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A new mechanistic growth model for simultaneous determination of lag phase duration and exponential growth rate and a new Bĕlehrádek-type model for evaluating the effect of temperature on growth rate☆

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ABSTRACT

A new mechanistic growth model was developed to describe microbial growth under isothermal conditions. The new mathematical model was derived from the basic observation of bacterial growth that may include lag, exponential, and stationary phases. With this model, the lag phase duration and exponential growth rate of a growth curve were simultaneously determined by nonlinear regression. The new model was validated using *Listeria monocytogenes* and *Escherichia coli* O157:H7 in broth or meat. Statistical results suggested that both bias factor (B_f) and accuracy factor (A_f) of the new model were very close to 1.0. A new Bĕlehrádek-type rate model and the Ratkowsky square-root model were used to describe the temperature dependence of bacterial growth rate. It was observed that the maximum and minimum temperatures were more accurately estimated by a new Bĕlehrádek-type rate model. Further, the inverse of square-roots of lag phases was found proportional to temperature, making it possible to estimate the lag phase duration from the growth temperature.

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1. Introduction

The growth of microorganisms in food systems usually exhibits three different phases, i.e., lag, exponential, and stationary phases, under normal conditions. The growth process under isothermal conditions can be described by mathematical models. Several mathematical models have been used in predictive microbiology to describe the microbial growth. These models may include an empirical modified Gompertz or logistic model (Gibson et al., 1987), and a semi-theoretical Baranyi model (Baranyi et al., 1995). These models can be used to fit the growth curves and obtain the growth parameters, such as lag phase duration and exponential growth rate. Each of these models has both advantages and disadvantages when used to fit growth curves.

Although various expressions have been used, the modified Gompertz model, as implied by its name, was modified from the original Gompertz function, and remains essentially similar. One of the most widely used expressions is

$$L(C) = L(C_0) - [L(C_{max}) - L(C_0)]\{\exp[-\mu_G(t-M)]\}. \quad (1)$$

In the above equation, L is the operator of logarithm. Although the logarithm of base-10 is more frequently used, the natural logarithm also can be used. C_0 and C_{max} are the initial and final cell concentrations (colony forming unit, or CFU, per unit weight or volume), μ_G is the relative growth rate at $t = M$, which is the inflection point of the curve. It is necessary to point out that μ_G does not represent the growth rate of a curve. From this equation, two of the most important kinetic parameters can be derived. The first is the maximum growth rate of an isothermal curve, K, in the unit of L CFU/g per unit time. The second parameter is the lag phase of the curve, λ. The major drawback of the modified Gompertz model is its empirical nature. It is just a sigmoid curve that resembles the growth curves, and it does not have any biological meaning. However, the modified Gompertz model is one of the earliest models adopted by food scientists for predictive microbial growth and, therefore, there is a large volume of kinetic data derived from this model. In Eq. (2), K is termed as the maximum growth rate if the base-10 logarithm of bacterial count is used. If the logarithm of natural base is used, K is termed as the specific growth rate (μ_{max}).

$$K = \frac{[L(C_{max}) - L(C_0)]\mu_G}{e}, \quad (2)$$

$$\lambda = M - 1/\mu_G. \quad (3)$$

☆ Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

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The Baranyi model is another growth model that was developed in mid 1990s (Baranyi and Roberts, 1994), and has gradually gained its acceptance in predictive microbiology. The fundamental characteristics that distinguishes this model from the empirical models is that the development of this model was based two basic hypotheses. The first hypothesis concerns the completion of the lag phase. It is proposed that the duration of the lag phase is dependent upon the formation of critical substances that are needed for bacterial growth, and the formation of critical substances follows some forms of Michaelis–Menten kinetics. Based on this hypothesis, the accumulation of critical substances within the cells affects the duration of the lag phase and, therefore, the formation of critical substances is significantly affected by the prior history. After the lag phase, the growth of bacteria is governed by the logistic kinetics, and this is the second major hypothesis of the Baranyi model. The Baranyi model has evolved and becomes

$$y(t) = y_0 + \mu_{max}A(t) - \ln\left\{1 + \frac{\exp[\mu_{max}A(t)] - 1}{\exp(y_{max} - y_0)}\right\}. \quad (4)$$

In the above equation, $y(t)$ is the natural logarithm of bacterial counts, or $\ln(C)$; y_0 and y_{max} are the natural logarithm of the initial and the stationary phase maximum bacterial counts; μ_{max} is the specific growth rate (based on natural logarithm); and $A(t)$ is defined by

$$A(t) = t + \frac{1}{\nu}\ln[\exp(-\nu t) + \exp(-h_0) - \exp(-\nu t - h_0)]. \quad (5)$$

