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Calendar and thermal time-based growth models for common carp and pikeperch, and the influence of stocking strategy in Lake Balaton, Hungary

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Abstract – Common carp *Cyprinus carpio* and pikeperch *Sander lucioperca* are widely distributed and economically important freshwater fishes. Because these species are extensively stocked both within and outside of their native ranges, it is important to assess the effect of these actions. We aimed to analyse growth rate and its variability related to stocking strategy (season × lake area × habitat × fish size) in common carp and pikeperch in Lake Balaton (Hungary), based on cooperative tagging experiments with anglers. In both species, length increment was more closely associated with thermal time (degree-day sum) over 8 °C threshold water temperature than calendar time. Except a marked decrease with increasing fish size, stocking parameters had little effect on length increment. Growth models based on the GROTAG method and the von Bertalanffy's asymptotic length (L_∞) and growth rate (K) are provided. Compared to other habitats, estimated growth rate proved to be high in common carp (128 mm year^{-1} at 300 mm standard length) and modest in pikeperch (61 mm year^{-1} at 250 mm standard length). We concluded that stocking rate even might be increased in common carp, while management of the pikeperch population should rather be based on catch restriction measures than intensified stockings.

Keywords: angling / degree-day sum / fisheries management / growth rate / mark and recapture

Résumé – Modèles de croissance basés sur le temps calendaire et thermique pour la carpe commune et le sandre; influence de la stratégie d'empoissonnement au lac Balaton, Hongrie. La carpe commune *Cyprinus carpio* et le sandre *Sander lucioperca* sont des poissons d'eau douce largement distribués et économiquement importants. Étant donné que ces espèces sont largement déversées à l'intérieur et à l'extérieur de leur aire de répartition naturelle, il est important d'évaluer l'effet de ces actions. Nous avons cherché à analyser le taux de croissance et sa variabilité liés à la stratégie d'empoissonnement (saison × superficie du lac × habitat × taille du poisson) chez la carpe commune et le sandre du lac Balaton (Hongrie), sur la base d'expériences de marquage en coopération avec les pêcheurs à la ligne. Chez les deux espèces, l'incrément de longueur était plus étroitement associé au temps thermique (somme des degrés-jours) au-dessus seuil de 8 °C pour la température de l'eau que le temps calendaire. Sauf une diminution marquée avec l'augmentation de la taille des poissons, les paramètres d'empoissonnement ont eu peu d'effet sur l'augmentation de la longueur. Des modèles de croissance basés sur la méthode GROTAG, et la longueur asymptotique de von Bertalanffy (L_∞) et le taux de croissance (K) sont fournis. Par rapport à d'autres habitats, le taux de croissance estimé s'est avéré élevé chez la carpe commune (128 mm année^{-1} à 300 mm de longueur standard) et modeste chez le sandre (61 mm année^{-1} à 250 mm de longueur standard). Nous avons conclu que le taux d'empoissonnement pourrait même être augmenté chez la carpe commune, alors que la gestion de la population de sandre devrait plutôt être basée sur des mesures de restriction des prises que sur des empoissonnements intensifiés.

Mots-clés : pêche à la ligne / somme de degrés-jours / gestion des pêches / taux de croissance / marquage et recapture

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1 Introduction

Common carp *Cyprinus carpio* and pikeperch *Sander lucioperca* are common native species of considerable ecological role, and high economic and game fishing importance in majority of Eurasian lowland freshwaters. However, due to overexploitation and human induced degradation of spawning and nursery areas, their natural recruitment is usually short to sustain abundant populations (Saulamo and Thoresson, 2005; Freyhof and Kottelat, 2008; Specziár and Erős, 2016). Moreover, there is a high demand for these species outside of their native ranges, too (Hickley and Chare, 2004; Copp *et al.*, 2005). Therefore, aquaculture-reared individuals of common carp and pikeperch are widely used to supplement or maintain their stocks (FAO, 2005-2018).

Since releasing fish to natural ecosystems, on the one hand, represents an ecological risk through food-web interactions (Fickling and Lee, 1983; Vilizzi *et al.*, 2015), and on the other hand, breeding and releasing of fish require high financial and labour investment, it is important to monitor the effect of stocking programs (Arlinghaus *et al.*, 2016). Growth rate of fish can provide valuable supplementary indications in these regards. In general, there is a strong relationship between the growth rate of fish and ecosystem productivity, the density and quality of the available food supply, and the degree of inter- and intraspecific competition (Kennedy and Strange, 1986; Keskinen and Marjomäki, 2003; Lorenzen, 2016). An insufficient growth rate could be an indication of overstocking and/or inappropriate environmental condition for the stocked species (Arlinghaus *et al.*, 2016). Information about the growth parameters is also essential for the assessment of stock status and sustainable fisheries yields (Lorenzen, 2016). Conditions of releasing, like season, area and body size, however, may also affect the survival rate, distribution and growth of the stocked fish (Gunn *et al.*, 1987; Vostradovský, 1991; Fielder, 1992; Michaletz *et al.*, 2008).

Balaton is a much preferred recreational lake, which fish populations are intensively harvested by angling. Therefore, regular stockings are needed to supplement stocks of the most preferred game fishes, and accordingly, about 350 tons of 2 and 3 years old common carp and 60 000 individuals (or 6 tons) of 1-year-old pikeperch are released to Lake Balaton, annually. In order to improve the efficiency of these stockings, a fish tagging program was implemented in cooperation with the anglers. Investigations revealed that both recapture rate and distribution of the stocked fish could considerably vary among releasing set-ups (Specziár and Turcsányi, 2014, 2017). However, it is not yet known how the releasing strategy influences the growth rate of fish and how the stocked fish grow?

