Effect of Temperature on Microbial Growth Rate–Mathematical Analysis: The Arrhenius and Eyring–Polanyi Connections

Lihan Huang, Andy Hwang, and John Phillips

Abstract: The objective of this work is to develop a mathematical model for evaluating the effect of temperature on the rate of microbial growth. The new mathematical model is derived by combination and modification of the Arrhenius equation and the Eyring–Polanyi transition theory. The new model, suitable for both suboptimal and the entire growth temperature ranges, was validated using a collection of 23 selected temperature–growth rate curves belonging to 5 groups of microorganisms, including *Pseudomonas* spp., *Listeria monocytogenes, Salmonella* spp., *Clostridium perfringens,* and *Escherichia coli,* from the published literature. The curve fitting is accomplished by nonlinear regression using the Levenberg–Marquardt algorithm. The resulting estimated growth rate (μ) values are highly correlated to the data collected from the literature ($R^2 = 0.985$, slope = 1.0, intercept = 0.0). The bias factor (B_f) of the new model is very close to 1.0, while the accuracy factor (A_f) ranges from 1.0 to 1.22 for most data sets. The new model is compared favorably with the Ratkowsky square root model and the Eyring equation. Even with more parameters, the Akaike information criterion, Bayesian information criterion, and mean square errors of the new model are not statistically different from the square root model and the Eyring equation, suggesting that the model can be used to describe the inherent relationship between temperature and microbial growth rates. The results of this work show that the new growth rate model is suitable for describing the effect of temperature on microbial growth rate.

Keywords: Arrhenius equation, Eyring–Polanyi transition theory, growth rate, mathematical analysis, temperature effect

Practical Application: Temperature is one of the most significant factors affecting the growth of microorganisms in foods. This study attempts to develop and validate a mathematical model to describe the temperature dependence of microbial growth rate. The findings show that the new model is accurate and can be used to describe the effect of temperature on microbial growth rate in foods.

Introduction

Among all factors that affect microbial growth, temperature is probably one of the most important factors directly affecting the growth of microorganisms in foods. Evaluating the effect of temperature on microbial growth is of paramount importance in predictive microbiology and predicting the shelf life of a product. Under normal conditions, microbial growth generally exhibits 3 characteristic temperatures—the minimum growth temperature (T_{min}), optimum growth temperature (T_{opt}), and maximum temperature (T_{max}). Below T_{min} or above T_{max}, microorganisms do not grow or may even die off. Between T_{min} and T_{opt}, or the suboptimal temperature range, the microbial growth rate increases with temperatures.

The effect of temperature on the rate of simple chemical and biological (for example, enzymatic) reactions is commonly described by the Arrhenius equation (Eq. 1), which is one of the most fundamental equations for describing the temperature dependence of chemical reaction rates:

$$\mu = Ae^{\frac{E_a}{RT}}, \quad (1)$$

where μ is the reaction rate, usually moles per unit time; A is often called the frequency factor, or the total number of collisions between reacting species per unit time; E_a is the activation energy, J/mol; R is the gas constant, 8.314 J/mol/K; and T is the temperature in Kelvin (K).

Although one of the most fundamental equations in reaction kinetics, the Arrhenius equation has not been found suitable for evaluating the effect of temperature on microbial growth, except in a few publications (Ingraham 1958; Daud and others 1978; Fu and others 1991; Taoukisa and others 1999; Nyati 2000; Cayre and others 2003; Valero and others 2007). The major drawback of the Arrhenius equation, as clearly illustrated in Figure 1A, is that the Arrhenius plots (natural logarithm of μ compared with $1/T$)

MS 20110621 Submitted 5/17/2011, Accepted 7/29/2011. *Authors Huang and Hwang are with U.S. Dept. of Agriculture, Agricultural Research Service, Eastern Regional Research Center, Residue Chemistry and Predictive Microbiology Research Unit,600 E. Mermaid Lane,Wyndmoor, PA 19038, U.S.A. Author Phillips is with USDA Agricultural Research Service, North Atlantic Area, 600 E. Mermaid Lane, Wyndmoor, PA 19038, U.S.A. Direct inquiries to author Huang (E-mail: lihan.huang@ars.usda.gov).*

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are not linear (Mohr and Krawiec 1980; Ratkowsky and others 1982; Daughtry and others 1997), although the plot may be linear within a certain temperature range. Due to the unique nature of the temperature dependence of microorganisms, despite the various attempts to modify the Arrhenius equation (Schoolfield and others 1981; Adair and others 1989; Davey 1989; 1991), this model still has not found a wider application in predictive microbiology.

One of the significant achievements in modern predictive microbiology is probably the development of the Ratkowsky square root model (Ratkowsky and others 1982, 1983). For bacterial growth under suboptimal temperature conditions, the square root model is a very simple mathematical equation (Eq. 2), suggesting a linear relationship between the square root of μ and temperature. The square root model can be extended to the entire temperature range that bacterial growth may occur (Eq. 3, Ratkowsky and others 1983):

$$\sqrt{\mu} = A(T - T_0), \tag{2}$$

$$\sqrt{\mu} = A(T - T_0)\,[1 - e^{B(T - T_{max})}]. \tag{3}$$

In Eqs. 2 and 3, A and B are regression coefficients; T_0 is the temperature at which $\mu = 0$; and T_{max} is the maximum growth temperature. T_0 is usually called the notional or nominal minimum growth temperature, and does not have any biological significance. Compared to T_0, T_{max} can be very close to the biological maximum growth temperature. Since its inception, the Ratkowsky square root model has become one of the most frequently used models for describing the effect of temperature on microbial growth rate. Numerous publications have documented the applicability of this model (McMeekin and others 1993). However, the major criticism to this model is that it is truly an empirical model used to describe the linear relationship between the temperature and square root of growth rate. Therefore, the objective of this work is to develop a new mathematical equation to describe the effect of temperature on microbial growth rate.

