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TOWARDS IMPROVING GROWTH ESTIMATION IN FISH: MULTI-MODEL INFERENCE AND ITS APPLICATION IN FRESHWATER FISH

ZORAN MARINOVIĆ[1], JELENA LUJIĆ[2], VIOLETA BOLIĆ-TRIVUNOVIĆ[1], GORAN MARKOVIĆ[3]
[1]Department of Biology and Ecology, Faculty of Sciences, University of Novi Sad, Novi Sad, Sebia
[2]Department of Aquaculture, Szent Istvan University, Godollo, Hungary
[3]Faculty of Agronomy, University of Kragujevac, Serbia

U SUSRET POBOLJŠANJU PROCENE RASTA RIBE: MULTI-MODELNA ANALIZA I NJENA PRIMENA KOD SLATKOVODNIH RIBA

Apstrakt

Cilj ovog istraživanja je bio da se uporedi multi-modelna analiza (MMI) u modelovanju rasta riba sa tradicionalnom metodom odabira najbolje odgovarajućeg modela kod slatkovodne ribe *Carassius gibelio* (Bloch 1782). Korištena su četiri modela (Von Bertalanffy, Gompertz, Robertson i power funkcije) za modelovanje rasta jedinki vrste *Carassius gibelio* iz reke Stari Begej. Iako je Power funkcija bila najbolje odgovarajuća, u svim slučajevima je više od jednog modela bilo značajno podržano te je stoga primenjeno usrednjavanje modela kako bi se dobili srednji model i tempo rasta. Kada je više od jednog modela podržano, preporučeno je da se koristi MMI koja omogućuje preciznije određivanje parametara rasta.

Ključne reči: srebrni karaš, usrednjavanje modela, multi-modelna analiza
Keywords: Prussian carp, model averaging, multi-model inference

INTRODUCTION

Information regarding fish age and growth is of great importance for stock assessment, fisheries management and conservation strategies (Liu et al., 2009; Wells et al., 2013). Therefore, a mathematical expression for relating fish size to its age is needed (Katsanevakis, 2006; Katsanevakis and Maravelias, 2008). Most of the studies dealing with fish growth are based on fitting one growth model (most commonly the von Bertalanffy growth function, hereafter VBGF) or several *a priori* determined models (such as Gompertz, Robertson and others) to the length-at-age data. In this case, one model is selected as the best fitting based on the principle of parsimony according to Akaike's Information Criterion (AIC) (Katsenevakis, 2006). However, this method leaves a high degree of uncertainty, leads to bias in estimates and overestimation of precision. In order to compensate for these deficiencies, a new approach was recently proposed, one that will have a significant advantage over the traditional picking of the 'best fitting model'. By model averaging, multi model inference (MMI) provides a more stable inference, reduces model selection bias and acquires higher precision when compared to the selection of 'best fitting model' (Burnham and Anderson, 2001; Katsanevakis, 2006).

Our aim was to implement multi-model analysis in evaluating growth of Prussian carp *Carassius gibelio*, use model-averaging to derive average growth parameters and growth rates and compare this method to the traditional one.

MATERIAL AND METHODS

Sampling was conducted along the Stari Begej River (45°15'17.60"N, 20°23'54.06"E) during July to October 2007 and July to October 2008 with gill nets of various mesh sizes and standard electrofishing device. Every individual was measured for total and standard length (±1 mm) and weighted for body weight (±1 g). Sex was determined by macroscopic observation of the gonads. Scales from the left side, above the lateral line in front of the dorsal fin, of every individual were removed for age determination.

Four models were fit to length-at-age data for both sexes independently: the asymptotic (1) von Bertalanffy growth function (VBGF): $L_t = L_\infty(1 - exp^{-k(t-t_0)})$, (2) Gompertz growth function (GGF): $L_t = L_\infty exp^{-exp^{-k(t-t_0)}}$, and (3) Robertson growth function (RGF): $L_t = L_\infty/(1 + exp^{-k(t-t_0)})$, where L_t is the total length, L_∞ is the asymptotic length, k is the growth coefficient, t is the age and t_0 is the theoretical age when length equals zero (L_t = 0) in all three models; and the non-asymptotic (4) power function (PF): $L_t = a_0 + a_1 t^b$. Models were fit using least squares non-linear regression in STATISTICA v12 software (Statsoft Inc., Tulsa, OK, USA). The best fitting models were compared between sexes by using F-statistic (Chen et al., 1992).

