

# Temperature Does Not Affect Model Performance when Predicting Microbial Population Growth

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Word Count:

## **Abstract**

Microorganisms constitute the most diverse and abundant life forms on Earth. Interest in their role on maintaining ecosystem function has grown in the context of climate change. This report aims to identify the best performing microbial population growth model between Gompertz, Logistic and cubic models. Moreover, trends between model performance and temperature will be inspected. 285 microbial population curves, grown under a range of environmental conditions were fit to the three models and model selection analyses were carried out. It was found that the Gompertz model was overall the strongest performer with no clear observable trends with temperature for any model. Though Gompertz was the best performer overall, the absence of a clear winner, suggested microbial populations are best predicted by models with parameters that align with the features of a specific curve. Thus explaining the use of many different models in the literature.

# 1 Introduction

1 Microorganisms make up the most diverse and plentiful group of life on Earth.  
2 They are essential for ecosystem function and stability [Shoemaker et al., 2021].  
3 In particular microbes play a critical role in processes such as the nitrogen  
4 cycle and carbon sequestration that are becoming increasingly significant in  
5 light of climate change [Gupta et al., 2016]. Microbes have immense abil-  
6 ity to multiply rapidly and exponentially whilst resources are abundant. As  
7 nutrients become limited, microorganisms must compete thus compromis-  
8 ing their ability to reproduce [Reviews, 2016]. This results in them typi-  
9 cally showing a sigmoidal pattern of growth whereby different stages of their  
10 growth curve infer different biology significance. Microbial growth curves  
11 typically consist of a lag phase (t<sub>lag</sub>), exponential growth phase, station-  
12 ary phase (K), and often a death phase [Zwietering et al., 1990]. The lag  
13 phase accounts for the time taken for a population to adjust to its envi-  
14 ronment before rapid reproduction [Buchanan et al., 1997]. Whereas, the  
15 stationary phase or carrying capacity is shown as an asymptote on a bacte-  
16 rial growth curve and indicates often compounding factors such as nutrient  
17 availability, predation, and crowding preventing further population growth  
18 [Wachenheim et al., 2003]. The maximum growth rate (R<sub>max</sub>) is also typi-  
19 cally annotated on microbial growth curves, illustrated by the steepest gra-  
20 dient.

21  
22 Models can be developed that effectively predict microbial populations  
23 at a given time point. They work under the assumption that microbial pop-  
24 ulation patterns are reproducible under the same environmental conditions  
25 [Pla et al., 2015]. Modelling microbial population dynamics has positive im-  
26 plications on agriculture and food security, as predictions on shelf life and  
27 product safety can be made [Zwietering et al., 1990]. In addition, predic-  
28 tive models assist in the decision making of large industrial processes such  
29 as fermentation [Garcia et al., 2021]. Models that are derived from exist-

ing theory and recorded observations are known as mechanistic; whilst phenomenological models are developed empirically and provide no explanation of patterns [Peleg and Corradini, 2011]. Two examples of commonly used non-linear mechanistic models are the the Gompertz model and the Logistic model.

The Logistic equation is popular for describing bacterial population growth. The Logistic model that was first developed by Pearl and Reed in 1920 was empirical. However, biological inferences are now commonly derived from its parameters [Wachenheim et al., 2003] [Pearl and Reed, 1920]. Therefore, it can be said that the Logistic model estimates the population at any given time point from the initial population ( $N_0$ ),  $K$  and  $R_{max}$  values [Wachenheim et al., 2003]. Whilst models consisting of fewer parameters are often preferred, the Logistic equation does lack parameters that captivate other typical stages of microbial growth curves such as a death or lag phase. The Gompertz equation is another sigmoidal model that takes into account the three parameters in the Logistic model but also includes a  $t_{lag}$ . The Gompertz model has been widely used across a range of applications such as predicting plant, fish or even cancerous tumour growth [Tjørve and Tjørve, 2017]. Finally, phenomenological cubic linear models are often used for predicting microbial populations. Garcia et al (2021) found that a cubic model accurately represents all aforementioned stages of bacterial population growth when applied to fermentation bacteria [Garcia et al., 2021]. However, biological inferences cannot be drawn from phenomoligcal model parameters, highlighting the importance of mechanistic models that provide parameter estimations, as well as predictions.

