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A Mathematical Equation for Describing Growth of Freshwater Species

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ABSTRACT

We introduced a new four-parameter growth equation and tested it with observed growth data sets for a variety of aquatic species. The equation is:

$$W = W_f - (W_f - W_0)/\{c \cdot (1 - W_0/W_f) \cdot [1 - \exp(kt)] + \exp(kt)\}$$

where W_f and W_0 are the upper asymptotic and initial values respectively, and c and k are constants. The new equation is a modification of the logistic and the Spillman equations with a special value of parameter c. Unlike the logistic and the Spillman functions, the new model has an unfixed value of the inflection point as dictated by the additional parameter c. We compared the model to the logistic, Spillman, Gompertz, and Bertalanffy equations using 10 sets of reference growth data of freshwater species ranging from protozoans to crustaceans to fishes. The new equation yielded excellent fits to each data set, which suggests that it is worthy of being considered by freshwater growth data analysts.

INTRODUCTION

Many growth functions have been used in the life sciences to provide mathematical summaries of time course data (Banks 1994, Begall 1997). Among models, the Gompertz (Gompertz 1825), logistic (Verhulst 1838), Spillman (Spillman and Lang 1924), and Bertalanffy (Bertalanffy 1957) equations are considered as the classic three-parameter growth models which are nested with many general models. In the study of freshwater species, the Bertalanffy equation has been extensively used to describe growth patterns by many authors (Ma et al. 1996, Jiang and Qin 1996, Wang and Jiang 1992).

Although these three-parameter models possess the advantage of mathematical simplicity, their theoretical assumptions are too simple and

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open to much criticism (Banks 1994). Kroops (1986) pointed out that it is hard to believe that a model with a few parameters can describe so complicated a process as growth from birth to death. Due to the deficiency in the number of parameters, these three-parameter equations usually have less flexibility and give poorer fits in describing many types of growth patterns than those with more parameters (Gille and Salomon 1995). For these reasons, many authors have attempted to modify these three-parameter equations to give better fits to data sets (Richards 1959, Cui and Lawson 1982, Jolicoeur et al. 1992, Wan 1998).

We derived a new flexible four-parameter growth equation which may be more suitable for depicting diverse growth courses of freshwater species, and we have tested the equation with 10 sets of observed growth data.

MATERIALS AND METHODS

In order to evaluate the fits of these models, we used 10 sets of referenced growth data of freshwater species (including protozoans, crustaceans and fishes) to fit each growth equation. Data set No.1 refers to the body length growth data of *Diaphanosoma brachyurum* (Huang 1986); No.2 refers to the body length growth data of *Daphnia hyalina* (Huang 1984); No.3 refers to the body length growth data of *Daphnia carinata* (Huang 1984); No.4 refers to the body length growth data of *Moina affinis* (Huang 1983); Nos.5-6 refer respectively to the population growth of *Paramecium aurelia* and *P. caudatum* at "one-loop" concentration of bacterial food (Gause 1934); Nos.7-8 refer to the body length and body weight growth data of crucian carp (*Carassius auratus*), respectively (Jiang and Qing 1996); and Nos.9-10 refer to the body length and body weight growth data of female paddlefish (*Psephurus gladius*, Ma et al. 1996).

RESULTS

The new equation takes the form of

$$W = W_f - (W_f - W_0)/\{c \cdot (1 - W_0/W_f) \cdot [1 - \exp(kt)] + \exp(kt)\} \qquad (1)$$

where W is the size at any convenient time unit t, parameters W_0 and W_f are the initial and final values of W, respectively. The values c and k are shape parameters, controlling the shape of growth curve. In addition, c is also a flexible parameter. For illustration, when c=0, the new model reduces to the Spillman equation (France et al. 1996): $W = W_f - (W_f - W_0) \cdot \exp(-kt)$

when c=1, the new model reduces to the logistic equation(Banks 1994)

$$W = W_0 \cdot W_f / [W_0 + (W_f - W_0) \cdot \exp(-kt)]$$

Setting the second derivative d^2W/dt^2 of equation (1) equals to zero yields the POI (point of inflection) of time t'

$$t' = \frac{1}{k} \ln\{c / [1/(1 - W_0/W_f) - c]\} \qquad (2)$$

Substituting equation (2) into equation (1) obtains the POI of size W'

$$W' = W_f - W_f / 2c \qquad (3)$$

Unlike these commonly applied three-parameter models, which have a fixed value of POI (POI located at $W_f/2$ for logistic, W_f/e for Gompertz, $(8/27)W_f$ for Bertalanffy, and no POI for Spillman), the new model possesses a variable value of POI according to its additional fourth parameter *c*. For this reason, the new equation has more flexibility in depicting diverse growth courses of freshwater species than the classic growth models.

