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Development of optimum feeding rate model for white sturgeon (*Acipenser transmontanus*)

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Establishing the optimum feeding rate (OFR; % body weight per day) for a cultured fish is a significant step toward the success of the aquaculture operation. Therefore, the objectives of this study were 1) the estimation of OFR for 19 datasets with different initial body weights by applying broken-line and quadratic regression models and 2) an investigation of potential OFR prediction models using 19 estimated OFRs from objective 1.

Objective 1) Nineteen datasets were obtained from five published studies (14 datasets) and one unpublished study (5 datasets) which were carried out to evaluate the effects of feeding rate on growth performance in white sturgeon of initial body weights varying from 0.05 g to 764 g. Each dataset, containing feeding rate (independent variable) and specific growth rate (% body weight increase per day; dependent variable) was used to estimate OFR by one-slope straight broken-line, two-slope straight broken-line, quadratic broken-line, and quadratic models for each body weight class. Calculations of model selection criteria, including the adjusted coefficient of correlation, Akaike information criterion, and corrected Akaike information criterion were performed to compare model performance on OFR estimation for each dataset. Three models (two-slope straight broken-line, quadratic broken-line, and quadratic models) were considered acceptable for the estimation of OFR, and the three sets of estimated OFRs obtained by these models were used in objective 2.

Objective 2) Several regression models, including polynomial models of order from 1 to 6, a simple exponential model with a constant, and a bi-exponential model, were fitted to each set of the 19 estimated OFRs against transformed initial body weights. A power function model was also fitted to the estimated OFRs against untransformed initial body weights. The model selection criteria for objective 2 were the same as those for objective 1.

Overall model performance on the estimation of OFR for the 19 datasets shows that the quadratic broken-line model performed best, followed by the quadratic, two-slope straight broken-line, and one-slope straight broken-line models. Given the overall performance of model fitness to the sets of the OFR estimates, the bi-exponential regression model emerged as the most favorable one. As a result, the bi-exponential model equation.

$$OFR\ (\%\ body\ weight\ per\ day) = 0.00344(\pm0.0123)\ e^{-5.684(\pm2.309)\ \ln(\sqrt{\text{body weight}})} + 8.695(\pm0.606)\ e^{-0.549(\pm0.065)\ \ln(\sqrt{\text{body weight}})}$$

obtained by fitting the estimated OFRs derived from the quadratic broken-line model analysis, can be used to predict the OFR for white sturgeon from about 0.05 g to 800 g.

1. Introduction

White sturgeon are a commercially important aquaculture species providing meat and caviar for human consumption, and France, Italy, and the USA are the main producers around the world. The total quantities of meat and caviar produced by these countries in 1996 were recorded as approximately 600 t and 1 t, respectively (Bronzi et al., 1999). Estimates of 2012 production for sturgeon aquaculture in the USA alone were approximately 1350 t of meat and between 15 and 20 t of caviar. The majority of this production came from the white sturgeon, 95% from California (F. S. Conte, University of California, Davis, CA, USA; personal communication).

Estimation of optimum feeding rate (OFR; % body weight per day) is an important component for the success of aquaculture operations because feeding rate, water temperature, and fish size are three critical elements for fish growth (Brett and Groves, 1979). Cui and Hung (1995) developed a prototype feeding model to provide OFR for white sturgeon

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from 50 g to 1000 g. However, the prototype model was developed on the basis of the outcomes of analysis of variance (ANOVA) and multiple range tests, assuming that the OFR is estimated as the minimum feeding rate that results in a response which is not significantly different from the maximum response. Generally, growth response to feeding rate is continuous, in that the response increases with increasing feeding rate up to a peak and then it plateaus at the feeding rate beyond the peak. Furthermore, the responses to nutrient or feeding levels show fairly similar patterns.

In his critique, Shearer (2000) stated that it is inappropriate to use the ANOVA and multiple range tests to determine optimum nutrient levels because the nutrient levels are treated as discrete rather than continuous. Shearer also provided a good example of the use of those statistical analyses giving less accurate estimates compared to the application of a regression model such as a second-order polynomial curve for the estimation of optimum nutrient levels. In order to find a more accurate estimate than the ANOVA and multiple range test yield, many researchers have commonly used regression models, such as broken-line and quadratic (also called second-order polynomial) models accounting for dose–response relationships (Pesti et al., 2009; Robbins et al., 1979, 2006; Shearer, 2000; Zeitoun et al., 1976). The broken-line model can be described as a linear line or a quadratic ascending line with either an ascending line, a plateau line, or a descending line, which represents the dose–response relationship between nutrient levels (or feeding rate) and growth. A breakpoint between the two lines indicates the optimum nutrient requirement or the OFR. The quadratic model is represented as a symmetric parabola having a unique maximum point which suggests the optimum nutrient requirement or the OFR that produces the maximum growth. However, a single model application for the estimation of OFR may not provide a best estimate because the design for that particular experiment and the resulting variations in the response can contribute to the selection of an inappropriate model (Shearer, 2000). In addition, the prototype model by Cui and Hung (1995) does not provide OFR for white sturgeon smaller than 50 g. Thus, testing various regression models is appropriate in order to select the best-fit model for the estimation of OFR.

Therefore, the objectives of this study were 1) the estimation of OFR for 19 datasets with different initial body weights by applying broken-line and quadratic regression models and 2) the development of an OFR prediction model that can predict OFR for white sturgeon from about 0.05 g to 800 g using the 19 estimated OFRs from objective 1.

2. Materials and methods

2.1. Description of dataset

Nineteen datasets were obtained from five published (De Riu et al., 2012; Deng et al., 2003; Hung and Lutes, 1987; Hung et al., 1993a, 1995) studies and one unpublished study, which were carried out to evaluate the effects of feeding rate on growth performance in white sturgeon of initial body weights varying from 0.05 g to 764 g. All the studies were carried out by the same laboratory (Dr. Silas Hung, Department of Animal Science, University of California, Davis, CA, USA) and at the same facility (the Center for Aquatic Biology and Aquaculture, University of California, Davis, CA, USA) except the Dataset 19 (a growth trial was performed at a local commercial farm; The Fishery, Galt, California, USA). The datasets, including initial body weight (weight class), number of replications, feeding rate (independent variable), and specific growth rate (SGR; % body weight increase per day) corresponding to the feeding rate (dependent variable) are listed in Table 1. The initial body weight was the average weight of the fish in all tanks when the growth trial began. The number of replications was the number of tanks assigned to each feeding rate. The feeding rate (% body weight per day) was the treatment tested for the evaluation of its effects on SGR. The SGR was the growth response at each feeding rate, calculated from the equation, $100 \times (ln(FBW) - ln(IBW))$ / *days of feeding*, where the *FBW* and *IBW* were the average final and initial body weights, respectively. The water temperature and the feed compositions used for the experiments are described in Table 1. In most of the experiments, continuous automatic feeders were used except the one experiment (Dataset 19) where a demand feeder was used. Other experimental conditions such as water quality (e.g. flow rate, total ammonia, dissolved oxygen, pH, etc.) and tank system, affecting growth performance can be found in the references as indicated in Table 1.