Statistical analysis whereby different models are selected or ranked in terms of performance have begun to gain traction in ecology and evolution [Johnson and Omland, 2004]. It offers an alternative to traditional hypoth-

60 esis testing techniques as it confronts multiple ‘competing’ hypotheses si-  
61 multaneously. It is crucial to identify the best performing models under  
62 various conditions, as the prediction of microbial population dynamics re-  
63 lies on selecting the best performing model that aligns with the conditions  
64 of unsampled populations. This report aims to identify trends in model  
65 performance between cubic, Gompertz and Logistic, under different tem-  
66 peratures. It is expected that the Gompertz model may drop in perfor-  
67 mance relative to the Logistic model with increasing temperatures. This  
68 is due to the tlag being significantly reduced by increasing temperatures  
69 [Aba et al., 2021] as populations can adapt to new conditions faster. Fur-  
70 thermore, I expect no changes in model performance for the Cubic model  
71 across temperatures as its parameters are not tied to any biological variables  
72 that are temperature dependent. Temperature is also known to influence  
73 the Rmax [Ward and Cockson, 1972] [Dey et al., 2020]. Rates of substrate  
74 uptake by bacteria reduce with lower temperatures thus negatively impact-  
75 ing a bacteria’s ability to grow [Nedwell and Rutter, 1994]. However as both  
76 mechanistic models contain an Rmax parameter this should not vary relative  
77 model performance.

78  
79 Finally, the model averaging application of model selection techniques  
80 will be carried out in this study. Robust parameter estimates for K and  
81 Rmax will be calculated using Akaike weights for demonstration and use in  
82 potential follow up studies.

## 83 **2 Methods**

### 84 **2.1 Data Collection**

85 This study is based on an amalgamation of microbial growth curves from 10  
86 different research papers. It includes populations of different species grown  
87 under varying temperatures (0 - 37C) and 18 different media. Observations in

the dataset were deemed from the same curve if they shared a temperature, species and citation. This facilitated the subsetting of the data into 285 individual growth curves for model fitting.

## Model Fitting

Only three candidate models were considered in this study as it is ill-advised to include many models that increase the chance of spurious findings [Johnson and Omland, 2004]. The Logistic model used in this study is the solution to the differential equation defining the classic Logistic population growth equation.

### 2.1.1 Logistic Model

$$N_t = \frac{N_0 K e^{r_{max} t}}{K + N_0 (e^{r_{max} t} - 1)} \quad (1)$$

The Gompertz model used in this study is a modified version by Zwietering et al (1990) [Zwietering et al., 1990] where Nmax represents carrying capacity.

### 2.1.2 Gompertz Model

$$\log(N_t) = N_0 + (N_{max} - N_0) e^{-e^{\frac{r_{max} \exp(1)}{(N_{max} - N_0) \log(10)} + 1} (t_{lag} - t)} \quad (2)$$

Finally, the equation below illustrates the cubic equation and its uninterpretable parameters.

### 2.1.3 Cubic Model

$$\log(N_t) = at + bt^2 + ct^3 + d \quad (3)$$

Fitting the non linear mechanistic models (Logistic and Gompertz) required reasonable starting values in addition to suitable upper and lower bounds. Sampling was used to vary the starting values around an appropriate mean to increase the likelihood of a non-linear least squares (NLLS) model fit after 100 attempts. After the 100 attempts for each growth curve,

only the fit with the highest  $R^2$  value was outputted alongside its respective AICc, BIC, and Akaike weight ( $A_w$ ) score. All three models were managed to be fit to 202 out of 285 growth curves. For consistency, when working out the statistical metrics for the Logistic model, the residuals were log transformed to facilitate comparison between the other models. In addition, log transformed population data is preferred as population is a multiplicative process therefore residuals naturally increase with time in a linear scale. This will increase the uniformity of the model residuals which leads to consistent predictive power across the range of time values [Freckleton, 2002].