Materials and Methods

Model development

One of the major extensions to the traditional Arrhenius equation for describing the effect of temperature on chemical reaction rate is the Eyring equation (Eq. 4, Evans and Polanyi 1935). This equation was derived from the transition state theory of chemical reactions. In Eq. 4, k_B is Boltzmann's constant, h is Planck's constant, and $\Delta G^{\ddagger}$ is the Gibbs free energy of activation:

$$\mu = \frac{k_B T}{h} e^{-\frac{\Delta G^{\ddagger}}{RT}}, \tag{4}$$

$$\mu = ATe^{-\left(\frac{E_a}{RT}\right)}. \tag{5}$$

In McMeekin and others (1993), the ratio of Boltzmann's constant and Planck's constant was replaced with a constant (Eq. 5). However, according to McMeekin and others (1993), the addition of the extra temperature term makes only a minor contribution to the goodness of fit of the model to real growth rate data. Therefore, Eq. 5 does not present a real advantage over the traditional Arrhenius equation (Eq. 1), and thus, it has not found further applications in predictive microbiology.

To describe the effect of temperature on bacterial growth rate, this study proposes a modification to the Eyring equation (Eq. 5),

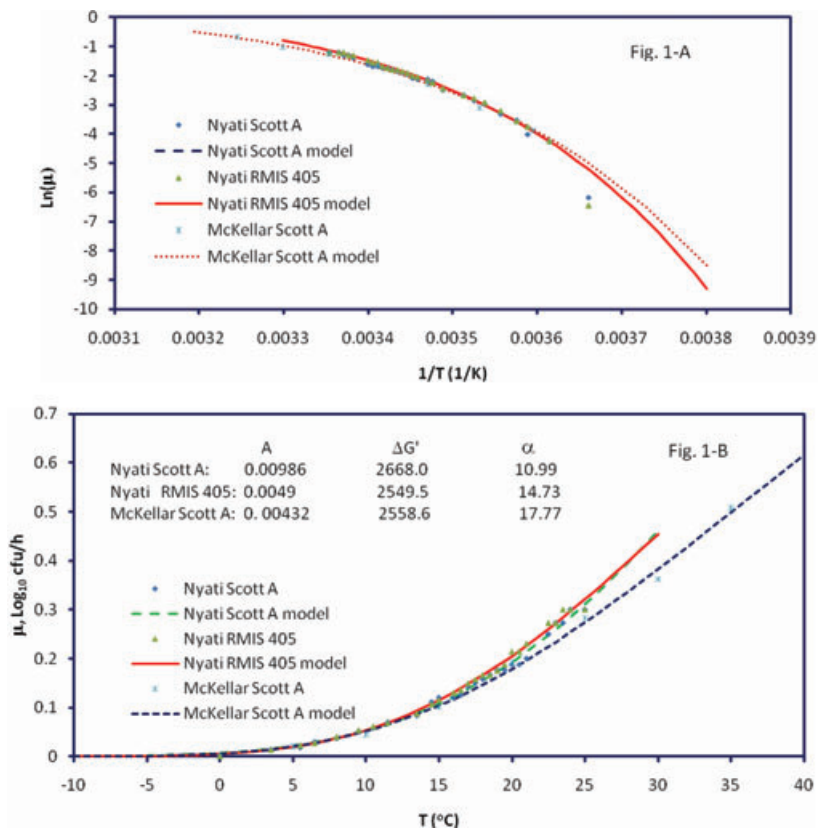

Figure 1–Effect of temperature on growth rate of *L. monocytogenes* and curve fitting using Eq. 6. (A) The traditional Arrhenius plot of μ compared with $1/T$ (in Kelvin); (B) the plot of μ compared with T (in celsius). Data sources: (A) *L. monocytogenes* Scott A in tryptose phosphate broth; (B) *L. monocytogenes* RMIT 405 in tryptose phosphate broth (data source: Table 1, Nyati (2000)); (C) *L. monocytogenes* Scott A in tryptic soy yeast extract broth (Table 1, McKellar [1997]).

allowing μ to be expressed

$$\mu = ATe^{-(\frac{\Delta G'}{RT})^{\alpha}}. \quad (6)$$

Equation 6 is termed as the modified Arrhenius–Eyring–Polanyi equation, or the new model in this study. In Eq. 6, $\Delta G'$ is equivalent to an energy term, with a unit of J/mol; α is an exponent. Eq. 6 is only suitable for suboptimal temperature conditions. To describe the effect of temperature on microbial growth over the entire temperature range, Eq. 6 can be expanded and expressed (Ratkowsky and others, 1983) as

$$\mu = ATe^{-\left(\frac{\Delta G'}{RT}\right)^{\alpha}}[1 - e^{B(T - T_{max})}]. \quad (7)$$

