Optimal prediction of adductor percentage for *Argopecten irradians concentricus* (Say) cultured in Beibu bay in China

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ABSTRACT

Adductor percentage is one of the economically most important traits in *Argopecten irradians concentricus*. Elucidation of its growth pattern is undoubtedly of great practical bearing. In the paper, according to Mallows' C_p criterion and a couple of other pertinent statistics, decision on the determination of the optimal math model, from several candidates that have been previously proposed, for depicting growth of adductor percentage in *A. irradians concentricus* was made. Results showed that under current environmental circumstances and culture management regime in the Beibu bay of South China Sea, the growth of adductor percentage was observed to exhibit the Brody pattern. von Bertalanffy, Gompertz, Logistic and Richards models were not advised for the depicture of growth of adductor percentage. Asymptotic growth of adductor percentage subtended in Brody model, estimated using Levengerg–Marquardt iteration, were 0.240 (95% confidence interval, 0.211–0.264). Results of the study are greatly instrumental to the formulation of culture production and breeding scenario of *A. irradians concentricus*.

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1. Introduction

The individual growth in organisms is rooted in physiological processes and is the net result of two opposing processes, anabolism and catabolism (von Bertalanffy, 1938). For population analysis, the expression of individual mean growth can be observed by relating the size of the species of interest to its age (Katsanevakis, 2006). Different mathematical models of weight or a morphometric character as a function of age (time) have been employed to depict the mean growth of individuals in a population. Generally, growth models are studied by fitting the data on information of the animal's entire life cycle (viz., a series of weight or dimension/age data) to readymade nonlinear functions in which a small set of biologically meaningful parameters are encompassed. In this way we can have an insight into the growth of organisms (Hernandez-Llamas and Ratkowsky, 2004). The significance lies in the fact that growth curves are important for research and recommendations about the efficiency of production and thus making a contribution to amelioration of productivity and profit (Fitzhugh, 1976). Growth models have also become the important tools used in genetic improvement programs, species selection and/or strains to be cultivated (Santos et al., 2008).

Argopecten irradians concentricus (Say), a subspecies of the bay scallop (*Argopecten irradians*) (Wilbur and Gaffney, 1997), was imported into China in 1991. At present the culture, due to some

advantages of the scallop such as fast growth, high percent adductor and availability of great returns, has been quickly extended in Beibu bay in South China Sea, and large-scale culture also has been successful (Guo et al., 1999). The total extension area in Beibu bay until now has amounted to 7380 hm². Now the scallop culture is gaining momentum and has become one of the pillar industries of aquaculture in Beibu bay of South China Sea (Liu et al., 2007).

Economic importance for the scallop, extensive and deep studies have been carried out about it both ecologically, genetically and in breeding (Tang and Fang, 1999; Zhang, 2006). In the case of the growth model of *A. irradians concentricus*, little information is now known. Liu et al. (2007) and Wang et al. (2007) fitted Logistic model to the morphometric characters/age and weight/age growth data, respectively. They concluded that the growth of morphometric and weight traits in *A. irradians concentricus* conform to Logistic pattern. Currently as the culture scale for the scallop in Beibu bay increasingly expands, it is necessary for the adductor percentage, the most important target trait in production and breeding, to be monitored any time over the entire culture or breeding process. However, study on the growth of adductor percentage has thus far not been reported both home and abroad. In the paper, by use of Mallows' C_p statistic (Neter et al., 1996; Kleinbaum et al., 1998) as the principal criterion, in conjunction with other relevant measures, an attempt was made of establishing the optimal growth model of adductor percentage in *A. irradians concentricus* (Say), with a purpose of making decisions about the improvement of production management and the determination of selection strategy in breeding scenario for *A. irradians concentricus* (Say) by applying the optimal growth model found.