According to Baranyi and Roberts (1994), the parameter υ is the rate at which the critical substances necessary to sustain the bacterial growth are formed in the lag phase. It is assumed that the critical substances are formed at the same rate that the bacteria grow and, therefore, υ is equal to μ_{max}. The parameter h_0 defines the physiological state of bacteria and is affected by prior history. According to Baranyi and Roberts (1994) and Baranyi et al. (1995), the lag phase duration can be calculated from

$$\lambda = \frac{h_0}{\mu_{max}}. \quad (6)$$

The physiological state coefficient h_0 of cells is basically a virtual parameter and is extremely difficult to be observed, validated, and quantified experimentally. According to Baranyi's hypothesis, the length of a lag phase depends upon the formation of "critical substances" and prior history (Baranyi and Roberts, 1994; Baranyi et al., 1995). This assumption sometimes is contradictory to experimental observations. When a population of healthy, fully developed, actively dividing cells are inoculated in a different environment containing all necessary components for healthy cells to grow, a lag phase may still exist, even though all the "critical substances" are available extracellularly and intracellularly. In addition, the parameter h_0 may vary from one curve to another. To use the Baranyi model, it is necessary to fit all the growth curves first, and then the average h_0 to fit individual growth curves again to obtain the growth rates.

The objective of this paper was to summarize and update the results of two recent studies (Huang, 2008, 2010) on the development and validation of a new mechanistic bacterial growth model. The new model was a theoretical growth model, and was based on the fundamental growth phenomenon of microorganisms in foods. It clearly defined the duration of lag phase and exponential growth rate in a single equation, and was more intuitive than the traditional growth models such as modified Gompertz and Baranyi models.

2. Materials and methods

2.1. Model development

For a growth curve without a lag phase, the microbial culture does not need to experience an adjustment process and can multiply exponentially until the population reaches a maximum density. This process can be described by

$$\frac{dC}{dt} = kC(C_{max} - C). \quad (7)$$

In this equation, C is the cell concentration; C_{max} is the maximum cell concentration, and kC_{max} is equal to μ_{max}, or specific growth rate in the exponential phase. Under isothermal conditions, it is assumed that k or μ_{max} does not change with time and is a constant. The bacterial population would start to increase immediately. Apparently, this equation is not suitable for growth curves with lag phases.

Since a lag phase is a transitional period through which bacteria enter the exponential phase of growth, a transitional function, $f(t)$, can be used to modify Eq. (7) so that it can describe a complete growth curve. A transitional function chosen for this application is

$$f(t) = \frac{1}{1 + \exp[-\alpha(t - \lambda)]}. \quad (8)$$

In Eq. (8), $f(t)$ is actually a unit transitional function. At $t \le \lambda$, it equal to zero. With $f(t) = 0$, dC/dt is also zero, which mathematically describes the lag phase during which no change in the cell population occurs. At $t > \lambda$, $f(t)$ equals to 1, and the process is governed by the 1st-order kinetics. The coefficient α is a constant that allows a smooth transition from 0 to 1. The coefficient α in the new model allows a smooth but sharp transition from the lag phase to the exponential phase in a growth curve. According to Huang (2008), a value of 25 is suitable for this coefficient. With $f(t)$, a new differential growth model can be developed, and is written as

$$\frac{dC}{dt} = \frac{kC(C_{max} - C)}{1 + \exp[-\alpha(t - \lambda)]}. \quad (9)$$

Denoting $y(t)$ as the natural logarithm of C, Eq. (9) can be solved analytically to produce a new growth model:

$$y(t) = y_0 + y_{max} - \ln\{\exp(y_0) + [\exp(y_{max}) - \exp(y_0)]\exp[-\mu_{max}B(t)]\}. \quad (10)$$

In Eq. (10), the function $B(t)$ is defined by

$$B(t) = t + \frac{1}{\alpha}\ln\frac{1 + \exp(-\alpha(t - \lambda))}{1 + \exp(\alpha\lambda)}. \quad (11)$$

Eq. (11) is particularly suitable for growth curves with all three phases. It is also suitable for growth curves without lag phases, as λ may approach zero in this special case. In experiments, sometimes it is not necessary to collect the stationary phase data. For these types of growth curves, a reduced model can be obtained for this special case (Eq. 12).

$$y(t) = y_0 + \mu_{max}\left\{t + \frac{1}{\alpha}\ln\frac{1 + \exp[-\alpha(t - \lambda)]}{1 + \exp(\alpha\lambda)}\right\}. \quad (12)$$

2.2. Microbiological experiments

The microbiological procedures are reported in detail in Huang (2008, 2010) for *Listeria monocytogenes* and *Escherichia coli* O157:H7, but briefly described in this section.

