Prediction of Competitive Microbial Growth

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Prediction of competitive microbial growth is becoming important for microbial food safety. There would be two approaches to predict competitive microbial growth with mathematical models. The first approach is the development of a growth model for competitive microbes. Among several candidates for the competition model considered, the combination of the primary growth model of the new logistic (NL) model and the competition model of the Lotka-Vorrttera (LV) model showed the best performance in predicting microbial competitive growth in the mixed culture of two species. This system further successfully predicted the growth of three competitive species in mixed culture. The second approach is the application of the secondary model especially for the parameter of the maximum cell population in the primary growth model. The combination of the NL model and a polynomial model for the maximum population successfully predicted Salmonella growth in raw ground beef. This system further successfully predicted Salmonella growth in beef at various initial concentrations and temperatures. The first approach requires microbial growth data in monoculture for analysis. The second approach to the prediction of competitive growth from the viewpoint of microbial food safety would be more suitable for practical application.

Key words : Competition model / Microbial growth / Logistic model / Growth prediction.

1. INTRODUCTION

Several primary growth models have been developed to analyze microbial growth in food so far. Those models have been thought to be good tools for the prediction of the growth of microbes including pathogens and spoilage microbes in food. This field of science has been called predictive food microbiology (McMeekin et al., 1993). Among those models, the modified Gompertz model and the Baranyi model are well known in many countries (Gibson et al., 1987; Baranyi and Roberts, 1995). However, the modified Gompertz model is not suitable for application at changing temperatures and the Baranyi model has a problem in structure (Baranyi and Roberts, 1995). A new growth model, which is an extended version of the logistic model, was also developed by the author; the model was called the new logistic (NL) model (Fujikawa et al., 2003, 2004). The NL model is described as below.

\[
\frac{dN}{dt} = rN \left\{ 1 - \left( \frac{N}{N_{\text{max}}} \right)^m \right\} \left\{ 1 - \left( \frac{N_{\text{min}}}{N} \right)^n \right\} \tag{1}
\]

Here \(N\) is the microbial population at time \(t\). \(N_{\text{max}}\) and \(N_{\text{min}}\) correspond to the maximum and the initial cell populations, respectively. \(m\) and \(n\) are the parameters for the curvature of the deceleration phase and the period of the lag phase, respectively. The NL model has been shown to precisely describe and predict microbial growth in broth and sterilized food at various patterns of temperature, similar to the Baranyi model (Sakha and Fujikawa, 2012, 2013).

However, there are a lot of microbial species contaminating actual raw food products and food materials such as meat, fish, vegetables, and liquid eggs. Especially, raw food materials are often contaminated with natural microflora, NM. If food-borne pathogens such as Salmonella, Staphylococcus aureus, and pathogenic Escherichia coli exist in raw food materials, the growth of these pathogens would be affected by the NM in the food materials.

There are several relationships among microbial species in the environment, including mutualism, competition, commensalism, and amensalism (Bailey and Ollis,
Among these relationships, competition would be the most common for interacting microbial species, because all microbial species need nutrients and space for growth in their environments (Bailey and Ollis, 1986). An example of the growth of SalmonellaEnteritidis spiked into raw ground chicken with low and high NM levels and into sterilized ground chicken is shown in Fig. 1 (Zaher and Fujikawa, 2011). With the higher NM population level in the ground chicken, more suppression was observed in Salmonella growth. Namely, Salmonella growth, which is characterized by both \( N_{\text{max}} \) and \( r \), was highest in sterilized chicken, followed by chicken with a low NM level. Similar results were observed at other temperatures.

Microbial growth models that can describe and predict the growth of a given microbe such as Salmonella in raw food with NM are needed for microbial food safety. From this viewpoint, studies on microbial growth kinetics in a food with NM are becoming important for the next stage of predictive food microbiology. The author and his group have studied the growth of a given microbe in raw food material and mixed culture with other microbial species and then have successfully predicted microbial growth with the NL model in those environments.