Growth rate data

The growth rate data of microorganisms were selected from the literature. The only criteria used for data selection were that the growth rate (μ) and the corresponding temperature were explicitly documented. Some authors used the generation time (GT) in the literature, and hence the GT was converted to growth rate by dividing the natural logarithm of 2 with the GT, or ln(2)/GT. All growth rate data were converted to maximum growth rates, which were $\log_{10}$ cfu per unit weight (or volume) per hour. Some publications reported temperatures in Kelvin (K), which were converted to celsius (°C) for plotting in this paper. However, the temperature data used in Eq. 6 and 7 were converted to Kelvin during curve fitting. Both spoilage and pathogenic microorganisms were selected in this study. These microorganisms include *Listeria monocytogenes, Escherichia coli, Pseudomonas* spp., *Salmonella* spp., and *Clostridium perfringens*. The sources of growth rate data will be presented as they appear in the Results and Discussion section.

Curve fitting

The nonlinear regression procedure (NLIN) of SAS Statistical Software (Version 9.2, SAS, Cary, N.C., U.S.A.) was used to fit the growth rate and temperature curves for Eq. 2, 3, 5, 6, and 7. The data were unweighted and analyzed using the Levenberg–Marquardt algorithm.

Model accuracy, goodness of fit, and comparison with other temperature models

The accuracy factor (A_f) and bias factor (B_f), commonly used in predictive microbiology, were calculated by comparing the estimated μ_i and the corresponding observed data (Eqs. 8 and 9). The A_f and B_f values of the curves were calculated used using the method originally proposed by Ross (1996), but modified by Baranyi and others (1999):

$$A_f = \exp\left(\frac{\sqrt{\sum_{i=1}^{n} 1 - [\ln(\mu_i) - \ln(\mu_{data,i})]^2}}{n}\right), \quad (8)$$

$$B_f = \exp\left(\frac{\sum_{i=1}^{n} 1[\ln(\mu_i) - \ln(\mu_{data,i})]}{n}\right). \quad (9)$$

The performance of the new kinetic model was compared with 2 existing secondary models. The 1st model for comparison was the Ratkowsky square root model (Eq. 2 for suboptimal temperature conditions and Eq. 3 for the entire growth range). The 2nd model for comparison was the Eyring equation (MeMeekin and other 1993), or Eqs. 5 and 10 (T in kelvin):

$$\mu = ATe^{-\frac{E_a}{RT}}[1 - e^{B(T - T_{max})}]. \quad (10)$$

The models were compared against 3 parameters. The 1st parameter was the mean square error, or MSE, calculated according to Eq. 11 ($df = n - p$, n = number of observations, and p = number of parameters to be estimated). The 2nd parameter was the Akaike information criterion, or AICc, estimated by Eq. 12 (von Boekel and Zwietering 2007). The 3rd parameter was the Bayesian information criterion, or BIC, calculated according to Eq. 13 (von Boekel and Zwietering 2007). In Eqs. 12 and 13, RSS was the residual sum of squares. For comparison of multiple models, models with smaller AICc and BIC values were more accurate than the ones with larger AICc and BIC values, that is, models with more negative AICc and BIC values are preferred:

$$MSE = \frac{\sum(\mu_{raw\ data} - \mu_{estimated})^2}{df}, \quad (11)$$

$$AICc = n\ln\left(\frac{RSS}{n}\right) + 2(p + 1) + \frac{2(p + 1)(p + 2)}{n - p - 2}, \quad (12)$$

$$BIC = n\ln\left(\frac{RSS}{n}\right) + p\ln(n). \quad (13)$$

Analysis of variance calculated by the ANOVA procedure (Version 9.2, SAS) was used to evaluate the effect of models on the means of A_f, B_f, AICc, BIC, and MSE, with a null hypothesis (H_0) that the selection of models did not affect the means of these parameters. Fisher's least-significant-difference (LSD) test (at the $\alpha = 0.05$ level) was used in ANOVA for multiple comparisons.

Results and Discussion

Curve fitting with the new model

Figure 1A shows the standard Arrhenius plots ($\ln(\mu)$ compared with $1/T$) of *Listeria* spp. using the data reported in Nyati (2000) and McKellar (1997). The raw data plots of $\ln(\mu)$ compared with $1/T$ clearly suggest the nonlinear relationship between these 2 variables, and the Arrhenius equation is not suitable for describing the temperature dependence of microbial growth rates. The continuous curves in Figure 1A are the results of the curve fitting using the new model (Eq. 6) and clearly demonstrate that it can be used to describe the nonlinear relationship between the growth rate and temperature. Figure 1B further illustrates the close agreement between the new model and μ–T (in celsius) relationship for the same set of data. As Figure 1B can directly present the relationship between temperature and growth rate (as compared to Figure 1A with the inverse of temperature in kelvin), the growth rates are directly plotted against temperature from this section forward.