2.2.1. Preparation of bacterial cultures

2.2.1.1. L. monocytogenes. Four strains of *L. monocytogenes* (H7763, H7776, H7778, and 46877) were obtained from the culture collection of USDA ARS Eastern Regional Center located at Wyndmoor, PA. The stock cultures were regularly propagated and maintained on Tryptic Soy agar (TSA, BD, Sparks, MD) plates and stored at 4 °C (Huang, 2008).

2.2.1.2. E. coli O157:H7. Five rifampicin-resistant strains of *E. coli* O157:H7 (Luchansky et al., 2008, 2009), were used in this study. The five strains of *E. coli* O157:H7 were 1) USDA/FSIS 011-82; 2) ATCC 43888; 3) ATCC 43889; 4) ATCC 43890; and 5) USDA-FSIS 45756. The bacterial cultures were stored in a refrigerator on individual Sorbitol-MacConkey Agar (SMAC, BD) plates supplemented with 100 μg/ml rifampicin (R-7382, Sigma, St. Louis, MO), or SMAC-R plates.

2.2.1.3. Culture preparation. One day before the experiment, a loopful of each strain of each bacterium was individually transferred to 10 ml Brain Heart Infusion broth (BHI broth, BD) and held at 37 °C on an orbital shaker (~100 rpm) for approximately 22–24 h. The bacteria cultures were harvested by centrifugation (2400 × g, 15 min, 4 °C), washed once with 10 ml 0.1% peptone water (PW, BD), re-centrifuged, and re-suspended in 1 ml PW. A cocktail of each bacterium was formed by combining and mixing the 1 ml culture cells. Each cocktail contained approximately $10^{9.5}$ CFU/ml of bacterial cells.

2.2.2. Growth studies

The growth studies were conducted in both liquid and solid media. To examine the growth of bacteria in liquid medium, *L. monocytogenes* was inoculated into Tryptic Soy broth (TSB, BD). To examine the growth of bacteria in solid media, both *L. monocytogenes* and *E. coli* O157:H7 were used.

2.2.2.1. L. monocytogenes in broth. The cocktail of *L. monocytogenes*, after proper dilution, was inoculated into 200 ml TSB to study isothermal growth in broth. Four differential initial concentrations (approximately 1, 2, 3, and 4 log CFU/ml) of *L. monocytogenes* were used. The sample flasks were incubated at 37 °C in a temperature controlled orbital shaker (Labline Environmental Shaker, Model 4628, Barnstead/Thermolyne) operated at 120 rpm, and were periodically retrieved and plated (after proper dilution) onto TSA to enumerate the bacteria counts. The TSA plates were held in an incubator for 48 h at 37 °C. The bacterial colonies were counted and converted to the logarithm of the natural base or base-10, and recorded as ln CFU/ml or $\log_{10}$ CFU/ml.

2.2.2.2. L. monocytogenes and E. coli O157:H7 in solid media. The diluted cocktail (0.1 ml) of *L.* monocytogenes or *E. coli* O157:H7 was inoculated into processed or raw meats. For *L.* monocytogenes, the bacteria were inoculated to beef frankfurters (1 ± 0.05 g). For *E. coli* O157:H7, the bacteria were inoculated into raw mechanically tenderized beef (5 ± 0.05 g). The inoculated samples were contained in filter bags (Whirl-Pak®, 7 oz., 95 mm × 180 mm × 0.08 mm, NASCO – Fort Atkinson, Fort Atkinson, WI). The initial inoculum level was approximately 3 $\log_{10}$ CFU/g in meat. For *L. monocytogenes*, the inoculated samples were placed in incubators maintained at 15, 25, 30, 37, or 40 °C. For *E. coli* O157:H7, the samples were incubated at 5, 10, 15, 20, 25, and 37 °C. At time intervals determined by the incubation temperature, samples were retrieved to determine bacterial counts. For *L.* monocytogenes, PALCAM *Listeria* selective agar (BD) plates were used. For *E. coli* O157:H7, SMAC-R plates were used. The plates were incubated at 37 °C for approximately 24–48 h. After incubation, typical colonies of *Listeria* and *E. coli* O157:H7 were counted, averaged, and converted to the logarithm (natural base or base-10) of CFU/g of meats.

2.3. Growth curves and curve fitting

Growth curves of *L. monocytogenes* and *E. coli* O157:H7, obtained from broth and meat samples, were analyzed and fitted with the modified Gompertz, Baranyi, and the new models. A nonlinear regression procedure based on Gauss-Newton method in Windows-based SAS Version 9.1.3 (SAS Institute Inc., Cary, NC) was used for curve fitting.