Generally, the growth of a given microbe competing with other microbes is lower in comparison with its growth in monoculture. There might be two approaches to describe and predict the growth of that microbe in competition. One approach is the development of a new mathematical model for competitive growth. Several researchers developed the models for microbial competition, which were made by the combination of primary growth models between competitors or the combination of a primary growth model and a competition model such as the Lotka-Volterra (LV) (Vandermeer and Goldber, 2003). The LV model is a very well-known and general model for the expression of competition between two species in ecology. Many researchers have introduced the LV model into the original logistic model in ecology (Vandermeer and Goldber, 2003). When species 1 grows in competition with species 2 in a given environment, the LV model is expressed by the following function.

\[
f(N_1, N_2) = 1 - \frac{N_1 + N_2}{N_{\text{max}}} \quad (2)
\]

\( N_1 \) and \( N_2 \) are the populations for the corresponding species at a given time. Here \( N_{\text{max}} \) can be set as the larger value between the maximum populations of the two species. As the sum of the two populations increases with time to the value of \( N_{\text{max}} \) in Eq. 2, the value for the fraction in the equation approaches one. This leads to zero as the value for Eq. 2, meaning no increase in the population when this model is incorporated in a growth model.

Another approach is the control of the parameter values of a primary growth model with the secondary models. Secondary models are developed for the parameters of a primary growth model which change with the environmental conditions (Whiting and Buchanan, 1994). Examples of the secondary models are the square root model and the Arrhenius model for the rate constant of growth at a given temperature. Thus, when the value for \( N_{\text{max}} \) at the stationary phase of a microbe in competition with other microbes changes with temperature regularly, a secondary model for \( N_{\text{max}} \) at the temperatures can be made.

In the present review, these two approaches to the prediction of competitive microbial growth are described and discussed using the results obtained by the author.

2. APPROACH WITH COMPETITION MODELS

2.1. Development of competition models.

Many researchers have modeled the growth of a foodborne pathogen competing with the natural microflora in food using competition models. Breidit and Fleming (1998) modeled the competitive growth of Listeria monocytogenes and Lactococcus lactis by modeling the concentration of lactic acid produced and the pH of vegetable broth. Gimenez and Dalgaard (2004) also developed a competition model for L. monocytogenes and lactic acid bacteria, which was based on the logistic model. This model, which is called GD model in this review, is consisted of the product of two logistic models for L. monocytogenes and lactic acid bacteria. The GD model requires the separate estimation of the period of the lag phase in advance, but the term of suppression in the model has successfully described the growth curves of these microorganisms. Le Marc et al. (2009)
developed a competition model by introducing the concept of critical population density for lactic acid bacteria against a competing bacterium (S. aureus). These models do seem to be specific to the species of concern, but not general enough to be applied to a number of microbial species.

On the other hand, Dens et al. (1999) proposed a microbial competition model constructed with the Baranyi model and the LV model, and studied the characteristics of the competition model. However, since their studies were mathematical simulations, it is necessary to evaluate whether their model is applicable to real microbial competition with microbial data. Similar studies were also reported by other researchers (Powell et al., 2004; Vereecken et al., 2000). Liu et al. (2006) studied interactions of microorganisms on pork with the modified Gompertz model coupled with a modified LV model. They showed the parameter values of microbial growth in their model, but not the actual growth curves. Koseki et al. (2011) studied the growth of L. monocytogenes and isolates from NM in raw minced tuna using the Baranyi model coupled with the GD model. They succeeded in describing the growth of L. monocytogenes and the species from the natural microflora at the temperatures tested, excepting low temperatures.

Several competition models can be developed by introducing the LV model or the GD model into the NL model to evaluate what model is the most suitable for application to competitive microbial growth between two competitive species (Table 1) (Fujikawa et al., 2014).

First, a model in which the LV model (Eq. 2) is incorporated directly in the term having \( N_{\text{max}} \) of the NL model (Eq. 1) can be developed. We call it the original LV model. Competition coefficients \( c_1 \) and \( c_2 \) are introduced to express the relative strengths of growth between two competing species (Vandermeer and Goldber, 2003). There are considered to be two types in terms of the competition coefficient, namely a multiplication type (type M) and a power type (type P), as shown in Eq. 3A, B and 4A, B, respectively (Table 1). Secondly, a model is created in which the LV model is

