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Comparison of four nonlinear growth models for effective exploration of growth characteristics of turbot *Scophthalmus maximus* fish strain

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This study was conducted to compare the effectiveness for non-linear growth models designated as Chapman-Richards, Gompertz, Logistic and von Bertalanffy for selection of fast-growing fish strain of turbot *Scophthalmus maximus*. These models were compared using the goodness of fit (the coefficient of determination (R^2) and the mean square error (MSE)) and the Akaike information criterion (AIC) and the growth characteristics of turbot from 3 to 27 months of age. The results in the present study showed that R^2 was the highest in Chapman-Richards, but the lowest in von Bertalanffy model. The MSE and AIC values were the highest in Chapman-Richards followed by von Bertalanffy model, whereas Gompertz model is the lowest compared to other models. The Gompertz model had the lowest mean square error (6421.8706) and Akaike information criterion (65.1322) and the second highest coefficient of determination (0.9908) (almost equal to the first highest coefficient of determination), suggesting being the best fit model for description of turbot growth trajectories. Furthermore, the results of turbot growth characteristics explored by the Gompertz model revealed that the fast-growth time interval of turbot were (10.23, 26.78) (unit: months) and the fast-growth time interval distance was 16.55 months. The results of this study suggested that the Gompertz model could be the best fit model for description of turbot growth trajectories, whereas the deduced mathematical formulas of growth intervals could be used in determining the growth characteristics of other fish.

Key words: *Scophthalmus maximus*, nonlinear models, comparison, growth characteristics.

INTRODUCTION

Turbot *Scophthalmus maximus* (L.) is a commercial flatfish inhabiting European waters (Ruan et al., 2011). It

was first introduced into China in 1992 (Ruan et al., 2011; Liang et al., 2012). However, as a result of technological

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problem-solving in the large-scale artificial breeding, the commercial culture of the species has been spreading rapidly along the coast of China (Wang et al., 2015). But, due to the degeneration of germplasm, it is necessary to carry out the selective breeding (Wang et al., 2015). However, the most important economic trait considered in an aquaculture breeding program has been growth rate which determine the total harvest yield (Wang et al., 2010). In this respect, the number of research has been carried out in turbot breeding for growth under the support of Chinese Government.

The selection for rapid growth breeding is commonly evaluated using the body weight collected from one single time point (usually in commercial-size fish), that is, point evaluations. But, the genes are expressed selectively at different growth stages in specific temporal and spatial patterns (Atchley and Zhu, 1997), whereas genetic mechanism controlling quantitative traits have significant changes at various developmental periods during ontogeny (Atchley and Zhu, 1997). This scenario could lead to uncertainty in determining fish growth rates under different space-time conditions and this could suggest probably that the use of point evaluations for determining fish growth rate could not be appropriate. However, the nonlinear growth models based on general system theory could be a good approach in solving this problem, that is, curve evaluations (Richards, 1959). The curve evaluations defined by nonlinear growth models has definite advantages over point evaluations. This is because point evaluations are based on constant ages, constant time periods or constant weight periods, whereas non-linear growth models provides parameters that can describe the biological growth along the entire lifetime (Masso et al., 2000).

The nonlinear growth models which have been extensively used in fish are Chapman-Richards (Richards, 1959), Gompertz (Gompertz, 1825), Logistic (Richards, 1959) and von Bertalanffy (Bertalanffy, 1938) models. The characteristics of these models have been studied in detail by Fitzhugh (1976), Deniel (1990), Tsangridis and Filippousis (1994), Imai et al. (2002), Tsoularis and Wallace (2002), Katsanevakis and Maravelias (2008), Lin and Tzeng (2009), Helidoniotis et al. (2011), Baer et al. (2011), Bilgin et al. (2014), Figueiredo et al. (2014), Ansah and Frimpong (2015); Drew et al. (2015), and Lugert et al. (2016). Moreover, some relevant mathematical formulas reflecting biological growth characteristics, such as time to inflection point, weight at inflection point, instantaneous growth rate and relative growth rate were reported by various authors (Fitzhugh, 1976; France et al., 1996; Tsoularis and Wallace, 2001; Koya and Goshu, 2013). However, the mathematical formulas of different growth intervals have not been previously reported. The whole growth process of fish can be divided into slow-growing, fast-growing and asymptotic period by two extreme points (starting point and ending point), that is, slow-growing, fast-growing

and asymptotic interval. In slow-growing period, the body weight increased slowly as the instantaneous growth rate is low and increased slowly. In fast-growing period, the instantaneous growth rate during the period is higher than that during both slow-growing and asymptotic period; body weight, therefore, also increase quickly. In asymptotic period, the instantaneous growth rate continues declining and reduces slowly to zero. Among, the fast-growing period, interval has important significance on the study of the growth characteristics of fish.

