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Lake Morphometry and Trophic Status Affect Life-history Characteristics of Populations of *Rutilus rutilus* (L., 1758) (Cyprinidae) in Temperate Lakes

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Abstract: We have tested the hypothesis that populations of roach, *Rutilus rutilus* (L., 1758), inhabiting temperate natural lakes differing in their morphological and limnological features exhibit environmentally-related variations in their life-history characteristics. Overall, a total of 1127 roach specimens were used for ageing and growth analysis. Growth parameters of the von Bertalanffy function were calculated for both the mean observed and the back-calculated lengths-at-age estimates. The estimated lifespan differed among lakes ranging from eight to eleven years. The growth index (φ') was higher in the population from the deepest and less eutrophic lake (2.28) as compared to those from the shallower and more eutrophic lakes, while natural mortality (M) exhibited the inverse pattern. Generally, all studied life-history characteristics varied among lakes with lakes' morphometry and trophic state being the main environmental variables imposing such variation. Our results suggest that much of the observed variations among roach populations represent adaptations to local environmental conditions and pressures.

Key words: Freshwater fish, growth parameters, mortality, lake morphometry, trophic state, Greece

Introduction

The study of the relationships between environmental parameters and life-history characteristics of fish species has been the focus of several studies concerning marine (e.g. Attrill & Power 2002), transitional (e.g. Araújo & Monteiro 2013) or inland ecosystems (e.g. Greene & Maceina 2000, Blanck & Lamouroux 2007). Many of these studies have focused mostly on the effect of the abiotic environment on the composition of fish assemblages, especially in lakes (Holmgren & Appelberg 2000, Mehner et al. 2005). However, there are still gaps in our knowledge on how strongly lake fish assemblages are affected by various abiotic variables (Mehner et al. 2007). Moreover, there is a need to understand how specific environmental factors like lake morphometry and water quality may affect population structure and growth parameters of the species inhabiting lake ecosystems.

In the beginning of 1980's, D. Pauly published his work on 175 fish stocks relating the natural mortality (M) and growth parameters with ambient mean temperature (Pauly 1980). Mann et al. (1984) confirmed the strong influence of local environment on fish life-history traits. Studies in reservoirs also revealed the relationship of fish growth with abiotic parameters, mainly trophic state (Dicenzo et al. 1995, 1996, Greene & Maceina 2000). Moreover, lake area and total dissolved solids were the main factors responsible for the differences observed in life-history characteristics of *Salvelinus namaycush* in 54 Ontario lakes (Shuter et al. 1998). More recently, Blanck & Lamouroux (2007) tested the effects of large-scale environmental factors on 11 fish traits of 25 European freshwater fish species. They concluded that traits such as growth and mortality

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varied more between populations than between species, thus making them more attractive for understanding and predicting fish community responses to their environment.

The roach, *Rutilus rutilus* (Linnaeus, 1758), is a freshwater cyprinid species, widely distributed across Europe and Asia (Kottelat & Freyhof 2007). In Greece it is abundant in several water systems of the northern and central parts of the country. The age and growth of the species have been studied across Europe (Froese & Pauly 2016). However, information about the environmentally related variations in its life-history characteristics is limited.

In the present study we aimed to (a) initially describe some aspects of the life history of roach populations inhabiting lentic temperate ecosystems differing in terms of morphological and limnological features and (b) test whether these life-trait characteristics were environmentally related. As a case study we selected three Greek lakes, representing natural temperate Mediterranean lake ecosystems.

Materials and Methods

Three lakes in Northern Greece (Southern Balkan Peninsula) were selected (Fig. 1). Fish sampling took place in September 2010 (Kastorias Lake) and October 2012 (Volvi and Vegoritida Lakes) using Nordic type benthic and pelagic gillnets (Appelberg 2000). Specimens were identified to species level and total length (TL, cm ± 0.1) and weight (W, g ± 0.01) were measured. A sufficient, representative subsample of roach specimens was chosen from each lake and used for age determination. All scales were read twice in random order by a single reader, at an interval of two months, to avoid bias in assigning ages (Bagenal & Tesch 1978).