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**Table 1: Growth models for two competitors developed with the NL model.**

| Type       | Equation                                                                 |
|------------|--------------------------------------------------------------------------|
| A. NL model coupled with the original LV model (type M) | \[
\begin{align*}
\frac{dN_1}{dt} &= r_1 N_1 \left[ 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right] \left[ 1 - \frac{(N_{1\max})^{n_1}}{N_1} \right] \\
\frac{dN_2}{dt} &= r_2 N_2 \left[ 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right] \left[ 1 - \frac{(N_{2\max})^{n_2}}{N_2} \right]
\end{align*}
\]  
| A. NL model coupled with original LV model (type P) | \[
\begin{align*}
\frac{dN_1}{dt} &= r_1 N_1 \left[ 1 - \frac{H_1 \min}{N_{1\max}} \right] \left[ 1 - \frac{(N_{1\max})^{n_1}}{N_1} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right] \\
\frac{dN_2}{dt} &= r_2 N_2 \left[ 1 - \frac{H_2 \min}{N_{2\max}} \right] \left[ 1 - \frac{(N_{2\max})^{n_2}}{N_2} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right]
\end{align*}
\]  
| C. LV-extended NL model (type M) | \[
\begin{align*}
\frac{dN_1}{dt} &= r_1 N_1 \left[ 1 - \frac{H_1 \min}{N_{1\max}} \right] \left[ 1 - \frac{(N_{1\max})^{n_1}}{N_1} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right] \\
\frac{dN_2}{dt} &= r_2 N_2 \left[ 1 - \frac{H_2 \min}{N_{2\max}} \right] \left[ 1 - \frac{(N_{2\max})^{n_2}}{N_2} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right]
\end{align*}
\]  
| C. LV-extended NL model (type P) | \[
\begin{align*}
\frac{dN_1}{dt} &= r_1 N_1 \left[ 1 - \frac{H_1 \min}{N_{1\max}} \right] \left[ 1 - \frac{(N_{1\max})^{n_1}}{N_1} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right] \\
\frac{dN_2}{dt} &= r_2 N_2 \left[ 1 - \frac{H_2 \min}{N_{2\max}} \right] \left[ 1 - \frac{(N_{2\max})^{n_2}}{N_2} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right]
\end{align*}
\]  
| D. LV-extended NL model coupled with GD model | \[
\begin{align*}
\frac{dN_1}{dt} &= r_1 N_1 \left[ 1 - \frac{H_1 \min}{N_{1\max}} \right] \left[ 1 - \frac{(N_{1\max})^{n_1}}{N_1} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right] \\
\frac{dN_2}{dt} &= r_2 N_2 \left[ 1 - \frac{H_2 \min}{N_{2\max}} \right] \left[ 1 - \frac{(N_{2\max})^{n_2}}{N_2} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right]
\end{align*}
\]  
| D. LV-extended NL model coupled with GD model | \[
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\frac{dN_1}{dt} &= r_1 N_1 \left[ 1 - \frac{H_1 \min}{N_{1\max}} \right] \left[ 1 - \frac{(N_{1\max})^{n_1}}{N_1} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right] \\
\frac{dN_2}{dt} &= r_2 N_2 \left[ 1 - \frac{H_2 \min}{N_{2\max}} \right] \left[ 1 - \frac{(N_{2\max})^{n_2}}{N_2} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right]
\end{align*}
\]  
| E. NL model coupled with GD model | \[
\begin{align*}
\frac{dN_1}{dt} &= r_1 N_1 \left[ 1 - \frac{H_1 \min}{N_{1\max}} \right] \left[ 1 - \frac{(N_{1\max})^{n_1}}{N_1} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right] \\
\frac{dN_2}{dt} &= r_2 N_2 \left[ 1 - \frac{H_2 \min}{N_{2\max}} \right] \left[ 1 - \frac{(N_{2\max})^{n_2}}{N_2} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right]
\end{align*}
\]  
| E. NL model coupled with GD model | \[
\begin{align*}
\frac{dN_1}{dt} &= r_1 N_1 \left[ 1 - \frac{H_1 \min}{N_{1\max}} \right] \left[ 1 - \frac{(N_{1\max})^{n_1}}{N_1} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right] \\
\frac{dN_2}{dt} &= r_2 N_2 \left[ 1 - \frac{H_2 \min}{N_{2\max}} \right] \left[ 1 - \frac{(N_{2\max})^{n_2}}{N_2} \left( 1 - \frac{c_1 H_1 + c_2 H_2 \min}{N_{\text{max}}} \right) \right]
\end{align*}
\]  

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introduced as an additional term in the NL model; it is called the LV-extended model here. There are also two types of this model according to the positions of the competition coefficients, that is, a multiplication type (type M) and a power type (type P), as shown in Eqs. 5A, B and 6A, B, respectively (Table 1). The GD model can be introduced in the NL model (Eq. 7A, B). Here \( l_1 \) and \( l_2 \) are competition coefficients of species 2 for species 1 and of species 1 for species 2, respectively.

