Rev Fish Biol Fisheries (2015) 25:587–602
DOI 10.1007/s11160-015-9398-6

REVIEWS

Patterns, latitudinal clines and countergradient variation in the growth of roach *Rutilus rutilus* (Cyprinidae) in its Eurasian area of distribution

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Received: 7 February 2015 / Accepted: 1 September 2015 / Published online: 5 September 2015
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Abstract The roach *Rutilus rutilus* is a eurythermal generalist that has been translocated and introduced mainly beyond the southern limits of its native Eurasian range of distribution. Although largely studied in most aspects of its ecology, no global assessment is available on its growth. Such information is critical for management purposes, especially in view of further dispersal of this 'potential pest' and climate change predictions. To address this knowledge gap, a meta-analysis was carried out of the age and growth of 301 roach populations from 231 water bodies across the species' native and translocated/introduced Eurasian range of distribution with the aim to identify habitat and climate-related differences in growth patterns, latitudinal clines, and the possible presence of countergradient growth variation (CGV). Faster growth rates were identified under warm relative to temperate and cold climates, and these were related to optimised resource allocation. Latitudinal clines indicated decreasing trends with increasing latitude in growth and body size, in line with life-history theory. However, the presence of thresholds encompassing the previously-reported 50°N latitude value suggested a 'plateau' or decrease in growth at lower latitudes, and CGV was identified for 1+ to 10+ fish. It is argued that increased water temperatures are likely to cause a northern shift in the observed thresholds and a 'homogenisation' of the species' population dynamics resulting in faster growth rates, but with more pronounced effects in continental Eurasia.

Keywords Growth index · von Bertalanffy growth function · Latitudinal clines · Countergradient growth variation · Köppen–Geiger · Piecewise regression · Mixed effects models

Electronic supplementary material The online version of this article (doi:10.1007/s11160-015-9398-6) contains supplementary material, which is available to authorized users.

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Introduction

The ideal life-history strategy of any species is one that maximises the number of offspring by increasing age-specific fecundity and survival (e.g. Roff 1992). In fish, a trade-off generally occurs between fecundity and size of offspring at hatching (Fleming and Gross 1990), so that a decrease in the former may be compensated by an increase in the latter, which in turn leads to enhanced survival (Brown and Shine 2005). Importantly, these life-history traits are intimately related to growth, which is tightly linked to environmental factors such as food availability and temperature, the latter being negatively related to latitude (e.g. New et al. 1999; Vázquez and Stevens 2004).

Growth rate in fish is known to increase with temperature first almost linearly and then, after reaching the optimal species-specific temperature, to decrease rapidly and finally cease totally (Kitchell et al. 1977; Magnuson et al. 1979). In a review study, Lappalainen et al. (2008) identified non-linear and unimodal relationships with latitude in three life-history traits for growth and reproduction in roach *Rutilus rutilus* (L., 1758), a generalist freshwater fish, and found that growth rate converged toward both the northern and southern limits of the species' range of distribution. Specifically, relatively lower growth rates were detected at the limits compared to the middle of the range, and this was explained in terms of deviation from optimum temperatures (either too high or too low in southern and northern populations), involving a decline in feeding efficiency. Based on these findings, it can be expected that populations of a widespread fish species at the limits of its range of distribution would experience a decline in growth. Also, as a decrease in growth rate is generally associated with an increase in lifespan (Metcalfe and Monaghan 2003), this should prove especially advantageous to fish in unstable environments.

Another growth mechanism observed in several fish species is countergradient growth variation (CGV: Conover and Present 1990). This involves latitudinal compensation with better growth performance in northern compared to southern populations of the same species. Typically, CGV has been studied in laboratory experiments mimicking the temperature conditions found at a range of latitudes (Conover and Present 1990; Conover et al. 1997), even though meta-analysis studies based on comparative age-growth data have also been used on occasion either in lieu or in support (e.g. Chavarie et al. 2010; Rypel 2012b, 2014).