The weight-length relationships (WLRs) were calculated using the equation (Le Cren 1951) $W = a \times L^b$, where a is the intercept and b is the slope of the logarithmically transformed equation. The back-calculated lengths-at-age estimates were determined based on the relationship between the total scale radius (S, cm) and the TL of the fish, according to the linear equation (Francis 1990) $TL = a + b \times S$, where a and b are the intercept and slope of the relationship. The back-calculated lengths-at-age estimates were then determined based on the equation

$$L_i = c + (L_c - c) \times (\frac{S_i}{S}),$$

where L_i is the back-calculated length-at-age estimates i, L_c is the observed TL at the time of capture, S_i is the radius of the i[th] annual ring, S is the total scale radius at the time of capture and c is a constant that corresponds to the constant a of the scale radius-fish total length relationship and expresses the length of the fish when its scales start forming. The growth parameters were calculated for both the mean observed and back-calculated lengths-at-age estimates using the von Bertalanffy growth function (VBGF, von Bertalanffy 1938): $L_t = L_\infty \times (1 - e^{-K \times (t-b)})$, where L_t is the total length (cm) at age t (y), L_∞ is the asymptotic TL (cm), K is a constant expressing the rate at which L_∞ is approached (y^{-1}) and t_0 is the theoretical age (y) at which mean length of the fish population is zero (Ricker 1975). The growth index φ', which is a combination of the growth parameters K and L_∞ and is expressed by the equation $\varphi' = \log K + 2 \log L_\infty$ (Munro & Pauly 1983), was calculated for each population. Natural mortality (M) was calculated according to two empirical equations: Pauly's (1980) equation, that includes the mean temperature of the water body, $\text{Log}(M) = -0.0152 - 0.279 \times \log(L_\infty) + 0.6543 \times \log(K) + 0.463 \times \log(T)$, where L_∞ (cm) and K (y^{-1}) are the growth parameters and T (°C) is the mean temperature of the water column, and Gislason's et al. (2010) equation, that is applied to each length class: $\text{Ln}(M) = 0.55 – 1.61 \times \ln(L) + 1.44 \times \ln(L_\infty) + \ln(K)$, where L is the TL (cm), L_∞ (cm) and K (y^{-1}) are the growth parameters. To determine significant differences of the estimated b values from the isometric value of $b = 3$, a one-sample t-test was applied (Zar 1999).

The environmental data were measured in each lake during the fish sampling periods. Nutrient and Chla analyses were done in accordance with APHA (1985). Before applying multivariate analysis, environmental data were checked for co-linearity. Principal Component Analysis (PCA) (Primer 6: Clarke & Gorley 2006) was applied to the log(x+1) transformed environmental data to identify those explaining the ordination of lakes in space. Components (PCs) with eigen-values >1.0 were further interpreted and the scores of the first two main PCs were plotted. Moreover, weighted Spearman's rank correlation analysis was run for evaluating the strength of the correlation among the PC1 and PC2 scores and the estimated fish growth parameters.

Results

The morphological and limnological features of the studied lakes are shown in Table 1.

Overall, 402 specimens (TL: 5.5 -33.0 cm) from Vegoritida Lake, 400 (TL: 6.5 - 22.8 cm) from Volvi Lake and 408 (TL: 6.2 and 20.8 cm) from