### 2.2. Growth of two species in mixed culture.

The above models were then validated using microbial data of three microbial species of non-pathogenic *Escherichia coli*, *Salmonella* Enteritidis, and *S. aureus* (Fujikawa et al., 2014). Namely, two species out of the three species were grown as competitors in sterilized ground chicken at a constant temperature (28°C). Here microbial cells were spiked at various populations.

Examples of competitive growth in mixed culture are shown in Fig.2A, B (Fujikawa et al., 2014). Suppression in growth is observed in *Salmonella* (Fig.2A) and *S. aureus* (Fig.2B); these two species can grow to the maximum population of about 10 log (CFU/g) in monoculture (sterilized ground chicken). Among the competition models proposed in Table 1, the LV-extended NL model (type P) described as Eq. 6A, B showed the best performance in describing the growth of two competitive species. Examples described with this model are shown in Fig.2A, B. As a reference, the growth described with the Baranyi model coupled with GD model is presented in Fig.2B; this model also described well the growth of competitive microbial growth of two species, similar to the LV-extended NL model. The competition coefficients in the LV-extended NL model (Eq. 6A, B) were almost constant at various initial concentrations of the species. The values of the competition coefficient for *E. coli*, *Salmonella*, and *S. aureus* were in total 0.04, 1.03, and 1, respectively. Here the value for *S. aureus* was set to be one.

### 2.3. Prediction of competitive growth among three species.

The LV-extended NL model can be extended to three competitive species by increasing the term for microbial species in the LV model. The whole equations for three species are thus described in the following equations 8A, B, C (Fujikawa and Sakha, 2014A).

\[
\frac{dN_1}{dt} = r_i N_i \left( 1 - \left( \frac{N_1}{N_{1\text{max}}} \right)^m \right) \left( \frac{N_{1\text{max}}}{N_{1\text{max}}} \right) \left( 1 - \frac{N_{2\text{max}}}{N_{1\text{max}}} \right) (8A)
\]

\[
\frac{dN_2}{dt} = r_i N_i \left( 1 - \left( \frac{N_2}{N_{2\text{max}}} \right)^m \right) \left( \frac{N_{2\text{max}}}{N_{1\text{max}}} \right) \left( 1 - \frac{N_{3\text{max}}}{N_{1\text{max}}} \right) (8B)
\]

\[
\frac{dN_3}{dt} = r_i N_i \left( 1 - \left( \frac{N_3}{N_{3\text{max}}} \right)^m \right) \left( \frac{N_{3\text{max}}}{N_{1\text{max}}} \right) \left( 1 - \frac{N_{1\text{max}}}{N_{1\text{max}}} \right) (8C)
\]

Here \( i \) corresponds to microbial species. \( i = 1, 2, 3 \). The value of \( N_{\text{max}} \) is the maximum value among the three species.

With the above data obtained between two competitors, the LV-extended NL model (Eq. 8A, B, C) can successfully predict the competitive growth of three species. An example for this is shown in Fig.3 (Fujikawa and Sakha, 2014A).

From these results, the general form of the NL-LV model could be expressed as Eq. 9 for species \( i \) in a microbial community consisting of a total of \( p \) species. Here \( i \) and \( p \) (>1) are natural numbers.
primary growth model in competition are modeled with the secondary models like the square root model, similar to the growth model in monoculture.

3.1. Microbial growth at a given initial concentration.

The growth of *Salmonella* in raw ground chicken varies with the temperature when the microbe is injected at a given concentration, as shown in Fig. 5 (Zaher and Fujikawa, 2011). Especially, the \( N_{\text{max}} \) value of the microbe is dependent on the temperature (Fig. 5A), while that of NM in the chicken is almost constant at various temperatures (Fig. 5B). Similar results have been obtained in raw ground chicken with a high level of NM contamination (7.1 log CFU/g) (Zaher and Fujikawa, 2011).

When the Baranyi-GD model is applied to three competitive species, the model cannot well predict microbial growth of the three species (Fujikawa and Sakha, 2014A). The reason for this is not understood.