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2. Materials and methods

2.1. Background

A. irradians concentricus (Say) scallops used for measurement in the trial came from descendants introduced from Florida of America in 1991. On 20 Oct. 2006, the same batch of juveniles (shell length 0.95 mm, shell height 1.07 mm, body weight 0.90 mg) was shifted to the field for nursery from the aquafarm, which is affiliated to Zhanjiang Silverwave Company and located at Caotan township, Suixi county, Guangdong province. The aquafarm has a culture area of 1700 hm^2. This batch of juveniles was transported by truck to the nursery site in 3 h, during which juveniles were kept in closed and oxygenated plastic bags, with the water temperature controlled at 29 °C. Over the nursery period (about 2 months), the scallop density was adjusted according to the practices of Zheng et al. (2004). Cylinder-shaped cages, whose length was 1.3 M and diameter 29 cm, were used for the culture in scallop grown-out period. The cages (10 layers/cage, 35–40 ind./layer) of juveniles were suspended at 1.5–4 M from under sea and placed in the central part of culture field (N21°03′368″E109°39′992″), 5.5 km off the coast. Mean water depth was 9.8 m, limpidity 3.6–5.6 m, salinity 27.2–32.8‰, water temperature 18.1–30.6 °C, pH 8.0–8.2 over the whole culture period (from 28 Oct. 2006 to 25 Jul. 2007). According to a survey, phytoplanktonic cell abundance averaged out at 4.8×10^4 cell·L^{-1} (1.8×10^4–7.8×10^4 cell·L^{-1}) during the culture period. Now in Beibu bay, the culture period of *A. irradians concentricus* spans three seasons of autumn, winter and spring, with autumn for juvenile nursery (juveniles stocking in 15 Oct.–15 Nov.), winter for intermediate cultivation, spring for growth-out. In July harvest begins . As regards the substantive culture procedure, refer to Wang et al. (1993).

2.2. Data measuring and processing

The study was intended to investigate the temporal growth pattern of adductor percentage through measurements over time (age/month) in *A. irradians concentricus*. Data were measured from the onset of juvenile nursery to the field. In order to gain representative data, 50 suspended cages were sampled at random each time from the culture area where 10,000 cages were suspended. 30–50 individuals were randomly sampled from 50 cages each. Each individual sampled was cleansed following removal of all foulings attached. Weight was determined, on each individual weighed by electronic balance (±0.001 g). Then the fresh adductor was taken out by vivisection and measured. Adductor percentage (%, AP) was formulated as the ratio of fresh adductor weight to total weight. The entire experiment lasted for 270 days (from 28 Oct. 2006 to 25 Jul. 2007), over which adductor percentage was monthly measured. Original data at varying temporal points were calculated as weighted means and weighted standard deviations for 50 cages (mean±S.D.). The statistical software Statistica6.0 was used to process the data on adductor percentage trait.

2.3. Growth models

The noted models that quantitatively describe the growth process of organisms chiefly include: Brody, von Bertalanffy, Gompertz, Logistic and Richards. Due to the fact that these models are not purely empirically based, but have a sound theoretical basis and are educed by differential equations associated with the metabolic processes (Xing et al., 1998), these models were, hence, chosen as the candidates from among which the optimal models are selected to best quantify the growth process of adductor percentage. Below are their forms:

Models	Substantive form
von Bertalanffy	$AP = B(1 - a \exp(-kt))^3$
Gompertz	$AP = B \exp(-a \exp(-kt))$
Logistic	$AP = B(1 + a \exp(-kt))^{-1}$
Brody	$AP = B(1 - a \exp(-kt))$
Richards	$AP^{1-m} = B^{1-m}(1 - a \exp(-kt))$

Where *AP* is adductor percentage at time *t* (month), parameter *B* is total growth amount or asymptotic value of adductor percentage, parameter *a* is the value of AP at time *t*=0, parameter *k* is maximum possible growth rate of AP, *m* is the parameter that shapes growth curve.

2.4. Model selection criterion

To decide on the optimal growth model from aforementioned classic models, Mallows' C_p statistic is chosen as the principal criterion for the selection of optimal growth model. The formula of Mallows' C_p statistic is as follows:

$$C_p = \frac{RSS_r}{\hat{\sigma}_f^2} + 2p$$

Where C_p, developed by Mallows in 1964, is the statistic employed to establish optimal model; RSS_r is the residual sum of squares for reduced model; $\hat{\sigma}_f^2$ is the estimate of error variance, generally estimated by error variance for full model (Neter et al., 1996); *p* is

Table 1
Parameter estimates and fitting of varying models to data

Growth models	Parameter	Estimate	Standard error	95% confidence interval		Prediction standard error	Adjusted multiple correlation R_a^2	Sig.
				Lower boundary	Upper boundary			
Bertalanffy	*B*	0.217	0.005	0.196	0.231	0.0042	0.992	<0.001
	a	0.475	0.019	0.427	0.520			
	k	0.322	0.030	0.248	0.394			
Gompertz	*B*	0.212	0.006	0.190	0.222	0.0050	0.990	<0.001
	a	1.828	0.108	1.567	2.100			
	k	0.387	0.035	0.291	0.465			
Logistic	*B*	0.204	0.008	0.178	0.216	0.0072	0.978	<0.001
	a	4.103	0.606	2.670	5.537			
	k	0.542	0.064	0.410	0.729			
Brody	*B*	0.240	0.010	0.211	0.264	0.0037	0.994	<0.001
	a	0.889	0.012	0.851	0.920			
	k	0.195	0.018	0.137	0.236			
Richards	*B*	0.235	0.021	0.175	0.287	0.0038	0.995	<0.001
	a	0.866	0.132	0.521	1.184			
	k	0.208	0.080	0.008	0.401			
	m	0.081	0.382	−0.843	1.018			