The growth rate of *L. monocytogenes* reported in Nyati (2000) was obtained anaerobically between 0 and 25 °C in tryptose

phosphate broth, but the curve of the new model is extrapolated to –10 and 30 °C in Figure 1B. It is also important to point out that there is no minimum temperature in Eq. 6, just as it is in the traditional Arrhenius equation. For endothermic reactions, the reaction rate approaches to zero in the Arrhenius equation as temperature decreases. This characteristic is preserved in the new model. The minimum growth temperature for *L. monocytogenes* is usually around 0 °C. At temperatures below the physical minimum growth temperature, the growth rates estimated by the new model (Eq. 6) are not negative. Rather, the estimates of μ decrease to close to zero. For example, the estimated growth rate at –10 °C is 3.7×10^{-4} $\log_{10}$ CFU/h for *L. monocytogenes* Scott A, and 9.2×10^{-5} $\log_{10}$ CFU/h for *L. monocytogenes* RMIT 405. The estimated growth rates for *L. monocytogenes* at –10 °C are basically negligible, as the GT is 34 and 137 d for *L. monocytogenes* Scott A and *L. monocytogenes* RMIT 405, respectively. The aerobic growth of *L. monocytogenes* in tryptic soy yeast extract broth (McKellar 1997) is also illustrated in Figure 1B. In McKellar (1997), the growth rate data were obtained at a 5 °C interval from 5 to 35 °C, but the growth rate is extrapolated again to down to –10 °C and up to 40 °C using Eq. 5. Again, no negative growth rate is obtained by Eq. 6, and the growth rates at temperatures below 0 °C are negligible. The estimated GT at –10 °C is 62 d.

Valero and others (2007) reported a study using neural network to evaluate the combined effects of temperature (4 to 30 °C), citric acid (CA, 0 to 0.3% w/v), and ascorbic acid (AA, 0 to 0.4% w/v) on the growth rate of *L. monocytogenes* in tryptone soya broth (TSB). This report contains a complete set of experimental data that can be analyzed using the new model proposed in this study. Since CA and AA change the pH of the broth, not all the data reported in Valero and others (2007) can be analyzed by the new model, which is more suitable for analyzing the pure temperature effect on bacterial growth. Therefore, the growth rate data with low CA contents (< 0.1% w/v) and AA contents (< 0.4%) are analyzed by Eq. 6. Figure 2 shows the effect of temperature and AA on the growth of *L. monocytogenes* in TSB.

Table 1 lists the results of observed and estimated μ values of 4 data sets of growth rates of *L. monocytogenes* and other microorganisms in various substrates. Among these 4 data sets, the $\Delta G'$ values are relative consistent, ranging from 2412 to 2559 J/mol. While the α values vary from 13.77 to 25.36, the A values change from 0.000391 to 0.0109. It is possible that both A and α determine the shape of the growth curve. For all these 4 data sets, the MSE values are relatively small. While the A_f values range from 1.03 to 1.18, the B_f values span from 1.00 to 1.06.

Table 1 also lists the curve-fitting results of 4 sets of growth rate data for *Salmonella* spp. Figure 3 shows the curve-fitting results for *Salmonella typhimurium* DT104 in pasteurized liquid whole egg and 10% sugared yolk (McQuestin and others 2010). The A values are basically the same between the 2 curves in Figure 3. Although there is some difference in the $\Delta G'$ values, the α value for the 10% sugared yolk curve is definitely smaller than that of the whole egg. As the growth rate of *S. typhimurium* DT 104 in 10% sugared yolk is smaller than that in liquid whole egg, the α value may play a significant role in defining the shape of the growth rate curve.

Figure 4 shows the curve fitting and the effect of temperature on the growth rate of *S. typhimurium* in cooked chicken breast meat. Unlike the previous figures, Figure 4 shows the results of curve fitting over the entire temperature range. Interestingly, the A, $\Delta G'$, and α values in Figure 4 are very close to those of *S. typhimurium* DT104 in liquid whole egg, suggesting that these values may represent some biological and physiological characteristics for *S. typhimurium* (Table 1). The maximum temperature

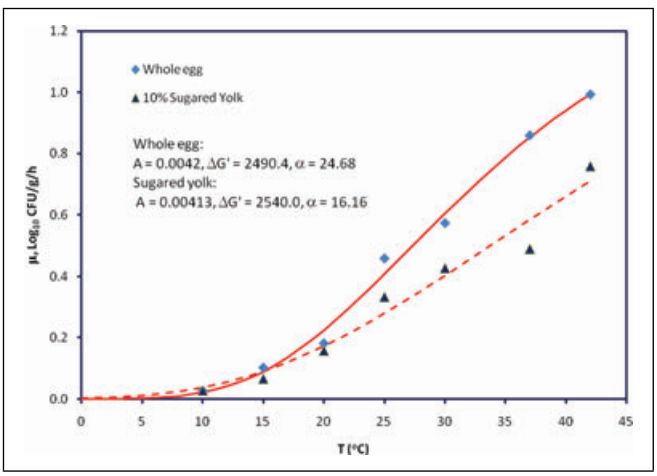

Figure 3–Modeling the effect of temperature on the growth rate of *Salmonella typhimurium* DT 104 in whole egg and 10% sugared yolk. Data source: McQuestin and others (2010).