2.4. Prediction of competitive growth at dynamic temperatures.

The competitive growth of microbial species at dynamic temperatures can be predicted with the NL-LV model. The growth of microbial species in monoculture has been successfully predicted with the combination of the primary growth model like the NL model and a secondary model for \( r \) like the square root model (Fujikawa et al., 2004). Similarly, in the competitive growth of microbial species at dynamic temperatures, the growth of each species can be predicted with the NL-LV model and a secondary model. Some examples with these models are shown in Fig. 4 (Fujikawa and Sakha, 2014B).

### 3. APPROACH WITH THE SECONDARY MODELS

Another approach to the prediction of the competitive growth of microbes is performed with secondary models. The point in this approach is whether \( N_{\text{max}} \) for a given species in a primary growth model can be modeled with a secondary model. In the competition models like the LV-extended NL model (Eq. 6A,B), the value for \( N_{\text{max}} \) of a given species is controlled by the LV model, as described above. Other parameters such as \( r \) in the primary growth model in competition are modeled with the secondary models like the square root model, similar to the growth model in monoculture.

3.1. Microbial growth at a given initial concentration.

The growth of *Salmonella* in raw ground chicken varies with the temperature when the microbe is injected at a given concentration, as shown in Fig. 5 (Zaher and Fujikawa, 2011). Especially, the \( N_{\text{max}} \) value of the microbe is dependent on the temperature (Fig. 5A), while that of NM in the chicken is almost constant at various temperatures (Fig. 5B). Similar results have been obtained in raw ground chicken with a high level of NM contamination (7.1 log CFU/g) (Zaher and Fujikawa, 2011).

With the above data in raw ground chicken with high and low levels of NM, the values for log \( N_{\text{max}} \) for *Salmonella* and NM are shown in Fig. 6 (Zaher and Fujikawa, 2011).

The value for log \( N_{\text{max}} \) for *Salmonella* is then expressed with a second-order polynomial equation (Eq. 10A, B). Here A and B are for low-NM and high-NM ground.
chicken, respectively.

\[
\log N_{\text{max}} = -0.00737T^2 + 0.4756T + 1.5922 \quad (10A)
\]
\[
\log N_{\text{max}} = -0.00477T^2 + 0.4343T + 0.2108 \quad (10B)
\]

The values for \(\log N_{\text{max}}\) for NM in chicken with low and high levels are both almost constant at various temperatures, with the average of 9.4 log (CFU/g) (Fig.6).

For the rate constant of growth, \(r\) for \(Salmonella\) at various temperatures in the low-NM and high-NM chicken, the square root model can be applied, similar to the growth in sterilized food and bacterial media. The equation of the square root model is expressed as follows. Here A and B are for the low-NM and high-NM chicken, respectively.

\[
\sqrt{T} = 0.0277 (T+4.40) \quad (11A)
\]
\[
\sqrt{T} = 0.0238 (T-1.45) \quad (11B)
\]

With these data analyzed, the growth of \(Salmonella\) in raw ground chicken can be successfully predicted with the primary model (the NL model) coupled with the secondary models of Eqs. 10 and 11. An example for

\[Salmonella\] and NM in the low-NM chicken is shown in Fig.7 (Zaher and Fujikawa, 2011). The growth of NM, whose \(\log N_{\text{max}}\) is constant in the chicken, is also successfully predicted (Fig.7).

### 3.2. Microbial growth at various initial concentrations.

The initial contamination level of a microbe of concern would vary in food products. Thus, the next stage of the secondary model approach is microbial growth at various initial concentrations.

The growth of \(Salmonella\) in raw ground beef at various initial concentrations of the pathogen ranging from 2.3 to 5.3 log CFU/g was studied at a constant temperature of 24°C (Sabike et al., 2015). The ground beef was originally contaminated with 5.7 log CFU/g of NM.
approach is the prediction of $N_{\text{max}}$ at various initial concentrations of a microbe and temperatures. This is because the temperature in actual raw food contaminated with microbes changes with time.

The results obtained for a microbe of concern in raw food material so far lead to the following assumptions:

- The value for $N_{\text{max}}$ of the microbe in raw food material might be determined with $I$ and $T$, using a polynomial equation with $I$ and $T$ and $r$.
- The value for $r$ at a given value of $I$ might be determined only with $T$, using a model like the square root model (Sabike et al., 2015).