The roach is a eurythermal cyprinid of native Eurasian distribution (Froese and Pauly 2014) and is abundant in rivers, lakes and reservoirs, but also encountered in brackish waters (Pęczalka 1968; Kozlovskiy 1992; Lappalainen et al. 2005, 2008). This species prefers slow-flowing or still, muddy waters (Hellawell 1972; Vostradovsky 1973), and spawning usually takes place in spring when water temperatures reach 8–17 °C (e.g. Holcik and Hruška 1966; Goldspink 1977; Mills 1981; Kozlovskiy 1992). Roach is known to be tolerant of temperature fluctuations (e.g. Papadopol 1970; Vøllestad and L'Abée-Lund 1987; Goldspink 1979; Papageorgiou 1979) and is valued for recreational fishing throughout Europe (Frimodt 1995). Its natural food items consist of phytoplankton, zoobenthos, zooplankton and detritus (e.g. Horppila 1994; Michel and Oberdoff 1995), which make it an omnivorous species with considerable food overlap with other fish (Persson 1983). In fact, the generalist feeding habits of this fish, combined with the high densities often achieved under favourable habitat conditions, make it a strong competitor with other species (Griffiths 1997), sometimes leading to severe population reductions or even localised extinctions in its introduced areas of distribution (Harrod et al. 2001). In this respect, intra-continentally roach has recently expanded its southern and western European range of distribution following introductions in the nineteenth century into the Italian (Volta and Jepsen 2008) and Iberian peninsulas (García-Berthou 1999) and into Ireland (Harrod et al. 2001); whereas translocations have occurred across much of Great Britain (Copp et al. 2005; Graham and Harrod 2009), Anatolia (Turkey; unpublished data), and in the Xinjiang Province of China (Hui Wei, pers. comm.).

Previous (semi-quantitative) comparative studies on the age and growth of roach have been generally limited to a certain study area (Hartley 1947; Williams 1967; Cragg-Hine and Jones 1969; Mann 1973; Chitravadivelu 1974; Goldspink 1978; White and Williams 1978; Burrough and Kennedy 1979; Przybylski et al. 2004; Epler et al. 2005) or based upon a sample of studies from different countries (Papageorgiou 1979; Ponton and Gerdeaux 1987; Zaugg 1987; Jamet and Desmolles 1994; Wiesky and Zalachowski 2000; Naddafi et al. 2005; Li et al. 2009; Okgerman et al. 2009). An exception are the reviews by Kas'yanov et al. (1995), on roach populations from water bodies of the former USSR, and by Zivkov and Raikova-Petrova (2001) from the entire species range of distribution. However, there is currently no study that has provided a global synthesis of growth patterns, types and rates in roach including any underlying mechanisms. This is important if a deeper understanding of the population dynamics of this and, in general, any fish species is to be achieved, and especially so in view of management purposes (e.g. Copp et al. 2004, 2009; Britton et al. 2012; Vilizzi et al. 2013, 2015).

The aim of the present study was to provide a global assessment, meta-analysis and synthesis of the growth of roach with the specific objectives to: (1) identify and compare the species' growth patterns across habitats and climates; (2) investigate the presence of

latitudinal clines in some life-history parameters for growth; and (3) assess the extent of CGV. Based on these outcomes, the implications for the potential further spread of the species within and beyond the limits of its Eurasian range of distribution are discussed and these are also related to current climate change projections of increased water temperatures.

Materials and methods

Data collation and analysis

Growth data for roach were obtained from tables, text or figures as available in publications from the peer-reviewed and gray literature, including both primary and secondary sources (i.e. data opportunistically retrieved through the former). Additionally, an unpublished dataset (available to the authors) was included for a translocated population from Porsuk Reservoir (Turkey). A necessary condition for inclusion of a study into the review was that it should provide mean length-at-age (LAA) values and/or von Bertalanffy growth function (VBGF) parameters for the population(s) under investigation. An exception was the study by Wilson (1971) on roach from Chew Valley Lake (England, UK), which was excluded from review due to likely errors in age estimates (see White and Williams 1978; Linfield 1979).

Growth data for populations of the Caspian roach [subspecies *R. rutilus caspicus* (Yakovlev, 1870)] were also included for both historical and taxonomical reasons. In the former case, a number of studies has incorporated this taxon into large-scale life-history trait comparisons (e.g. Kas'yanov et al. 1995; Zivkov and Raikova-Petrova 2001; Lappalainen et al. 2008), and for consistency this approach was followed in the present study. In the latter case, phylogenetic studies have so far provided inconclusive evidence to categorise the Caspian roach as a different species (i.e. *R. caspicus*), hence contrary to Froese and Pauly (2014; see also 'interoperability of database requirements': Nicolas Bailly, pers. comm.). Thus, despite low genetic divergence between *R. caspicus* and *R. frisii* (Nordmann, 1840) (the latter from the Black and Azov Sea basins, but also from part of the Caspian basin and Lake İznik in Anatolia) (Ketmaier et al. 2008; Larmuseau et al. 2009), haplotypes of *R. r. caspicus* have been found to be highly similar to those of *R. rutilus* from Lake Volvi in Northern Greece, which is considered to be the home of the west-European and Ponto-Caspian *R. rutilus* clades (Tsoumani et al. 2014). The latter finding would not only support historical evidence for the existence of a subspecies at most [www.briancoad.com/Species%20Accounts/FFI%20Complete.htm (accessed 04/06/2015)] but may also benefit from further studies focussing on comparative ontogenies and ecomorphology (Vilizzi and Kováč 2014).