Various nonlinear growth models have been proposed to explain the growth pattern of individuals for a particular species (Bilgin et al., 2014). Growth pattern of turbot or other flatfish species are mainly described by von Bertalanffy model (Deniel, 1990), von Bertalanffy, Schnute, and Gompertz model (Baer et al., 2011) and logistic, Gompertz, von Bertalanffy, Kanis, and Schnute models (Lugert et al., 2016), due to goodness of fit of the data. And Chapman-Richards model encompasses Gompertz ($m \rightarrow 1$), Logistic ($m = 2$) and von Bertalanffy ($m = 2/3$) models for particular values of parameter m . So, the four nonlinear growth models including Chapman-Richards, Gompertz, Logistic and von Bertalanffy were applied to turbot to obtain reliable and suitable growth parameters to explore the growth characteristics of turbot. The objective of this study was to identify appropriate non-linear growth model which best fit for determining the growth rate and establish mathematical formulas exploring growth intervals of rapid growing turbot fish strain. It is anticipated that the identified model and deduced mathematical formula of growth intervals could help in evaluating the effects of selection in the process of turbot breeding.

MATERIALS AND METHODS

Study area

This study was carried out in China Tianyuan Aquaculture Ltd.

Source and management experimental turbot fish strain

The fast growing strain of turbot fish were obtained from China Tianyuan Aquaculture Ltd. The fifty fish were weighed using an electronic balance with a precision of 0.01 g (Table 1) at every 3-month intervals from 3 to 27 months of age. The rearing conditions of experimental fish at different stages of growth periods were same as recommended by Wang et al. (2010).

Analytical procedure

Analysis of parameters of non-linear growth models

The Chapman-Richards, Gompertz, Logistic and von Bertalanffy models were compared by fitting the data to model the relationship between weight and age. The goodness of fit was assessed by

Table 1. Mean body weight of turbot in different month of age (mean values ± standard deviations).

| Month | 3 | 6 | 9 | 12 | 15 | 18 | 21 | 24 | 27 |
|-----------------|-------------|---------------|----------------|----------------|----------------|------------------|------------------|------------------|------------------|
| Body weight (g) | 2.09 ± 0.51 | 47.21 ± 10.68 | 162.02 ± 33.46 | 311.07 ± 60.94 | 619.85 ± 97.42 | 1001.07 ± 129.67 | 1203.59 ± 244.91 | 1784.54 ± 328.28 | 1865.48 ± 401.56 |

using the coefficient of determination (R^2) and mean square error (MSE) according to Gbangboche et al. (2008) and the lower Akaike information criterion (AIC) (Akaike, 1974). The models parameters (A , B , k and m), the R^2 and MSE were calculated using SAS software package (SAS 1999). The four models used in this study are as follows:

Chapman-Richards: $W_t = A(1 - Be^{-kt})^{1/(1-m)}$ (Richards 1959);
 Gompertz: $W_t = Ae^{-Be^{-kt}}$ (Gompertz, 1825);
 Logistic: $W_t = A(1 + Be^{-kt})^{-1}$ (Richards 1959);
 von Bertalanffy: $W_t = A(1 - Be^{-kt})^3$ (Bertalanffy, 1938).

where W_t is the body weight at time t , t is time, A is the asymptote value, B is the scale parameter, k is the intrinsic growth rate representing growth rate per capita and m is the inflection parameter, which determines the shape of the function.

AIC is a measure to help in the selection between candidate models. Using this criterion, the best model is the one with the lowest AIC results. AIC was calculated as (Bilgin et al., 2014):

$$AIC = \text{Mog}(WSS) + 2M,$$

where N is the number of data points, WSS is the weighted sum of squares of residuals, and M is the number of model parameters.

Analysis for growth intervals for turbot

The growth intervals of turbot were determined by deducing the mathematical formulas of three growth intervals of the four non-linear models shown subsequently. The growth curves of the four models had inflection points and the growth processes were divided into accelerated and decelerated periods using the point of inflection. The instantaneous growth rate of the four models had two inflection points and the growth process were divided into slow, fast and asymptotic periods using these two points (starting point and ending point).