2.4. Model evaluation

The bias factor (B_f) and accuracy factor (A_f) proposed by Ross (1990) were used to evaluate the performance of each growth model. RMSE, or root mean square error, an estimate of the standard error of a model, was also calculated for evaluation of the models. Analysis of variance (ANOVA) was conducted to compare of the mean of K (or μ_{max}), λ, B_f, A_f, and RMSE among different models. The Tukey's studentized range (HSD) test procedure was used to group the means of K, λ, B_f, A_f, and RMSE. The statistical analyses were conducted using Windows-based SAS Version 9.1.3 (SAS Institute, Cary, NC).

2.5. Secondary model

2.5.1. Growth rates as a function of temperature

The growth rate was fitted to two secondary models modified from the Ratkowsky square-root model:

$$\sqrt{\mu_{max} \text{ or } K} = a(T - T_{min})\{1 - \exp[b(T - T_{max})]\}, \quad (13)$$

$$\mu_{max} \text{ or } K = a(T - T_{min})^{\gamma}\{1 - \exp[b(T - T_{max})]\}. \quad (14)$$

In Eq. (14), γ was either 1.0, 1.5, or 2.0. For *L. monocytogenes*, the full model of Eqs. (13) and (14) were used, as the growth temperature almost spanned the entire temperature range suitable for this microorganism. For *E. coli* O157:H7, the exponential term was dropped. Eq. (13) became the original square-root model, and Eq. (14) became a Bělehrádek-type model (McMeekin et al., 1993) A nonlinear regression procedure based on Gauss–Newton method in Windows-based SAS Version 9.1.3 (SAS Institute Inc., Cary, NC) was also used for curve fitting.

2.5.2. Lag phase as a function of growth rate

A simple equation was used to describe the interdependence between lag phase and temperature (Eq. (15)).

$$\frac{1}{\sqrt{\lambda}} = a(T - T_{min})\{1 - \exp[b(T - T_{max})]\}. \quad (15)$$

3. Results and discussion

3.1. Comparison of primary model

3.1.1. Growth of L. monocytogenes in broth

Fig. 1 illustrates the growth and curve fitting of *L. monocytogenes* in broth at 37 °C. With the new model, all three phases of bacterial growth are clearly defined and distinguishable from each other. For the modified Gompertz and Baranyi models, however, the lag phases are not clearly distinguishable from the exponential phases, and the calculated bacterial population starts to increase

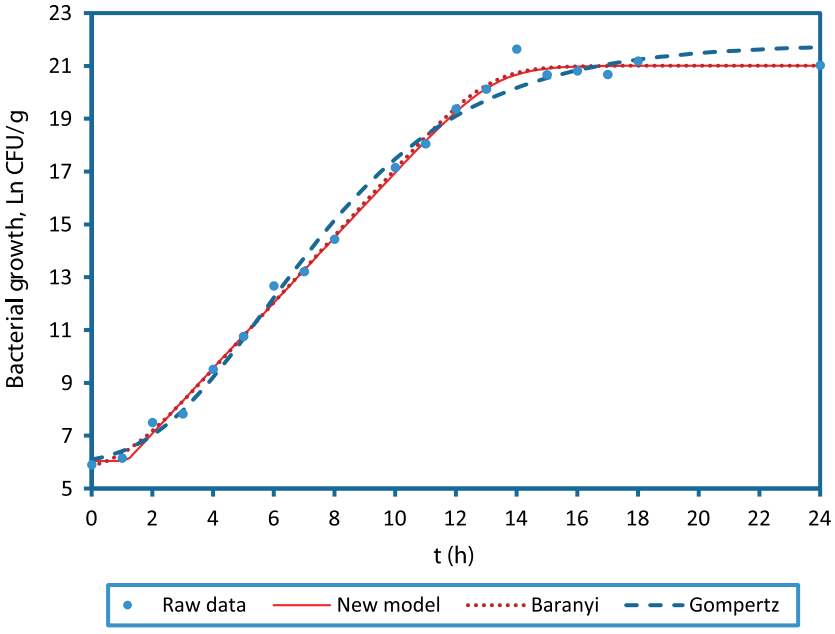

Fig. 1. Growth of *L. monocytogenes* in broth at 37 °C and curve fitting with the modified Gompertz, Baranyi, and new models.

immediately for these two models (Fig. 1). The ANOVA analysis suggests that the initial inoculum level did not affect the growth rate of the exponential growth phase ($p = 0.15$). The lag phase, growth rate, and maximum cell concentration determined from the modified Gompertz were significantly higher than those determined from the Baranyi and new model. No statistical difference in the lag phase duration, growth rates, and specific growth rate was found between the new and Baranyi models (Huang, 2008).

3.1.2. Growth of *L. monocytogenes* and *E. coli* O157:H7 in solid medium

Figs. 2 and 3 show the curve fitting of three models to growth curves of *L. monocytogenes* and *E. coli* O157:H7 in solid media. Again, the lag phases are more clearly defined by the new model. No statistical difference was found in the maximum (or specific) growth rates and lag phase determined by the new and Baranyi models. However, the maximum (or specific) growth rates and lag phase derived from the modified Gompertz model was significantly higher than the new model.