Note: Sig. stands for the right-tailed probability of observed *F* value in ANOVA.

number of parameters embraced in model. When parameter m equals to 0, 2/3 and 2 respectively, Richards model can transform into Brody, von Bertalanffy and Logistic models. When parameter m tends to 1, Richards model can transform into Gompertz model. Richards model is consequently taken as the full model, others, as specific cases of Richards model, are reduced models. According to Mallows' C_p criterion, the model that has the smallest C_p value is optimal.

2.5. Approach to estimating growth parameters

In the paper the Levenberg–Marquardt iteration method (Wang and Li, 1986) was used to estimate the growth parameters covered in the above models, with the iterative precision set to be equal to 10^{-5}. At the end of the iterative process, the converged outcomes or estimates were final values of parameters to be estimated. According to the attributes of various models cited above and practical growth situation of *A. irradians concentricus*, the initial values of growth parameters included in the above models were preset, $B=0.25$, $a=5$, $k=0.3$, $m=2.5$.

3. Results

3.1. Parameter estimating and model fitting

When utilizing the preceding models to fit the growth process of AP, growth parameter estimates, estimated standard errors, 95% confidence intervals and several statistics such as prediction standard error and adjusted multiple correlation coefficient R_a^2 that gauge the goodness of fit of models are presented in Table 1. It could be seen that in the context of the goodness of fit, all models fitted were statistically significant (ANOVA, $P<0.001$), with the adjusted multiple correlations all over 0.90 ($P<0.001$). Prediction standard errors were all very small. Estimates of parameter B varied from model to model. B values of Bertalanffy, Gompertz and Logistic models, e.g., were close to one another, while those of Brody and Richards models were approximately equal. For parameter a, those estimates of parameter a in Bertalanffy, Gompertz and Logistic models were greatly inconsistent, whereas those in Brody and Richards models came near mutually. The same case was as above for the estimates of parameter k. In addition, the estimated standard error of parameter m in Richards model was relatively larger, and minus estimates emerged in 95% confidence interval thereof. This case, corresponding to a decrease and/or an eventual tissue absorption, is of biological relevancy especially in mollusks and other invertebrates.

3.2. Fast growth interval for adductor percentage

The fast growth intervals, growth inflection points and corresponding values of AP are given in Table 2. It could be seen that there existed inflection points with von Bertalanffy, Gompertz and Logistic models each. The respective temporal points from which AP ceased fast growing differed from one another, with that of Logistic model being the last to emerge, roughly at the beginning of the 4th month from nursery in the sea. This obviously was not in accordance with the actual situation. For Brody and Richards models, whose growth inflection points were absent, their temporal points from which AP

Table 3
C_p values of varying growth models

Models	RSS	Number of parameters	Mallows' C_p
Bertalanffy	1.78×10^{-4}	3	14.92
Gompertz	2.34×10^{-4}	3	17.73
Logistic	4.48×10^{-4}	3	28.45
Brody	1.32×10^{-4}	3	12.61
Richards	1.30×10^{-4}	4	14.54

was no longer fast growing were very close to the termination of lifespan of *A. irradians concentricus* scallop. At the moment, AP, is almost commensurate with each other for the two models and all are not far from their respective asymptotes, would start going into steady growth. This showed that Brody and Richards models were more characteristic of AP than others involved.

3.3. Determination of optimal model according to C_p value

The residual sum of squares for the models given above, number of parameters subsumed and values of Mallows' C_p statistic are presented in Table 3. It could be found that C_p of the Brody model was the smallest. In the light of Mallows' C_p criterion, Brody model should be the optimal model of depicting the pattern of AP growth over time.