Following Begg et al. (1999), in the present study a population (stock) was defined as a 'semi-discrete group of fish with some definable attributes of interest for management purposes' (see also Begg and Waldman 1999). Populations sampled at different sites and/or times from the same water body were regarded as different (e.g. due to genetic composition, immigration/emigration, recruitment and mortality, stocking and fishing), and were treated as independent samples (see Rypel 2012a). Also, due to only a fraction (≈ 8 %) of the reviewed studies providing mean LAA values for males and females separately, these were averaged over the combined sexes.

Water bodies for which mean LAA data were available were categorised into lentic (i.e. streams and rivers) and lotic (i.e. ponds, natural lakes and artificial reservoirs), and in case of different sections of a river/stream a separate 'water body' was considered. For each water body, the altitude (m a.s.l.; unless already reported in the study) and mean annual air temperature of the nearest weather station (T_a^*, °C) were obtained from monthly climate statistics tables [Meteorologisk Institutt: www.yr.no (accessed 04/06/2015)]. However, due to differences in some cases between the altitude of the nearest weather station and that of the water body under investigation, a correction factor (CF) was applied to estimate more accurately the mean annual air temperature at the water body location (T_a, °C):

$$\mathrm{CF} = \left(\mathrm{Alt}_a^* - \mathrm{Alt}_a\right) \times \mathrm{Lapse}/1000 \quad (1)$$

where Alt_a^* is the altitude of the weather station, Alt_a the altitude of the water body, and Lapse is the lapse rate at which the atmospheric temperature decreases with increasing altitude, which in the present study was grossly estimated at 0.6 °C per 100 m (http://global.britannica.com/EBchecked/topic/330402/lapse-rate [accessed 04/06/2015]). Based on T_a, the mean annual water temperature T_w (°C) of the water body was then computed as (after Erickson and Stefan 1996):

$$T_w = 3.47 + 0.898\,T_a \quad (2)$$

Additionally, the latitude and longitude of each water body were used to identify the corresponding Köppen–Geiger climate class and type (after Peel et al. 2007; Appendix Table S1 in Electronic Supplementary Material), which were obtained by reference to a regular 0.5° latitude/longitude grid for the period 1951–2000 [Kottek et al. 2006; available at http://koeppen-geiger.vu-wien.ac.at/data/Koeppen-Geiger-ASCII.zip (accessed 04/06/2015)].

For comparative purposes and consistency with other studies (e.g. Hickley and Dexter 1979; Britton 2007), fork length (FL) was the reference length measurement employed across all reviewed studies. Consequently, whenever required mean LAA values were expressed as FL (mm; converted from cm or inches, if originally reported as such) using the following species-specific conversion factors from SL (standard length) or TL (total length) (Froese and Pauly 2014):

$$\mathrm{FL} = 1.152\,\mathrm{SL} \quad (3a)$$

$$\mathrm{FL} = 0.802\,\mathrm{TL} \quad (3b)$$

Notably, for those studies (mainly from former USSR countries) providing no indication of the length measurement employed, this was taken to be SL (see Vilizzi et al. 2015). On the contrary, for those studies (8 % in total) where no indication of the length used was reported, this was taken to be FL, which represented the nearest-accurate and 'most judicious' choice given possible conversion from SL or TL.

Overall, data on mean LAA and/or VBGF parameters were obtained from 231 Eurasian water bodies (latitude: ≈36°–66°N; longitude: ≈8°W–87°E: Fig. 1 and Appendix Table S2 in Electronic Supplementary Material) for 301 roach populations in total (Appendix Table S2 in Electronic Supplementary Material). Introduced populations were those from lakes Maggiore and Piediluco (Italy), whereas the population from the River Funshion (Ireland) was semi-naturalised, and those from Ulungur and Sayram lakes (China) as well as from Porsuk and Seyhan reservoirs (Turkey) were translocated.

Growth patterns

The growth index (GI, %; Hickley and Dexter 1979) was used to assess the extent of growth in roach. The GI is computed as the mean value of the growth in each age class for a certain population relative to a reference age class-specific global growth value for the species as (after Hickley and Dexter 1979):

$$\mathrm{GI} = \sum \mathrm{FL_{oi}}/\mathrm{FL_{ri}} \times 100 \quad (4)$$

where $\mathrm{FL_{oi}}$ and $\mathrm{FL_{ri}}$ are the observed and reference mean fork length, respectively, of the roach population at age i (i = 1–4). Notably, because of the likely high level of noise in the estimated LAAs in the reviewed dataset, only the first four age classes (whenever available) of each population were included in the computations.