3.1.3. Reduced model

Another major advantage of the new model is that partial growth curves without stationary phase can be precisely and directly defined by the reduced form of the new model. Fig. 4 shows the fitting of the partial growth curves using the reduced model. According to the results of ANOVA, no statistical difference was

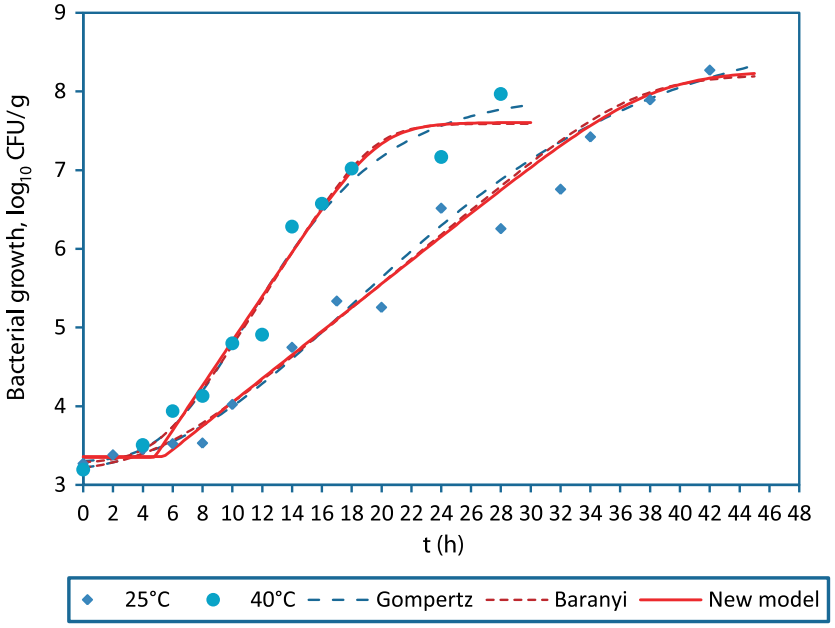

Fig. 2. Growth of *L. monocytogenes* in beef frankfurter at 25 and 40 °C.

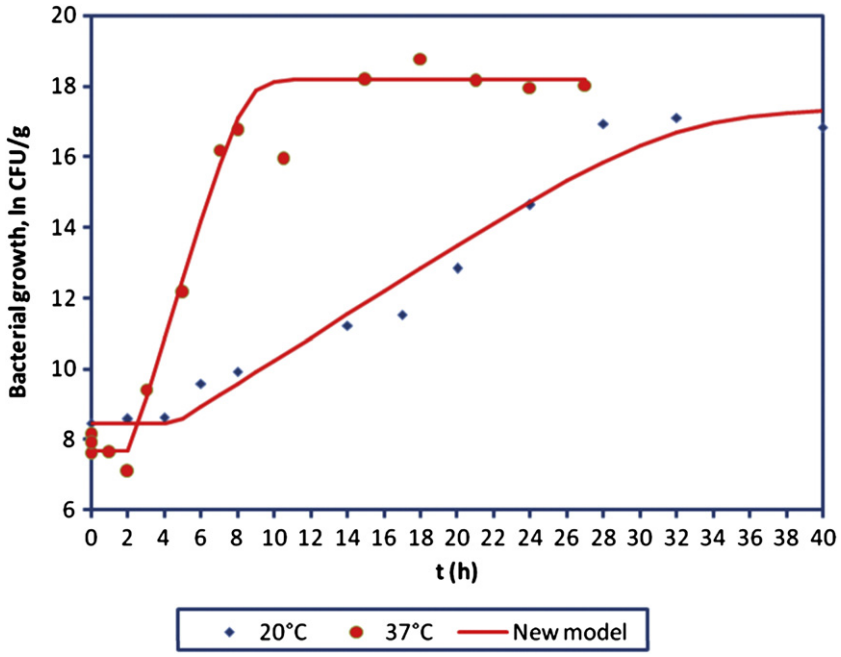

Fig. 3. Growth of *E. coli* O157:H7 in raw beef at 20 and 37 °C.

found in the growth rates and lag phases determined by the full and reduced forms of the new model.

3.1.4. Performance of models

For *L. monocytogenes*, either in broth or in beef frankfurter, the bias factor (B_f) calculated from all three models were almost identical to 1.0 ($\sim$1.001), and the accuracy factor (A_f) ranged from 1.02 to 1.04. The RMSE values of the new and Baranyi models were almost identical (Huang, 2008). In broth, the RMSE of the modified Gompertz model was higher than that of the new model.