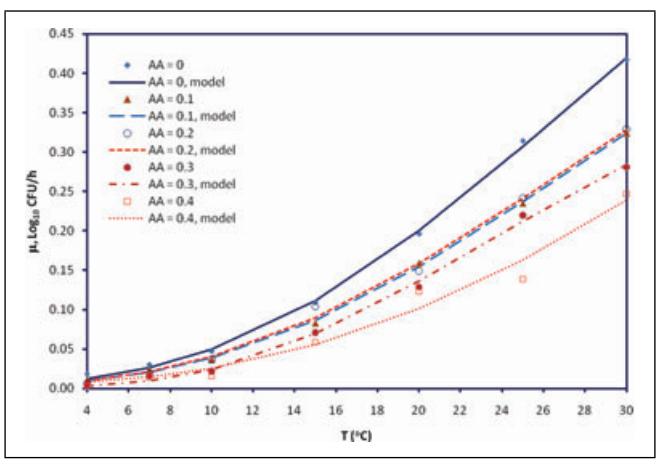

Figure 2–Effect of temperature on the growth of *L. monocytogenes* in tryptone soya broth in the presence of ascorbic acid (AA 0—0.4% w/v). Data source: Table 5, Valero and others (2007).

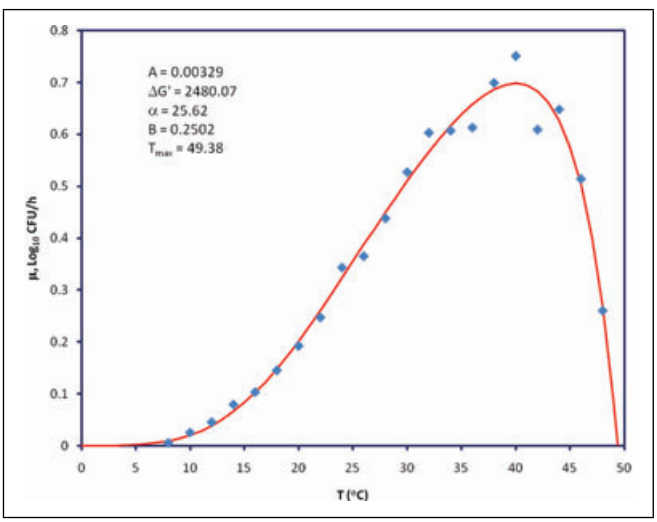

Figure 4–Modeling the effect of temperature on the growth rate of *Salmonella typhimurium* in cooked breast meat. Data source: Oscar (2002).

estimated by the new model (Eq. 7) is very close to the results reported in Oscar (2002).

Figure 5 demonstrates the curve-fitting results for 3 data sets of *Pseudomonas* spp. in various substrates, and Table 1 also lists the kinetic parameters for each curve. Among 3 data sets, the A values are relatively similar, ranging from 0.00272 to 0.00661. The $\Delta G'$ and α vary in a very narrow range (2503 to 2531 J/mol for $\Delta G'$ and 11.94 to 14.46 for α).

Figure 6 depicts the results of curve fitting for 3 selected curves of *E. coli*. The A values of the 2 suboptimal curves (Ratkowsky and others 1991; Daughtry and others 1997) are very close (0.00702 and 0.00858, respectively), and so are the $\Delta G'$ values (2551.4 and 2528.0). The α value for Ratkowsky and others (1991) is 17.56, while this value is 19.98 for Daughtry and others (1997).

For the growth rates of *E. coli* K-12 in trypticase-soy broth at temperatures between 8 and 46 °C (Ingraham, 1958), the maximum growth temperature (T_{max}) estimated by Eq. 7 was 48.6 °C. The A value for this rate curve was 0.00649, $\Delta G'$ was 2555.0 J/mol, and α was 21.69. Interestingly, the A, $\Delta G'$, and α values are very close to the suboptimal temperature curves shown in Figure 6.

The full model (Eq. 7) can also be used to describe the temperature dependence of *C. perfringens* in various meat products (Juneja and others 2008, 2009, 2010), with the curve-fitting results shown in Figure 7. The estimated $\Delta G'$ values of *C. perfringens* are 2648.9, 2570.6, and 2613.8 J/mol in pork, chicken, and beef, respectively (Table 2). While the α for *C. perfringens* is 13.5 in pork, the α values in chicken and beef are very close to each other (18.31 and 18.46, respectively). The A values range from 0.0133 to 0.0223. The T_{max} values estimated by the new model are very consistent with the maximum growth temperature of *C. perfringens.*

Comparison of models

The mean A_f values were 1.24, 1.19, and 1.59 for the new model, square root model, and Eyring equation, and the corresponding B_f values were 0.996, 1.004, and 0.852, respectively. According to the ANOVA/LSD test results, there was no significant statistical difference in the means of A_f and B_f values between

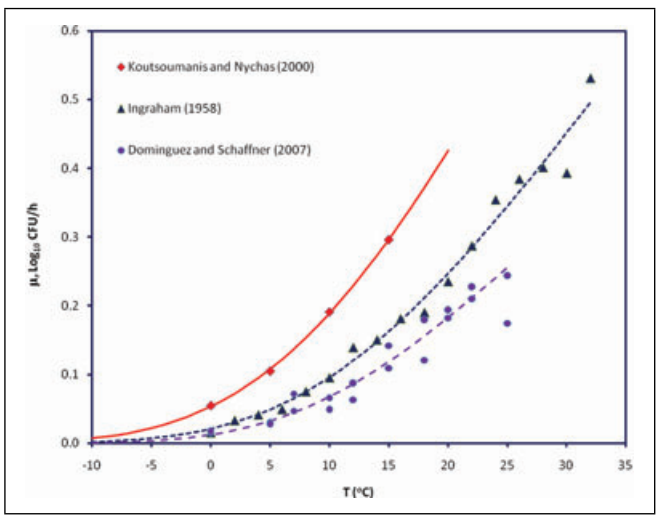

Figure 5–Modeling the effect of temperature on the growth rate of *Pseudomonas* spp. Data source: Dominguez and Schaffner (2007), Ingraham (1958), and Koutsoumanis and Nychas (2000).

