion

The mean matrix is defined in general as

$$\mathbf{R} = \sum_i p_i \mathbf{P}_i, \quad \sum_i p_i = 1, \quad p_i > 0. \tag{55}$$

Thus, theorem (31) holds in general. Caswell (2001) showed the following relation when $t \to \infty$,

$$\log N(t) \to \mathrm{Normal}\left(t \log \lambda_s, t\sigma^2\right). \tag{56}$$

Therefore, $N(t)$ distributes lognormally and

$$\log \Lambda = \log \lambda_s + \frac{\sigma^2}{2} \geq \log \lambda_s. \tag{57}$$

He considered that the intrinsic rate of natural increase $r_s = \log\lambda_s$ is better than $\log\Lambda$ for the population growth rate. However, we think it is not optimal to compare these logarithms. We had better compare $\log\lambda_s$ with Λ, which is equivalent to comparing $\log N$ with N for the population size. We consider that N is better than $\log N$ due to two reasons. One is that we use the population size N in fisheries management, not the logarithm population size $\log N$. The other is that the analysis for raw data is better than the analysis for transformed data in statistics. If there is no advantage for raw data, the lognormal distribution is not necessary for data analysis. Therefore, Λ is better than $\log\lambda_s$ for population projection matrix models.

Cautionary T- and C-models have very large eigenvalues in **Tables 2, 3**. When these models approximate the A-model, their large values become very important. Thus, we had better estimate the distribution of the growth rate λ_1 as a histogram. Calculating λ_1 for all permutations in the short-term is more basic than many computer simulations carried out over the long-term in the random walk matrix model. In general projection population matrix models, the vector $\mathbf{n}(t)$ has much more information than the scalar $N(t)$ for the population size.

Caswell (2001) showed that the negative correlation between environments is important for good population growth in the C-model, which is approximately equal to the A-model. However, we discussed that the periodicity is more important than the correlation in many environmental states, for which we expanded the A-model to a 3-dimesional model in Section 6.

9. Conclusion

In population projection matrix models, the distribution of the maximum eigenvalues of all permutations approaches to the lognormal distribution. Their arithmetic mean converges to the maximum eigenvalue of the mean matrix. Thus, it is relevant that the population growth rate be defined as the maximum eigenvalue of the mean matrix, not the average of growth rates calculated by computer simulations.

The negative correlation between environments is not so important in many conditional environments. We consider that the periodicity is more important than the correlation.

doi:10.5047/absm.2011.00403.0095

Acknowledgments

The authors thank Dr. Kazuhiko Hiramatsu of the University of Tokyo, Dr. Ichiro Oohara of the National Research Institute of Fisheries Science and the two anonymous referees for their useful comments on earlier drafts of the manuscript. The authors also thank Ms. Tomoko Yamakoshi for her help with our work.

References

Akamine T. Non-linear and graphical methods for fish stock analysis with statistical modeling. *Aqua-BioSci. Monogr*. 2009; **2**(3): 1–45.

Akamine T. *Suisan Sigen no Data Kaiseki Nyuumon*. Kouseisha Kouseikaku, Tokyo. 2010a; 178 pp.

Akamine T. Mathematical study of matrix models for fish population dynamics in random environments. *Bull. Jpn. Soc. Fish. Oceanogr*. 2010b; **74**: 208–213 (in Japanese).

Akamine T. Proof of a theorem for the growth rate in matrix models of fish population dynamics. *Bull. Jpn. Soc. Fish. Oceanogr*. 2011; **75**: 29–31 (in Japanese).

Caswell H. *Matrix Population Models*, 2nd ed. Sinauer Associates, Sunderland. 2001; 722 pp.

Cohen JE, Christensen SW, Goodyear CP. A stochastic age-structured population model of striped bass (*Morone saxatilis*) in the Potomac river. *Can. J. Fish. Aquat. Sci*. 1983; **40**: 2170–2183.

Matsuda H, Iwasa Y. Nani ga zetsumetsu wo motarasunoka?: hozen seitaigaku no riron. *Kotaigun seitaigakkai kaihou*. 1993; **50**: 2–9.

Quinn TJ, Deriso RB. *Quantitative Fish Dynamics*. Oxford Univ. Press, New York. 1999; 542 pp.

Tuljapurkar S. An uncertain life: demography in random environments. *Theor. Popul. Biol*. 1989; **35**: 227–294.

Yano K. *Senkei Daisuu, Bekutoru to Gyouretsu*. Nippon-Hyoron-Sha, Tokyo. 1974; 177 pp.

doi:10.5047/absm.2011.00403.0095