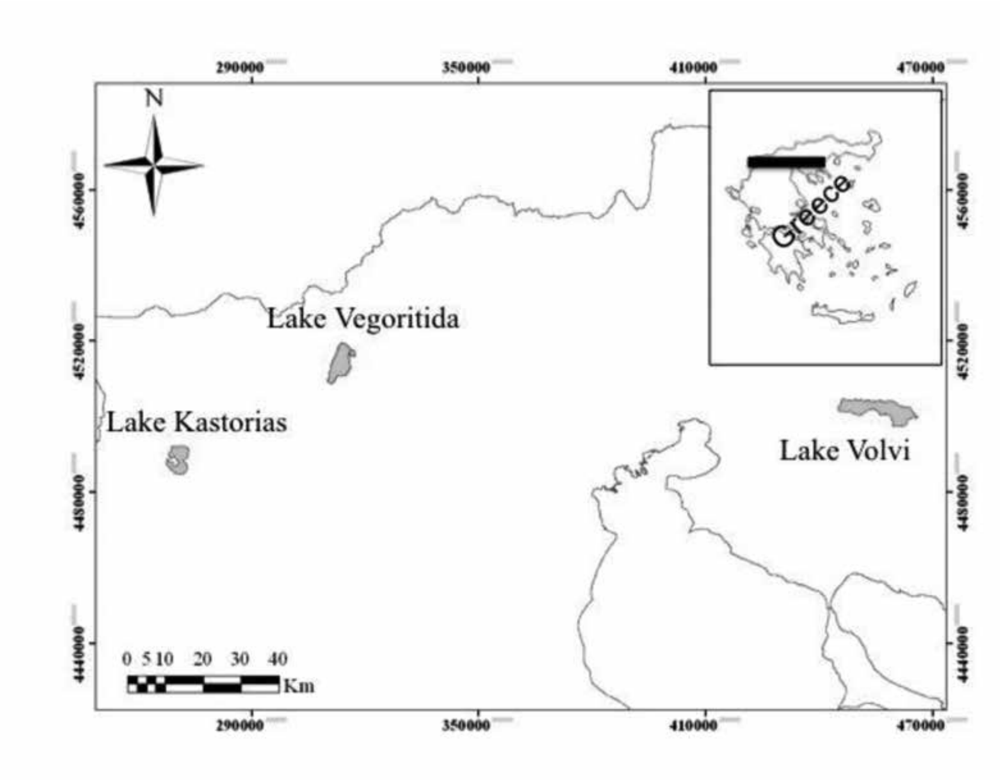

Fig. 1 The studied lakes

Table 1. Main morphological and limnological features of the studied lakes

		Lakes	
Parameters	**Kastorias**	**Volvi**	**Vegoritida**
Latitude	40°31′ N	40°40′ N	40°45′ N
Longitude	21°17′ E	23°28′ E	21°47′ E
Altitude (Alt, m)	625	37	524
Surface area (Area, km^2)	28.9	68.4	40.6
Mean depth (Dmean, m)	4.1	13.5	20.0
Maximum depth (Dmax, m)	9.0	23.5	48.0
Catchment basin (Basin, km^2)	271.6	1,247	1,853
Conductivity (Cond, μS/cm)	320	985	621
pH	8.88	9.00	8.94
Transparency (Trans, m)	0.45	1.95	1.90
TP (μg/l)	0.23	0.13	0.09
Chla (mg/m^3)	122.53	32.15	16.81
N/P	7.4	9.23	10
Trophic state	Eutrophic/ Hypertrophic	Eutrophic	Mesotrophic/ Eutrophic

Kastorias Lake were used. The slopes of the WLRs (Table 2) were significantly higher for all lakes than the theoretical value of 3.

Age and Growth

For ageing and growth analysis a total of 374, 371 and 382 specimens were used from Vegoritida, Volvi and Kastorias Lakes, respectively. About 6.5% of the scales in each lake were not readable or damaged and therefore rejected. The lifespan of roach in Vegoritida Lake was 11 years, while in Volvi and Kastorias lakes it was shorter (eight years). The majority of fish successfully aged were one (113 individuals; 30.2%) and two (108; 28.9%) years old in Vegoritida Lake, three (107; 28.8%) and four (68; 18.3%) years old in Volvi Lake, and two (93; 24.3%) and three (107; 28%) years old in Kastorias Lake. In all studied lakes, the annual growth of roach was