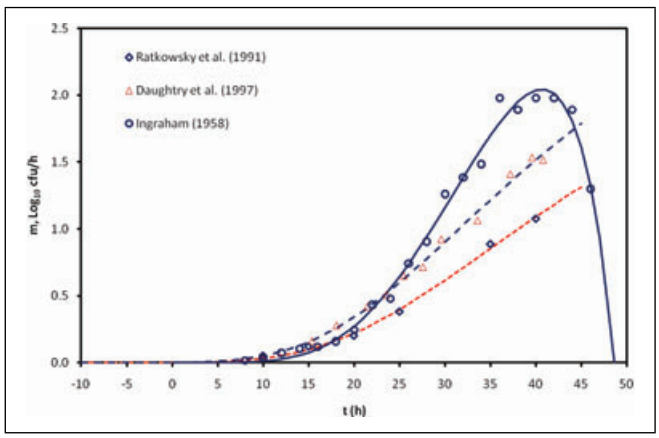

Figure 6–Modeling the effect of temperature on growth rate of *E. coli.*

Table 1–Comparison of observed and estimated maximum growth rates (μ, $\log_{10}$ CFU/h), the estimated parameters (A, $\Delta G'$, and α), model mean square error (MSE), accuracy factor (A_f), and bias factor (B_f).

Source	Substrate	A	$\Delta G'$ (J/mol)	α	MSE	A_f	B_f
L. monocytogenes							
Diez-Gonzalez and others (2007)	Tryptic soy broth	0.00295[a](0.00089[b])	2493.4(44.5)	18.44(5.23)	0.000533	1.18	1.02
Valero and others (2007)	Tryptone soya broth	0.00326(0.00051)	2498.6(21.93)	18.00(2.00)	0.000034	1.17	1.06
McKellar (1997)	Tryptic soy yeast extract broth	0.00432(0.0017)	2558.6(70.77)	13.77(3.55)	0.0002	1.04	1.00
Koseki and Isobe (2005)	Iceberg lettuce	0.00109(0.00031)	2411.8(30.73)	25.36(7.65)	0.000062	1.12	1.04
Salmonella. Spp							
McQuestin and others (2010)	Liquid whole egg	0.0042(0.0006)	2490.4(18.2)	24.68(5.11)	0.00141	1.16	1.04
McQuestin and others (2010)	10% sugared yolk	0.00413(0.00291)	2540.0(121.1)	16.16(10.44)	0.00392	1.22	0.921
Mackey and Kerridge (1988)	Minced beef	0.0098(0.0056)	2585.2(93.7)	14.70(5.00)	0.00196	1.22	0.949
Oscar (2002)	Cooked chicken meat	0.00329(0.00067)	2480.2(21.7)	25.62(5.25)	0.000895	1.18	0.989
Pseudomonas spp.							
Koutsoumanis and Nychas (2000)	Mediterranean gilt-head seabream (*Sparus aurata*) stored aerobically	0.00661(0.00429)	2523.4(109.3)	11.94(3.29)	0.000015	1.02	1.00
Ingraham (1958)	Trypticase-soy broth	0.00428(0.00188)	2531.1(83.01)	12.84(3.62)	0.000502	1.12	0.979
Domingquez and Schaffner (2007)	Raw poultry	0.00272(0.00223)	2503.3(128.6)	14.46(6.68)	0.000291	1.25	0.997
E. coli							
Ratkowsky and others (1991)	Unknown	0.00702(0.00208)	2551.4(46.2)	17.56(4.24)	0.00989	1.23	1.09
Daughtry and others (1997)	Unknown	0.00858(0.00136)	2528.0(23.3)	18.98(3.00)	0.0018	1.12	0.972
Ingraham (1958)	Trypticase-soy broth	0.00649(0.00412)	2555.0(65.82)	21.69(7.55)	0.00109	1.60	1.22

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

the new and square root models, while the Eyring model has significantly higher A_f values and lower B_f values than the other 2 models.

According to the ANOVA test, however, there was no significant difference in the means of AICc, BIC, and MSE among all 3 models, which indicates that all 3 models are equally suitable for describing the effect of temperature on microbial growth rate. The mean MSE values are 0.00419, 0.00466, and 0.00627 for the new, square root, and Eyring models, respectively. The average AICc and BIC values are −107 and −110, respectively, for the new model. The average AICc and BIC values for the square root model are −103 and −109, respectively. The average AICc and BIC values for the Eyring equation are −98 and −101, respectively.