Accordingly, in this study we set the goals: (i) to evaluate the effect of releasing strategy (*i.e.* season × lake area × habitat × fish size) on the length increment of stocked two summer old common carp and one summer old pikeperch, and (ii) to provide models about the length increment of these species in Lake Balaton, by using the information obtained from tagging experiments. Most often, size increment of fish is examined relative to calendar time (Francis, 1988a; Wootton, 1998). However, since instantaneous rate of growth of fish is largely affected by the ambient water temperature, it is suggested that period of growth should preferably be defined as degree-day sum (also known as thermal time approach) at a species-specific threshold temperature, which is an index of the metabolically relevant thermal energy that was experienced over the period of observation (Neuheimer and Taggart, 2007; Chezik *et al.*, 2014). Therefore, to provide more comprehensive analyses, we used both approaches. For research point (i) we hypothesised that length increment of fish, related either to number of days or to degree-day sum, will not be influenced by the stocking season over several years of post-stocking observation period. On the other hand, since primary production increases toward the south-western end (Keszthely basin) of the lake (Istvánovics *et al.*, 2007), we predicted that length increment of fish released at different areas should reflect this pattern. We also predicted that due to the moderate distances between the relevant releasing sites (*ca.* 2 km), fish could rapidly shift between offshore and inshore habitats, and therefore, habitat of stocking will not influence their growth rate. Finally, in accordance with the general pattern of individual lifetime growth trajectories (von Bertalanffy, 1957; Wootton, 1998), we predicted a marked variance in the growth rate related to fish size at stocking, with smaller length increment in larger size-groups.

2 Materials and methods

2.1 Study area

This study was conducted on large and shallow Lake Balaton (surface area: 593 km^2; mean depth: 3.2 m) situated in Hungary, Central Europe (at 46° 42′–47° 04′ N, 17° 15′–18° 10′ E and 104.8 m above sea level). The lake has recently been recovered from eutrophication to an oligo-mesotrophic state with mean annual chlorophyll-*a* concentrations of 3.6–18.7 mg m^{-3}, and moderate zooplankton and zoobenthos biomass (Istvánovics *et al.*, 2007). The fish fauna is dominated by cyprinids, of which common bream *Abramis brama*, bleak *Alburnus alburnus*, razor fish *Pelecus cultratus* and the introduced hybrid bigheaded carp *Hypophthalmichthys molitrix* × *H. nobilis* are the most abundant in biomass. Common carp occurs mainly in the littoral zone and its abundance basically depends on the actual stocking rate. While, pikeperch, the main piscivorous fish of the lake, lives primarily offshore (Specziár *et al.*, 2009; Specziár, 2010).

2.2 Tagging and recapture

For the purpose of this study, all common carp belonging to the same, fully scaled, less domesticated aquaculture strain and pikeperch of semi-natural progeny of Lake Balaton stock (eggs were collected by plastic spawning nets placed into the lake) were hatched and reared in the fish farm of the Balaton Fish Management Non-Profit Ltd (BFMnP). We tagged altogether 4500 two summers old (170–350 mm standard length, *L*) common carp and 3000 one-summer old (170–310 mm *L*) pikeperch with Floy® FD-68BC T-Bar Anchor Tags (2 × 38 mm; www.floytag.com) of orange colour, and with unique tag numbers and a reference to the address of the institute to be contacted. Each fish was measured for *L* and body mass (*M*) to the nearest 1 mm and 1 g, respectively. Common carp was released in March, July and November–December 2010, while pikeperch in December 2012 and March 2013 into the three major basins (Siófok, Szemes and

Keszthely) of Lake Balaton, from shore and offshore according to a symmetrical experimental design with 250 fish in each group (season × lake area × habitat). Only healthy and vigorous fish were used. More detailed description of the tagging procedure, size ranges of fish by stocking trials and releasing of fish is provided in our previous studies (Specziár and Turcsányi, 2014, 2017).

Tagged fish were recaptured and reported by the anglers according to the guide provided to each angling licence and also published in written and electronic media. Anglers were asked to report time and location of the catch, and L and M of the fish at capture. To encourage reporting activity we offered a modest reward (*ca.* 10 EUR until the end of 2012 and 13 EUR afterwards) for each tag returned. Anglers were distinctly instructed to indicate if they were not able to provide precise data with no effect on their rewarding. Ambiguous data were excluded from the analyses.

2.3 Data analysis

Length increment (ΔL, mm) of fish was modelled both relative to calendar and thermal time; that is we related ΔL to number of days (d) and degree-day sum (D, °C) elapsed between the release and recapture. Degree-day sum calculates as:

$$D = \sum_{i=1}^{d} (T_i - T_{\text{threshold}}) T_i > T_{\text{threshold}} \qquad (1)$$

where T_i is the mean daily water temperature at day i, d the number of days of the observation period and $T_{\text{threshold}}$ is the set threshold water temperature. The $T_{\text{threshold}}$ of growth of common carp and pikeperch was assessed by maximizing the coefficient of determination (R^2) in the regression of ΔL on D via testing all possible round $T_{\text{threshold}}$ values between 0 and 20 °C. Daily water temperature data measured at Siófok were obtained from the Hungarian Meteorological Service.