## 2.2 Model Comparison and Weighted Averages

Johnson and Omland outlined model selection metrics and described the differences between them. Firstly,  $R^2$  is used that simply suggests the proportion of the variance in the data that is explained by a given model.  $R^2$  is not commonly used and is described as ‘naive’ as it does not consider model complexity and therefore does not penalise overfitted models [Johnson and Omland, 2004]. Secondly, Akaike information criterion (AIC) is another measure of model performance that counts for goodness of fit and model complexity. Furthermore, AICc includes bias correction when the model is applied to small sample sizes. Finally bayesian information criterion (BIC), similar to AICc, considers fit, complexity and sample size. However, AIC is often favoured as it is based on Kullback-Leibler information theory [Johnson and Omland, 2004] - though some statisticians still argue that BIC is preferable as it is less tolerant of overcomplex models. When comparing model AIC and BIC values, models with the smallest AIC and BIC by at least 2, are considered the better performing model [Johnson and Omland, 2004]. Model comparison occurs between models fit onto the same data and an overall model winner is defined as the model that performed best the most number of times. In addition, model performances were compared under all different temperature values to identify trends in model performance.

137

138 Omland and Johnson further explain the use of a more interpretable  
139 metric, Akaike weights that consider the relative probabilities of a model  
140 being the best performer. In this study, for a model to be selected as the best  
141 performer an  $A_W$  score of over 0.9 is necessary [Dash et al., 2023]. This is an  
142 arbitrary threshold suggesting a model can only be deemed the best if there  
143 is more than 90 percent chance that that is the case. These probabilities can  
144 consequently be used for robust parameter estimations. In this study,  $A_W$   
145 averages were made for comparison between all three models. However, for  
146 parameter estimations  $A_W$  were recalculated for just Gompertz and Logistic  
147 as the Cubic model does not contain interpretable parameters associated  
148 with stages of bacterial growth.

## 149 **2.3 Computational Tools**

150 Firstly the pandas package in python 3.10.12 [Van Rossum and Drake, 2009]  
151 was used for initial data manipulation and exportation as it is a compu-  
152 tationally efficient and popular tool. R version 4.1.2 [R Core Team, 2021]  
153 was consequently used for model fitting, analysis, and plotting. For NLLS  
154 model fitting, minpack.lm package was used to access the nlsLM function that  
155 uses the Levenberg-Marquardt algorithm, known to be more robust than the  
156 Gauss-Newton algorithm. The purrr package, which incorporates the pos-  
157 sibly function, was employed to continue the iterative process in the model  
158 fitting and plotting functions in the presence of errors. The dplyr package  
159 was used for appending model winners to respective IDs before tables and  
160 graphs could be plotted. Finally, ggplot2 was used for producing all graphs  
161 included in the report.

### 3 Results

All 202 growth curves with fitted models were plotted with both log transformed and linear population values. Subset 225 is a good example for illustrating the differences between plot types:

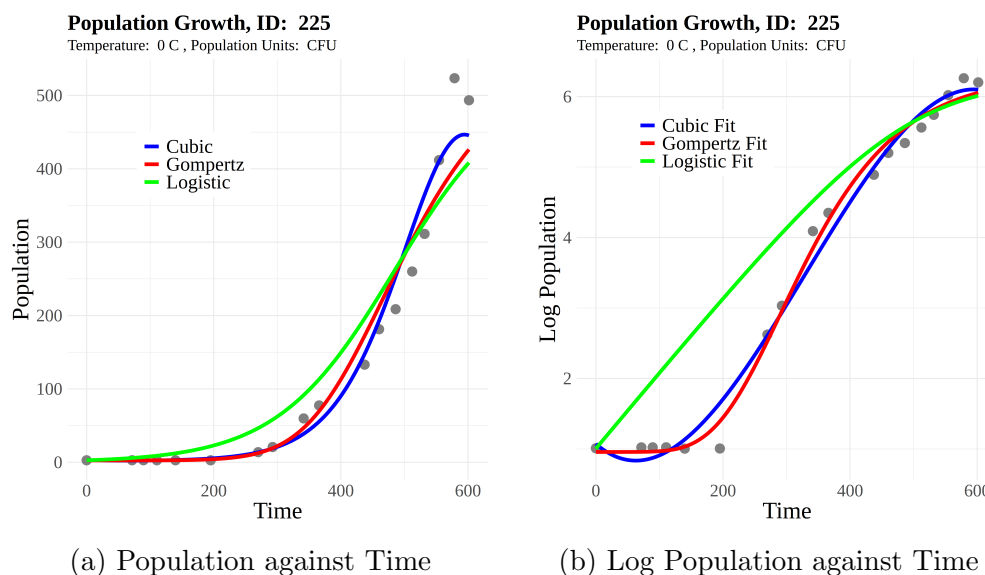


Figure 1: Graphs showing the relationship between log and linear microbial populations against time for subset 225.