(1) Chapman-Richards: $W_t = A(1 - Be^{-kt})^{1/(1-m)}$

The instantaneous growth rate (dW/dt) can be written as follows:

$$dW/dt = kW_t / (1-m) [(A/W_t)^{1-m} - 1]$$

Growth acceleration (d^2W/dt^2) can be described as follows:

$$d^2W/dt^2 = g(t) \cdot k \cdot \{m/(1-m) \cdot (W_t/A)^{m-1} \cdot [1 - (W_t/A)^{1-m}] - 1\}$$

where $g(t) = dW/dt$ and $d^3W/dt^3 = Amk^3Be^{-kt}(1 - Be^{-kt})^{m-3} [m^2(Be^{-kt})^2 - (3m-1)Be^{-kt} + 1]$

Setting $d^3W/dt^3 = 0$ produces the following equation:

$$Amk^3Be^{-kt}(1 - Be^{-kt})^{m-3} [m^2(Be^{-kt})^2 - (3m-1)Be^{-kt} + 1] = 0$$

Solving this equation produces the following:

$$t = \ln X/k,$$

$$\text{where } X_{1,2} = B(m+2 \pm \sqrt{m^2 + 4m}) / [2(m-1)]$$

The rate of change in the instantaneous growth rate has two extreme values and the responding body weight W_t is as follows:

$$W_t = A[1 + (m-1)(m+2 \pm \sqrt{m^2 + 4m})/2]^{1/(1-m)}$$

The time interval distance Δt between the two extreme values can be written as follows:

$$\Delta t = t_2 - t_1 = \ln[(m+2 + \sqrt{m^2 + 4m}) / (m+2 - \sqrt{m^2 + 4m})] / k$$

(2) Gompertz: $W_t = Ae^{-Be^{-kt}}$

Instantaneous growth rate (dW/dt) based on Gompertz

model can be written as follows:

$$dW/dt = kW_t(\ln A - \ln W_t)$$

Growth acceleration (d^2W/dt^2) can be written as follows:

$$d^2W/dt^2 = Bk^2W_t e^{-kt}(Be^{-kt} - 1)$$

$$d^3W/dt^3 = ABk^3 e^{-kt-B} e^{-kt} [Be^{-kt} - (3 + \sqrt{5})/2] [Be^{-kt} - (3 - \sqrt{5})/2]$$

Setting $d^3W/dt^3 = 0$ produces the following equation:

$$[Be^{-kt} - (3 + \sqrt{5})/2] [Be^{-kt} - (3 - \sqrt{5})/2] = 0$$

Solving this equation produced the following:

$$Be^{-kt} - (3 + \sqrt{5})/2 = 0 \Rightarrow t_1 = -\ln[(3 + \sqrt{5})/(2B)]/k \Rightarrow W_1 = Ae^{-(3 + \sqrt{5})/2}$$

$$Be^{-kt} - (3 - \sqrt{5})/2 = 0 \Rightarrow t_2 = -\ln[(3 - \sqrt{5})/(2B)]/k \Rightarrow W_2 = Ae^{-(3 - \sqrt{5})/2}$$

The time interval distance Δt between the two extreme values is written as follows:

$$\Delta t = t_2 - t_1 = \ln[(3 + \sqrt{5}) / (3 - \sqrt{5})] / k.$$

(3) Logistic: $W_t = A(1 + Be^{-kt})^{-1}$

Instantaneous growth rate (dW/dt) based on Logistic model can be written as follows:

$$dW/dt = kW_t(1 - W_t/A)$$

Growth acceleration (d^2W/dt^2) can be written as follows:

$$d^2W/dt^2 = k^2W_t(1 - W_t/A)(1 - 2W_t/A)$$

$$d^3W/dt^3 = ABk^2 e^{-kt} [Be^{-kt} (2 + \sqrt{3})] [Be^{-kt} (2 - \sqrt{3})] / (1 + Be^{-kt})^4$$

Setting $d^3W/dt^3 = 0$ produces the following equation:

$$[Be^{-kt} (2 + \sqrt{3})] [Be^{-kt} (2 - \sqrt{3})] = 0$$

Solving this equation produced the following:

$$Be^{-kt} (2 + \sqrt{3}) = 0 \Rightarrow t_1 = -\ln[(2 + \sqrt{3})/B]/k \Rightarrow W_1 = A/(3 + \sqrt{3})$$

$$Be^{-kt} (2 - \sqrt{3}) = 0 \Rightarrow t_2 = -\ln[(2 - \sqrt{3})/B]/k \Rightarrow W_2 = A/(3 - \sqrt{3})$$