Table 2. The weight (W, g) - total length (TL, cm) relationship for roach *Rutilus rutilus* in Vegoritida, Volvi and Kastorias Lakes; n: sample size, min: minimum, max: maximum, *a* and *b*: the parameters of the weight-length equation, SE_b: standard error of the parameter *b*, r^2: the coefficient of determination, P: significance level

Lake	n	TL (cm)		W (g)		$W = a\,(TL)^b$					
		min	max	min	max	*a*	$SE_{(a)}$	*b*	SE_b	r^2	P
Vegoritida	402	5.5	33.0	1.27	504.13	0.005	0.032	3.283	0.012	0.995	0.000
Volvi	400	6.5	22.8	2.37	167.41	0.004	0.043	3.392	0.017	0.991	0.000
Kastorias	408	6.2	20.8	2.55	129.30	0.004	0.047	3.425	0.018	0.989	0.000

Table 3. Mean observed and back-calculated total lengths-at-age for *Rutilus rutilus* in Vegoritida, Volvi and Kastorias Lakes. In parenthesis, the mean annual increment in fish size compared to the maximum attainable total length

Lake	n	Mean observed TL (cm) at age										
		1	2	3	4	5	6	7	8	9	10	11
Vegoritida	374	8.35	12.37	15.26	18.04	20.53	22.76	24.75	26.65	28.28	29.75	30.65
		(27.24)	(13.11)	(9.44)	(9.06)	(8.12)	(7.29)	(6.49)	(6.20)	(5.30)	4.81)	(2.94)
Volvi	371	7.10	10.00	12.13	14.00	15.62	16.85	18.00	19.05			
		(37.27)	(15.25)	(11.13)	(9.82)	(8.53)	(6.45)	(6.03)	(5.52)			
Kastorias	382	7.09	10.73	12.48	14.22	15.83	17.29	18.41	19.18			
		(36.98)	(18.98)	(9.13)	(9.09)	(8.40)	(7.59)	(5.86)	(4.00)			
Lake	**n**	**Mean back-calculated TL (cm) at age**										
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Vegoritida	374	7.78	11.38	14.40	17.09	19.43	21.51	23.41	25.11	26.68	28.12	29.32
		(2.53)	(12.28)	(10.29)	9.18	7.97	7.11	6.48	5.80	5.35	4.93	4.09
Volvi	371	7.36	9.82	11.78	13.48	14.92	16.17	17.33	18.39			
		(40.02)	(13.40)	(10.63)	(9.28)	(7.79)	(6.80)	(6.33)	(5.77)			
Kastorias	382	7.67	10.09	11.88	13.54	15.03	16.34	17.48	18.46			
		(41.54)	(13.14)	(9.69)	(8.95)	(8.08)	(7.12)	(6.14)	(5.34)			

higher during the first year of life and gradually declined with age.

The relationships estimated between total scale radius and total length were: TL=3.311+5.195S (r^2=0.954; *P*<0.001) for specimens from Vegoritida Lake, TL=4.149+4.014S (r^2=0.905; *P*<0.001) for specimens from Volvi Lake and TL=4.559+4.435S (r^2=0.902; *P*<0.001) for specimens from Kastorias Lake. Back-calculated total lengths–at-age estimates, based on the above-mentioned equations, as well as the mean observed total lengths-at-age measured, are shown in Table 3. In all lakes, the annual growth of roach was higher during the first year, reaching up to 41.54% of the maximum attainable length at Kastorias Lake. Then, growth rate was gradually declining. Generally, the mean back-calculated lengths-at-age estimates were lower compared to the mean observed lengths-at-age (Table 3). The growth parameters of the VBGF based on the observed and the back-calculated lengths–at-age are shown in Fig. 2.

The highest value of the asymptotic length L_∞ (39.71 cm) and the lowest value of rate K (0.12 y^{-1}) were observed for roach in Vegoritida Lake, whereas the values of these parameters in the other two lakes were similar, with the lowest value of L_∞ (23.09 cm) and the highest value of K (0.20 y^{-1}) observed in Kastorias Lake.