Recaptured fish were classified into three size groups representing ranges of ≤245, 246–265 and >265 mm L at release and fish size was included to stocking variables. Accordingly, based on four predictor variables (season × lake area × habitat × fish size), we could evaluate the variability of ΔL among 54 and 36 different stocking strategies in the common carp and pikeperch, respectively. The effect of stocking variables and their interactions on ΔL at alternative covariates, the d and D, was tested with general linear models (GLM). Because preliminary analysis of variance (ANOVA) indicated that fish size at release differed slightly between stocking seasons (common carp: d.f. = 2; 678, $F = 87.6$, $P < 0.001$; pikeperch: d.f. = 2; 505, $F = 9.2$, $P = 0.003$), but not between lake areas (common carp: d.f. = 2; 678, $F = 1.8$, $P = 0.167$; pikeperch: d.f. = 2; 505, $F = 0.3$, $P = 0.777$) and habitats (common carp: d.f.=1; 678, $F = 0.0$, $P = 0.893$; pikeperch: d.f. = 1; 505, $F = 0.0$, $P = 0.867$) of release in both species, therefore, the effect of stocking season on ΔL was tested both for the total samples (full GLMs) and for each size group as well. Further, since we expected a strong influence from the lake area on fish growth and many fish moved to other areas after stocking, we also tested the effect of the recapture area on ΔL at the same alternative covariates, the d and D. GLM and ANOVA were performed with Statistica 8.0 software (www.statsoft.com).

Then, length increment of recaptured fish was modelled using the GROTAG method proposed by Francis (1988a). This method uses a maximum likelihood approach to fit the following function on tagging data to estimate ΔL for an individual i:

$$\Delta L_i = \left[\left(\beta g_\alpha - \alpha g_\beta \right) \left(g_\alpha - g_\beta \right)^{-1} - L_i \right] \left\{ 1 - \left[1 + \left(g_\alpha - g_\beta \right) (\alpha - \beta)^{-1} \right]^{\Delta t_i} \right\} \qquad (2)$$

where L_i is the standard length at release, Δt_i the observation period in years, and g_α and g_β are the estimated growth rates at preselected standard lengths α and β ($\alpha = 200$ mm and $\beta = 300$ mm in common carp and $\alpha = 200$ mm and $\beta = 250$ mm in pikeperch in this study). In general, Δt_i is calculated by dividing d_i, the number of days fish i was at liberty by 365 (Francis, 1988a; Simpfendorfer, 2000), which approach served as the basis of our calendar time based growth model:

$$\Delta L_i = \left[\left(\beta g_\alpha - \alpha g_\beta \right) \left(g_\alpha - g_\beta \right)^{-1} - L_i \right] \left\{ 1 - \left[1 + \left(g_\alpha - g_\beta \right) (\alpha - \beta)^{-1} \right]^{\left(d_i 365^{-1} \right)} \right\}. \qquad (2a)$$

Our alternative model was based on the thermal time and Δt_i was calculated by dividing D_i by the mean annual degree-day sum (D_{annual}) calculated for the whole study period (*i.e.* from 2010 to 2016 in common carp, and from 2013 to 2016 in pikeperch):

$$\Delta L_i = \left[\left(\beta g_\alpha - \alpha g_\beta \right) \left(g_\alpha - g_\beta \right)^{-1} - L_i \right] \left\{ 1 - \left[1 + \left(g_\alpha - g_\beta \right) (\alpha - \beta)^{-1} \right]^{\left(D_i D_{\text{annual}}^{-1} \right)} \right\}. \qquad (2b)$$

This modified approach (Eq. 2b) proportionally incorporates both intra- and inter-annual variability of temperature into the model and more directly than approaches introducing additional seasonal parameters to be estimated (*e.g.* Cloern and Nichols, 1978; Francis, 1988a). Growth models were optimized by maximizing the following likelihood function:

$$\lambda = \sum_i log \left[(1 - p) \lambda_i + p (\Delta L_{\max} - \Delta L_{min})^{-1} \right] \qquad (3)$$

where

$$\lambda_i = \left[e - 0.5 (\Delta L_i - \mu_i - m)^2 \left(\sigma_i^2 + s^2 \right)^{-1} \right] \left[2\pi \left(\sigma_i^2 + s^2 \right) \right]^{-0.5},$$

p is the outlier probability, μ_i the expected value of growth increment of fish i, m and s the mean and the standard deviation of the measurement error (assumed to be normally distributed), and σ_i is the standard deviation of the growth variability (v) assumed to be $\sigma_i = v\mu_i$ (Francis, 1988a). The likelihood value (λ) was maximized using the macro developed by Simpfendorfer (2000) based on the Solver function in

Microsoft® Excel. Although the GROTAG method allowed the use of six parameters (*i.e.* g_α, g_β, v, s, m and p), the number of parameters retained in the final model was determined according to the likelihood ratio test, assuming that the addition of a new parameter is significant if λ increases by >1.92 (Francis, 1988a). Ninety-five percent confidence intervals (CIs) were calculated for each model parameter by bootstrapping the observed ΔL data 10 000 times. In situations where the GLM did not unequivocally reject the effect of season, lake area and habitat of stocking, or lake area of recapture on the ΔL, separate growth models (Eqs. 2a and/or 2b) were composed based on the whole samples and for the relevant releasing set-up variants as well. Note that stocking fish size is *a priori* included in the growth model.