3.4. Absolute and relative growth of adductor percentage

Records of AP measured at specific time point in the trial described only the accumulative growth pending the point. If the growth rate at a specific time over the whole growth process is desired to manifest itself, the instantaneous and relative growth rates should be used (Liu et al., 2007; Wang et al., 2007). It could be seen from Fig. 1 that the patterns of instantaneous growth for von Bertalanffy, Gompertz and Logistic models were nearly identical. That is, rapid declining resulted subsequent to a single peak. As opposed to this case, Brody and Richards models differed a lot from above. But the patterns of the two growths were roughly the same. In the case of the relative growth (Fig. 2), rates of AP for Bertalanffy, Gompertz and Logistic models slowly decreased at the early phase of culture in the sea, as was contrary to those of AP for Brody and Richards models. The relative growth rates of all models concerned were very marginal after 8 months' culture. In the later culture stage close to the finish of life cycle for the scallop, both instantaneous and relative growths all tended to stagnation.

4. Discussion

Statistic C_p is a measure of standardized model prediction error. In its formula, first right-hand term denotes the extent of fitting of

Table 2
Fast growth interval, growth inflection point and corresponding adductor percentage

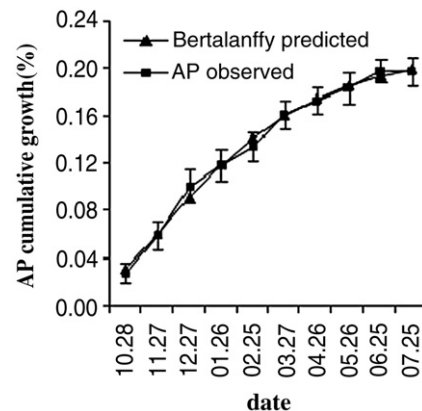| Growth models	Fast growth interval (month/AP)		
	Start point (month/AP)	Inflection point (month/AP)	End point (month/AP)
Bertalanffy	–	1.091/0.058	3.540/0.135
Gompertz	–	1.569/0.082	4.039/0.149
Logistic	0.168/0.048	2.587/0.108	4.992/0.162
Brody	–	–	9.256/0.206
Richards	–	–	9.714/0.209

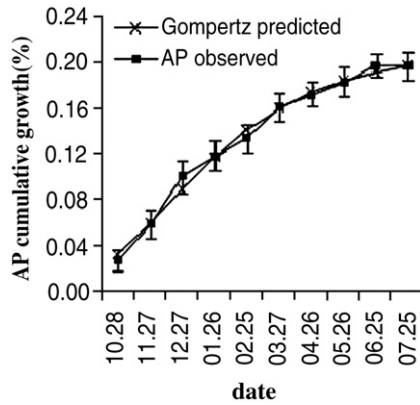**Fig. 1.** Instantaneous growth of adductor percentage.
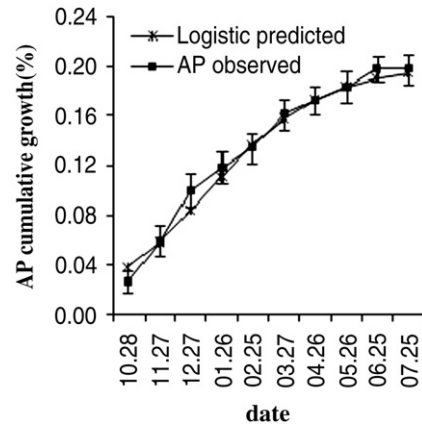
Fig. 2. Relative growth of adductor percentage.

Fig. 3. Fitting Bertalanffy model to adductor percentage data.

selected model to data, and second right-hand term can be deemed as penalty for adding parameter(s) to model. C_p is at present one of the widely applied model selection criteria (Neter et al., 1996). It is hence chosen in the paper as the criterion for determination of optimal growth model of adductor percentage in *A. irradians concentricus*.

When attempting to enunciate the pattern embraced in trait-age data on a certain organism, most pervasive approach used is, based on the shape of the observed trait-age curve and on a small set of biological assumptions, to fit existent growth models to the data mustered. The model that has minimum residual sum of errors or maximum adjusted multiple correlation is usually thought of as optimal (Katsanevakis, 2006). But adjusted multiple correlation doesn't perform well in model selection (Pasternak and Shalev, 1994; Hernandez-Llamas and Ratkowsky, 2004). As in the paper, adjusted multiple correlation coefficient predicted a different "optimal" model than did Mallows' C_p (Table 1). Unlike the above method, in the paper upon establishing the optimal model for describing the growth of adductor percentage in *A. irradians concentricus*, besides the use of adjusted multiple correlation, Mallows' C_p as primary criterion, concurrently coupled with other measures such as parameter estimated standard error, confidence interval, prediction standard error, growth inflection point, instantaneous and relative growth rates, was used. In terms of the said measures, particularly the Mallows' C_p value, Brody model should be optimal rather than Richards or others. Richards model, as a general form for describing organismal growth (Xing et al., 1998), seems not optimal for the description of growth pattern of adductor percentage. Although Richards model has the smallest residual sum of squares, it encompasses the most parameter number. Relative to Brody model, increase of C_p value for Richards model is nearly completely caused by addition of one parameter m to model. As per C_p criterion, the model with both high fitting goodness and least parameter number is preferable. Mere smaller residual error of squares is no indication of optimal model.