The VBGF, based on the back-calculated lengths-at-age, gave a better estimation for L_∞ (i.e. closer to the L_{max}, $L_{max}/L_\infty = 0.85$) and for t_0 (i.e. closer to zero, $t_0 = -0.80$ y) in Vegoritida Lake. Also, the growth index φ' estimated from the parameters K and L_∞, of either the observed ($\varphi' = 2.09$, $\varphi' = 1.80$ and $\varphi' = 1.84$ for specimens from Vegoritida, Volvi and Kastorias Lakes, respectively) or the back-calculated lengths ($\varphi' = 2.28$, $\varphi' = 2.01$, and $\varphi' = 2.03$ for individuals from Vegoritida, Volvi and Kastorias Lakes, respectively), corresponded to much higher values in Vegoritida Lake than in the other two lakes.

The average value of M, calculated for roach from Vegoritida Lake was the lowest, ranged between 0.27 and 0.66 y^{-1} with an average of 0.47 ± 0.28 y^{-1}. Roach from Volvi Lake exhibited M values between 0.52 and 0.58 y^{-1} and an average of 0.55 ± 0.04 y^{-1}, while roach from Kastorias Lake had M values between 0.47 and 0.65 y^{-1} and an average of 0.56 ± 0.13 y^{-1}. According to the length-based equa-