Based on the optimized model parameters, the von Bertalanffy growth rate (K) and asymptotic length (L_∞) were also estimated according to Francis (1988a):

$$K = -\ln\left[1 + \left(g_\alpha - g_\beta\right)(\alpha - \beta)^{-1}\right] \quad (4)$$

$$L_\infty = \left(\beta g_\alpha - \alpha g_\beta\right)\left(g_\alpha - g_\beta\right)^{-1}. \quad (5)$$

3 Results

3.1 Recaptures

Until 31 December, 2016, anglers reported recaptures of altogether 829 common carp and 522 pikeperch of which 684 and 513, respectively, were reported with approved L data. The number of recaptures decreased considerably in time in both species; 83.3% of recaptures happened in the first, 11.3% in the second, 2.9% in the third, 1.5% in the fourth and altogether 1% in the fifth year or later after stocking in common carp, while 39.6% of recaptures happened in the first, 34.5% in the second, 18.1% in the third and 7.8% in the fourth year after stocking in pikeperch. Observed ΔL ranged from −20 to 470 mm (−69 to 11 770 g increment in M) in common carp and from −10 to 350 mm (−48 to 2574 g increment in M) in pikeperch.

3.2 Water temperature threshold of growth

For majority of the tested $T_{\text{threshold}}$ range, ΔL proved to be more closely associated with D than d (Fig. 1). In both species, R^2 values of the correlation between the ΔL and D increased very slightly or showed a plateau with increasing $T_{\text{threshold}}$ from 0 °C to 8–9 °C and then decreased progressively. Therefore, and also in agreement with the temperature related shift in recapture rate by angling (Specziár and Turcsányi, 2014, 2017), we chose $T_{\text{threshold}} = 8$ °C for modelling growth of common carp and pikeperch in Lake Balaton.

3.3 Effect of stocking strategy

In the common carp, at either d or $D_{8\,°C}$ covariant, ΔL varied with fish size (specifically, ΔL decreased with L at stocking), but not with lake area and habitat of stocking (Tab. 1). Although the full GLM with d as covariant indicated some stocking season related variability in ΔL as well, this effect was not clearly approved when the influence of fish size at stocking was controlled. Therefore, differences in the L distribution of fish between the stocking seasons could explain (at least in part) the observed seasonal variability, too. However, no seasonal variability at all was found in ΔL at covariant $D_{8\,°C}$. Lake area of recapture proved also not to influence ΔL in common carp at neither covariates (Tab. 1). Moreover, no considerable factor interactions were revealed, except the marginal effect of fish size × season ($P = 0.045$) on ΔL at covariant d.

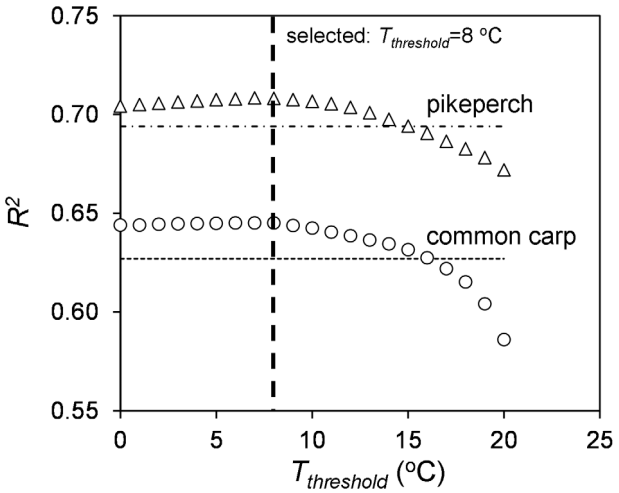

Fig. 1. Goodness of fit (R^2) of regression between degree-day sum (D) and standard length increment (ΔL) in relation to the threshold water temperature ($T_{\text{threshold}}$) in tagged common carp (o; $n = 684$) and pikeperch (Δ; $n = 513$) in Lake Balaton. For reference, R^2 values of the regression between calendar days and ΔL are indicated by horizontal lines (· · · · in common carp and — · - · in pikeperch), while the vertical line (- — —) represents the set $T_{\text{threshold}}$.

In pikeperch, ΔL varied with fish size (again, ΔL decreased with L at stocking), while the lake area and habitat of stocking had no effect on ΔL at neither covariant d nor $D_{8\,°C}$ (Tab. 1). In addition, GLM indicated some pure seasonal effect at covariant d. Contrary to common carp, however, a weak effect ($P = 0.031$) from the lake area of recapture was also found on the ΔL at covariant d; pikeperch recaptured in the Siófok basin showed less increment then in the Szemes and Keszthely basins. We found no significant factor interaction in the models.

3.4 Growth models

Based on the likelihood values, growth of common carp and pikeperch was most efficiently described by four or five parameters GROTAG models (Tab. 2). Adjusted coefficient of determination ($R^2_{\text{adj.}} = 0.576$–$0.795$) indicated that these models explained a large proportion of variation in the ΔL data, especially in models, which included $D_{8\,°C}$ ($R^2_{\text{adj.}} = 0.739$ in the common carp and $R^2_{\text{adj.}} = 0.780$ in the pikeperch).

In common carp, the overall model based on $D_{8\,°C}$ predicted mean ΔL of 174, 94, 51 and 28 mm for the first, second, third and fourth year after stocking for individuals released at 200 mm L. The same values for common carp

Table 1. General linear model (GLM) analysis on the effect of fish size (standard length classes, L1-3), lake area (I – Keszthely, II – Szemes, III – Siófok basin), habitat (shore, offshore) and season (spring – Sp, summer – S, autumn – A) of stocking on the length increment (ΔL) of common carp and pikeperch in Lake Balaton, with days (d) or degree-day sum at 8 °C threshold water temperature ($D_{8\,°C}$) as covariant. Since size of the stocked fish varied between seasons, thus when the full GLM indicated a seasonal variability, main effect of season was also tested for each size group separately. Effect of the recapture area and interaction of stocking area × recapture area is also shown on ΔL at covariates d and D. Note that since factor interactions, except the marginal effect of fish size × season ($P = 0.045$) in common carp at covariant d, proved to be insignificant at $P < 0.05$, these results are not presented. Results of the Tukey HSD *post hoc* tests are also shown for significant factor effects.