2.2. Estimation of OFR for the 19 datasets (objective 1)

One-slope straight broken-line (One-slope BL), two-slope straight broken-line (Two-slope BL), quadratic broken-line (Quadratic BL), and quadratic (Quadratic) models are common regression models used to estimate optimum nutrient levels or feeding rates. The functional equation forms and the graphical illustrations of the models are shown in Table 2 and Fig. 1, respectively. A brief description of each model is given here.

The One-slope BL model (Equation [1] and Fig. 1[A]) represents a single breakpoint which is the intersection of a positive slope line and a plateau line. The breakpoint is the OFR where SGR is at a maximum.

The Two-slope BL model (Equation [2] and Fig. 1[B]) represents a single breakpoint which is the intersection of a positive slope line and a positive or a negative slope line. The breakpoint is the OFR where SGR is at a maximum.

The Quadratic BL model (Equation [3] and Fig. 1[C]) represents a single breakpoint which is the intersection of a quadratic line and a plateau line. The breakpoint is the OFR where SGR is at a maximum.

The Quadratic model (Equation [4] and Fig. 1[D]) is a second-order polynomial where the OFR is the vertex of the polynomial curve.

The statistical model for the *i*th SGR (y_i) was stated as follows:

$$y_i = f(\boldsymbol{\theta}, x_i) + e_i$$

where x_i was the *i*th feeding rate and e_i was an error term, assumed to have a mean of zero and a variance of σ^2 (assumption of variance homogeneity was evaluated using the Levene's test ($p > 0.05$; Ritz and Streibig, 2008) in all but one dataset (Dataset 19; $p = 0.0406$); the Dataset 19 was included in the datasets for the development of OFR model because this probability was sufficiently close to 0.05). The vector θ was the functional parameters as described in Table 2.

Estimation of OFR for each dataset was performed through the application of the One-slope BL, Two-slope BL, and Quadratic BL models using a nls (nonlinear least-squares) function and of the Quadratic model using a lm (linear model) function, located in the standard library of R 3.0.1 (R Development Core Team, 2013). The R codes for fitting each model to the 19 datasets are provided in Supplementary Material.

To produce a criterion for the comparisons of model performance on OFR estimation for each dataset, the adjusted coefficient of correlation (R^2_{adj}), Akaike information criterion (AIC), and corrected AIC (AICc) were calculated as follows:

$$R^2_{adj} = 1 - \frac{MSE}{MST} = 1 - \frac{SSE/(n-k-1)}{SST/(n-1)}$$

$$\mathrm{AIC} = -2ln(L) + 2k$$

$$\mathrm{AICc} = -2ln(L) + \frac{2nk}{n-k-1} = AIC + \frac{2k(k+1)}{n-k-1}$$

where *SSE* and *SST* are residual sum of squares and total sum of squares corrected for the mean, respectively, *n* is the total number of observations, *k* is the number of parameters, and *L* is the maximum of the likelihood function. All three aforementioned criteria balance goodness-of-fit and model complexity to different extents. AICc penalizes model

Table 1
List of the 19 datasets obtained from the five published studies and the one unpublished study used for the estimation of optimum feeding rate (% body weight per day).

Dataset number	Source	IBW[1](g)	Number of replications[2]	FR[3] (%)	SGR[4] (%)	IE[5] (KJ)	CP[6] (%)	CL[7] (%)	Temperature[8] (°C)
1	Deng et al. (2003)	0.05	4	10, 20, 30, 40, 50, 60	7.5, 9.9, 11.0, 11.2, 11.1, 11.7	19.1	52.5	10.3	19.2
2	Deng et al. (2003)	0.09	4	5, 10, 15, 20, 25, 30	5.3, 9.6, 11.5, 12.1, 12.1, 13.0	19.1	52.5	10.3	19.3
3	Deng et al. (2003)	0.18	4	2.5, 5.0, 7.5, 10.0, 12.5, 15.0	2.0, 5.5, 6.8, 9.2, 10.1, 10.8	19.1	52.5	10.3	19.3
4	Deng et al. (2003)	0.37	4	2.5, 5.0, 7.5, 10.0, 12.5, 15.0	3.9, 7.6, 8.9, 9.2, 8.9, 9.6	19.3	50.0	12.9	19.0
5	De Riu et al. (2012)	2.8	4	3, 4, 5, 6, 7, 8	4.5, 5.8, 6.4, 7.1, 7.6, 7.6	19.0	48.8	12.3	18.0
6	De Riu et al. (2012)	4.5	4	2, 3, 4, 5, 6, 7	2.7, 4.3, 5.2, 6.3, 6.4, 6.2	19.0	48.8	12.3	18.2
7	De Riu et al. (2012)	8.6	4	1, 2, 3, 4, 5, 6	0.9, 2.9, 4.3, 5.5, 6.0, 6.1	19.0	48.8	12.3	18.0
8	De Riu et al. (2012)	10.0	4	1, 2, 3, 4, 5, 6	0.6, 2.6, 3.9, 4.8, 5.6, 5.6	19.0	48.8	12.3	18.0
9	Hung and Lutes (1987)	27.9	3	0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0	0.0, 1.0, 1.6, 2.2, 2.5, 2.6, 2.9, 2.8	21.2	43.0	16.0	20.2
10	Hung and Lutes (1987)	37.0	3	0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0	0.5, 1.1, 1.8, 2.3, 2.4, 2.7, 2.2, 2.3	21.2	43.0	16.0	20.2
11	Hung and Lutes (1987)	49.0	3	0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0	0.3, 1.1, 1.5, 2.0, 2.2, 1.9, 1.7, 1.7	21.2	43.0	16.0	20.2
12	Hung and Lutes (1987)	62.0	3	0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0	0.5, 1.1, 1.6, 1.9, 1.6, 1.1, 1.1, 1.4	21.2	43.0	16.0	20.2
13	Hung et al. (1993a)	30.5	3	2.0, 2.5, 3.0, 3.5	2.2, 2.5, 2.7, 2.8	20.5	40.9	13.8	23.1
14	Unpublished data	359.9	3	0.4, 0.8, 1.2, 1.6, 2.0	0, 0.9, 1.2, 1.5, 1.7	21.9	41.8	19.0	18.0
15	Unpublished data	418.8	3	0.4, 0.8, 1.2, 1.6, 2.0	0.4, 0.7, 1.0, 1.0, 1.0	21.9	41.8	19.0	17.9
16	Unpublished data	470.4	3	0.4, 0.8, 1.2, 1.6, 2.0	0.6, 1.1, 1.1, 1.2, 1.1	21.9	41.8	19.0	18.0
17	Unpublished data	543.5	3	0.4, 0.8, 1.2, 1.6, 2.0	0.6, 1.0, 1.0, 1.0, 0.9	21.9	41.8	19.0	18.1
18	Unpublished data	616.7	3	0.4, 0.8, 1.2, 1.6, 2.0	0.5, 0.9, 0.9, 0.9, 0.9	21.9	41.8	19.0	18.3
19	Hung et al. (1995)	764.0	3	0.5, 0.9, 1.3, 1.7	0.3, 0.6, 0.8, 0.7	N/A[9]	44.0	15.0	22.4

[1] Initial body weight: The average initial weight of fish in all tanks when the growth trial began.
[2] A number of tanks assigned to each feeding rate.
[3] Feeding rate: % body weight per day.
[4] Specific growth rate: % body weight increase per day calculated from the equation, *100 × (ln(FBW) − ln(IBW))/ days of feeding*, where the *FBW* and *IBW* were the average final and initial body weights. The values in the SGR column represented the average SGR of the replicates corresponding to the respective feeding rate shown in the FR column.
[5] Intake energy: The energy content in the diet as fed was calculated using the following values: crude protein 23.6 kJ/g, crude lipid 39.3 kJ/g, and NFE 17.7 kJ/g.
[6] Crude protein: % crude protein contained in the diet as fed.
[7] Crude lipid: % crude lipid contained in the diet as fed.
[8] Average water temperature during a period of the growth trial.
[9] Not available: the IE value was not available because the moisture and ash contents were not recorded in the reference.

complexity the most, whereas R^2_{adj} provides more insight into the goodness-of-fit of a regression model.