3.2. Secondary model

3.2.1. Growth rate as a function of temperature

Fig. 5 depicts the effect of temperature on the maximum growth rate of *L. monocytogenes* in beef frankfurter, and the curve fitting using the secondary models. Table 1 lists the estimates of parameters for each secondary rate model.

L. monocytogenes is a nonsporeforming, psychrotrophic bacterium that can grow at refrigerated temperatures. According to the literature, this microorganism can grow at temperatures between

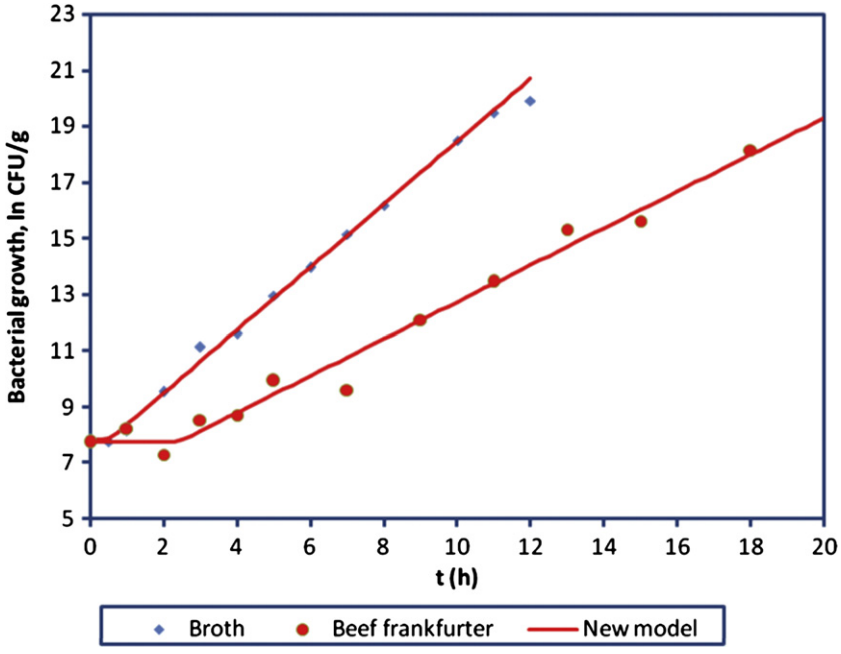

Fig. 4. Partial growth curves of *L. monocytogenes* in broth and beef frankfurter incubated at 37 °C and curve fitting using the reduced new model.

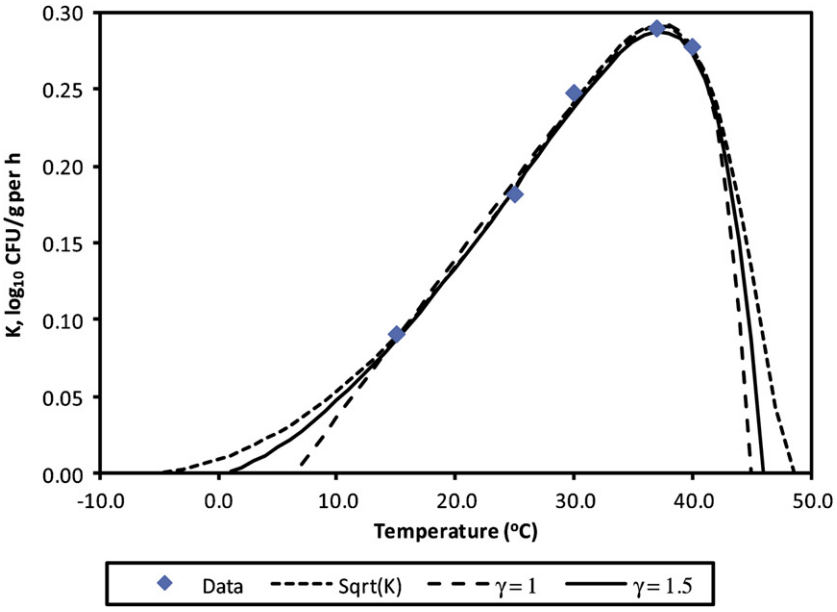

Fig. 5. Effect of temperature on average growth rate of *L. monocytogenes* in beef frankfurter and the curve fitting of secondary models. The legend Sqrt(K) represents the growth determined from the modified Ratkowsky model (Eq. (13)). The legend γ is the parameter used in Eq. (14).