	Common carp								Pikeperch							
	ΔL *vs.* d				ΔL *vs.* $D_{8\,°C}$				ΔL *vs.* d				ΔL *vs.* $D_{8\,°C}$			
	d.f.	F	P	Tukey HSD	d.f.	F	P	Tukey HSD	d.f.	F	P	Tukey HSD	d.f.	F	P	Tukey HSD
Covariant: d	1	962.2	<0.001		–	–	–		1	962.7	<0.001		–	–	–	
Covariant: $D_{8\,°C}$	–	–	–		1	1040.8	<0.001		–	–	–		1	1082.9	<0.001	
Stocking fish size	2	11.4	<0.001	L 3 < L2 < L1	2	9.4	<0.001	L 3 < L2 < L1	2	6.8	0.001	L3 < L2 < L1	2	9.7	<0.001	L3 < L2 < L1
Stocking lake area	2	0.1	0.863		2	0.1	0.944		2	1.9	0.148		2	2.6	0.076	
Stocking habitat	1	1.6	0.202		1	0.8	0.386		1	2.6	0.109		1	2.1	0.152	
Stocking season	2	7.5	<0.001	S < Sp < A	2	0.2	0.843		1	12.4	<0.001	NS	1	0.0	0.867	
Error	629				629				474				474			
Main effect of stocking season by size groups																
L1 (≤245 mm)	2;157	0.4	0.680						1;160	4.4	0.037	NS				
L2 (246–265 mm)	2;212	1.6	0.202						1;152	2.5	0.117					
L3 (>265 mm)	2;258	11.3	<0.001	S<Sp, A					1;160	5.5	0.021	NS				
Effect of recapture area																
Covariant: d	1	1086.5	<0.001		–	–	–		1	1000.0	<0.001		–	–	–	
Covariant: $D_{8°C}$	–	–	–		1	1177.1	<0.001		–	–	–		1	1142.1	<0.001	
Stocking lake area	2	2.4	0.095		2	1.2	0.310		2	0.0	0.996		2	0.0	0.961	
Recapture lake area	2	2.3	0.102		2	0.8	0.432		2	3.5	0.031	III<II, I	2	2.9	0.054	
Stocking area × recapture area	4	1.3	0.288		4	1.9	0.102		4	1.1	0.339		4	1.2	0.331	
Error	674				674				500				500			

NS indicates non-significant post hoc results.

Table 2. Estimated parameters and their 95% confidence intervals (CI) of models assessing standard length increment (ΔL) of stocked common carp and pikeperch in Lake Balaton according to the GROTAG method of Francis (1988a) and using number of days (d) and degree-day sum at 8 °C threshold water temperature ($D_{8\,°C}$) as predictors. Estimated values (mean and CI) of von Bertalanffy growth parameters, growth rate (K) and asymptotic length (L_∞) are also shown. Since some stocking season and recapture area (I – Keszthely, II – Szemes, III – Siófok basin) related variability was found in the ΔL when related to d in both species and in pikeperch, respectively (Table 1), thus growth models based on d were composed both for the total samples and each relevant subsample as well. Only the best model according to the likelihood ratio test is shown for each model type.

Model type predictor – season	g_α (mm year^1) (CI)	g_β (mm year^{-1}) (CI)	v (CI)	s (CI)	m (mm) (CI)	P (CI)	Likelihood	$R^2_{adj.}$	n	K (year^{-1}) (CI)	L_∞ (mm) (CI)
Common carp											
d – spring	221.6	153.2	0.34	0.0	–	–	−1085.3	0.576	226	1.153	524
	(211.7–230.3)	(136.0–168.4)	(0.28–0.37)	(0.0–12.8)	–	–				(0.899–1.473)	(476–581)
d – summer	225.7	133.7	0.36	11.7	5.0	–	−1588.0	0.621	332	2.536	445
	(215.4–235.9)	(122.7–144.8)	(0.31–0.40)	(9.2–14.0)	(1.3–8.8)	–				(2.165–2.973)	(431–460)
d – autumn	143.0	113.4	0.21	34.9	–	–	−654.5	0.731	126	0.351	683
	(132.1–154.2)	(105.0–121.3)	(0.05–0.30)	(23.7–43.6)	–	–				(0.233–0.504)	(578–856)
d – all	144.3	99.7	0.40	26.4	32.4	–	−3430.6	0.643	684	0.590	524
	(132.9–156.8)	(90.9–107.6)	(0.34–0.45)	(24.0–28.8)	(27.4–37.2)	–				(0.445–0.768)	(481–579)
$D_{8\,°C}$ – all	173.6	128.0	0.30	12.6	3.7	–	−3277.5	0.739	684	0.609	581
	(166.4–181.6)	(121.8–134.2)	(0.27–0.32)	(10.5–14.6)	(0.2–6.9)	–				(0.512–0.723)	(542–624)
Pikeperch											
d – spring	94.7	82.0	0.00	29.6	25.3	–	−961.2	0.795	211	0.291	574
	(78.3–114.1)	(71.0–96.0)	(0.00–0.12)	(24.9–32.1)	(12.7–36.2)	–				(0.145–0.463)	(497–780)
d – autumn	101.3	89.8	0.18	22.4	–	–	−1450.3	0.752	302	0.262	640
	(94.4–109.1)	(85.6–94.6)	(0.14–0.22)	(18.3–26.3)	–	–				(0.188–0.352)	(564–755)
d – basin III	106.6	89.5	0.10	28.6	–	–	−429.8	0.709	89	0.419	512
	(91.3–120.3)	(81.0–97.6)	(0.00–0.19)	(21.6–33.4)	–	–				(0.216–0.660)	(445–669)
d – basins I and II	103.4	89.0	0.18	29.2	15.1	–	−2131.5	0.698	424	0.338	560
	(87.4–119.5)	(77.8–101.3)	(0.13–0.22)	(24.9–33.0)	(3.6–25.3)	–				(0.217–0.464)	(51–652)
d – all	93.6	82.7	0.14	27.8	14.5	–	−3430.6	0.643	513	0.590	524
	(81.8–104.9)	(74.1–90.8)	(0.09–0.18)	(24.6–30.7)	(6.5–22.5)	–				(0.156–0.341)	(560–783)
$D_{8\,°C}$ – all	98.5	85.0	0.20	17.0	12.7	–	−2334.2	0.780	513	0.315	565
	(89.7–107.8)	(78.5–91.8)	(0.17–0.22)	(14.1–19.6)	(6.6–18.2)	–				(0.239–0.402)	(521–630)