2.3. Development of an OFR prediction model (objective 2)

Three models (Two-slope BL, Quadratic BL, and Quadratic models) for the estimation of OFR were considered acceptable on the basis of the model selection criteria from objective 1, and the 3 sets of OFR estimates obtained by these models were used for developing an OFR prediction model.

Table 2
The functional equation forms of the regression models used to estimate optimum feeding rate (OFR; % body weight per day) for the 19 datasets.

[Equation] Model name	$f(\boldsymbol{\theta},x)$[1]	OFR
[1] One-slope BL[2]; Fig. 1[A][6]	$\begin{cases}\beta_0-\beta_1(\beta_2-x), & x<\beta_2\\ \beta_0, & x\geq\beta_2\end{cases}$	β_2
[2] Two-slope BL[3]; Fig. 1[B]	$\begin{cases}\beta_0-\beta_1(\beta_2-x), & x<\beta_2\\ \beta_0+\beta_3(x-\beta_2), & x\geq\beta_2\end{cases}$	β_2
[3] Quadratic BL[4]; Fig. 1[C]	$\begin{cases}\beta_0-\beta_1(\beta_2-x)^2, & x<\beta_2\\ \beta_0, & x\geq\beta_2\end{cases}$	β_2
[4] Quadratic[5]; Fig. 1[D]	$\beta_0+\beta_1x+\beta_2x^2$	$-\beta_1/2\beta_2$

[1] The parameter vector $\boldsymbol{\theta}$ was composed of the parameters β_0, β_1, β_2, and β_3, which were specific to the individual function, and the argument x was feeding rate (% body weight per day). The value of the function $f(\boldsymbol{\theta},x)$ at x was specific growth rate (% body weight increase per day).
[2] One-slope straight broken-line model.
[3] Two-slope straight broken-line model.
[4] Quadratic broken-line model.
[5] Quadratic model (second-order polynomial). The OFR was calculated by solving for x when the derivative of the function was set to zero.
[6] The graphical illustrations of the Equations [1], [2], [3] and [4] are shown in [A], [B], [C], and [D] in Fig. 1, respectively.

After estimating the OFRs from objective 1, the three sets of OFR estimates were plotted against the corresponding *IBWs* (see Supplementary Fig. S1). A variable transformation was needed to obtain a good fit for most regression models because of the rapid decrease in the estimated OFRs at the lower body weights. A good transformation was found to be the natural logarithm of the square root of the *IBW*, so a new variable w was defined as $w = \ln\left(\sqrt{IBW}\right)$. Plots of the estimated OFRs against the transformed *IBWs* (w) are shown in Supplementary Fig. S2.

The regression models (see Table 3), including polynomial models of order from 1 to 6 (Equations [5] to [10], respectively), a simple exponential model with a constant (Equation [11]), and a bi-exponential model (Equation [12]), were applied to fit each set of 19 estimated OFRs against w. A power function regression model (Equation [13]) was also fitted to each set of estimated OFRs against the untransformed *IBWs*.

Fitting the regression models to the sets of estimated OFRs was performed using the lm function for the polynomial models and the nls function for the two exponential models as well as the power function model. Both functions can be found in the standard library of R 3.0.1. The model selection criteria for objective 2 were the same as those for objective 1.

3. Results and discussion

3.1. The OFR estimates (objective 1)

Although the regression models, such as the broken-line and quadratic models, reflect the dose–response relationship better than do the ANOVA and multiple range tests, the use of a single model among the possible regression models can be disputed unless a relevant justification for choosing that model is given. Shearer (2000) pointed out in his critical review that selection of appropriate methods and models for statistical analysis in the estimation of nutrient requirements should

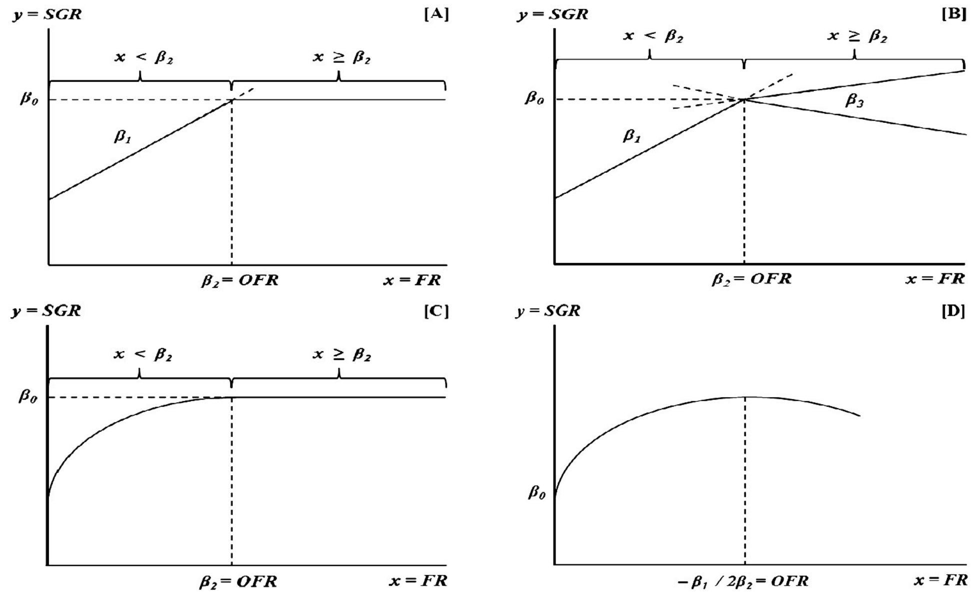

Fig. 1. The graphical illustrations of the one-slope straight broken-line ([A]; Equation [1]), two-slope straight broken-line ([B]; Equation [2]), quadratic broken-line ([C]; Equation [3]), and quadratic ([D]; Equation [4]) models shown in Table 2. The SGR, OFR, and FR represented the specific growth rate (SGR; % body weight increase per day), optimum feeding rate (OFR; % body weight per day), and feeding rate (FR; % body weight per day), respectively. The β_0, β_1, and β_3 in the figures [A] and [B] were defined as the asymptote of the first segment, slope of the first segment, and slope of the second segment, respectively. The β_3 in the figure [B] can be either a positive or a negative slope. The β_0 in the figure [C] was defined as the asymptote of the first segment. The β_0, β_1, and β_2 in the figure [D] were defined as the intercept at $x = 0$, coefficient of the argument x, and coefficient of the argument x^2, respectively (adopted from Zeitoun et al., 1976; Robbins et al., 1979, 2006).

be considered by the researcher. He showed that the re-evaluation of the published data with the Quadratic model resulted in optimum nutrient levels that varied 20% to 400% from the original broken-line models. Thus, it is necessary to test various models for the estimation of OFR and to justify the model that should be chosen based on specific model selection criteria.