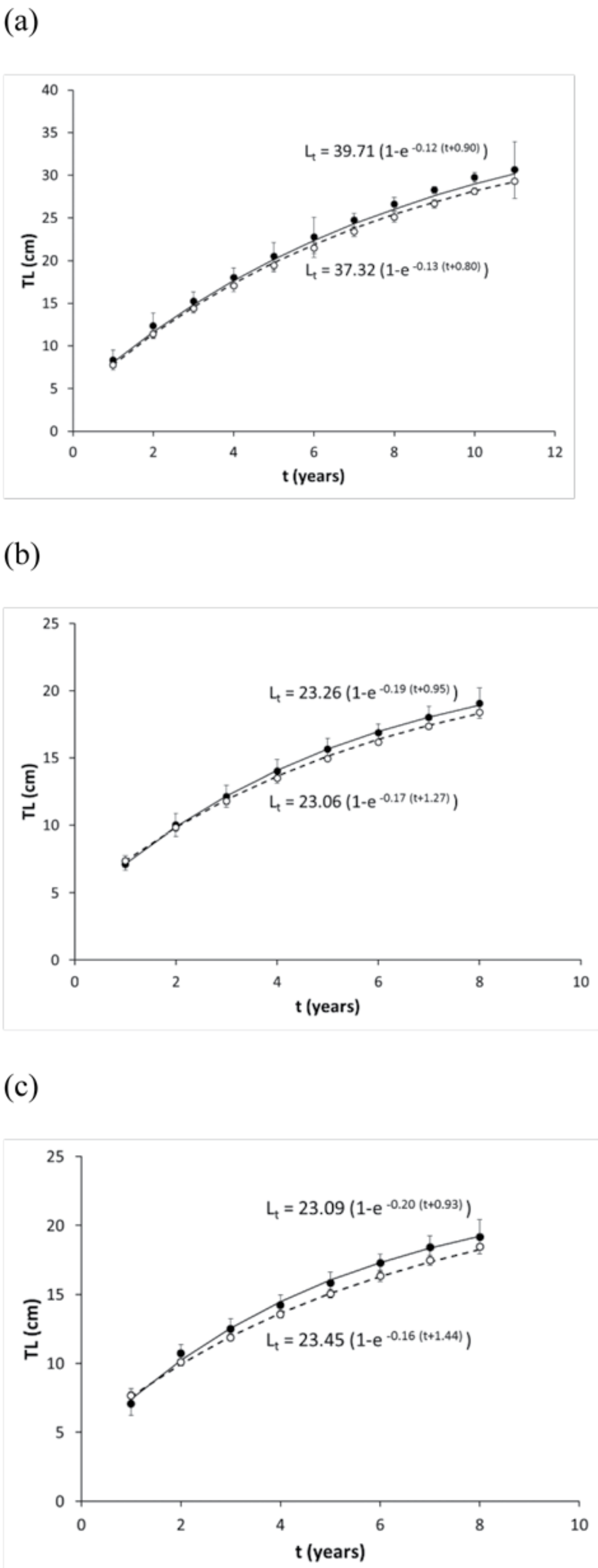

Fig. 2 Growth curves of the roach *Rutilus rutilus* in Vegoritida (a), Volvi (b) and Kastorias (c) Lakes, with the mean observed lengths-at-age (continuous line with black markers) ± SD (vertical lines) and the mean back-calculated lengths-at-age (dashed line with white markers) ± SD (vertical lines)

tion of Gislason et al. (2010), in all three lakes, M of roach was initially higher and declined as L_∞ was approached. In Vegoritida Lake the initial M was 3.13 y^{-1} and declined to 0.15 y^{-1}at maximum length. In Volvi Lake the initial M was 1.71 y^{-1} and declined to 0.20 y^{-1} at maximum length, while in Kastorias Lake the initial M was 1.78 $y^{-1}$and declined to 0.24 y^{-1} at maximum length.

Relationships with Limnological Characteristics

Both growth parameters (K and L_∞) exhibited strong correlation (r_s>|0.797|, p<0.01) with the drainage basin and lakes' depth (Table 4). Significant correlations (r_s>|0.619|, p<0.01) were also revealed with the concentrations of total phosphorus (TP) and chlorophyll (Chla; Table 4). Mortality was also related with the limnological characteristics of the studied lakes (Table 4), having strong negative correlation with TP and Chla concentrations (r_s>|0.646|, p<0.01), while it was positively related with the morphological features of the lakes (r_s>|0.817, p<0.01).

PCA analysis produced two statistically significant principal components (PCs) explaining 69.6% and 30.4% of the total variance, respectively. The first axis (PC1) was positively correlated to Chla (r=0.409) and negatively to drainage basin, minimum and maximum lake depth (r=-0.422, r=-0.387 and r=-0.373, respectively). The deeper lakes (Vegoritida and Volvi) with the lower Chla concentrations were ordinated on the negative side of PC1, while the shallow and eutrophic to hyper-hytrophic Kastorias Lake was ordinated on the positive side (Fig. 3). The second axis (PC2) was positively correlated to altitude (r=0.861) separating Volvi Lake, situated at lower altitude. Negative correlation was evident among L_∞ and M and PC1 scores (r_s>|0.529|, *P*<0.01), while K values were positively related (r_s=0.617, *P*<0.01) with the same axis. Furthermore, t_0, and *φ'* were positively correlated to PC2 scores (r_s>0.912, *P*<0.01), whereas *b* values were negatively related (r_s>-0.944, *P*<0.01).

Discussion

Based on the WLRs, the roach grew hyperallometrically in all lakes. This is in accordance with previous studies in Greek inland waters (e.g. Kleanthidis et al. 1999, Tsoumani et al. 2013) and elsewhere (e.g. Specziár et al. 1997, Tarkan et al. 2006). The values of the parameter *b* in all three lakes generally fall within the usually reported range for fish (from 2.7 to 3.4; Froese 2006) and, moreover, within the reported range for roach (from 2.78 to 3.61: Froese & Pauly 2016). Generally, the differences in *b* values observed among the three populations may be related

Table 4. Spearman's rank correlation analysis of the estimated growth parameters (L_∞ cm; K, y^{-1}) and mortality (M) of *Rutilus rutilus* and the limnological characteristics of the studied lakes