Selection of the best fitting model among the candidate models was done by using the Akaike's Information Criterion corrected for small sample sizes (AIC_c) (Katsanevakis, 2006): $AIC_c = N \log \frac{RSS}{N} + 2k + \frac{2k(k+1)}{(N-k-1)}$ where N is the sample size, RSS is the residual sum of squares, k is the number of estimated parameters. The model with the smallest AIC_c ($AIC_{c,min}$) was considered to be the best fitting model among the candidate models. Furthermore, differences from the $AIC_{c,min}$ were calculated as $\Delta_i = AIC_{c,i} - AIC_{c,min}$ where i indexes the growth models. Models with $\Delta_i > 10$ were considered to have no support, models with $2 < \Delta_i < 10$ were considered to have little support, and models with $\Delta_i < 2$ were considered to have significant support. In addition, Akaike's weight (w_i) was used to assess the best fitting model and was calculated as: $w_i = \frac{exp^{(-0.5 \times \Delta i)}}{\sum_{i=1}^{8} exp^{(-0.5 \times \Delta i)}}$. The model with the highest Akaike's weight was considered to be the best fitting among the candidate models. In many cases more than one model was significantly supported ($\Delta_i < 2$) and Akaike's weight displayed no 'clear winner' ($w_i < 0.9$). Therefore, we included multi-model inference (MMI) by model-averaging in the study and calculated average model and average growth rate as described in Katsanevakis and Maravelias (2008).

RESULTS

Among the 515 individuals sampled, 240 individuals were females (W: 7-128 g; TL: 8.5-19 cm), 178 were males (W: 13-144 g; TL: 9.5-20.5 cm) and 97 were juveniles (W: 2-35 g; TL: 5.5-12.5 cm). Female: male sex ratio differed significantly from the expected value of 1:1 (χ^2=9.196, d.f.=1, p<0.01). ANOVA showed no significant differences in weight and total length between sexes (p > 0.05). Age of juvenile individuals ranged from 0^+ to 2^+, while age of females and males ranged from 1^+ to 4^+.

Considering that length-at-age data did not significantly differ between sexes, length-at-age data for the juvenile individuals was added to both sexes for growth modeling. Based on AIC_c, PF was the best fitting model in describing growth for both sexes (Table 1, Fig. 1A). However, it was not the only model significantly supported by the data since all chosen models had Δ_i values below 2 and Akaike's weights above 0.1. Since the F statistic displayed no significant difference between sexes in the best fitting growth model ($F = 0.14$, $p > 0.05$), data for both sexes were pooled and growth models were recalculated. PF was the best fitting model for the combined sexes, followed by VBGF and GGF which were also significantly supported, and RGF which had little support (Table 1).

Table 1. Estimated growth models for *Carassius gibelio* from the Begej River per sex using the asymptotic von Bertalanffy (VBGF), Gompertz (GGF) and Robertson (RGF) growth functions and the non-asymptotic power function (PF). Parameters estimated: Akaike's Information Criterion (AIC_c), differences from $AIC_{c,min}$ (Δ_i) and Akaike's weights (w_i) for each model. The best fitting models are bolded.

Sex	Model	AIC_c	Δ_i	w_i
Females	VBGF	111.44	0.45	0.28
	GGF	111.97	0.98	0.21
	RGF	112.48	1.50	0.16
	PF	**110.99**	**0.00**	**0.35**
Males	VBGF	81.13	0.73	0.27
	GGF	81.81	1.42	0.19
	RGF	82.48	2.08	0.14
	PF	**80.39**	**0.00**	**0.39**
Combined	VBGF	161.66	0.85	0.28
	GGF	162.53	1.73	0.18
	RGF	163.41	2.61	0.12
	PF	**160.80**	**0.00**	**0.43**

Since more than one model was significantly supported, multi-model inference by model averaging was used to develop an average growth rate (Fig. 1B).