The OFRs were estimated for the 19 datasets using the One-slope BL, Two-slope BL, Quadratic BL, and Quadratic models (see Table 4 and Fig. 2). The One-slope BL model for the Datasets 15 and 16 and the Quadratic BL model for the Dataset 16 could not estimate the OFR because the estimation algorithm failed to achieve convergence. The OFR estimates produced by each of the aforementioned models were not identical within each dataset with the magnitude of the difference between the smallest and largest OFR estimates, ranging from 15.4% (between the Two-slope BL and Quadratic models in the Dataset 16) to 162.5% (between the Two-slope BL and either the Quadratic BL or Quadratic models in the Dataset 14). Robbins et al. (2006) stated that optimum levels will be underestimated if a dataset is less adequately fitted by the One-slope BL and Two-slope BL models than by the Quadratic BL model. The results showed that the OFR estimates from the One-slope BL and Two-slope BL models were smaller than those from the Quadratic BL model in all but two datasets (Datasets 12 and 17).

The model selection criteria were calculated for the evaluation of model performance (see Table 4). The duplicate model selection criteria values within a dataset for each of the models were counted individually. The R^2_{adj} values show that the Quadratic BL and Quadratic models (9 out of the 19 datasets, for each model) are the best fit to the datasets, followed by the Two-slope BL (7 datasets) and One-slope BL (3 datasets) models. The AIC and AICc values indicate that the Quadratic BL model (9 out of the 19 datasets) performed best for the estimation of OFR, followed by the Quadratic (8 datasets), Two-slope BL (4 datasets), and One-slope BL (3 datasets) models. The three models (Two-slope BL, Quadratic BL, and Quadratic models) were considered acceptable for the estimation of OFR on the basis of the outcomes of the model selection criteria, and each set of OFR estimates obtained from the three model analyses was used to develop an OFR prediction model in objective 2.

Table 3
The functional equation forms of the regression models used to fit the three sets of optimum feeding rate (OFR; % body weight per day) estimates from the two-slope broken-line, quadratic broken-line, and quadratic model analyses for the development of the OFR prediction model.

[Equation] Model name	Function: $f(w)$ or $f(IBW)$ = predicted OFR
[5] 1st order polynomial model[1]	$f(w) = a_0 + a_1w^1$
[6] 2nd order polynomial model	$f(w) = a_0 + a_1w^1 + a_2w^2$
[7] 3rd order polynomial model	$f(w) = a_0 + a_1w^1 + a_2w^2 + a_3w^3$
[8] 4th order polynomial model	$f(w) = a_0 + a_1w^1 + a_2w^2 + a_3w^3 + a_4w^4$
[9] 5th order polynomial model	$f(w) = a_0 + a_1w^1 + a_2w^2 + a_3w^3 + a_4w^4 + a_5w^5$
[10] 6th order polynomial model	$f(w) = a_0 + a_1w^1 + a_2w^2 + a_3w^3 + a_4w^4 + a_5w^5 + a_6w^6$
[11] Simple exponential model with a constant[2]	$f(w) = ae^{-kw} + z$
[12] Bi-exponential model	$f(w) = ae^{-k_1w} + be^{-k_2w}$
[13] Power function model	$f(IBW) = aIBW^b$

[1] The a_0 to a_6 are estimated parameters unique to the Equations [5] to [10].
[2] The a, b, k, k_1, k_2, and z are estimated parameters unique to the Equations [11] to [13]. The w represents the natural logarithm of the square root of the initial body weight (IBW; g) ($w = \ln(\sqrt{IBW})$).

Table 4
The optimum feeding rate (OFR; % body weight per day) estimates from the one-slope straight broken-line (One-slope BL), two-slope straight broken-line (Two-slope BL), quadratic broken-line (Quadratic BL), and quadratic (Quadratic) model analyses and the values calculated by the model selection criteria, including the adjusted coefficient of correlation (R^2_{adj}), Akaike information criterion (AIC), and corrected AIC (AICc).