Evaluation of the overall growth in roach across its Eurasian range of distribution and comparisons between/amongst habitats, climate classes and climate types were based on the VBGF (Ricker 1975):

$$\mathrm{FL} = \mathrm{FL}_\infty\left(1 - e^{(-K(\mathrm{age}-t_0))}\right) \quad (5)$$

where FL_∞ is the asymptotic FL, K the Brody growth coefficient (years^{-1}), and t_0 the age of the fish at 0 mm FL. Following Vilizzi et al. (2015), comparisons between/amongst groups for the VBGF were made by fitting eight models in total: (1) a general model with separate parameter estimates for each group (e.g. $\mathrm{FL}_{\infty 1} \neq \mathrm{FL}_{\infty 2}$, $K_1 \neq K_2$, $t_{01} \neq t_{02}$; where 1 and 2 are the two different groups in the comparison); (2) three models with one parameter in common between/amongst groups (e.g. FL_∞, $K_1 \neq K_2$, $t_{01} \neq t_{02}$; $\mathrm{FL}_{\infty 1} \neq \mathrm{FL}_{\infty 2}$, K, $t_{01} \neq t_{02}$; $\mathrm{FL}_{\infty 1} \neq \mathrm{FL}_{\infty 2}$, $K_1 \neq K_2$, t_0); (3) three models with two parameters in common between/amongst groups (e.g. FL_∞, K, $t_{01} \neq t_{02}$; FL_∞, $K_1 \neq K_2$, t_0; $\mathrm{FL}_{\infty 1} \neq \mathrm{FL}_{\infty 2}$, K, t_0); and (4) one common model with the same parameter estimates for all groups (i.e. FL_∞, K, t_0). Both the Akaike (AIC) and Bayesian Information Criterion (BIC) were computed to select the best-fitting model, with preference given to BIC in case of major disparity of outcomes for reasons of model parsimony (i.e. fewer parameters), otherwise to AIC for biological meaningfulness (Burnham and Anderson 2003). Fitting of models was in R x64 v3.0.3 (R Core Team 2014) using packages 'FSA' (Ogle 2014) with 1000

Fig. 1 Water bodies for which growth data for roach *Rutilus rutilus* were reviewed (see also Table S2 in Electronic Supplementary Material)

bootstrap confidence interval estimates of the parameters (and with additional supporting code written by the second author).

For those populations in the dataset for which no original VBGF parameters were provided in the source study, a VBGF was fitted to the available mean LAA data. To this end, a maximum FL_∞ value of 576 mm (based on the maximum reported SL = 500 mm for roach: Froese and Pauly 2014) was set as the upper limit (threshold) for asymptotic growth. Fitting of the VBGF was in the FAO-ICLARM FiSAT II v1.2.2 package (Gayanilo et al. 2005), under the constraint of there being more than six mean LAA values for a population, using the above-defined FL_∞ threshold, and with a starting value of t_0 ranging between −2 and 2 (which was otherwise fixed at 0 in case of lack of fit). In case of overall lack of fit for a population (i.e. estimated FL_∞ value above the threshold resulting from real non-asymptotic growth, lack of sampling of the older age classes, or underestimation of older ages in the corresponding population), no VBGF parameters were assigned.

Overall, LAA data were available for 299 of the 301 populations reviewed, and parameters for the VBGF were originally provided for 30 populations in total (parameters for one population were discarded because of unrealistic estimates in the source study and re-fitted accordingly). Parameters were then successfully fitted to the mean LAA values of an additional 159 populations. Of the remaining 112 populations, VBGF parameters could not be fitted to eight of them, whereas 104 had less than seven mean LAA values to allow fitting (including the two populations for which no LAA values were originally provided). In total, VBGF parameter triplets (L_{inf}, K, t_0) were obtained for 189 populations (Appendix Table S3 in Electronic Supplementary Material).

Latitudinal clines

Latitudinal clines were investigated based on GI and FL_{Age4}. The latter parameter was computed as mean length at age 4 and used as an indicator of fish size due both to the species reaching full maturity at this age (e.g. Tarkan 2006) and to the largest number of corresponding LAA data points in the dataset at this age. Both parameters were regressed against latitude to detect the possible presence of a trend and a corresponding threshold, i.e. the latitudinal value at which a shift in trend would occur. Fitting of piecewise linear relationships was in R with package 'SiZer' (Sonderegger 2012; see also Sonderegger et al. 2009), which allows to detect significant thresholds in ecological data, with 1000 bootstrap estimates for computation of confidence intervals. Following identification of the threshold for each life-history

parameter, a linear model was fitted to each of the two resulting (piecewise) regressions. Because of fitting two models in total to the same dataset, tests of significance were Bonferroni-corrected at $\alpha = 0.05/2 = 0.025$.