The suitability of the new model for describing the effect of temperature on the growth rates of microorganisms can be further illustrated by the linear correlation between the growth rate data collected from the literature and the corresponding growth rate data calculated by the new model. A total of 348 raw μ data points were collected from the literature and analyzed using the newly proposed mathematical model. The resulting linear regression is

$$\mu_{\text{raw data}} = -0.00027 + 1.0002\,\mu_{\text{estimated}}, \quad R^2 = 0.985. \tag{14}$$

The fact that the slope of the correlation curve is almost equal to 1.0 (1.0002) and the intercept is also almost zero (−0.00027) clearly suggests the close agreement between the μ values collected

Table 2–*Clostridium perfringens*—the estimated parameters (A, $\Delta G'$, α, B, and T_{max} in Eq. 6) and model mean square error (MSE).

Source/substrate rate	A	$\Delta G'$ (J/mol)	α	B	T_{max} (°C)	MSE
Juneja and others (2010), Pork	0.0181(0.0137)	2648.9(136.9)	13.50(6.06)	0.5346(0.2502)	52.18(0.46)	0.0258
Juneja and others (2009), Chicken	0.0133(0.0073)	2570.6(77.3)	18.31(7.49)	0.3479(0.1474)	52.05(0.36)	0.0286
Juneja and others (2008), Uncured beef	0.0223(0.0181)	2613.8(96.3)	18.46(7.33)	0.2167(0.1252)	53.31(0.55)	0.0123

Table 3–List of parameters for the Ratkowsky square root model, and Eyring equation (please use Table 1 and 2 for cross-reference of microorganisms). Units: T_{min} and T_{max}, °C.

	Ratkowsky square root model		Eyring equation	
Source/substrate	Estimated value	Approx. STD	Estimated value	Approx. STD
Diez-Gonzalez and others (2007)	$A = 0.0190$	0.0009	$A = 5.06 \times 10^5$	1.35×10^6
	$T_{min} = -2.32$	1.05	$E_\alpha = 5.03 \times 10^4$	6.07×10^3
Valero and others (2007)	$A = 0.0206$	0.0006	$A = 1.51 \times 10^8$	3.73×10^8
	$T_{min} = -1.53$	0.61	$E_\alpha = 6.39 \times 10^4$	6.15×10^3
McKellar (1997)	$A = 0.0193$	0.0006	$A = 1.91 \times 10^6$	5.59×10^6
	$T_{min} = -1.97$	0.70	$E_\alpha = 5.34 \times 10^4$	4.74×10^3
Koseki and Isobe (2005)	$A = 0.0154$	0.0009	$A = 1.38 \times 10^7$	5.29×10^7
	$T_{min} = -4.46$	1.15	$E_\alpha = 5.88 \times 10^4$	9.38×10^3
McQuestin and others (2010)	$A = 0.0268$	0.0018	$A = 2.02 \times 10^5$	5.64×10^5
	$T_{min} = 2.76$	1.66	$E_\alpha = 4.69 \times 10^4$	7.18×10^3
McQuestin and others (2010)	$A = 0.0215$	0.0017	$A = 1.63 \times 10^5$	4.60×10^5
	$T_{min} = 1.48$	2.12	$E_\alpha = 4.73 \times 10^4$	7.26×10^3
Mackey and Kerridge (1988)	$A = 0.0313$	0.0011	$A = 1.52 \times 10^8$	2.86×10^8
	$T_{min} = 3.42$	0.69	$E_\alpha = 6.29 \times 10^4$	4.76×10^3
Oscar (2002)	$A = 0.0297$	0.0012	$A = 2.62 \times 10^{11}$	6.06×10^{12}
	$T_{min} = 4.93$	0.55	$E_\alpha = 7.98 \times 10^4$	4.53×10^3
	$B = 0.141$	0.017	$B = 0.0214$	0.136
	$T_{max} = 51.83$	0.48	$T_{max} = 49.36$	0.39
Koutsoumanis and Nychas (2000)	$A = 0.0208$	0.0007	$A = 1.08 \times 10^9$	2.00×10^9
	$T_{min} = -10.98$	0.64	$E_\alpha = 6.63 \times 10^4$	4.39×10^3
Ingraham (1958)	$A = 0.0181$	0.0001	$A = 5.26 \times 10^5$	6.87×10^5
	$T_{min} = -7.24$	0.65	$E_\alpha = 4.96 \times 10^4$	3.25×10^3
Dominguez and Schaffner (2007)	$A = 0.0156$	0.0009	$A = 5.20 \times 10^7$	1.05×10^8
	$T_{min} = -7.01$	1.18	$E_\alpha = 6.14 \times 10^4$	4.92×10^3
Ratkowsky and others (1991)	$A = 0.0281$	0.0011	$A = 1.08 \times 10^7$	2.72×10^7
	$T_{min} = 2.73$	0.92	$E_\alpha = 5.68 \times 10^4$	6.47×10^3
Daughtry and others (1997)	$A = 0.0343$	0.0011	$A = 1.06 \times 10^6$	1.59×10^6
	$T_{min} = 3.11$	0.79	$E_\alpha = 4.99 \times 10^4$	3.88×10^3
Ingraham (1958)	$A = 0.0303$	0.0013	$A = 3.01 \times 10^{12}$	3.11×10^{11}
	$T_{min} = 7.15$	0.71	$E_\alpha = 8.79 \times 10^4$	2.44×10^4
Juneja and others 2010	$A = 0.0416$	0.0022	$A = 3.83 \times 10^8$	1.44×10^9
	$T_{min} = 9.03$	1.07	$E_\alpha = 6.50 \times 10^4$	9.47×10^3
	$B = 0.414$	0.129	$B = 0.213$	0.098
	$T_{max} = 53.51$	0.82	$T_{max} = 52.70$	0.455
Juneja and others 2009	$A = 0.0459$	0.0026	$A = 7.81 \times 10^{10}$	6.57×10^{11}
	$T_{min} = 8.98$	1.03	$E_\alpha = 7.74 \times 10^4$	2.09×10^4
	$B = 0.269$	0.055	$B = 0.0807$	0.0876
	$T_{max} = 53.52$	0.56	$T_{max} = 52.39$	0.34
Juneja and others 2008	$A = 0.0516$	0.0017	$A = 2.14 \times 10^{11}$	1.41×10^{12}
	$T_{min} = 10.89$	0.56	$E_\alpha = 7.99 \times 10^4$	1.61×10^4
	$B = 0.275$	0.045	$B = 0.0916$	0.0730
	$T_{max} = 54.44$	0.59	$T_{max} = 53.06$	0.35