In both plots it is clear that the Gompertz and Cubic models were best fit to the data. This would suggest their  $R^2$  values would be stronger however, as the Logistic model contains fewer parameters, AIC and BIC values may tell a different story. Furthermore, both plots illustrate the Logistic models struggle to fit curves with a time lag phase. The Gompertz and Cubic manage to captivate the lag phase, growth phase and stationary phase, with the cubic even predicting a death phase shown by a slight decline in predicted population.

The number of times each model performed best for a given criteria is



176 shown in this table below:

Model	AICc	BIC	R <sup>2</sup>	A <sub>w</sub>
Logistic	56	28	26	47
Cubic	52	73	84	40
Gompertz	72	76	92	59

Table 1: The number of top performances for all models according to each criteria

177 Table 1 shows that Gompertz was the best performing model the most  
178 number of times for each criteria. The Gompertz model's quality of fit clearly  
179 outweighed its penalty for having an extra parameter than the Logistic model  
180 for AICc and BIC. Furthermore, the Cubic and Gompertz models clearly out-  
181 performed the Logistic according to R<sup>2</sup>, aligning with expectations due to  
182 their greater number of parameters. Despite this, the number of A<sub>w</sub> best fits  
183 is fairly similar across all three models. The Gompertz model had a prob-  
184 ability of being the best model of more than 0.9 only 59 times out of the  
185 202 growth curves. It is important to note that the columns may not add  
186 up to 202 due to 'no clear winner' outcomes where threshold values were not  
187 attained.

188

189 The proportions of best fits for each model were calculated and plotted for  
190 each unique temperature value in the dataset. Observing the plot there is  
191 no clear trend between performance for any model and temperature. Whilst  
192 there are temperatures which certain models perform best at, for example  
193 cubic at 16 degrees, drawing definitive trends is challenging due to small  
194 sample sizes for each temperature.

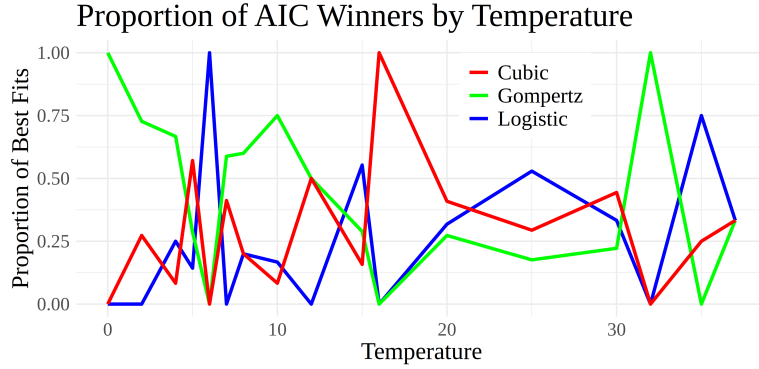


Figure 2: Line graph showing best model proportions against temperature

## 195 4 Discussion

196 This study ultimately aimed to identify which models were best predictors of  
 197 microbial growth at different temperatures to inform quantitative biologists,  
 198 under which conditions should certain models be used for predictions. The  
 199 Gompertz model was found to be the best predictor of microbial population  
 200 growth - implying that the additional parameter compared to the Logistic  
 201 model provides sufficient explanation of the data to justify extra model com-  
 202 plexity. However, there was no evidence from figure 2 to suggest that the  
 203 efficacy of any model is influenced by temperature. Therefore, this report  
 204 encourages the use of the Gompertz model for predicting microbial popula-  
 205 tions across a range of temperatures.

206

207 The trade off between parsimony and complexity is an important dilemma  
 208 to address in this case. Parsimonious theories advocate for simplicity of ex-  
 209 planation [Coelho et al., 2019] thus the most straightforward model that ad-  
 210 equetly explains the data is best. Simplicity is often favoured as it is more  
 211 interpretable and overfitting is less likely. In contrast, complex models with  
 212 more parameters than its competitors (such as Gompertz) explain intricacies  
 213 in the data, thus providing a better fit. Therefore, metrics that quantify

the balance of parsimony and complexity, AICc and BIC, were used in this study to identify the best performing models. The inclusion of  $R^2$  in Table 1 highlights its insuitability and the need for parameter penalisation, as it expectedly more strongly favoured the cubic and Gompertz models than the other metrics.