We cited 10 observed growth data sets of freshwater species ranging from protozoans to crustaceans to fishes to fit the logistic, Spillman, Gompertz, and Bertalanffy equations and the new one to compare the fitness. All parameters were obtained through the least squares method. The values of RSS (residual sum of squares) were used to evaluate the fit of each model. This results are presented in Tables 1-2 and Figure 1.

Table 1. Estimated parameter values, POI of time t' and size W', residual sum of squares (RSS), and percent of variation accounted for (R^2) obtained by fitting the new growth function to each data set.

Data	k	W_0	W_f	c	t'	W'	RSS	R^2
No.1	0.0079	0.102	1.42	-1.769	--	--	0.002323	0.998
No.2	0.0036	0.524	2.66	-0.142	--	--	0.02665	0.996
No.3	0.0027	0.419	2.66	-2.953	--	--	0.02077	0.996
No.4	0.0076	0.334	1.76	0.274	--	--	0.01567	0.994
No.5	0.7103	-11.4	451	0.938	4.53	211	7711	0.985
No.6	1.116	-5.04	245	0.957	3.35	117	2240	0.983
No.7	0.1839	3.26	29.2	-0.018	--	--	4.378	0.993
No.8	0.2979	-13.1	703	0.843	6.04	286	3840	0.996
No.9	0.0119	67.0	645	-2.95	--	--	867.7	0.986
No.10	0.2471	-0.04	143	0.960	12.9	68.5	273.6	0.977

DISCUSSION

In the logistic hypothesis, the peak growth rate occurs at $W_f/2$, which is not necessarily the truth. A lot of authors have revealed that in many organisms, including microorganisms, plants and animals, the maximum growth velocity does not occur at exactly half equilibrium (Thompson 1952, Ricklefs 1968, Cui and Lawson 1982, Wan 1998). In these cases, the ordinary logistic equation may fail to give a suitable fit to growth data sets. Like the logistic equation, Bertalanffy and Gompertz equations also have fixed values of POI, which leads to less flexibility in portraying various growth patterns. On the contrary, the new model possesses a unfixed value of POI, which enables it to have good flexibility in describing diverse growth patterns of freshwater species. For example, in many crustacean species (Nos.1-4), the value of parameter *c* is somewhat lower than 1/2, in these cases equation (3) gives $W' < W_0$ or $W' > W_f$ and therefore there is no POI; in some other situations, equation (3) may give any value of POI. For illustration, in the population growth of protozoans and the body weight