The growth process of organisms can be generally delineated by a sigmoid curve. This curve will take on varying forms, depending upon species, ecological environment, etc (Xing et al., 1998). When parameter m changes, not only does Richards model subsume Brody, Gompertz, Logistic and von Bertalanffy models, but also it subsumes those transient and even more general categories in between. Therefore, Richards model is of great generality. When it is employed for depicting growth, the fitting should be no doubt the best. On the other hand, one point should be seen that the generality of Richards model is derived at the cost of the addition of one more parameter m to model, whereas this additional parameter in turn brings about some instability both in parameter estimating and model prediction (Table 1). Thus, going extremes is not advisable, we should arrive at a compromise between the model generality and the number of parameter(s) contained in model. This is just what C_p criterion tells.

Wang et al. (2007) reported that both body weight and adductor weight in *A. irradians concentricus* all conformed to Logistic growth pattern, and adductor weight grew more quickly than adductor weight. Adductor percentage, expressed as the ratio of adductor weight to body weight, does not continue to grow in Logistic mode, in Brody mode instead. This is inconsistent with Craeymeersch et al. (1986), Griffiths and Griffiths (1987), Reaburn and Edwards (2003), Miguel et al. (2004), Ohnishi and Akamine (2006), Soderberg (2006), most likely as a result of the distinctions in species, traits involved, age and environment etc.

Katsanevakis (2006) thought that the usual model selection procedures were simplistic. For this reason, he, based on information theory, developed an "average" model to describe growth trajectory of several marine organisms by assigning different "Akaike weights" prior to classic growth models. In the authors' opinion, simplicity and utility should be the first thing to ponder on when the research objective is only pragmatic application. It would be best if we can find the optimal growth model out of extant classic models. These classic models, after all, have solid theoretical underpinnings (Xing et al., 1998). Santos et al. (2008), under the existence of heteroscedasticity, estimated the growth curves of tilapia by weighting data at different temporal points in growth process. In terms of those data acquired in the study, variability at various temporal points, due to larger sample size, is so small that taking into account the heteroscedasticity seems to be unnecessary (Figs. 3–7). In fish, due to the particularity in growth, Gamito (1998) deemed that fitting models to fish growth should be done stagewise, and he concluded that the Gompertz or the parabolic growth models seemed more appropriate for the description of young fish growth, for older fish the von Bertalanffy equation or some modified form adjusted to seasonal change was preferable. It
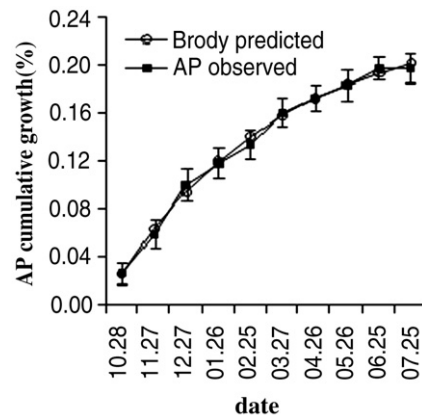

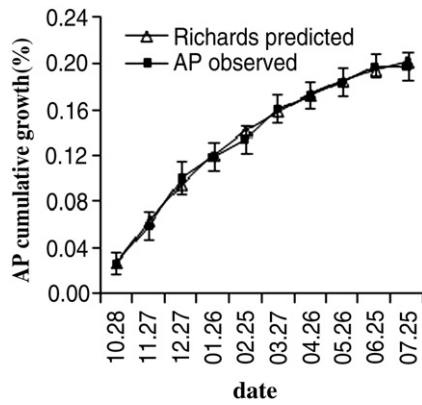Fig. 4. Fitting Gompertz model to adductor percentage data.

Fig. 5. Fitting Logistic model to adductor percentage data.