The results do not align with the expectation that the Logistic model would outperform the Gompertz model at higher temperatures. Reasons for this may be due to the limitations of this study such as the other confounding factors at play. Firstly, the length and extent of different stages of microbial growth will depend on the environmental conditions relative to the conditions that it is best adapted for [Dey et al., 2020]. For example, lag increases for microbes placed in novel environments to allow for time taken to adapt to new conditions [Rolfe et al., 2012]. This favours the Gompertz model where a lag parameter is present. Secondly, growth mediums are known to affect metabolic rates in bacteria [Kim and Kim, 2017]. Kim and Kim (2017) found that microbes grown in nutrient rich media had increased  $K$  and  $R_{max}$ , and decreased lags than those grown in nutrient poor media. This indicates that the Logistic equation is more suitable for nutrient rich media. To address the limitations of this study, more specified experiments that record enough data for each unique set of conditions would provide a more nuanced understanding of when each model works best.

The limited data set also reduces the significance of the findings of the study. Whilst the Gompertz model performed best for all criteria, no statistical analyses were conducted to address whether or not Gompertz would likely be the best performing model in another set of growth curves. Furthermore, the  $A_W$  scores illustrate no overwhelming winner and therefore suggest model selection should be more specific to the conditions that a microbe is grown under. However, to combat the drawbacks of a limited dataset, the  $A_W$

parameter estimations could be used to predict microbial population growth - particularly when there is no clearly best performing model. Model averaging using  $A_W$  is mostly useful when multiple models exhibit roughly equal AICc values [Johnson and Omland, 2004], so equally performing models are both considered when calculating parameters. This study generated Akaike estimated parameter values regardless of whether or not there was a clear best performer ( $A_W > 0.9$ ). However, a potential improvement to the estimations, as suggested by Johnson and Omland (2004), would be to only use model averaging when the best performing models  $A_W$  is less than 0.9. And otherwise just use the given parameters of the best performing model. This is to prevent the influence of poor performing models on parameter estimates.

Finally, whilst  $A_W$  scores are great for model comparison and assessing relative performance. They do not illustrate how well each model really fits to the data as they are just probabilities. Therefore, their use alongside raw AICc or even  $R^2$  may be necessary. For example, through inspecting each growth curve used in this study (found in the plots directory), there are some instances where a death phase is present. Therefore, regardless of relative performance between Gompertz and Logistic models, both would have failed to capture a major phase of microbial population change.

## 5 Conclusion

In conclusion the results of this study provides explanation and evidence for why the Gompertz model should be used to gain a general idea of microbial population growth. Secondly, it is concluded that temperature does not influence model performance. However, it is likely that selecting models that perform best for particular conditions, or using  $A_W$  is a more reliable method for predicting growth curves and parameters. The study also generated robust parameter estimates for  $R_{max}$  and  $K$  (found in the supplementary

information) that may be used in future studies.

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**SUPPLEMENTARY INFORMATION**

# 1 Figure 1 Data [Roth and Wheaton, 1962]

Time	PopBio	Temp	Species	Medium
601.626016260162	493.476250996515	0	Arthrobacter sp. 62	TGE agar
578.861788617886	523.483270316647	0	Arthrobacter sp. 62	TGE agar
554.471544715447	411.804687494928	0	Arthrobacter sp. 62	TGE agar
531.707317073171	311.310143129459	0	Arthrobacter sp. 62	TGE agar
512.195121951219	260.026157859915	0	Arthrobacter sp. 62	TGE agar
486.178861788618	208.658959315772	0	Arthrobacter sp. 62	TGE agar
460.162601626016	181.333035948067	0	Arthrobacter sp. 62	TGE agar
437.39837398374	133.044356243192	0	Arthrobacter sp. 62	TGE agar
365.853658536585	77.4961483452263	0	Arthrobacter sp. 62	TGE agar
341.463414634146	59.7604174563915	0	Arthrobacter sp. 62	TGE agar
292.682926829268	20.748959485739	0	Arthrobacter sp. 62	TGE agar
269.918699186992	13.779738449309	0	Arthrobacter sp. 62	TGE agar
195.121951219512	2.73595599371223	0	Arthrobacter sp. 62	TGE agar
139.837398373984	2.73093667864603	0	Arthrobacter sp. 62	TGE agar
110.569105691057	2.78319996924522	0	Arthrobacter sp. 62	TGE agar
89.430894308943	2.78124657266229	0	Arthrobacter sp. 62	TGE agar
71.5447154471544	2.77959476950685	0	Arthrobacter sp. 62	TGE agar
0	2.74550329401221	0	Arthrobacter sp. 62	TGE agar