g_α and g_β are the estimated growth rates at preselected standard lengths α and β ($\alpha = 200$ mm and $\beta = 300$ mm for common carp and $\alpha = 200$ mm and $\beta = 250$ mm for pikeperch in this study); v, s, m and p are additional model parameters to be estimated; likelihood is a function to be maximized during the model optimization and is calculated according to equation (3); R^2_{adj} is the adjusted coefficient of determination, while n is the sample size. "–" indicates that the concerning parameter was not retained in that model.

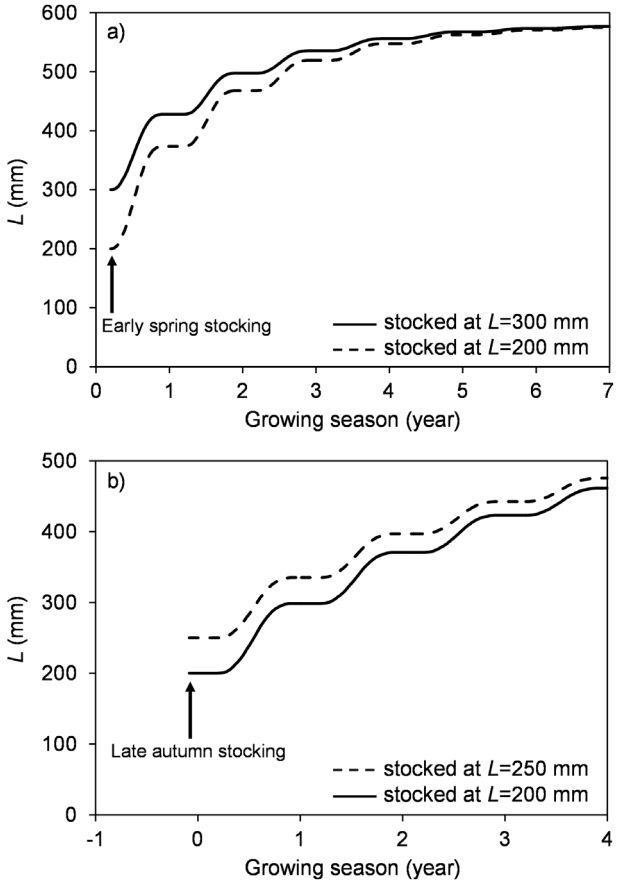

Fig. 2. Mean growth trajectories of stocked and recaptured common carp (a) and pikeperch (b) in Lake Balaton for the suggested stocking season (early spring in common carp, Specziár and Turcsányi 2014; and late autumn in pikeperch, Specziár and Turcsányi 2015) and according to the temperature adjusted GROTAG model of Francis (1988a). Modelled growth is calculated as: $L_{\Delta t} = L_0 + \Delta L_{\Delta t}$, where $L_{\Delta t}$ is the standard length at Δt (years) time after stocking calculated as degree-day sum above 8 °C threshold water temperature and divided by the mean annual degree-day sum of the concerning study period above the same threshold temperature, L_0 is the standard length at stocking and ΔL_t is the modelled standard length increment according to equation (2b). Modelled growth is shown for two stocking sizes in each species of which the more typical is indicated by continuous whereas the less typical with broken line.

released at 300 mm *L* were 128, 70, 37 and 21 mm, respectively (Fig. 2a). Note that these predicted ΔL values are based on the mean annual $D_{8\,°C}$ value of 2323 °C for the whole study period between 2010 and 2016 in Lake Balaton, and actual ΔL depends on the temperature regime of the considered period as well. Estimated von Bertalanffy parameters of growth based on the same model proved to be $K = 0.609$ (95% CI: 0.512–0.723) year^{-1} and $L_\infty = 581$ (542–624) mm (Tab. 2). It should be noted, however, that estimated values of the GROTAG parameters as well as the K and L_∞ varied substantially among models and had quite wide 95% confidence ranges.