Fig. 7. Fitting Richards model to adductor percentage data.

should be said that this is not suitable for the fitting of growth of adductor percentage in *A. irradians concentricus*, reasons of which being that this experiment endured for exactly a whole life cycle of the scallop and the growth pattern has been completely displayed over the course. It is, therefore, unnecessary for the growth of adductor percentage to be fitted stagewise, as done by Gamito (1998).

Genetically, the growth pattern of various traits in organisms is completely imputable to the sequential expression of genes, interactions between varying genetic components and between genotype and environment, and to environment in which organisms live (Hedgecock et al., 1991). Subject to relative invariance of environmental conditions, the intracellular genetic control mechanism can guarantee that biological traits grow in a regular fashion (Marinova et al., 2007). In this sense, not only can the optimal Brody model given in the paper be used for the portrayal of growth process for the trait adductor percentage, but also for projections of growth and rates at any time throughout culture period. In turn predicated on these, the efficacy of production management and breeding work may be tested. It can be found that since the adductor percentage trait goes into rapid growth from the start of culture in the sea, the first 8 months in whole culture process is the fastest growth period for adductor percentage. This period is, therefore, of critical significance for culture practitioners. This clearly shows that, for better economic returns, creation of optimal growth conditions for the scallop by virtue of intensive management in this culture period should be considered. Additionally, it should be seen that the prosecution of breeding programs is likely to alter estimates of growth parameters, but the growth pattern may not vary, as has been proven by the trial done in poultry (Marks, 1978). Fresh estimation of growth parameters, consequently, should be carried out every other year in breeding process.
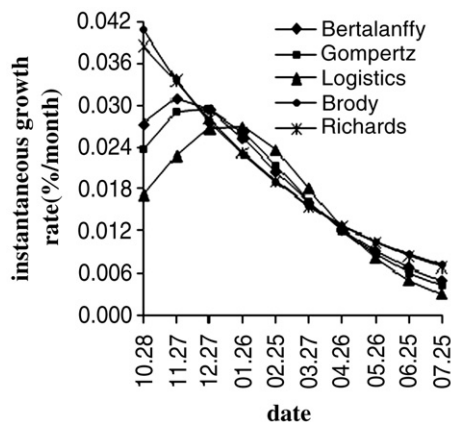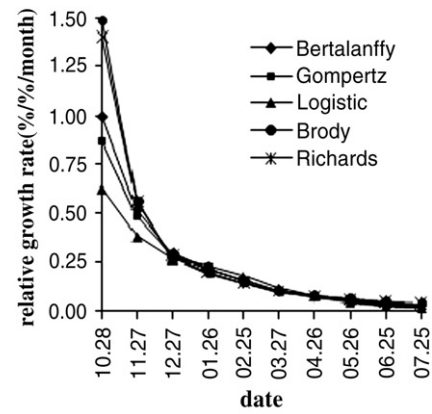
An alternative approach to the study of the bivalve growth is that based on the energy balance equation. Here the growth potential is estimated from physiological measurements of the various constituents of the energy budget (West et al., 2004). When integrated over time and applied to individuals of different sizes, these data can be used to derive an average growth curve. It can provide an excellent method for quantifying the responses of individuals to changing environmental conditions such as food supply, salinity and contaminants. In this respect, this research has yet to be further undertaken. In addition, temperature no doubt has a very important effect on the growth of bivalves (Almada-Villela et al., 1982). During this trial, minimum temperature was 18.1 °C. It could be found that the growth of adductor percentage was very regular, demonstrating that *A. irradians concentricus* has well acclimated itself to the environment of the Beibu bay in South China Sea since its introduction in 1991, and that temperature seemingly does not matter for the growth of the scallop. This accords with Loo and Rosenberg (1983). Unlike Rodhouse et al. (1984a), it appears that no necessity of incorporating temperature as an independent variable into the growth model of adductor percentage should be considered in the study. Perhaps what is really important is planktonic abundance (Page and Hubbard, 1987).

The initial values contained in various growth models should be roughly set predicated on the actual situation of the trait under consideration, or parameter estimates may be not obtained owing to the nonconvergence following iteration. Global instead of local optima can be typically attained because the Levenberg–Marquardt iteration method is not demanding for the setting of parameter initial values. For the parameter initial values and iterative precision as given in the study, convergence arrived at approximately after 20–30 rounds of iteration. The setting of initial values of growth parameters generally doesn't affect the acquisition of global optima in parameter space upon estimating the parameters encompassed in growth models using iteration, but affects only the number of times of iteration (Wang and Li, 1986).

Fig. 6. Fitting Brody model to adductor percentage data.

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