Parameters	Basin (km^2)	Dmin (m)	Dmax (m)	TP (mg/l)	N/P	Chla (mg/m^3)
L_∞ (cm)	0.797	0.930	0.976	-0.727	0.735	-0.619
K (y^{-1})	-0.856	-0.964	-0.994	0.795	-0.802	0.698
M (y^{-1})	0.817	0.942	0.983	-0.750	0.758	-0.646

Table 5. Growth parameters (L_∞, K, t_0) and growth index (φ') of *Rutilus rutilus* from 13 populations in lake systems of the Balkan Peninsula and from one population of Central Europe

Lake / year	Country	L_∞ (cm)	K (1/y)	t_0 (y)	φ'	Reference
Vegoritida (2012)	Greece	32.02	0.12	-0.92	2.09	1
Kastorias (2010)	Greece	17.41	0.23	-0.64	1.84	1
Volvi (2012)	Greece	19.82	0.16	-1.06	1.80	1
Volvi (1978)	Greece	25.12	0.09	-1.12	1.75	2
Volvi (1997-1999)	Greece	25.39	0.09	-3.10	1.76	3
Batak (1966-1976)	Bulgaria	27.50	0.10	-1.24	1.89	4
Batak (1977-1992)	Bulgaria	32.50	0.22	-0.12	2.37	4
Dospat (1971-1982)	Bulgaria	26.20	0.31	0.23	2.33	4
Ovcharitsa (1976-1985)	Bulgaria	28.10	0.44	-002	2.54	4
Ovcharitsa (1986-1989)	Bulgaria	35.20	0.30	-0.45	2.57	4
Dimitrov (1973-1977)	Bulgaria	38.23	0.23	-	2.53	5
Balaton (1995-1996)	Hungary	31.90	0.16	0.03	2.21	6
Rosu (1977)	Romania	28.54	0.28	-	2.36	7
Puiu (1977)	Romania	26.68	0.55	-	2.59	7

[1]Present study, [2]Papageorgiou (1979), [3]Kiritsi et al. (2008), [4]Zivkov & Raikova-Petrova (2001), [5]Marinov (1989), [6]Speczíár et al. (1997), [7]Papadopol & Chisalesku (1981).

to the particular environmental conditions of each ecosystem (Froese 2006, Pauly et al. 2008), as well as to the diet preferences of the species related to the trophic state of the waters, which can affect the WLR of fish species in freshwater systems (Kleanthidis et al. 1999). Indeed, the higher *b* values in the present study were estimated for roach from the shallow, small, eutrophic-hypertrophic Kastorias Lake, and from the deeper, large eutrophic Volvi Lake, compared to specimens from the very deep, mesotrophic to eutrophic Vegoritida Lake. However, a reverse pattern has been observed for the non-native *Carassius gibelio* in 12 Greek lakes (Tsoumani et al. 2006).

The lifespan of roach in Vegoritida Lake (11 years) is considered quite high. The absence of the older age classes and the small number of individuals at ages 7 and 8 in Volvi and Kastorias Lakes was probably due to the higher fishing pressure on roach in these two lakes as compared to Vegoritida Lakes. Salvarina et al. (2008) report an annual decrease in the mean trophic level of the catches in Kastorias Lake, due to fishing pressure. Overexploitation of fish populations (including roach's), has also been observed in Volvi Lake (Bobori & Psaltopoulou 2012). Moreover, the majority of the captures in the three lakes were at the smaller ages, denoting that fishing regulations should be considered for the protection of species populations.