1 and 45 °C (Busta et al., 2001). All three secondary models used to describe the temperature dependence of growth rate can accurately estimate the growth rates at temperatures between 15 and 40 °C (Fig. 5). However, the minimum temperature (T_{min}) estimated by the Ratkowsky square-root model (Eq. (13)) or modified Ratkowsky model $\gamma = 2$ in Eq. (14) is −6.83 or −6.05 °C, respectively. Apparently, the minimum temperatures estimated by the Ratkowsky models were significantly lower than the true minimum temperature for *L. monocytogenes*. With $\gamma = 1.0$ in Eq. (14), the theoretical maximum growth temperature (T_{max}) is 45 °C, which agrees very well with the biological nature of *L. monocytogenes*. However, the theoretical minimum growth temperature is overestimated. With $\gamma = 1.5$ in Eq. (14), the theoretical minimum temperature estimated by the model is 0.109 °C, which is very close to the minimum growth temperature reported in the literature. The maximum growth temperature estimated by the model is 46.03 °C, also agrees well with the biological nature of the bacteria. It is evident that a γ value of 1.5 is more suitable for describing the temperature dependence of growth rate.

That the γ value of 1.5 is also suitable for evaluating the effect of temperature on growth rate of *E. coli* O157:H7 in raw beef (Table 2). As the growth studies were conducted below 37 °C. The exponential function in Eqs. (13) and (14) is not needed to calculate the maximum growth temperature, and therefore must be dropped from the equation.

E. coli O157:H7 is a mesophilic bacterium, and does not grow well at refrigerated temperatures. The minimum growth temperature is around 8–10 °C under optimal conditions (Buchanan and Bagi, 1994; Buchanan and Doyle, 1997). The minimum growth temperature estimated by the Ratkowsky square-root model (Eq. (13)) is 4.1 °C, which is below the biological minimum growth temperature for this microorganism. In the paper published by Ratkowsky et al. (1982), the estimated T_{min} of *E. coli* was reported as 275, 276, 277, or 280 K, depending on the source of the data. The theoretical minimum growth temperature obtained from this study was very close to the values listed in Ratkowsky et al. (1982). Apparently, the original Ratkowsky model may underestimate the minimum growth temperature of *E. coli* O157:H7.

With the Bělehrádek-type model (Eq. (14)), the estimated minimum growth temperature is 12.7 °C, if using a γ value of 1. Accordingly, this would lead to an overestimation of the minimum growth temperature. With $\gamma = 1.5$, the minimum growth temperature estimated by the Bělehrádek-type model is 7.8 °C, and this value matches well with the biological minimum growth temperature of *E. coli* O157:H7.

3.2.2. Lag phase as a function of temperature

The effect of temperature on lag phase of *L. monocytogenes* can be evaluated using Eq. (15) (Fig. 6), and the resulting equation is

$$\frac{1}{\sqrt{\lambda}} = 0.0179(T - 0.109)\{1 - \exp[0.2417(T - 46.03)]\}. \quad (16)$$

For *E. coli* O157:H7 in raw beef, the exponential function is also dropped, resulting a simple linear model to describe the relationship between the lag phase duration and temperature (Eq. (17)). The adjusted R^2 value of this equation is 0.87.

$$\frac{1}{\sqrt{\lambda}} = 0.0234T \quad (17)$$

Table 1
Parameters for secondary rate models of *L. monocytogenes* in beef frankfurter.

Parameter	a	b	T_{min} (°C)	T_{max} (°C)
$\sqrt{K}$	0.0137[a] (0.0015)[b]	0.198 (0.100)	−6.83 (2.79)	48.66 (3.51)
K ($\gamma = 1$)	0.0103 (0.0013)	0.328 (0.287)	6.53 (2.06)	44.97 (3.85)
K ($\gamma = 1.5$)	0.00153 (0.00032)	0.210 (0.136)	0.109 (2.86)	46.03 (2.99)
K ($\gamma = 2.0$)	0.000199 (0.000062)	0.163 (0.103)	−6.05 (3.92)	46.51 (2.70)

[a] Estimated value.
[b] Approximate standard error.

Table 2
Parameters for secondary rate models (without the exponential function) of *E. coli* O157:H7 in raw beef meat.

Parameter	a	T_{min} (°C)
$\sqrt{\mu_{max}}$	0.0362 (0.0023)	4.10 (1.33)
μ_{max} ($\gamma = 1$)	0.0542 (0.0046)	12.7 (1.27)
μ_{max} ($\gamma = 1.5$)	0.00859 (0.00072)	7.77 (3.68)