Dataset (IBW[1], g)	Model	Estimated OFR (standard error)	R^2_{adj}	AIC[2]	AICc[2]
1	One-slope BL	30.7 (2.5)	0.751	60.74	61.94
(0.05)	Two-slope BL	24.3 (3.2)	0.766	60.03	62.13
	Quadratic BL	37.0 (5.4)	0.769	58.89	60.09
	Quadratic	49.2 (4.2)	0.726	63.00	64.20
2	One-slope BL	15.9 (0.7)	0.923	57.75	58.95
(0.09)	Two-slope BL	11.9 (0.6)	0.958	43.95	46.05
	Quadratic BL	19.6 (1.3)	0.945	49.59	50.79
	Quadratic	25.3 (1.3)	0.912	60.88	62.08
3	One-slope BL	11.2 (0.6)	0.910	69.54	70.74
(0.18)	Two-slope BL	10.1 (1.7)	0.910	70.15	72.25
	Quadratic BL	16.5 (2.1)	0.920	66.59	67.79
	Quadratic	16.5 (2.1)	0.920	66.59	67.79
4	One-slope BL	6.1 (0.3)	0.903	50.32	51.52
(0.37)	Two-slope BL	5.8 (0.4)	0.907	50.01	52.11
	Quadratic BL	8.3 (0.7)	0.905	49.91	51.11
	Quadratic	11.9 (0.6)	0.833	63.29	64.49
5	One-slope BL	6.5 (0.4)	0.824	39.38	40.58
(2.8)	Two-slope BL	6.4 (0.6)	0.815	41.35	43.46
	Quadratic BL	8.1 (0.9)	0.836	37.63	38.83
	Quadratic	8.1 (0.9)	0.836	37.63	38.83
6	One-slope BL	4.8 (0.2)	0.958	12.19	13.39
(4.5)	Two-slope BL	5.1 (0.2)	0.956	14.14	16.24
	Quadratic BL	6.1 (0.3)	0.955	13.95	15.15
	Quadratic	6.1 (0.2)	0.958	12.32	13.52
7	One-slope BL	3.9 (0.2)	0.933	39.53	40.73
(8.6)	Two-slope BL	4.2 (0.4)	0.934	40.00	42.11
	Quadratic BL	5.7 (0.4)	0.944	35.48	36.68
	Quadratic	5.7 (0.4)	0.944	35.43	36.63
8	One-slope BL	4.4 (0.2)	0.954	26.97	28.17
(10.0)	Two-slope BL	4.4 (0.3)	0.952	28.94	31.04
	Quadratic BL	5.9 (0.3)	0.970	16.95	18.15
	Quadratic	5.9 (0.3)	0.970	16.95	18.15
9	One-slope BL	2.6 (0.1)	0.931	7.63	8.83
(27.9)	Two-slope BL	2.1 (0.2)	0.946	2.37	4.47
	Quadratic BL	3.6 (0.2)	0.953	−1.72	−0.52
	Quadratic	3.6 (0.2)	0.953	−1.68	−0.48
10	One-slope BL	1.9 (0.1)	0.931	−7.97	−6.77
(37.0)	Two-slope BL	2.1 (0.1)	0.931	−7.08	−4.98
	Quadratic BL	2.7 (0.2)	0.926	−6.20	−5.00
	Quadratic	3.0 (0.1)	0.928	−6.91	−5.71
11	One-slope BL	1.8 (0.2)	0.797	9.80	11.00
(49.0)	Two-slope BL	2.2 (0.1)	0.861	1.44	3.55
	Quadratic BL	2.3 (0.3)	0.799	9.57	10.77
	Quadratic	2.7 (0.1)	0.839	4.17	5.37
12	One-slope BL	1.4 (0.3)	0.473	17.46	18.66
(62.0)	Two-slope BL	1.7 (0.2)	0.642	8.97	11.08
	Quadratic BL	1.7 (0.5)	0.464	17.85	19.05
	Quadratic	2.5 (0.1)	0.415	19.95	21.15
13	One-slope BL	3.1 (0.2)	0.670	−6.15	−3.15
(30.5)	Two-slope BL	2.7 (0.3)	0.666	−5.59	0.12
	Quadratic BL	3.4 (0.5)	0.705	−7.47	−4.47
	Quadratic	3.4 (0.4)	0.704	−7.46	−4.46
14	One-slope BL	1.4 (0.2)	0.702	15.62	17.80
(359.9)	Two-slope BL	0.8 (0.2)	0.729	14.76	18.76
	Quadratic BL	2.1 (0.5)	0.733	13.98	16.16
	Quadratic	2.1 (0.5)	0.733	13.98	16.16
15	One-slope BL	N/A[3]			
(418.8)	Two-slope BL	1.3 (0.1)	0.936	−34.01	−30.01
	Quadratic BL	1.6 (0.2)	0.905	−28.48	−26.30
	Quadratic	1.6 (0.1)	0.912	−29.69	−27.51
16	One-slope BL	N/A			
(470.4)	Two-slope BL	1.3 (0.3)	0.403	−3.62	0.38
	Quadratic BL	N/A			
	Quadratic	1.5 (0.1)	0.559	−8.74	−6.56
17	One-slope BL	0.8 (0.1)	0.560	−15.98	−13.80
(543.5)	Two-slope BL	0.9 (0.1)	0.610	−17.22	−13.22
	Quadratic BL	0.9 (0.5)	0.560	−15.98	−13.80
	Quadratic	1.4 (0.1)	0.618	−18.08	−15.90
18	One-slope BL	0.8 (0.1)	0.792	−30.65	−28.46
(616.7)	Two-slope BL	0.8 (0.1)	0.771	−28.67	−24.67
	Quadratic BL	1.0 (0.2)	0.792	−30.65	−28.46
	Quadratic	1.5 (0.1)	0.666	−23.58	−21.39

(continued on next page)

Table 4 (*continued*)

Dataset (IBW[1], g)	Model	Estimated OFR (standard error)	R^2_{adj}	AIC[2]	AICc[2]
19	One-slope BL	1.1 (0.2)	0.614	−10.36	−6.93
(764)	Two-slope BL	1.3 (0.1)	0.676	−11.98	−5.32
	Quadratic BL	1.4 (0.4)	0.608	−10.19	−6.76
	Quadratic	1.3 (0.1)	0.668	−12.00	−8.57

[1] Initial body weight: The average initial weight of fish in all tanks when the growth trial began.
[2] The smaller AIC and AICc values indicate the better model for its performance.
[3] Not available: Either the One-slope BL or Quadratic model was not able to estimate OFR due to failure of the estimation algorithm to achieve convergence.

Morgan et al. (1975) developed the general saturation equation as a general model for the nutritional responses of higher organisms from observation that the nutrient–response curves resembled either the hyperbolic saturation curves of the Michaelis–Menten type (Michaelis and Menten, 1913) or the sigmoidal saturation curves described by the Hill equations (Hill, 1913). The shape of the curve for the general saturation model shows that the rate of growth with increasing nutrient levels decreases as the nutrient levels approach their optimum levels, which implies that a nutrient response to the graded levels of nutrients up to the optimum level is more likely curvilinear. Thus, it is reasonable to choose models encompassing the curve-like dose–response relationship of the Quadratic BL and Quadratic models, consistent with our findings.

The Quadratic model has been commonly used by researchers to estimate optimum nutrient levels and/or to estimate an economical proportion of the optimum nutrient level based on diminishing returns (e.g. 95% of optimum level) (Pesti et al., 2009; Shearer, 2000; Zeitoun et al., 1976). The Quadratic model represents a typical dose–response relationship with the growth responses reaching a maximum with increasing nutrient levels, then decreasing when the nutrient levels increase to intolerable levels. Shearer (2000) showed that re-evaluation of published nutrient requirements, using the Quadratic model, provided the best fit based on residual analysis in 18 out of the 30 cases. In spite of the advantages of using the Quadratic model for the estimation of nutrient requirement levels, this model does not seem to represent the feeding rate–response relationship as well as the Quadratic BL model does. A number of the similar feeding rate–response patterns, exhibiting that the response tends to plateau when fish are fed above the OFR rather than decreasing, can be observed in the literature (De Riu et al., 2012; Deng et al., 2003; Eroldogan et al., 2004; Ghosh et al., 1984; Hung and Lutes, 1987; Hung et al., 1989, 1993a,b; Okorie et al., 2013; Santiago et al., 1987). The plots shown in Fig. 2 also represent the typical feeding rate–response relationship. The behavior of farmed fish generally shows cessation of feeding once they are satiated, and the growth response to overfeeding seems not to change unless excessive uneaten feeds deteriorate rearing water quality. Thus, given the overall performance of the estimation of the OFR for the 19 datasets, the Quadratic BL model emerged as the most favorable one.

Shearer (2000) stated that the selection of dietary input levels is critical to the estimation of optimum nutrient requirements because inappropriately selected levels, resulting in an atypical dose–response curve, cannot be salvaged even by the best statistical test. He suggested that the allocation of the input levels should be distributed as 1/4 in the ascending portion of the curve, 1/2 near the estimated requirement, and 1/4 where the curve begins to decline (or to plateau). In this study, the selected feeding rate levels of the 19 datasets did not completely meet these criteria; however, the typical feeding rate–response curve was observed in most of the datasets (see Table 1 and Fig. 2).

Data quality is also critical to the estimation of OFR because the R^2_{adj}, AIC, and AICc values are correlated with the deviations of observations from estimates. Although the Quadratic BL model was chosen as the best one among the tested regression models based on the model performance and the observation of the feeding rate–response pattern, the efficiency of out-performance by this model was nearly 50% (9 out of the 19 datasets), which might call into question its feasibility. The low efficiency (but highest among the tested models) may be attributed to the high deviations of the responses from the typical curve (Datasets 12, 16, and 17; see Table 4 and Fig. 2), numerically indicated by the small R^2_{adj} values of all the models in these datasets. It is unclear why the unusual responses were observed; however, they could be attributed to the high variations of the initial body weights when the growth trials began (e.g. 61.9 ± 16.7 g (mean ± SD) in the Dataset 12 compared to 2.8 ± 0.1 g in the Dataset 5).