The time interval distance Δt between the two extreme values is as follows:

$$\Delta t = t_2 - t_1 = \ln[(2 + \sqrt{3})/(2 - \sqrt{3})]/k.$$

(4) von Bertalanffy: $W_t = A(1 - Be^{-kt})^3$

Instantaneous growth rate (dW/dt) based on von Bertalanffy model can be written as follows:

$$dW/dt = 3kW_t[(A/W_t)^{1/3} - 1]$$

Growth acceleration (d^2W/dt^2) can be written as follows:

$$d^2W/dt^2 = 3ABk^2 e^{-kt} (W_t/A)^{1/3} (3 - Be^{-kt})$$

$$d^3W/dt^3 = 3ABk^3 e^{-kt} [Be^{-kt} (4 + \sqrt{7})/9] [Be^{-kt} (4 - \sqrt{7})/9]$$

Setting $d^3W/dt^3 = 0$ produces the following equation:

$$[Be^{-kt} (4 + \sqrt{7})/9] [Be^{-kt} (4 - \sqrt{7})/9] = 0$$

Solving this equation produces the following:

$$Be^{-kt} (4 + \sqrt{7})/9 = 0 \Rightarrow t_1 = -\ln[(4 + \sqrt{7})/(9B)]/k \Rightarrow W_1 = A[1 - (4 + \sqrt{7})/9]^3$$

$$Be^{-kt} (4 - \sqrt{7})/9 = 0 \Rightarrow t_2 = -\ln[(4 - \sqrt{7})/(9B)]/k \Rightarrow W_2 = A[1 - (4 - \sqrt{7})/9]^3$$

The time interval distance Δt between the two extreme values can be written as follows:

$$\Delta t = t_2 - t_1 = \ln[(4 + \sqrt{7})/(4 - \sqrt{7})]/k.$$

These new formulas deduced are summarized in Table 2.

RESULTS

Parameters of non-linear growth models

The model R^2 , MSE, A , B , k , m and AIC of the four compared models are shown in Table 3. The results showed that all the compared models had R^2 with a narrow range of 0.11, but the R^2 values were the highest in Chapman-Richards and lowest in von Bertalanffy model compared to other models. Moreover, the results

showed a wide range of MSE values among studied models but Gompertz model had the lowest, whereas Chapman-Richards model had the highest MSE value compared to their counterparts. The AIC value ranged from 65.1322 to 68.4522 and the Gompertz was ranked 1st in term of the lowest AIC value. The AIC of the four models had same change trend as MSE. The parameter 'A' values was the highest in the von Bertalanffy, but was the lowest in logistic model. The parameter 'B' value was the highest in Logistic, but the lowest in Chapman-Richards model. The parameter 'k' value was the highest in Logistic, but the lowest in von Bertalanffy.

The growth intervals for turbot

The non-linear growth models in the present study showed different growth intervals for the turbot fish strain (Table 4). Logistic model had the longest (13.63 month), whereas the Chapman Richards model had the shortest (7.58 month) slow growth interval distance compared to the other models. The longest (22.72 month) fast growth interval distance was noted in the von Bertalanffy model, whereas the shortest (10.53 month) was revealed in the Logistic model. Moreover, the asymptotic growth interval was the longest (30.8 month) in von Bertalanffy model, but the shortest in Chapman Richards model.

DISCUSSION

As typical sigmoid growth curves, the properties of Chapman-Richards, Gompertz, Logistic and von Bertalanffy models in the past few decades have been studied in detail and some property formulas were obtained from the first and second differentials of the models, that is, the instantaneous growth rates, the relative growth rate, and the growth acceleration. All instantaneous growth rates of the four models have a vertex (maximum value). These vertexes are the inflection points of the sigmoid curves [the inflection point coordinates of Chapman-Richards, Gompertz, Logistic and von Bertalanffy is $(\ln[B/(1-m)]/k, Am^{1/(1-m)})$, $(\ln B/k, A/e)$, $(\ln B/k, A/2)$ and $(\ln 3B/k, 8A/27)$, respectively]. This indicates that the instantaneous growth rate has an inverted bell-shaped curve (Figure 1). The curve characteristics of the relative growth rates have already been reported and are always decreasing according to Minot's law (Figure 1) (Medawar, 1941). The growth accelerations of the four models all have two vertexes (a maximum and a minimum), which indicates that the growth accelerations have a transverse S-shaped curve (Figure 1). The transverse S-shaped curve of the growth acceleration shows that the two extreme points are the point of inflection of the instantaneous growth rate. In this way, the growth process can be divided into slow, fast and asymptotic periods using these two points (starting