Countergradient growth variation

Computation of CGV was based on the equation (Power and McKinley 1997; see also Rypel 2012a):

$$G = FL/(GDD \times age) \quad (6)$$

where G is growth rate (mm GDD^{-1}) and GDD is the number of growing degree days >10 °C for the corresponding water body and computed as:

$$GDD = \sum ((((T_{max_m} + T_{min_m})/2) - T_{base}) \times days_m) \quad (m = 1, \ldots, 12) \quad (7)$$

where T_{maxm} and T_{minm} are the averages of the maximum and minimum air temperatures (corrected as per Eq. 1), respectively, of month *m* [Meteorologisk Institutt: www.yr.no (accessed 06/02/2015)], $T_{base} = 12.5$ °C, $days_m$ is the number of days in any month, and Σ indicates summation over the 12 months of the year. Choice of the standardised value for T_{base} was according to the median value reported in Chezik et al. (2014), which is also in line with the reported >12 °C threshold for inception of growth in roach (van Dijk et al. 2002). Notably, no conversion from T_a to T_w was made, as this has been recommended against for GDD computations (Chezik et al. 2014).

Relationships between CGV and latitude were assessed for roach ages 1 through to 10 (due to small sample sizes, older ages were excluded from analysis). Fitting was by linear mixed effects (LME) modelling (Bates 2010), with two main models fitted including G as the response variable, Latitude and Altitude as fixed effects (covariates) and Age as random effect. The first was a random intercept model, under the assumption that G varies depending on age but at the same rate across ages:

$$G \sim Lat + Alt + (1|Age) \quad (8)$$

and the second was a random intercept and slope model, under the assumption that G varies not only depending on age but also at a different rate across ages:

$$G \sim Lat + Alt + (Lat|Age) \quad (9)$$

where in both models the terms outside the parentheses are the fixed effects and inside the parentheses are the random effects.

The statistical significance of the two models was tested by both AIC and ANOVA and also relative to a 'null' model (i.e. no random effects and no random slope) to see whether inclusion of a random intercept or a random intercept and slope was justified. Fitting of LME models was in R with package 'lme4' (Bates et al. 2014), and the AIC-based comparison was with package 'bbmle' (Bolker and R Development Team 2014).

Fig. 2 Growth in length for roach as described by the von Bertalanffy growth function (VBGF; parameters in Table 2) fitted: **a** globally to the entire dataset (range max − min of FL values for each age class at top of chart.); **b** by habitat; **c** by climate class; **d** by climate type II B; **e** by climate type II C; and **f** by climate type D (see Table S1 in Electronic Supplementary Material). In the scatterplots, each *point* represents one mean length-at-age (LAA) value (see Table S2 in Electronic Supplementary Material) and the *shaded area* indicates 95 % bootstrapped confidence intervals. The *points* in scatterplots **b–f** are slightly jittered to improve visibility

Results

In total, 2251 mean LAA data points (=FL values) in 18 age classes were retrieved and there was considerable spread especially at ages 8–10 and 12, for which the range (i.e. difference between max FL and min FL) was ≥300 mm (Fig. 2a). The longest-lived populations were those from Orava Reservoir, Czech Republic (18 years), and from Lake Øyeren, Norway (17 years) (Appendix Table S2 in Electronic Supplementary Material). Except for climate type Dfa, for which realistic VBGF parameters could not be fitted, the upper confidence interval for FL_∞ in all models was always below the FL = 576 mm threshold, indicating good fit to the data (Table 1). For Habitat, there was no difference in growth rate between lentic and lotic populations, and a common VBGF was fitted (Fig. 2b). For Climate class, three VBGFs were fitted differing in the *K* parameter values, which decreased progressively from class B to C to D (Fig. 2c). For Climate type II B, due to low sample sizes and modelling constraints the FL_∞ value was fixed to