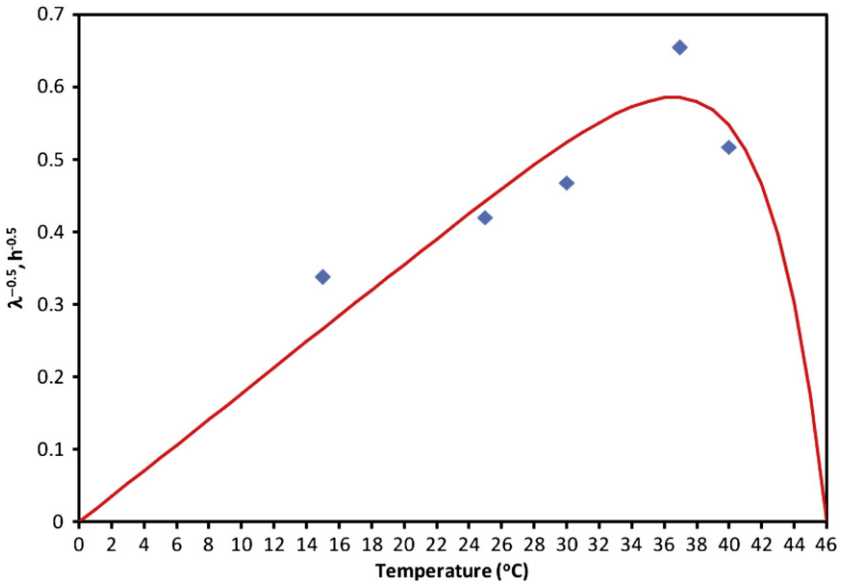

Fig. 6. The correlation between the average lag phase duration and temperature using a modified Ratkowsky model.

4. Conclusion

This study clearly demonstrates that the new integrated model is very accurate in describing the isothermal growth kinetics of microorganisms in foods. The new model is essentially identical to the Baranyi model, but without the need for the presumption of the effect of prior history and the physiological states of bacteria. The model is intuitive and straightforward with clearly defined lag exponential growth, and stationary phases. In addition, this model can be simplified to produce a reduced form that can be used to describe isothermal growth curves without a stationary phase. This study also reports a new secondary model can accurately capture the relationship between the growth and temperatures, and precisely estimate the minimum and maximum growth temperatures of bacteria.

References

Baranyi, J., Roberts, T.A., 1994. A dynamic approach to predicting bacterial growth in food. Int. J. Food Microbiol. 23, 277–294.

Baranyi, J., Robinson, T.P., Kaloti, A., Mackey, B.M., 1995. Predictive growth of *Brochothrix thermosphacta* at changing temperature. Int. J. Food Microbiol. 27, 61–75.

Buchanan, R.L., Bagi, L.K., 1994. Expansion of response surface models for the growth of *Escherichia coli* O157:H7 to include sodium nitrite as a valuable. Int. J. Food Microbiol. 23, 317–322.

Buchanan, R.L., Doyle, M.P., 1997. Foodborne disease significance of *Escherichia coli* O157:H7 and other enterohemorrhagic *E. coli*. Food Technol. 51 (10), 69–76.

Busta, F.F., Bledsoe, G.E., Flick, G.J., Gram, L., Herman, D., Jahncke, M.L., Ward, D.R., 2001. J. Food Sci., S-1055–S-1133.

Gibson, A.M., Bratchell, N., Roberts, T.A., 1987. The effect of sodium chloride and temperature on the rate and extent of growth of *Clostridium botulinum* type A in pasteurized pork slurry. J. Appl. Microbiol. 62, 479–490.

Huang, L., 2008. Growth kinetics of *Listeria monocytogenes* in broth and beef frankfurters – determination of lag phase duration and exponential growth rate under isothermal conditions. J. Food Sci. 73, E235–242.

Huang, L., 2010. Growth kinetics of *Escherichia coli*O157:H7 in mechanically-tenderized beef. Int. J. Food Microbiol. 140, 40–48.

Luchansky, J.B., Phebus, R.K., Thippareddi, H., Call, J.E., 2008. Translocation of surface-inoculated *Escherichia coli* O157:H7 into beef subprimals following blade tenderization. J. Food Prot. 71, 2190–2197.

Luchansky, J.B., Porto, A.C.S., Shoyer, B., Phebus, R.K., Thippareddi, H., Call, J.E., 2009. Thermal inactivation of *Escherichia coli* O157:H7 in blade-tenderized beef steaks cooked on a commercial open-flame gas grill. J. Food Prot. 72, 1401–1411.

McMeekin, T.A., Olley, J.N., Ross, T., Ratkowsky, D.A., 1993. Predictive Microbiology: Theory and Application. Research Studies Press LTD/John Wiley & Sons Inc., Taunton, Somerset, England/New York.

Ratkowsky, D.A., Olley, J., McKeekin, T.A., Ball, A., 1982. Relationship between temperature and growth rate of bacterial cultures. J. Bacteriol. 149, 1–5.

Ross, T., 1990. Indices for performance evaluation of predictive models in food microbiology. J. Appl. Bacteriol. 81, 501–508.