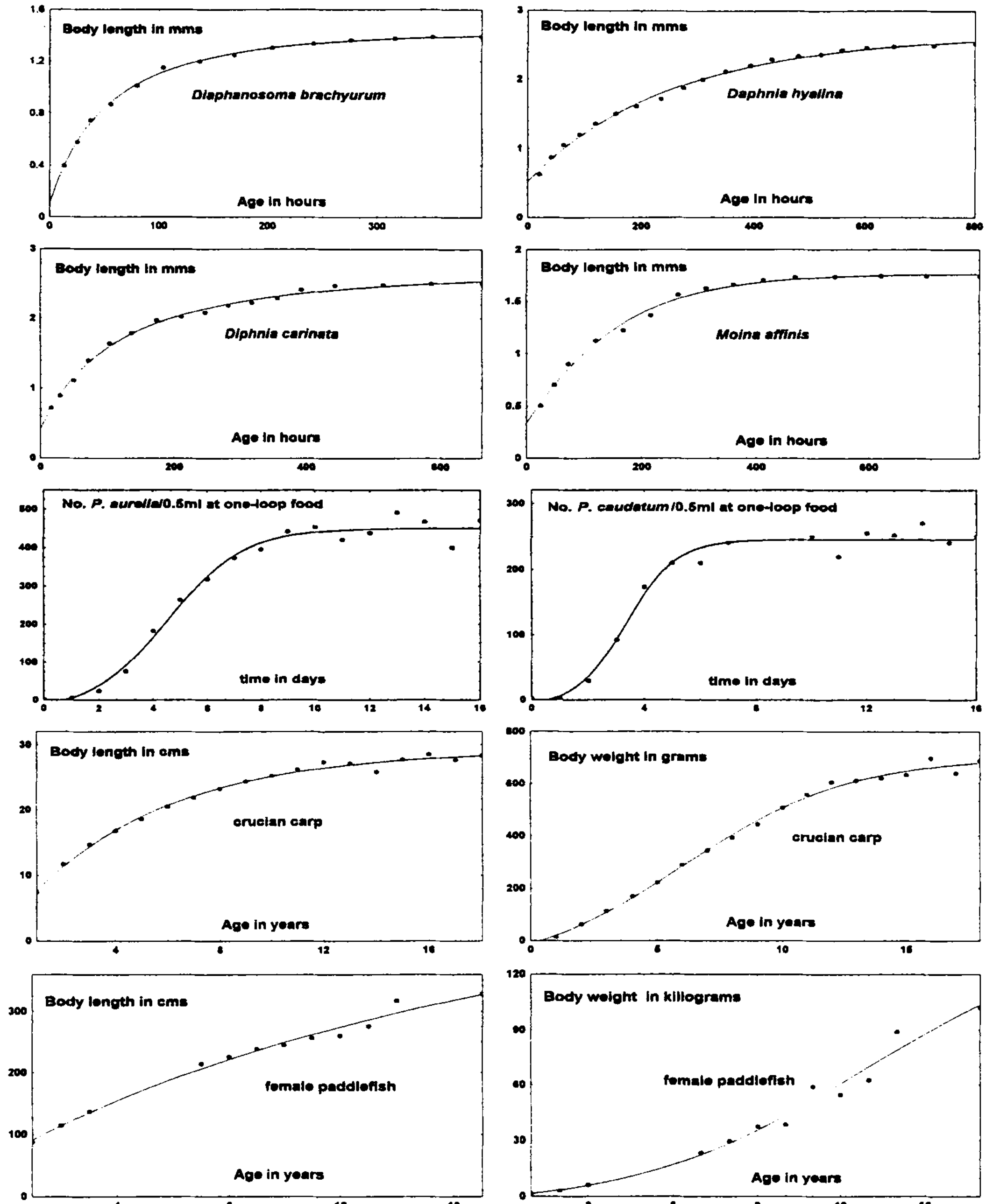

Figure 1. Growth curves obtained by fitting the new model to observed data sets of freshwater species.

growth of fishes (Nos.5-6, No.8, No.10), there are different values of POI. For these reasons, the new equation possesses the ability to depict diverse growth courses ranging from no POI to every value of POI.

In fisheries management, one of the central activities is the setting of harvest regulations on populations of recreationally and commercially important species to maintain a sustainable yield. Based on the RSS values presented in Table 2, the new model has better fits than the logistic, Spillman, Gompertz, and Bertalanffy equations in 10, 10, 8, and 10 out of 10 cases respectively. Considering the fact that the new equation can provide a more accurate estimations than other commonly used growth models, the new function is significant not only in theory, but also in practice. Therefore, the new model proposed here appears to be a worthy successor to the ordinary logistic and the Spillman equations and should be considered by data analysts.

Table 2. The values of RSS (residual sum of squares) obtained through least square method by fitting each model to observed growth data sets.

Data Set	Gompertz	logistic	Spillman	Bertalanffy	New model
No.1	0.01387	0.02335	0.00558	0.01083	0.00232
No.2	0.04455	0.07090	0.02687	0.03717	0.02665
No.3	0.08105	0.12790	0.04060	0.06624	0.02077
No.4	0.01893	0.02626	0.01626	0.01725	0.01567
No.5	6818	8640	33366	8303	7711
No.6	1910	2364	6929	2595	2240
No.7	5.939	8.778	4.378	5.204	4.378
No.8	4476	6676	11919	4929	3840
No.9	1091	1331	893.5	1019	867.7
No.10	282.4	291.0	733.9	289.3	273.6

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