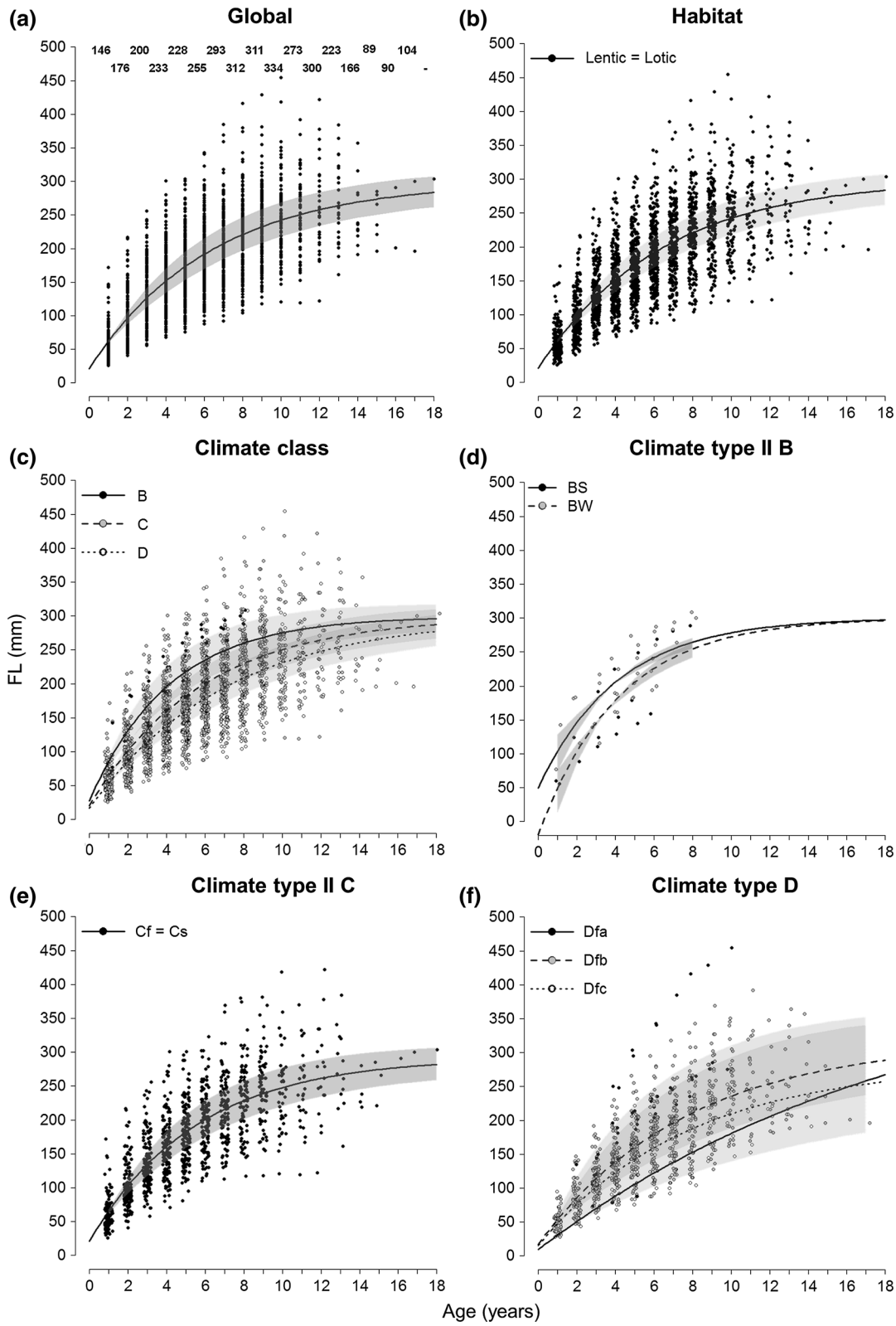
(a)
Global
146 200 228 293 311 273 223 89 104
176 233 255 312 334 300 166 90 -
(b)
Habitat
Lentic = Lotic
(c)
Climate class
B
C
D
(d)
Climate type II B
BS
BW
(e)
Climate type II C
Cf = Cs
(f)
Climate type D
Dfa
Dfb
Dfc
FL (mm)
Age (years)

Table 1 Growth in roach *Rutilus rutilus* across its Eurasian range of distribution (see Fig. 1) as described by the von Bertalanffy growth function (VBGF)

Parameter	Estimate	SE	LCI	UCI	t	P
Global—$n = 2251$, $N = 299$						
FL_∞	299.96	8.94	284.08	319.01	33.55	**<0.001**
K	0.16	0.01	0.14	0.18	13.77	**<0.001**
t_0	−0.46	0.12	−0.71	−0.24	−3.74	**<0.001**
Habitat—Lentic: $n = 1572$, $N = 213$; Lotic: $n = 679$, $N = 88$						
FL_∞	299.96	8.94	284.31	319.51	33.55	**<0.001**
K	0.16	0.01	0.13	0.18	13.77	**<0.001**
t_0	−0.46	0.12	−0.72	−0.24	−3.74	**<0.001**
Climate class—B: $n = 52$, $N = 10$; C: $n = 1143$, $N = 149$; D: $n = 934$, $N = 124$						
FL_∞	299.60	8.74	284.37	318.47	34.26	**<0.001**
K_B	0.24	0.02	0.19	0.29	9.92	**<0.001**
K_C	0.17	0.01	0.15	0.20	13.42	**<0.001**
K_D	0.14	0.01	0.12	0.16	14.60	**<0.001**
t_0	−0.40	0.12	−0.65	−0.19	−3.35	**<0.001**
Climate type II B—BS: $n = 35$, $N = 7$; BW: $n = 17$, $N = 3$						
FL_∞[a]	299.45	8.83	283.90	319.77	33.96	**<0.001**
K	0.24	0.03	0.19	0.29	8.81	**<0.001**
t_{0BS}	−0.75	0.50	−1.92	0.03	−1.49	0.142
t_{0BW}	0.26	0.36	−0.52	0.84	0.72	0.477
Climate type II C—Cf: $n = 1100$, $N = 141$; Cs: $n = 43$, $N = 8$						
FL_∞	292.52	9.84	274.80	313.08	29.74	**<0.001**
K	0.18	0.01	0.15	0.21	11.30	**<0.001**
t_0	−0.41	0.15	−0.70	0.15	−2.82	**0.005**
Climate type D—Dfa-: $n = 49$, $N = 10$; Dfb: $n = 643$, $N = 80$; Dfc: $n = 241$, $N = 34$						
$FL_{\infty Dfa}$[b]	873.29	439.94	468.71	4522.49	1.98	**0.047**
$FL_{\infty Dfb}$	317.93	18.65	286.90	363.58	17.05	**<0.001**
$FL_{\infty Dfc}$	283.58	29.59	236.92	368.32	9.58	**<0.001**
K_{Dfa}	0.05	0.03	0.01	0.12	1.62	0.104
K_{Dfb}	0.13	0.02	0.10	0.16	7.94	**<0.001**
K_{Dfc}	0.13	0.02	0.08	0.18	5.21	**<0.001**
t_0	−0.43	0.21	−0.86	−0.07	−2.05	**0.040**