## 2 Figure 2 Data

Temperature	Logistic	Gompertz	Cubic	LogisticProp	GompertzProp	CubicProp
0	0	4	0	0	1	0
2	0	8	3	0	0.727	0.273
4	3	8	1	0.25	0.667	0.083
5	2	4	8	0.143	0.286	0.571
6	1	0	0	1	0	0
7	0	10	7	0	0.588	0.412
8	1	3	1	0.2	0.6	0.2
10	2	9	1	0.167	0.75	0.083
12	0	2	2	0	0.5	0.5
15	21	11	6	0.553	0.289	0.158
16	0	0	2	0	0	1
20	7	6	9	0.318	0.273	0.409
25	9	3	5	0.529	0.176	0.294
30	3	2	4	0.333	0.222	0.444
32	0	1	0	0	1	0
35	6	0	2	0.75	0	0.25
37	1	1	1	0.333	0.333	0.333

### **3 Parameter Estimations for use in follow up study**

Species	Temperature	Rmax	K	Group
Chryseobacterium	5	0.04	-5.26	1
Enterobacter	5	0.1	-0.57	1
Pantoea	5	0.15	-0.74	1
Pantoea	5	0.1	-0.72	1
Clavibacter	5	0.03	-0.99	1
Pseudomonas	5	0.03	0.2	1
Pseudomonas	5	0.04	-1.24	1
Acinetobacter	5	0.01	0.12	1
Acinetobacter	5	0.03	-2.25	1
Stenotrophomonas	5	0.03	0.21	1
Stenotrophomonas	5	0.04	-1.25	1
Klebsiella	5	0.04	-0.96	1
Pantoea	5	0.09	-0.88	1
Acinetobacter	5	0.01	0.05	1
Stenotrophomonas	5	0.03	-1.66	1
Clavibacter	5	0.01	0.22	1
Chryseobacterium	15	0.04	0.31	1
Enterobacter	15	0.37	0.83	1
Bacillus	15	0.05	0.13	1
Clavibacter	15	0.06	0.49	1
Pseudomonas	15	0.1	0.11	1
Pseudomonas	15	0.07	0.26	1
Acinetobacter	15	0.11	-0.39	1
Acinetobacter	15	0.15	-0.21	1
Stenotrophomonas	15	0.08	0.18	1
Klebsiella	15	0.3	0.8	1
Pectobacterium	15	0.8	-0.68	1
Dickeya	15	0.17	0.32	1
Acinetobacter	15	0.08	0.11	1
Stenotrophomonas	15	0.14	-1.2	1
Klebsiella	15	0.27	0.61	1
Bacillus	15	0.11	-1.64	1
Chryseobacterium	25	0.15	-1.02	1
Pantoea	25	0.06	0.56	1
Pantoea	25	0.07	0.49	1
Bacillus	25	0.31	-1.43	1
Pseudomonas	25	0.17	0.18	1
Pseudomonas	25	0.17	0.29	1
Stenotrophomonas	25	0.24	0.2	1
Stenotrophomonas	25	0.13	0.51	1
Klebsiella	25	0.63	0.95	1