In pikeperch, the overall model based on $D_{8\,°C}$ predicted mean ΔL of 99, 72, 52 and 39 mm for the first, second, third and fourth year after stocking for individuals released at 200 mm *L*. The same values for pikeperch released at 250 mm *L* were 85, 62, 45 and 33 mm, respectively (Fig. 2b). Note again that these predicted ΔL values are based on the mean annual $D_{8\,°C}$ value of 2407 °C for the period between 2013 and 2016 and actual ΔL depends on the temperature regime of the considered period. Estimated von Bertalanffy parameters of growth based on the same model proved to be $K = 0.315$ (0.239–0.402) year^{-1} and $L_\infty = 565$ (521–630) mm (Tab. 2). Again, estimated values of the GROTAG parameters as well as the K and L_∞ varied substantially among model types and had quite wide 95% confidence ranges.

4 Discussion

Our tagging experiments with long observation periods resulted in useful amount of growth data for the stocked common carp and pikeperch in Lake Balaton. Results support the judgement that thermal time based growth models provide greater explanatory power than conventional calendar time based models. Moreover, the application of thermal time enables to integrate growth data of fish tagged at different time of the year into a common analysis even in the temperate region.

Calculation of the thermal time, however, requires the assessment of the lower $T_{\text{threshold}}$ of growth of the species studied (Neuheimer and Taggart, 2007). Since we could not find direct estimates about the $T_{\text{threshold}}$ value of the common carp and pikeperch, an attempt was made to assess it from the tagging data. The observed patterns of R^2 values as function of $T_{\text{threshold}}$ were very similar to that found by Chezik *et al.* (2014) in eight freshwater species and 81 walleye *Sander vitreus* populations. Namely, R^2 values were similar and high for small values of $T_{\text{threshold}}$, and then dropped of progressively in both common carp and pikeperch. Therefore, considering the proof for a daily growth rate as high as 0.7% of body mass even at 12 °C water temperature (Goolish and Adelman, 1984), the intensive feeding to as low as 8 °C water temperature (Specziár and Turcsányi, 2014), and the pattern of R^2 values for the regression between D and ΔL, we assumed that the lower $T_{\text{threshold}}$ of growth of common carp could be 8 °C in Lake Balaton. Mooij *et al.* (1994) estimated the $T_{\text{threshold}}$ of zero growth for 9.8 °C in planktivorous and 8.6 °C in piscivorous age-0 pikeperch in Lake Tjeukemeer. At the same time, Frisk *et al.* (2012) concluded that the temperature optima of the adult pikeperch could range from 10 to 27 °C in term of >80% of the maximal metabolic scope (related to growth potential). Therefore, the minimum temperature of growth of adult pikeperch actually seems to be lower than the commonly applied $T_{\text{threshold}} = 10$ °C (Kjellman *et al.*, 2001; Lappalainen *et al.*, 2009), and accordingly, we adopted the $T_{\text{threshold}} = 8$ °C value resulted from the R^2 approach in Lake Balaton.

Either related to calendar or thermal time, growth rate of common carp and pikeperch depended most on their length at release, which is in accordance with our understanding on the general nature of fish growth. Although this finding contributes little to stock management strategies, it is important from the point of view of growth modelling and validates the selection of the Francis (1988a) method, which was derived from the von Bertalanffy (1957) framework.

Variation in food resource is one of the most important factors influencing fish growth. For example, Keskinen and Marjomäki (2003) revealed a strong correlation between primary production and size of age-3 pikeperch across 41 lakes in central Finland. While, Weber *et al.* (2010) found a marked relationship between primary production and condition of common carp in 84 lakes and impoundments in the upper Midwest United States. In this study, result on the effect of lake area representing a trophic gradient, however, proved to be less clear-cut. The locality of stocking had no effect on the length increment of fish. This indicates that we cannot influence the growth of stocked common carp and pikeperch in Lake Balaton by varying the area of release, but it does not necessarily mean that growth rate of fish does not respond to spatial differences in lake productivity. It is well known that stocked fish reared in aquaculture may exhibit considerable post-releasing foraging movement and travel long distances (Bolland *et al.*, 2009). Such movements were observed in stocked pikeperch and common carp in Lake Balaton, also (Specziár and Turcsányi, 2014, 2017). On the other hand, since acclimatised common carp and pikeperch generally show strong site fidelity (Keskinen *et al.*, 2005; Jones and Stuart, 2007), we could suppose that length increment of stocked fish that spent long enough time in the lake should reflect differences in productivity between areas of recapture. After all, the area of recapture had also no effect on the growth of common carp and only slightly influenced the growth of pikeperch. The better growth of stocked pikeperch recaptured in the Keszthely and Szemes basins compared to the Siófok basin is in accordance with the productivity gradient of Lake Balaton (Istvánovics *et al.*, 2007). Moreover, this result coincides also with the higher survival rate (monitored as recapture rate) of pikeperch stocked into the Keszthely and Szemes basins than into the Siófok basin likely due to the better feeding conditions (Specziár and Turcsányi, 2017). Finally, post-releasing movements of pikeperch also prevailed towards the more productive areas (Specziár and Turcsányi, 2017). Therefore, Keszthely and Szemes basins are likely more favourable areas for pikeperch than the Siófok basin. Contrary to pikeperch, common carp lives primarily in the littoral zone and feeds mainly on dreissenid mussels in Lake Balaton (Specziár and Rezsu, 2009). Food resources in the littoral zone are distributed more heterogeneously and do not reflect the trophic gradient of the offshore area (Balogh *et al.*, 2008; Árva *et al.*, 2015). The uniform growth rate of common carp in the lake coincides with the area independent pattern of its survival (recapture) rate and post-stocking movements as well (Specziár and Turcsányi, 2014).