The mean back-calculated lengths-at-age were lower compared to the observed lengths, indicating that the specimens were caught before the formation of the annual marks. Indeed, all lakes were sampled in autumn, while the annual marks in most roach populations are usually formed in spring (April-May), in the beginning of the growth period (Mann 1973). Consequently, the estimated growth parameters differed, depending on the type of length-at-age used. Generally, growth parameters were underestimated up to 6% (e.g. in the case of L_∞ in Vegoritida Lake), when the mean back-calculated lengths were used. However, the growth parameters calculated in the present work that were based on the mean observed lengths-at-age, fall within the reported range for the European species populations (L_∞: 26.2- 51.3 cm, K: 0.08 and 0.44 y^{-1}, Froese & Pauly 2016), with the excep-

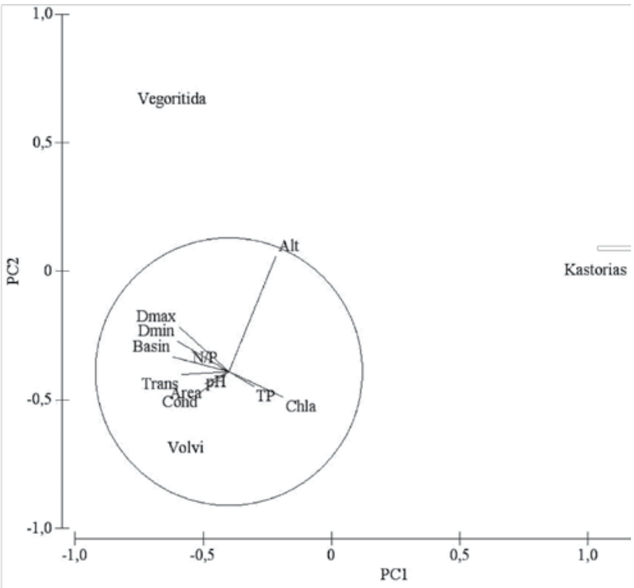

Fig. 3 Principal Component Analysis (PCA) plot of the two PC axes on the transformed morphological and limnological features of the three studied lakes. The length of the lines in this plot reflects the significance of each variable contribution to each axis. If the line reaches the circle, then none of the variable's coefficient differs from 0

tion of the L_∞ values of roach from Volvi and Kastorias Lakes, which were lower. These lower L_∞ values could be attributed to differences in lakes' eutrophication, as well as to the absence of large-sized specimens from the catches. Moreover, the growth index *φ*′, which indicates the ability for growth of each fish population (Munro & Pauly 1983, Pauly 1998), was higher in Vegoritida (2.28) as compared to Volvi and Kastorias Lakes (2.01 and 2.03, respectively). All these values of *φ*′ fall within the reported range in Fishbase for roach, i.e. from 1.89 to 2.57 (Froese & Pauly 2016).

The estimated, natural mortality for species population in Vegoritida Lake, was similar to that reported in Fishbase (0.47 y^{-1}). However, higher values were calculated for the populations in Kastorias and Volvi Lakes. Such intraspecific variations could be attributed to ecological differences of the studied systems, as well as to differences in food availability, the physiological status of the fish and/or the fishing pressure (Biswas 1993).

Generally, the roach populations in Volvi and Kastorias Lakes showed a similarity in their growth pattern but they differed from the respective pattern for Vegoritida Lake, as well as from other roach populations in Balkan lakes (Table 5).

Conclusion

We observed that the life-history characteristics of the studied roach varied among the three lakes. The main abiotic variables that imposed such variation were related to lakes' morphometry and trophic state. As the area of the drainage basin and lake's depth decreased and its trophic state (concentrations of Chla) increased, the values of K declined and species mortality increased, while the values for *φ*'and *b* varied depending on the altitude. These results suggest that much of the observed variation among roach populations represent adaptations to local conditions and pressures. Moreover, it is important to note the correlation of the selected life-history characteristics studied here for roach with the lakes' drainage basin. Since the amount of the terrestrial particulate organic matter reaching the lakes is expected to increase in the near future as a result of climate change (Lischke et al. 2014), this will further alter the strophic status in lakes, especially the shallow ones and consequently affecting fish populations. As knowledge of the life–history characteristics of the fish species is essential for assessing, among others, their status and improving their conservation (Paret & Schrimi 1995), the information provided by the present study is of crucial importance, especially for management of species that are target of commercial fisheries, as is the case of roach (Jennings et al.1998).

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