For each model, parameter estimates are provided with SE (standard errors) and 95 % lower and upper confidence intervals (LCI and UCI, respectively; 1000 bootstrap iterations) for best fit models. FL_∞ = asymptotic fork length (mm); K = Brody growth coefficient (years^{-1}); t_0 = age of the fish at 0 mm FL. Statistically significant tests (in bold) are Bonferroni-corrected at $\alpha = 0.05/6 = 0.01$ because of fitting six models to the same dataset (or subsets thereof). n = number of mean LAA values; N = number of populations. Climate classes and types as in Appendix Table S1 in Electronic Supplementary Material. See also Fig. 1a–e

[a] FL_∞ value constrained to be equal to that of the global model because of low sample sizes

[b] FL_∞ value above maximum reported length for roach (FL = 576 mm: Froese and Pauly 2014)

equal that of the global model and two separate VBGFs were best fitted but only differing in parameter t_0 (Fig. 2d). For Climate type II C, a common VBGF was best fitted due to no significant differences between any of the parameters (Fig. 2e). Finally, for Climate type D three VBGF curves were best fitted with different FL_∞ and K parameter values, which progressively decreased from type Dfa to Dfb to Dfc

(even though for type Dfa growth was non-asymptotic) (Fig. 2f).

Piecewise regression highlighted significant decreasing trends and thresholds for both GI and FL_{Age4}. For GI, a significantly decreasing trend was present above 48°N, below which no significant trend was identified, even though this was possibly the result of low sample sizes (Fig. 3a; Table 2). For FL_{Age4}, a significantly decreasing trend was present both above and below 54°N, but with a higher decrease in the latter case (Fig. 3b; Table 2).

Growth degree days could be estimated for 149 water bodies in total and ranged from 167 GDD (Lake Pyhäjärvi, Finland) to 2753 GDD (Gomishan wetland, Iran) (Appendix Table S2 in Electronic Supplementary Material). Linear mixed effects (LME) modelling indicated a significant improvement after inclusion of both latitude and altitude as fixed effects and of age as a random effect, whereas additional inclusion of a random slope did not improve the model significantly (i.e. over one consisting of a random intercept only). The final LME model of choice pointed to a significant increase in growth rate per GDD across all age classes 1–10, which occurred at a similar rate (Table 3; Fig. 4).

Discussion

Growth patterns

The observed lack of differences in the growth of roach between lentic and lotic habitats is not surprising given the cosmopolitan nature of the species and its adaptability to different aquatic environments (Graham and Harrod 2009; Froese and Pauly 2014). This contention is further supported by the fairly high proportion in the reviewed dataset of populations from lotic ($\approx$30 % of the entire sample) relative to lentic habitats, hence contrary to studies on other fish species indicating similar lack of differences but characterised by under-represented riverine populations (e.g. Rypel 2012b, Vilizzi et al. 2015). On the other hand, K (but not FL_{∞}) differed at the broad scale between climate classes, and the lower and higher values observed for cold (D) and warm (B) climates, respectively, were a likely reflection of the harsher conditions of temperature extremes and hypoxia (either winter- or summertime: Bajer and Sorensen 2010) experienced by roach compared to temperate climate (C) conditions. At the smaller scale (i.e. climate type), whilst the lack of differences in growth between both B and C climate types II was likely a result of limited sample sizes in the former case and under-represented populations from Cs climate type II in the latter, the differences observed amongst climate types D are noteworthy. Thus, despite similar growth rates between Dfb and Dfc climates, based on the present findings the cold-summer conditions experienced by roach under Dfc would lead to lower asymptotic size; whereas, the hot-summer conditions under Dfa would allow to achieve non-asymptotic growth.

