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Thermal performance curves of *Paramecium caudatum*: A model selection approach

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Abstract

The ongoing climate change has motivated numerous studies investigating the temperature response of various organisms, especially that of ectotherms. To correctly describe the thermal performance of these organisms, functions are needed which sufficiently fit to the complete optimum curve. Surprisingly, model-comparisons for the temperature-dependence of population growth rates of an important ectothermic group, the protozoa, are still missing. In this study, temperature reaction norms of natural isolates of the freshwater protist *Paramecium caudatum* were investigated, considering nearly the entire temperature range. These reaction norms were used to estimate thermal performance curves by applying a set of commonly used model functions. An information theory approach was used to compare models and to identify the best ones for describing these data. Our results indicate that the models which can describe negative growth at the high- and low-temperature branch of an optimum curve are preferable. This is a prerequisite for accurately calculating the critical upper and lower thermal limits. While we detected a temperature optimum of around 29 °C for all investigated clonal strains, the critical thermal limits were considerably different between individual clones. Here, the tropical clone showed the narrowest thermal tolerance, with a shift of its critical thermal limits to higher temperatures.

Keywords: Ciliate; Ecophysiological characteristics; Non-linear models; *Paramecium*; Population growth rate; Temperature

Introduction

Temperature is one of the main abiotic factors influencing the physiological performance of ectothermic organisms. Recently, investigations on the effect of temperature on biological processes have experienced a renaissance in current climate change research. Scientists started to re-evaluate the biological consequences of elevated temperatures to determine potential shifts in phenology, geographic distribution, species diversity and primary productivity (Daufresne et al. 2009; Hill et al. 1999; Richardson and Schoeman 2004; Ruess et al. 1999; Weitere et al. 2009). To estimate the impact of global warming on ectothermic organisms, thermal tolerances as well as the capability of thermal adaptation are essential components. This is especially the case for microbial eukaryotes, where growth and division rates are directly dependent on temperature.

Often, developmental or growth rates are used to estimate an organism's breadth of tolerance or its performance as a function of temperature. Here, the determination of thermal performance curves (TPCs) provides a suitable framework to evaluate an organism's operative range based on such data and is a prerequisite to calculate key ecophysiological characteristics such as the lower (CT_{min}) or upper (CT_{max})

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Table 1. Model comparison based on the required number of parameters (*K*), the coefficient of determination (R^2), the second order Akaike information criterion (AICc) and the Akaike weight (w_i) for the four investigated natural *P. caudatum* clones NO*E*-1, G*LA*-1, PO*E*-1, and IN*L*-1.

Model	*K*	NO*E*-1			G*LA*-1			PO*E*-1			IN*L*-1		
		R^2	AICc	w_i	R^2	AICc	w_i	R^2	AICc	w_i	R^2	AICc	w_i
Gaussian	3	0.499	0.23	0.00	0.507	−3.94	0.00	0.689	−7.61	0.00	0.815	−10.84	0.00
Modified Deutsch	4	0.977	−24.91	0.00	0.923	−20.38	0.04	0.934	−20.89	0.06	0.954	−24.41	0.00
Spain	4	0.994	−37.15	0.66	0.951	−25.00	0.44	0.948	−23.35	0.22	0.936	−20.54	0.00
Ratkowsky	4	0.918	−13.19	0.00	0.861	−14.19	0.00	0.928	−19.91	0.04	0.950	−23.30	0.00
Briere-2	4	0.785	−4.40	0.00	0.830	−12.15	0.00	0.898	−16.32	0.01	0.954	−24.30	0.00
Lactin-2	4	0.991	−32.96	0.08	0.947	−24.32	0.31	0.952	−24.18	0.33	0.980	−34.31	0.70
O'Neill	4	0.898	−11.20	0.00	0.853	−13.66	0.00	0.944	−22.58	0.15	0.938	−20.80	0.00
Polynomial	5	0.907	−8.59	0.00	0.934	−18.68	0.02	0.938	−18.29	0.02	0.980	−30.92	0.13
Logan-10	5	0.994	−33.61	0.11	0.951	−21.77	0.09	0.955	−21.61	0.09	0.956	−21.75	0.00
Jöhnk	5	0.994	−33.79	0.12	0.951	−21.79	0.09	0.953	−21.19	0.07	0.980	−31.29	0.15
Sharpe-Schoolfield	6	0.922	−6.11	0.00	0.799	−3.53	0.00	0.875	−7.33	0.00	0.920	−11.48	0.00
Stevenson	6	0.994	−29.57	0.02	0.951	−18.16	0.01	0.955	−17.97	0.01	0.956	−18.41	0.00