Table 2. Properties of four nonlinear growth models (time).

| Type of model | Chapman-Richards | Logistic |
|-------------------------------|---|---|
| Slow-growth interval | $\left(0, \frac{1}{k} \ln \left[-\frac{B(m+2-\sqrt{m^2+4m})}{2(m-1)} \right] \right)$ | $\left(0, -\frac{1}{k} \ln \frac{2+\sqrt{3}}{B} \right)$ |
| Fast-growth interval | $\left(\frac{1}{k} \ln \left[-\frac{B(m+2-\sqrt{m^2+4m})}{2(m-1)} \right], \frac{1}{k} \ln \left[-\frac{B(m+2+\sqrt{m^2+4m})}{2(m-1)} \right] \right)$ | $\left(-\frac{1}{k} \ln \frac{2+\sqrt{3}}{B}, -\frac{1}{k} \ln \frac{2-\sqrt{3}}{B} \right)$ |
| Asymptotic growth interval | $\left(\frac{1}{k} \ln \left[-\frac{B(m+2+\sqrt{m^2+4m})}{2(m-1)} \right], +\infty \right)$ | $\left(-\frac{1}{k} \ln \frac{2-\sqrt{3}}{B}, +\infty \right)$ |
| Fast-growth interval distance | $\ln[(m+2+\sqrt{m^2+4m})/(m+2-\sqrt{m^2+4m})]/k$ | $\ln[(2+\sqrt{3})/(2-\sqrt{3})]/k$ |
| Type of model | Gompertz | von Bertalanffy |
| Slow-growth interval | $\left(0, -\frac{1}{k} \ln \frac{3+\sqrt{5}}{2B} \right)$ | $\left(0, -\frac{1}{k} \ln \frac{4+\sqrt{7}}{9B} \right)$ |
| Fast-growth interval | $\left(-\frac{1}{k} \ln \frac{3+\sqrt{5}}{2B}, -\frac{1}{k} \ln \frac{3-\sqrt{5}}{2B} \right)$ | $\left(-\frac{1}{k} \ln \frac{4+\sqrt{7}}{9B}, -\frac{1}{k} \ln \frac{4-\sqrt{7}}{9B} \right)$ |
| Asymptotic growth interval | $\left(-\frac{1}{k} \ln \frac{3-\sqrt{5}}{2B}, +\infty \right)$ | $\left(-\frac{1}{k} \ln \frac{4-\sqrt{7}}{9B}, +\infty \right)$ |
| Fast-growth interval distance | $\ln[(3+\sqrt{5})/(3-\sqrt{5})]/k$ | $\ln[(4+\sqrt{7})/(4-\sqrt{7})]/k$ |

Table 3. The parameter values and goodness of fit of four nonlinear curve models of family.

| Model | Logistic | Gompertz | von Bertalanffy | Chapman-Richards |
|--|-----------|-----------|-----------------|------------------|
| Coefficient of determination (R^2) | 0.9906 | 0.9908 | 0.9898 | 0.9909 |
| Mean square error (MSE) | 6574.1773 | 6421.8706 | 7127.1754 | 7436.3161 |
| A | 2156.69 | 2788.11 | 3584.70 | 2788.24 |
| B | 112.61 | 8.60 | 1.28 | 0.0013 |
| k | 0.25 | 0.12 | 0.07 | 0.12 |
| m | / | / | / | 0.9998 |
| Akaike's Information Criteria (AIC) | 65.3431 | 65.1322 | 66.0700 | 68.4522 |

Table 4. Properties of four nonlinear growth models for Turbot fish strain (month).