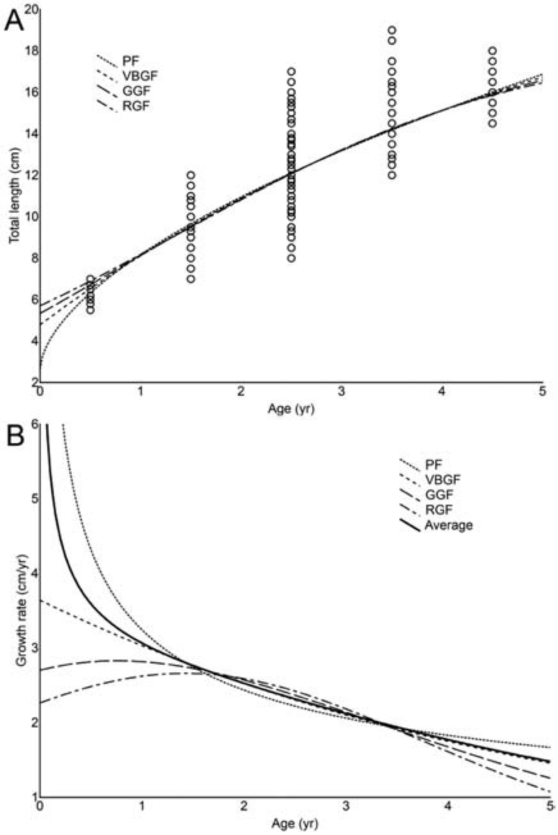

Figure 1 (A, B). Estimated growth functions (A) and growth rates (B) for *Carassius gibelio* sampled from the Stari Begej River. VBGF – Von Bertalanffy growth function; GGF – Gompertz growth function; RGF – Robertson growth function; PF – Power function. Lines indicate growth functions while circles indicate observed length-at-age data.

DISCUSSION

Growth assessment in fish is essential for stock assessment and management strategies (Liu et al., 2009; Wells et al., 2013). The most commonly applied growth model in fisheries science is the VBGF (Katsanevakis, 2006; Katsanevakis and Maravelias, 2008). However, several studies have reported that this growth model is not always the best fitting one. This was observed for *Thunnus albacores*, *Carcharhinus plumbeus* (Katsanevakis, 2006), *Bathyraja interrupta* (Ainsley et al., 2014), *Galeus sauteri* (Liu et al., 2011) and other. Therefore, the usage of different competing growth models in fitting length-at-age data can offer an advantage in providing a more realistic growth assessment. Furthermore, using methods as *AIC* which is indicative of the robustness of the fit can reduce error of growth fits and point out the 'best fitting' model.

In the present study we have successfully implemented multi-model analysis in growth assessment of Prussian carp. To the authors’ knowledge, this is one of the first studies to implement multi-model analysis in growth estimation of this species, and in freshwater species in general. According to AIC_C, PF was the best fitting model in all cases. Since this model was not the only one significantly supported, picking only this model as the best fitting would leave a great deal of uncertainty and overestimate precision. Therefore, an average growth model which would account for the left uncertainty and would provide a more stable inference was developed. When looking at the average growth rate (Fig. 1B), the average model follows the pattern of the power model during the first year, but then changes and completely follows the pattern of the VBGF. When taking biometric data into account, young of the year individuals have length span from 5 cm to 7 cm, and after gain on average 2 – 3 cm per year afterwards. Therefore we believe that the average model did provide a more stable and precise inference than any of the chosen models.

CONCLUSION

As discussed above, model averaging has significant advantages over the picking of the ‘best fitting’ model. Since this method was most commonly applied in marine species, we demonstrate that model averaging should be used in freshwater species as well. Since many of these species are threatened or endangered because of overfishing and other anthropogenic activities, precise growth estimates may provide a more suitable and successful management strategies for endangered species, but may also provide a better insight into life-history characteristics of invasive species and enable creating better management strategies for them as well.

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