3.2. The OFR prediction models (objective 2)

Although the Quadratic BL model performed best among the tested models for the estimation of OFR for the 19 datasets, the Two-slope BL and Quadratic models were still chosen for the development of OFR prediction model because they are commonly used in nutrient requirement research for fish. The results of the Two-slope BL and Quadratic models are provided in Supplementary Table S1 and Fig. S3, and Supplementary Table S2 and Fig. S4, respectively.

The three plots of the estimated OFRs from the aforementioned models, plotted against the corresponding *IBWs*, are presented in Supplementary Fig. S1. Due to the sharp "drop and turn" of the OFR estimates when the *IBWs* were small it was difficult to fit most regression models using the original data. Therefore, the data was transformed using the natural logarithm of the square root of the *IBWs*, $w = ln\left(\sqrt{IBW}\right)$, where w is the transformed *IBW*. As the result of the transformation, the more gradually declining trend on the OFR estimates against w was attained (see Supplementary Fig. S2).

The OFR prediction model equations of the polynomial, exponential, and power function regression models were obtained by fitting these regression models to the three sets of OFR estimates (see Table 5 for the Quadratic BL model; Supplementary Table S1 for the Two-slope BL model; and Supplementary Table S2 for the Quadratic model). The plots of the predicted OFRs, determined by the OFR prediction model equations, and the observed OFRs, estimated by the Quadratic BL, Two-slope BL, and Quadratic models, plotted against w and against the untransformed *IBW* are presented in Fig. 3 and in Supplementary Fig. S3 and S4, respectively. The plots showed that the predicted OFRs, determined by the simple exponential and bi-exponential regression models, were fitted to the observed OFRs just as good as the polynomial regression model of higher orders. Noticeably, the power function regression model performed poorly when the *IBWs* were small.

The R^2_{adj}, AIC, and AICc values for the comparison of model performance on the fitness of the polynomial, exponential, and power function regression models to each set of estimated OFRs are shown in Table 6, using the data from the Quadratic BL model analysis and in Supplementary Table S3, using the data from the Two-slope BL and Quadratic model analyses. Due to its simplicity the power function regression model was selected by the AICc in two out of the three cases; however, the goodness-of-fit was relatively poor compared to the exponential regression models, indicated by the small R^2_{adj} values. The model's poorness-of-fit was also shown on the figures, especially when the *IBWs* were small. The performance of the 6th order polynomial regression model

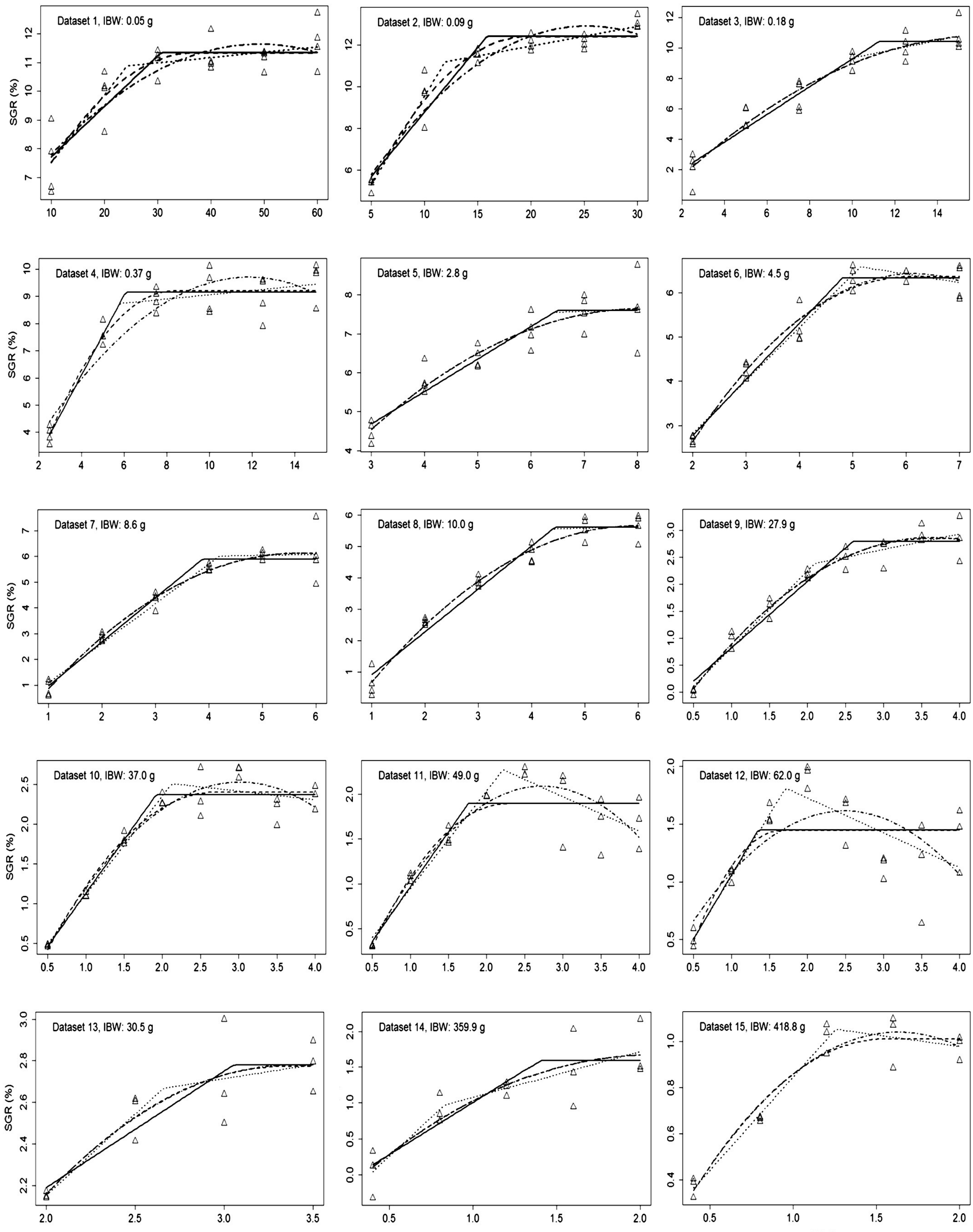

Fig. 2. The plots of the line/curve fits to the 19 datasets, performed by the one-slope straight broken-line (———), two-slope straight broken-line (·········), quadratic broken-line (- - - -) and quadratic (—·—·—·) model analyses. The symbol (Δ) indicated the specific growth rate (SGR; % body weight increase per day) responding to each feeding rate (FR; % body weight per day). The initial body weight (*IBW*; g) was the average initial weight of fish in all tanks when the growth trial began. The one-slope straight broken-line model for the Datasets 15 and 16 and the quadratic broken-line model for the Dataset 16 were not able to estimate the optimum feeding rate (% body weight per day), due to failure of the estimation algorithm to achieve convergence.