| Type of model | Slow-growth interval | Fast-growth interval | Asymptotic growth interval | Fast-growth interval distance |
|------------------|----------------------|----------------------|----------------------------|-------------------------------|
| Chapman-Richards | (0, 7.58) | (7.58, 23.62) | (23.62, 0) | 16.04 |
| Logistic | (0, 13.63) | (13.63, 24.16) | (24.16, 0) | 10.53 |
| Gompertz | (0, 10.23) | (10.23, 26.78) | (26.78, 0) | 16.55 |
| von Bertalanffy | (0, 7.86) | (7.86, 30.58) | (30.58, 0) | 22.72 |

point and ending point). However, the property formulas from three differentials have not been previously

deducted. To evaluate deeply the effects of selection of fast-growing strain of turbot, we have deducted the

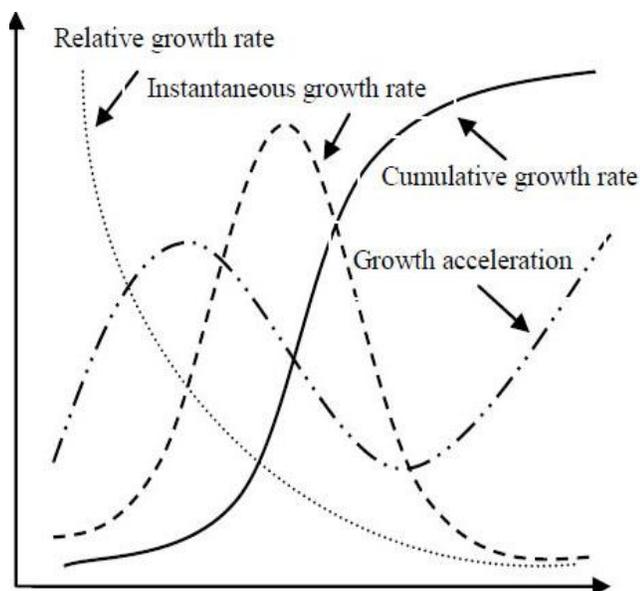


Figure 1. The curve shape characteristics of sigmoid growth curve (cumulative growth curve), instantaneous growth rate, relative growth rate and growth acceleration. The meaning and scale of coordinate axis, for the four curves, are different.

mathematical formulas of the three special growth intervals and explored the growth characteristics of turbot using the formulas.

The model selection was a daunting task, given the broad range of criteria for goodness of fit, as the coefficient of determination (R^2), the mean squares errors (MSE), the loglikelihood ($\ln L$) values, the AIC (Akaike, 1974; Gbangboche et al., 2008), and the least average prediction error (APE) (Lambe et al., 2006; Gbangboche et al., 2008). The goodness of fit, in this study, was assessed using R^2 , MSE and AIC, and the model with the higher R^2 and the lower MSE and AIC were selected as the optimal model (Akaike, 1974; Gbangboche et al., 2008). All competing models had high R^2 from 0.9898 to 0.9909, suggesting overall good fits to the data. The MSE value ranged from 6421.8706 to 7436.3161 and the Gompertz was ranked 1st according to the lowest MSE value. The AIC value ranged from 65.1322 to 68.4522 and the Gompertz was ranked 1st according to the lowest AIC value. Among the four models, although the Chapman-Richards model showed the highest R^2 (0.9909), its MSE value was also the highest (7436.3161), which indicated that the Chapman-Richards model was not the best model to describe the growth data of turbot; by contrast, the Gompertz model showed the lowest MSE (6421.8706) and AIC (65.1322) and the second highest R^2 value (0.9908) (almost equal to the first highest R^2 of the Chapman-Richards model). Hence, the Gompertz model has been considered as the best fit according to MSE, AIC and R^2 value and was optimal for the description of turbot growth trajectories. Research