Although littoral and offshore habitats differ considerably in their environmental characteristics, including a marked divergence in food resources, habitat of stocking did not influence the growth of common carp and pikeperch in Lake Balaton. Recapture patterns indicated that these species could find their suitable habitat rapidly; the common carp moves to the littoral zone while the pikeperch to the offshore zone (Specziár and Turcsányi, 2014, 2017).

Our results did not categorically support the hypothesis that season of stocking do not influence the growth of the stocked fish when post-stocking observation period covers several years. Some season related variability was revealed in the calendar time-based growth rate of the largest size group of common carp and the smallest and largest size groups of pikeperch. Since such effect did not exist in analyses based on thermal time, the observed seasonal effect likely is a consequence of the limit of calendar time predicting fine changes in the growth rate, especially at the beginning of the post-stocking period between fish released in or out of the growing season.

Growth rate of the common carp proved to be high during the first 2 years after stocking, but then the growth curve started to approach an asymptote (Fig. 2a). The observed initial growth rate (128 mm year^{-1} at 300 mm L, according to the thermal time based overall model) was similar to that found in Lake Balaton in the late 1990s based also on cooperative tagging study (132 mm year^{-1} at 294 mm L; recalculated from M data of Tölg *et al.* (1997), according to the L–M relationship given in Specziár, 2010), but higher than values assessed based on scale analysis (98 mm year^{-1} at 289 mm L; Specziár, 2010). Analysing the huge amount of information available world-wide on age-length relationship of common carp, Vilizzi and Copp (2017) provided a reference review. Unfortunately, growth parameters (*i.e.* von Bertalanffy parameters) obtained from age-length and tagging data are not directly comparable (Francis, 1988b). Therefore, to compare our results to average growth rate of common carp, we calculated 1 year length increment of an $L = 300$ mm common carp based on the relevant von Bertalanffy growth functions of Vilizzi and Copp (2017, see Tab. 1 of that publication) and the conversion function between fork and standard length (see Eq. 3a in Vilizzi and Copp, 2017). The calculated average growth rates at 300 mm L proved to be 53 mm year^{-1} at global scale and 57 mm year^{-1} in the temperate zone, which are less than half of the values observed in Lake Balaton. The prominently high growth rate of common carp indicates plentiful food supply related to high abundance of dreissenid mussels in Lake Balaton. *Dreissenia polymorpha* and *D. bugensis*, form large beds, have high productivity (Balogh *et al.*, 2008) and are not utilized to a significant extent by other fish species except the oldest age classes of roach, *Rutilus rutilus* (Specziár and Rezsu, 2009). In addition, although common carp is stocked regularly into the lake, its mean density is still low (Specziár *et al.*, 2009; Specziár, 2010) because of the intensive catch-and-take angling, and therefore, no significant intra-species competition can be expected.

Present results indicated a somewhat higher average growth rate (85 mm year^{-1} at 250 mm L, according to the thermal time based overall model) of pikeperch, than found in the 1960s (61 mm year^{-1} at 250 mm L; Bíró, 1970) and 1970s (66–79 mm year^{-1} at 250 mm L, calculated from the von Bertalanffy functions provided for different lake areas by Bíró, 1985). Compared to other habitats, the growth rate of pikeperch is low in Lake Balaton (Bíró, 1970; Harka, 1977; Bíró, 1985; Copp *et al.*, 2003), because of the unfavourable feeding conditions, at least to 500 mm L (Bíró, 1973; Specziár, 2011). For example, even though the colder climate, tagging experiments revealed much higher growth rate of pikeperch in Lake Mälaren (Sweden) (Andersson *et al.*, 2015). Based on the published function (Eq. 1 in Andersson *et al.*, 2015), pikeperch released at 250 mm L could have an average growth rate of 128 mm year^{-1} in 1995, at annual degree-day sum above 10 °C of 934 °C (*cf.* 1611–1984 °C in Lake Balaton, during 2010–2016), in Lake Mälaren.

Compared to ordinary field studies relying upon age estimates of varying reliability (Campana, 2001), tagging experiments provide direct information about the time period of the observed size increment for each individual recaptured, and therefore, could support more sophisticated analysis of fish growth. However, present study is based on stocked individuals and recaptures by anglers, which circumstances may limit the generalization of the observed growth rates for the whole stocks at least due to two reasons. First, common carp but not pikeperch (which were direct and diversified progeny of the natural population of Lake Balaton) was obtained from aquaculture stocks domesticated to a degree and therefore may differ in their growth potential genetically from those of the small existing natural stock in the lake. Second, it has been shown that anglers tend to catch individuals that grow faster than the stock average (Raat, 1985; Miranda *et al.*, 1987), and therefore, cooperative tagging studies may overestimate average growth rate of the whole stock. Nevertheless, these limits do not influence the conclusions related to study goals and fisheries management issues.

To conclude, using thermal time instead of the calendar time we can model the length increment of tagged common carp and pikeperch with better explanatory power, including seasonal patterns also. We demonstrated that within the range of relevant variants, stocking strategy has little or no direct effect on the growth rate of these species in Lake Balaton. Analyses revealed that growth rate of common carp is great and the present stocking rate is likely well within the carrying capacity of Lake Balaton. On the other hand, the moderate growth rate of pikeperch indicates that there could not be too much potential to increase population density without adverse environmental and population level effects. Therefore, the management of this species should rather be based on restrictive measures (like sharpening catch quotas) then on intensified stockings.

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