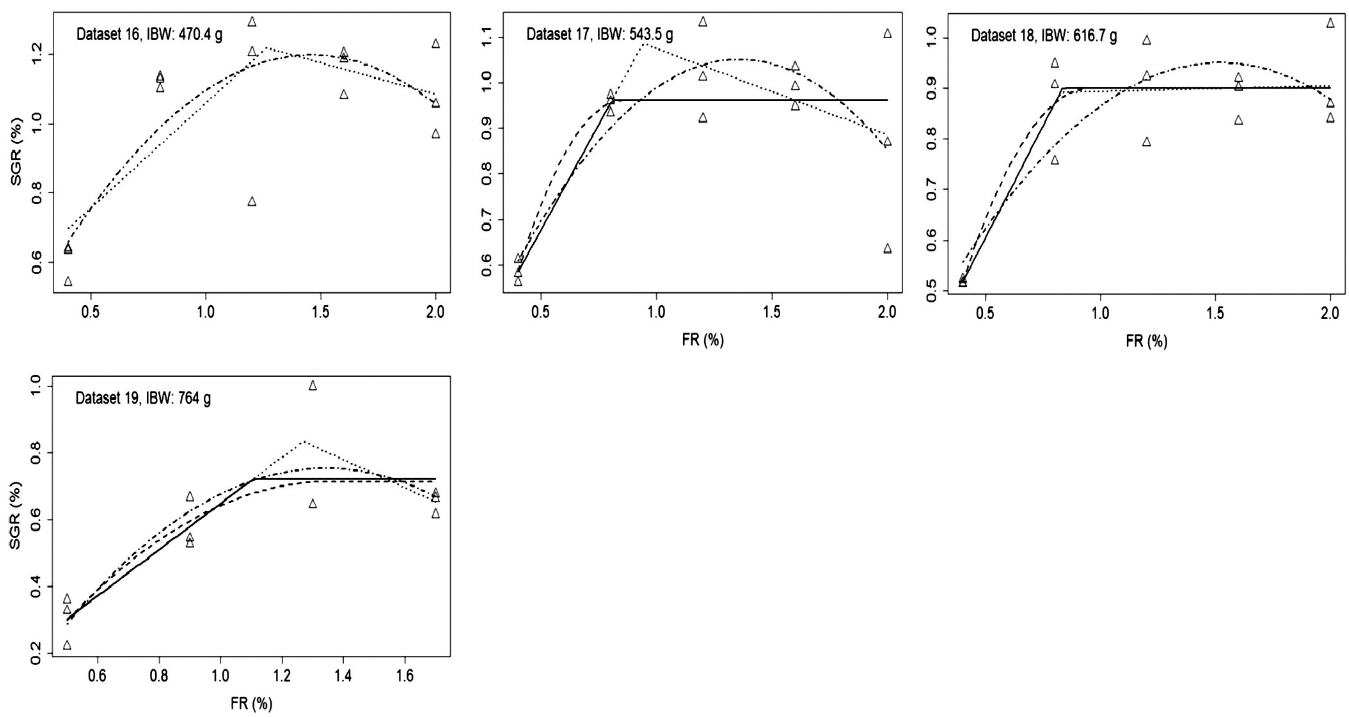

Fig. 2 (*continued*).

was considered good on the basis of the larger R^2_{adj} and smaller AIC values compared to the other models' values; however, the model performance was penalized by the AICc showing the largest value among all the models because of the number of parameters. The bi-exponential model, less complex than the polynomial regression model of higher orders, showed the largest R^2_{adj} values in two out of the three cases and the comparatively small AICc values in all the cases. Otherwise, there are the caveats of using the bi-exponential model, which are 1) that this model provides an asymptotic estimate, almost zero OFR, when the body weight is very large and 2) that the

Table 5
The optimum feeding rate (OFR; % body weight per day) prediction model equations, obtained by fitting the polynomial, exponential, and power function regression models to the OFR estimates from the quadratic broken-line model analysis.

Polynomial regression model ($f(w)^1 = a_0 + a_1w^1 + \cdots + a_dw^d$, $d = 1,\ldots,6$)

Order	Estimated coefficients (standard error) $\hat{a}_0$	$\hat{a}_1$	$\hat{a}_2$	$\hat{a}_3$	$\hat{a}_4$	$\hat{a}_5$	$\hat{a}_6$
1	13.681	−4.895	–	–	–	–	–
	(1.617)	(0.798)					
2	11.344	−8.276	1.677	–	–	–	–
	(1.244)	(0.961)	(0.390)				
3	7.146	−7.114	4.773	−0.993	–	–	–
	(1.543)	(0.806)	(0.946)	(0.288)			
4	6.647	−2.185	4.335	−3.561	0.706	–	–
	(0.949)	(1.113)	(0.586)	(0.549)	(0.143)		
5	8.212	−1.123	1.111	−3.695	1.863	−0.265	–
	(0.937)	(0.967)	(1.219)	(0.443)	(0.420)	(0.093)	
6	8.637	−1.516	0.205	−3.033	2.105	−0.501	0.039
	(1.288)	(1.270)	(2.207)	(1.401)	(0.649)	(0.480)	(0.078)

Exponential and power function regression models

Model	Estimated coefficients (standard error) $\hat{a}$	$\hat{b}$	$\hat{k}$	$\hat{k}_1$	$\hat{k}_2$	$\hat{z}$
Simple exponential	3.339	–	1.515	–	–	2.786
($f(w) = a\,e^{-kw} + z$)	(1.043)		(0.220)			(0.646)
Bi-exponential	0.00344	8.695	–	5.684	0.549	–
($f(w) = a\,e^{-k_1w} + b\,e^{-k_2w}$)	(0.0123)	(0.606)		(2.309)	(0.065)	
Power function	8.761	−0.427	–	–	–	–
($f(IBW)^2 = aIBW^b$)	(1.111)	(0.050)				

[1] $f(w)$ = the predicted OFR at w, where the w represented the natural logarithm of the square root of the initial body weight (IBW; g) ($w = \ln\left(\sqrt{IBW}\right)$).
[2] The value of the function $f(IBW)$ at IBW indicates the predicted OFR.