has shown that the Gompertz model, in fish population such as *Spicara smaris* and *Tribolodon nakamurai*, can be deemed as the best fit based on AIC lowest value (Tsangridis and Filippousis, 1994; Imai et al., 2002). The conclusion was consistent with the result of this study. Even so, it cannot be assumed that the Gompertz model could produce the goodness of fit in the other breeding farm when the environmental conditions change. Therefore, the model parameters can be routinely re-adjusted, allowing even the possibility of testing all other nonlinear models (Gbangboche et al., 2008). The growth of turbot is influenced by rearing conditions, especially water temperature. In this study, during the larval period, water temperature is 18°C and during sub-adult and adult period are 13 to 15°C. In the appropriate temperature range, turbot can show a rapid growth as temperature rises. But, the growth rate of turbot will decrease when the water temperature is too high or too low, for example, the water temperature of larval period is lower than 16°C or higher than 23°C and the water temperature of sub-adult and adult period are lower than 10°C or higher than 22°C. Various nonlinear growth models have been proposed to explain the growth characteristics of turbot (Baer et al., 2011; Lugert et al., 2016). Baer et al. (2011) used three different growth models, the von Bertalanffy model, the Gompertz model and the Schnute model, to analyze the growth of turbot (*Psetta maxima*) in a commercial recirculation system. The results indicate that the Schnute model was the optimal model to simulate the growth data collected. In the present study, we were unable to determine whether the Schnute model was the optimal model, because the model was not used. But, in the paper of Baer et al. (2011), the Gompertz model was more suitable to simulate the growth data than the von Bertalanffy model according to AIC and sum of squared residuals (SSE) without considering the Schnute model. The conclusion, to some extent, was consistent with our research result. Lugert et al. (2016) used five nonlinear growth functions, the logistic model, the Gompertz model, the von Bertalanffy model, the Kanis and Schnute model, to model the collected growth data in a recirculation aquaculture system (RASs). The fitting weight showed that the Gompertz model gave the best results with the lowest residual standard error (RSE) and AIC among the applied five growth models and was considered to be the best model to simulate the weight collected. The conclusion was consistent with our research findings. Furthermore, the asymptotic values A of the Gompertz model are also very similar in two studies and are more realistic in biological terms; the asymptotic value A and the intrinsic growth rate k .

The asymptotic body weight A was estimated as 2156.69 g by the logistic model and 2788.11 g by the Gompertz model and 3584.70 g by the von Bertalanffy model and 2788.24 g by the Chapman-Richards model, and correspondingly the intrinsic growth rate k of the four models was 0.25, 0.12, 0.07 and 0.12, respectively.

Obviously, the parameter A and k estimated by the Gompertz model were almost the same as the Chapman-Richards model. On the whole, the larger the asymptotic body weight A (mature weight), the less the intrinsic growth rate k , the longer it tends to take to mature. Clearly, the A value from the logistic model was too low (2156.69 g) and was not consistent with the breeding goal for the body weight. The A value from the von Bertalanffy model was the highest (3584.70 g), but its k value was the lowest (0.07) and the individual will take a longer time to mature and was not consistent with the breeding objectives since prolonging breeding generation interval. Although the A and k from the Gompertz model were almost the same as the Chapman-Richards model, the Gompertz model was considered as the most suitable growth models to simulate the present growth data according to both MSE, AIC and R^2 value and biological meaning. In addition to the asymptotic value A and the intrinsic growth rate k , the third parameter point of inflection is often used to partition the growth curve into two stages (Fitzhugh, 1976). To explore deeply the growth characteristics of turbot, we further investigated the curve property of growth models used in this paper and deduced the starting point and ending point formulas. And thus, the growth process can be divided into slow, fast and asymptotic periods using the two points (starting point and ending point) but not two stages based on point of inflection. In fact, the point of inflection, starting point and ending point of a growth curve is determined by the same parameters of the curve. In the present study, based on the optimal model selection, we have explored the growth characteristics of turbot using the Gompertz model. Three kinds of growth time intervals of the four models were quite different according to starting- and ending-point, and the corresponding fast-growth time interval distance were radically different (The fast-growth time interval distances of Chapman-Richards, Logistic, Gompertz and von Bertalanffy models were 16.04, 10.53, 16.55 and 22.72 months, respectively). In this study, the Gompertz model was used to describe the growth trajectories of turbot based on the goodness of fit (R^2 , MSE and AIC), and decided that the fast-growth time interval of turbot and the fast-growth time interval distance were (10.23, 26.78) (unit: months) and 16.55 months. The conclusion calculated by Gompertz model was more in accordant with the realistic growth characteristics of fast-growth turbot from selective breeding than by the other three models.

Conclusion

In this paper, the Gompertz model gave the best results with the lowest MSE ((6421.8706)) and AIC (65.1322) and the second highest R^2 value (0.9908) (almost equal to the first highest R^2 value) among the applied four growth models and was considered to be the best model to simulate the weight collected. On this basis, we have

explored the growth characteristics of turbot using the Gompertz model selected and decided that the fast-growth time interval of turbot and the fast-growth time interval distance were (10.23, 26.78) (unit: months) and 16.55 months, respectively.

Conflict of interests

The authors have not declared any conflict of interests.

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