critical thermal limits that circumscribe a species' thermal niche. Thermal performance curves have a general shape, with a gradual increase from CT_{min} to a thermal optimum (T_{opt}) where the investigated biological function (e.g., growth rate) reaches its maximum. With a further increase in temperature above T_{opt} the TPCs show a rapid decline towards CT_{max} (Fig. 1). A variety of mathematical models have been proposed to describe such temperature response curves. Sometimes linear relationships are used, but these can be misleading when investigating performance over the whole temperature range (Bulté and Blouin-Demers 2006). The same arguments apply to exponential and power functions that describe temperature dependence as a strictly increasing chemical reaction. Therefore, the current study considered only non-linear functions that describe temperature reaction norms at the increasing (low-temperature) branch as well as over a broader range of temperatures including the decreasing (high-temperature) branch. Numerous models of this type with different properties and with a different number of parameters are available (cf. e.g., Table 1; Appendix A). These models have been used to illustrate TPCs in bacteria, algae, fungi, arthropods or reptiles (e.g., Dauta et al. 1990; Logan et al. 1976; Ratkowsky et al. 1983; Smits et al. 2003; Stevenson et al. 1985), but have not been tested for protozoan species.

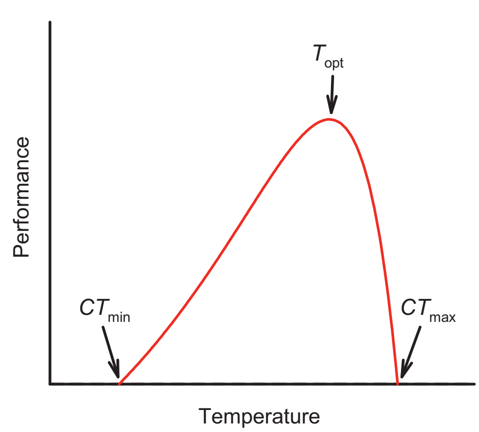

Fig. 1. General shape of a thermal performance curve describing the relationship between temperature and physiological rate in ectotherms. The thermal optimum (T_{opt}) defines the temperature at maximum performance. The critical thermal minimum (CT_{min}) and maximum (CT_{max}) are the temperatures where performance reaches zero; they express the limits of an organism's thermal niche.

The first aim of this study was to examine nearly the entire temperature range for growth (7–35.5 °C) of the eukaryotic microbe *Paramecium caudatum* with detailed analyses of the decreasing, high-temperature branch. Higher temperatures have often been disregarded because of the improbable occurrences in nature as well as due to experimental difficulties. However, due to climate change and the increase of high-temperature extremes (Clark et al. 2006; Fischer and Schär 2010), these temperatures have gained new significance.

In addition, this study aimed to compare a set of commonly used models to sufficiently describe the temperature reaction norms of different natural isolates of this ciliate species. One method to select the best model from a set of plausible candidates is based on information theory (cf. Johnson and Omland 2004), which allows finding the most appropriate model that does not over-fit the data without prior information from similar experiments. This method further permits the ranking or weighting of the selected models. The best model from our set of candidate models should also allow the estimation of temperature-dependent ecophysiological parameters (CT_{min}, T_{opt}, CT_{max}, and μ_{max} – maximal growth rate). These estimated key characteristics can then be used to compare the current thermal tolerances of natural *P. caudatum* isolates of differing geographic origin. Such key ecophysiological parameters will be useful for investigating the thermal adaptation capabilities of *P. caudatum* in