Species	Temperature	Rmax	K	Group
Dickeya	25	1.13	-0.45	2
Pectobacterium	25	0.74	-0.54	2
Dickeya	25	0.37	0.73	2
Acinetobacter	25	0.27	0.11	2
Stenotrophomonas	25	0.22	0.21	2
Bacillus	25	0.19	-1.07	2
Clavibacter	25	0.15	0.3	2
Chryseobacterium	35	0.08	0.19	2
Bacillus	35	0.18	-0.3	2
Clavibacter	35	0.29	0.72	2
Pseudomonas	35	0.27	-0.19	2
Acinetobacter	35	0.31	0.36	2
Stenotrophomonas	35	0.25	0.21	2
Stenotrophomonas	35	0.28	0.13	2
Bacillus	35	0.24	-0.58	2
Tetraselmis tetrahele	8	0.04	9.83	2
Tetraselmis tetrahele	32	0.09	6.23	2
Staphylococcus spp	2	0.05	8.16	2
Staphylococcus spp	4	0.06	5.9	2
Staphylococcus spp	7	0.12	0.34	2
Staphylococcus spp	10	0.21	7.67	2
Staphylococcus spp	15	0.27	6.96	2
Staphylococcus spp	20	0.43	2.53	2
Staphylococcus spp	2	0.04	7.96	2
Staphylococcus spp	4	0.01	457.01	2
Staphylococcus spp	7	0.11	7.56	2
Staphylococcus spp	10	0.15	10.67	2
Staphylococcus spp	15	0.22	8.64	2
Staphylococcus spp	20	0.39	9.39	2
Staphylococcus spp	2	0.06	0.01	2
Staphylococcus spp	4	0.08	5.79	2
Staphylococcus spp	7	0.08	6.42	2
Staphylococcus spp	15	0.25	8.22	2
Staphylococcus spp	20	0.38	10.29	2
Pseudomonas spp	2	0.09	6.08	2
Pseudomonas spp	4	0.1	48.99	2
Pseudomonas spp	7	0.11	6.5	2
Pseudomonas spp	10	0.2	7.63	2
Pseudomonas spp	15	0.25	17.08	2
Pseudomonas spp	20	0.43	9.21	2

Species	Temperature	Rmax	K	Group
Pseudomonas spp	2	0.09	5.75	3
Pseudomonas spp	4	0.1	6.28	3
Pseudomonas spp	7	0.1	5.61	3
Pseudomonas spp	10	0.2	6.14	3
Pseudomonas spp	15	0.2	7.74	3
Pseudomonas spp	2	0.06	8.05	3
Pseudomonas spp	4	0.01	1266.95	3
Pseudomonas spp	7	0.14	6.76	3
Pseudomonas spp	10	0.26	8.44	3
Pseudomonas spp	15	0.34	15.08	3
Pseudomonas spp	20	0.65	8.34	3
Aerobic Psychotropic	2	0.06	6.69	3
Aerobic Psychotropic	4	0.02	1294.25	3
Aerobic Psychotropic	10	0.22	5.9	3
Aerobic Psychotropic	15	0.32	7.97	3
Aerobic Psychotropic	2	0.06	5.95	3
Aerobic Psychotropic	4	0.04	325.83	3
Aerobic Psychotropic	7	0.09	201.35	3
Aerobic Psychotropic	10	0.15	6.52	3
Aerobic Psychotropic	15	0.24	6.01	3
Aerobic Psychotropic	20	0.13	258.08	3
Aerobic Psychotropic	2	0.08	7.73	3
Aerobic Psychotropic	4	0.08	8.44	3
Aerobic Psychotropic	7	0.13	7.49	3
Aerobic Psychotropic	10	0.19	6.99	3
Aerobic Psychotropic	15	0.26	8.03	3
Aerobic Psychotropic	20	0.42	7.16	3
Aerobic Mesophilic	2	0.06	6.23	3
Aerobic Mesophilic	7	0.14	7.56	3
Aerobic Mesophilic	4	0.08	6.32	3
Aerobic Mesophilic	10	0.26	6.72	3
Aerobic Mesophilic	15	0.38	7.43	3
Aerobic Mesophilic	20	0.52	7.21	3
Aerobic Mesophilic	2	0.05	6.57	3
Aerobic Mesophilic	4	0.08	7.53	3
Aerobic Mesophilic	10	0.23	5.95	3
Aerobic Mesophilic	15	0.3	6.4	3
Aerobic Mesophilic	2	0.06	6.81	3
Aerobic Mesophilic	4	0.01	11669.6	3
Aerobic Mesophilic	7	0.17	9.08	3