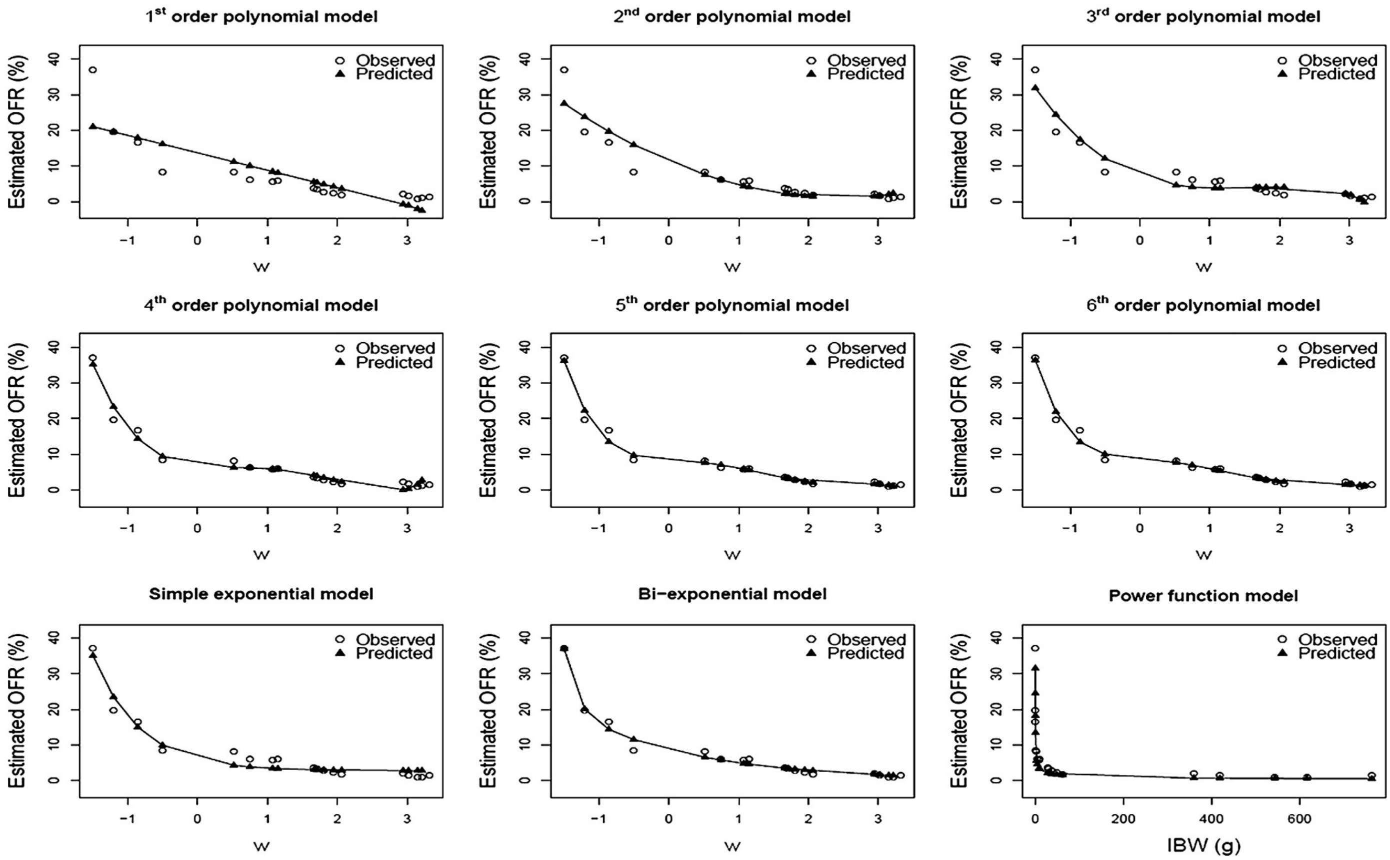

Fig. 3. The plots of the observed and predicted optimum feeding rates (OFR; % body weight per day) against the transformed initial body weights (*IBW*; g) ($w = \ln\left(\sqrt{IBW}\right)$) and the untransformed *IBW* (g). The observed OFRs were identical to the OFRs estimated by the quadratic broken-line model analysis. The predicted OFRs were determined by each one of the OFR model equations shown in Table 5.

standard errors of the estimated coefficients (especially, $\hat{a}$) are relatively large compared to the power function and 6th order polynomial regression models. The establishment of restriction from using this model for white sturgeon larger than about 800 g will prevent underestimation of OFR with large body weights. Also, the large standard errors may be negligible because the overall fitness of the model to the observations is good, indicated by the larger R^2_{adj} and smaller AICc values and the very good fit as shown in Fig. 3 and in Supplementary Fig. S3 and S4. Thus, given the overall performance of model fitness, the bi-exponential regression model emerged as the most favorable one.

Table 6
The values calculated by the model selection criteria, including the adjusted coefficient of correlation (R^2_{adj}), Akaike information criteria (AIC), and corrected AIC (AICc), for the polynomial, exponential, and power function models fitting the estimated optimum feeding rates (% body weight per day) from the quadratic broken-line model analysis.

Regression model	R^2_{adj}	AIC[1]	AICc[1]
1st order polynomial	0.662	113.81	119.06
2nd order polynomial	0.838	101.36	119.76
3rd order polynomial	0.905	92.30	131.59
4th order polynomial	0.964	75.29	144.98
5th order polynomial	0.977	67.91	179.91
6th order polynomial	0.975	69.50	238.96
Simple exponential	0.941	83.09	101.49
Bi-exponential	0.979	65.53	104.81
Power function	0.910	89.95	95.20

[1] The smaller AIC and AICc values indicate the better model for its performance.

3.3. Applications and limitations of the OFR prediction model

The approach used in this study is unique and informative because of the large number of datasets (19), the use of multiple statistical criteria, the wide range of starting body weights (0.05 g to 764 g), and lack of similar studies in the literature.

The main purpose of the development of the OFR prediction model is the provision of an OFR estimate providing a maximum growth, applicable for both experimental settings and aquaculture facilities. In general, experimental or aquaculture conditions, such as water quality (temperature, dissolved oxygen, nitrogenous waste, pH, etc.), nutrient composition of feeds, and stocking density, can affect growth performance. The experimental conditions of the studies that provided the 19 datasets for the development of the OFR prediction model were well maintained facilitating favorable growth conditions. When the OFR prediction model is applied in sophisticated culture systems with high stocking densities (e.g. recirculating system), a good water quality management program is essential to achieve desirable outcomes and to avoid low oxygen and high nitrogenous waste levels.

Reduction in feed costs and maximization of growth are two major goals for an aquaculture operation. The OFR prediction model, however, does not necessarily provide the highest feed efficiency by feeding fish at the predicted OFR because this model was developed using the datasets obtained by the feeding trials with the specific continuous feeding regime, resulting in potentially undesired feed wastes. However, feed costs of feeding small fish is relatively low compared to costs of feeding large fish as a total amount of feed increases with increasing fish size even though OFR decreases. Lower nutritional status in young fish, resulting from underfeeding, leads to lower final weight and reduced tolerance to stress (Buckley et al., 1999; Deng et al., 2009), which will negatively affect the aquaculture operation. Thus, application of the OFR prediction model can be a cost-effective technique to maximize growth of white sturgeon, resulting in higher productivity which will likely override any potential loss due to feed costs.

4. Summary

The three best models to estimate the OFR for 19 datasets were the Two-slope BL, Quadratic BL, and the Quadratic models. Based on the results from objective 1, the estimation of OFR for a given dataset requires the consideration of various possible models and then choosing a best-fit model based on specific model selection criteria in order to have an accurate estimate. In addition, selection of appropriate input levels and conditions are essential to control data quality and to ensure that the chosen model provides the most accurate estimate based on the specific model selection criteria.

The OFR estimates from objective 1 were used to develop a prediction equation that could estimate the OFR at different body weights. The model that was superior, after testing several models, was the bi-exponential model and is recommended for use with white sturgeon from about 0.05 g to 800 g. The newly developed bi-exponential OFR prediction equation, obtained by fitting the estimated OFRs derived from the Quadratic BL model analysis, is

$$OFR(\%\ body\ weight\ per\ day) = 0.00344(\pm 0.0123)e^{-5.684(\pm 2.309)\ \ln(\sqrt{\text{body weight}})} + 8.695(\pm 0.606)e^{-0.549(\pm 0.065)\ \ln(\sqrt{\text{body weight}})}.$$

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.aquaculture.2014.06.007.

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