Thus, the growth of *Salmonella* in the above raw ground beef at various initial concentrations and temperatures was studied (Fujikawa et al., 2015). From a total of 12 (4 x 3) growth curves, the values of log $N_{\text{max}}$ were obtained from the stationary phases of the corresponding growth curves. A cubic polynomial equation for log $N_{\text{max}}$ was then developed to fit the values at these combinations of the initial concentration, $I$ and temperature, $T$, as

\[
\log N_{\text{max}} = 0.030I^3 - 0.52I^2 + 3.2I + 2.2 \quad (12)
\]

Using Eq. 12, the value for log $N_{\text{max}}$ can be estimated at a given value for $I$. With the measured value for $I$ (3.8 log CFU/g), a growth curve was predicted and the curve was very close to the observed data (Fig.8C), suggesting that the polynomial model with $I$ is applicable to estimate log $N_{\text{max}}$ at a constant temperature.

### 3.3. Microbial growth at various initial concentrations and temperatures.

The third and final stage of the secondary model approach is the prediction of $N_{\text{max}}$ at various initial concentrations of a microbe and temperatures. This is because the temperature in actual raw food contaminated with microbes changes with time.

The results obtained for a microbe of concern in raw food material so far lead to the following assumptions:

- the value for $N_{\text{max}}$ of the microbe in raw food material might be determined with $I$ and $T$, using a polynomial equation with $I$ and $T$ and $r$.
- the value for $r$ at a given value of $I$ might be determined only with $T$, using a model like the square root model (Sabike et al., 2015).

Thus, the growth of *Salmonella* in raw ground beef at various initial concentrations of 2, 3, and 4 log CFU/g at 16, 20, 24, and 28°C was studied (Fujikawa et al., 2015). From a total of 12 (4 x 3) growth curves, the values of log $N_{\text{max}}$ were obtained from the stationary phases of the corresponding growth curves. A cubic polynomial equation for log $N_{\text{max}}$ was then developed to fit the values at these combinations of the initial concentration, $I$ and temperature, $T$, as
growth in raw beef, the value for $r$ at a given temperature is estimated with the square root model, as shown below (Sabike et al., 2015).

$$\sqrt{r} = 0.0401 (T-3.47) \quad (14)$$

The prediction system consisting of the growth model (the NL model), the polynomial model for log $N_{max}$, and the square root model for $r$ successfully predicted the growth of the pathogen in ground beef at a constant temperature (Fig. 10). Furthermore, this system precisely predicted the growth at dynamic temperatures as well (Fig. 11). The growth of NM in ground beef was also successfully predicted with the NM model and the square root model (Figs. 10 and 11) (Fujikawa et al., 2015).

4. CONCLUSION

There have been two approaches to predict competitive microbial growth with mathematical models up to the present. The first approach is the development of a competition growth model for microbes. Several candidates for the competition model were considered. Among them the combination of a primary growth model such as the NL model and the LV model for competition showed the best performance in describing and predicting microbial competitive growth in mixed culture. The second approach is the application of secondary models especially for the parameter of $N_{max}$ in the primary growth model. The combination of the NL model and a polynomial model for $N_{max}$ successfully predicted the growth of *Salmonella* in raw meat. This system
moreover successfully predicted *Salmonella* growth in raw meat at various initial concentrations and temperatures. The application of both approaches for competitive microbes in a food for prediction would not be necessary. Either of the two would be sufficient for prediction of growth.

The point to be noticed in the first approach is that growth data in monoculture for microbes of concern are needed in advance for prediction with the LV model from the nature of the model. Data in monoculture can be obtained with microbial experiments in broth and sterile food. For example, when a competitive model with the LV model is used to predict the growth of *Salmonella* in raw beef, the monoculture data for *Salmonella* in sterile raw beef is needed for the LV model. However, it is actually very hard or impossible to obtain such data. A high-temperature treatment can sterilize the raw beef, but it might also change the nature of the meat. In contrast, the second approach needs no data for the monoculture of a microbe of concern, because the secondary models control the growth of a microbe by the primary growth model. In this sense the second approach is thought to be a practical one. Thus, the second approach to the prediction of competitive growth from the viewpoint of microbial food safety would be more suitable for practical application.

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