Species	Temperature	Rmax	K	Group
Aerobic Mesophilic	10	0.25	7.94	4
Aerobic Mesophilic	15	0.38	6.88	4
Aerobic Mesophilic	20	0.63	8.16	4
Spoilage	8	1.14	16964.74	4
Spoilage	10	1.43	13657.26	4
Escherichia coli	10	1.3	2790.35	4
Spoilage	12	1.08	11924.51	4
Escherichia coli	15	2.26	9203.08	4
Salmonella Typhimurium	15	2.17	5492.1	4
Salmonella Typhimurium	15	2.32	231.64	4
Spoilage	20	3.26	13025.86	4
Escherichia coli	20	10	14849.08	4
Salmonella Typhimurium	20	10	10981.48	4
Escherichia coli	20	4.35	9485.78	4
Salmonella Typhimurium	20	10	5631.68	4
Escherichia coli	30	10	10903.89	4
Salmonella Typhimurium	30	10	6021.7	4
Salmonella Typhimurium	30	10	6583.32	4
Serratia marcescens	15	0.02	8.1	4
Serratia marcescens	15	0.01	2765.93	4
Serratia marcescens	15	0.01	2352.13	4
Serratia marcescens	15	0	2353.35	4
Serratia marcescens	15	0.01	2052.97	4
Serratia marcescens	15	0.01	2868.8	4
Arthrobacter sp	0	0.04	6.18	4
Arthrobacter sp	7	0.1	6.19	4
Arthrobacter sp	20	0.1	281.3	4
Arthrobacter sp	30	0.59	1.03	4
Arthrobacter sp	0	0.05	4.99	4
Arthrobacter sp	7	0.03	188.1	4
Arthrobacter sp	20	0.31	1.01	4
Arthrobacter sp	30	0.03	881.06	4
Arthrobacter sp	37	0	1.88	4
Arthrobacter sp	0	0.04	6.32	4
Arthrobacter sp	7	0.09	144.65	4
Arthrobacter sp	20	0.35	6.69	4
Arthrobacter sp	37	0	1.12	4
Arthrobacter aureescens	7	0.11	1.81	4
Arthrobacter aureescens	20	0.16	125.08	4
Arthrobacter aureescens	37	0.03	76.2	4



Species	Temperature	Rmax	K	Group
Arthrobacter citreus	0	0.14	4.26	5
Arthrobacter citreus	7	0.14	5.22	5
Arthrobacter citreus	20	0.21	6.27	5
Arthrobacter citreus	30	0.27	1.91	5
Arthrobacter citreus	37	0.39	19.77	5
Arthrobacter globiformis	7	0.01	115.39	5
Arthrobacter globiformis	20	0.16	7.14	5
Arthrobacter globiformis	30	0.04	191.89	5
Arthrobacter globiformis	37	0.08	205.38	5
Arthrobacter simplex	0	0	1.78	5
Arthrobacter simplex	7	0.06	1.01	5
Arthrobacter simplex	20	0.16	20.14	5
Arthrobacter simplex	30	0.13	23.55	5
Lactobacillus plantarum	8	0.06	16.47	5
Lactobacillus plantarum	12	0.17	465918.97	5
Lactobacillus plantarum	20	0.47	2410978170.25	5
Lactobacillus plantarum	30	1.94	134.52	5
Weissella viridescens	4	0.06	2327.55	5
Weissella viridescens	8	0.2	20.35	5
Weissella viridescens	12	0.55	443.85	5
Weissella viridescens	16	0.18	1362211190.39	5
Weissella viridescens	20	0.38	1723868483.05	5
Weissella viridescens	30	0.88	1478475784.42	5
Lactobacillus sakei	4	0.1	661.92	5
Lactobacillus sakei	8	0.23	19.35	5
Lactobacillus sakei	12	0.52	40.75	5
Lactobacillus sakei	16	0.23	1281403231.49	5
Lactobacillus sakei	20	1.16	79612582.68	5
Lactobacillus sakei	30	1.09	1479234929.71	5
Oscillatoria agardhii Strain 97	15	0.01	4.27	5
Oscillatoria agardhii Strain 97	20	0.01	4.29	5
Oscillatoria agardhii Strain 97	25	0.01	5.55	5
Oscillatoria agardhii StrainCYA 128	15	0.01	3.69	5
Oscillatoria agardhii StrainCYA 128	30	0.01	5.35	5
Pseudomonas sp	15	0.2	1030130.44	5
Pseudomonas sp	12	0.81	56048.24	5
Pseudomonas sp	6	0.13	1670868.96	5
Pseudomonas sp	2	0.05	558158.05	5
Lactobacillus plantarum	10	0.14	7.95	5
Lactobacillus plantarum	15	0.39	0.91	5
Lactobacillus plantarum	25	0.87	395.32	5

## References

- [Roth and Wheaton, 1962] Roth, N. G. and Wheaton, R. B. (1962). Continuity of psychrophilic and mesophilic growth characteristics in the genus *arthrobacter*. *Journal of Bacteriology*, 83(3):551–555.