from the literature and estimated by the new mathematical model. The R^2 value of 0.985 also points to the fact that the μ values from the 2 sets of data are highly correlated.

This study shows that the Eyring equation is also suitable for describing the effect of temperature on microbial growth rate, but it also has some inherent shortcomings. For example, the mean A_f and B_f values are substantially higher than those of the new and square root models. Another disadvantage of the Eyring equation is relatively large standard errors of coefficient A in some estimates (Table 3), and some standard errors of A can be 10 times the value of A in the model estimates (Table 3). Large standard errors associated with a parameter usually increase the uncertainties in the estimation for a model.

The parameters of the new model

For all the curves analyzed, $\Delta G'$ seems to be narrowly distributed. The average of $\Delta G'$ of all growth rate curves (including the data in the table and figures) was 2532.5 J/mol, and with a standard deviation of only 60.0 J/mol, which was only 2.4% of the mean $\Delta G'$ value. Ranking by microorganisms, the average $\Delta G'$ was 2510.3, 2519.3, 2524.0, 2544.8, and 2611.1 J/mol, for *L. monocytogenes, Pseudomonas* spp., *Salmonella* spp., *E. coli,* and *C. perfringens.* Since *C. perfringens* grows very fast at temperatures between room temperature and 50 °C. It may need more energy to support its growth, and that may explain the slightly higher $\Delta G'$ value for this microorganism.

The parameter α in the new model seems to shape the growth rate curve, and may reflect the unique relationship between temperature and growth rate. For some microorganisms, this value is very consistent within the group. For example, this value was fairly consistent for *Pseudomonas* spp. (11.9 to 15.0) and *E. coli* (17.6 to 21.7). The variation in α was slightly wider for *C. perfringens* (13.5 to 18.5) and *Salmonella* spp. (14.7 to 25.6). The largest variation in α was found with *L. monocytogenes* (11.0 to 25.4). Overall, the mean α value was 18.1 with a standard deviation of 4.5.

Finally, for the A values, the microorganisms could be divided into 3 groups. It was highest with *C. perfringens.* The average A value was 0.0179 ± 0.0045 (mean and standard ± deviation). Included in the 2nd group were *Pseudomonas* spp. (0.00454 ± 0.020), *L. monocytogenes* (0.00462 ± 0.0030), and *Salmonella* spp. (0.00536 ± 0.0030). The A value was relatively higher with *E. coli* (0.00736 ± 0.0011).

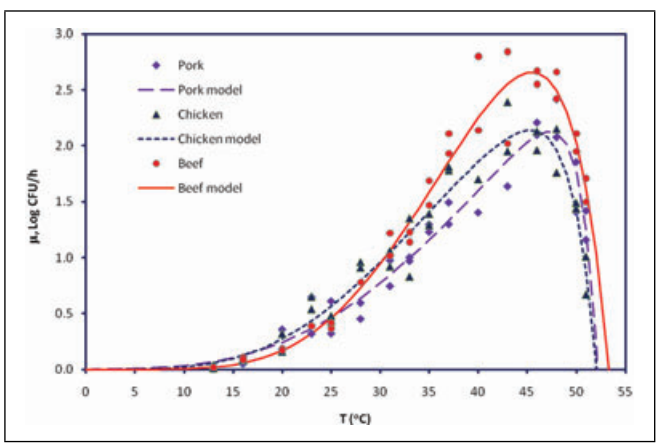

Figure 7–Modeling the effect of temperature on the growth rate of *Clostridium perfringens*. Data source: beef, Juneja and others (2008); chicken, Juneja and others (2009); and pork, Juneja and others (2010).

Conclusions

This limited study attempts to develop a new mathematical model to describe the effect of temperature on microbial growth rate. The new model is related to the Arrhenius equation and the Eyring–Polanyi transition theory, and can be used to evaluate the temperature dependence of bacterial growth in the suboptimal temperature range (Eq. 6) and over the entire biokinetic temperature range (Eq. 7). This study is not a simple curve-fitting exercise, but rather an extension of the Arrhenius and Eyring equations with an integration of an exponential term. This model is therefore a new model that has not been tested before in microbiology, and thus, more study is needed to test this new model under various extrinsic and intrinsic conditions (temperature, water activity, pH, and among other factors).

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