Overall, the observed differences in roach growth can be explained in terms of optimisation of resource allocation between growth and reproduction (Kozlowski 1992, 1996) under different climatic conditions (abiotic constraints), and with a positive effect of temperature on the species' growth (e.g. Lappalainen et al. 2008) as commonly observed in temperate cyprinid fishes (Mann 1991). Conversely, the observed lack of differences between lentic and lotic populations may have been the result of the species' capability to maximise opportunistically the utilisation of available resources (biotic factors). However, further evidence is needed to support this contention, given that variation in growth is known to be influenced by a wide range of biotic and abiotic factors including genetic effects (Silverstein et al. 1999), density dependence (Pierce et al. 2003) and exploitation (Kipling 1983), which could not be investigated in the present study. A high level of phenotypic plasticity may allow roach to maintain a 'predefined' growth trajectory regardless of the influence of a/biotic variables and above possible intraspecific variation at the system or regional level. As recently observed in common carp *Cyprinus carpio* (L., 1758) (Vilizzi et al. 2015), the mechanisms responsible for these patterns may result from evolutionary inter-relationships between genotype and developing phenotype (Vilizzi and Kováč 2014).

Two caveats would apply to the present findings. Firstly, similar to most literature-based comparative fish age-growth studies, the modelling of relationships based on mean LAA values as opposed to the use of individual fish lengths measurements has allowed in the present study for an approximation of the underlying patterns of growth variation in roach, contrary to the higher resolution possible with the availability of

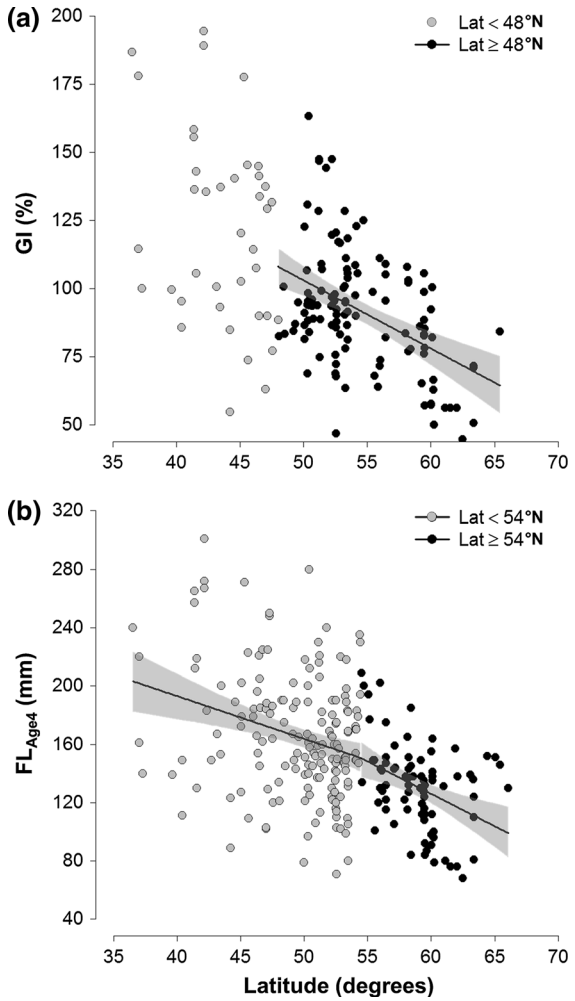

Fig. 3 Piecewise regression relationships for two life-history parameters of roach along its latitudinal gradient of distribution. **a** Growth index, GI; **b** mean length at age 4, FL_{Age4}. Each *dot* in a chart corresponds to a roach population, with *gray* and *black dots* indicating populations below and above the latitudinal threshold shift value along the trend (see Table 3)

individual fish lengths (e.g. Kas'yanov et al. 1995). Secondly, the evaluation of growth patterns in roach for both sexes combined due to the limited availability of data for males and females separately has likely masked sex-related growth differences due to females generally growing larger and older than males (e.g. Goldspink 1979; Cowx 1988; Naddafi et al. 2005).

Latitudinal clines

The significant decreasing trends with increasing latitude in roach growth (as described by parameters GI and FL_{Age4}) were in agreement with other studies (e.g. Mills 1988; Lobón-Cerviá et al. 1996; Blanck and Lamouroux 2007) and in line with life-history theory predictions for ectothermic animals of faster growth at high temperatures (Angilletta and Dunhan 2003). In the case of fish, these are generally accompanied by larger sizes (hence, contrary to Bergmann's rule: Belk and Houston 2002) from south to north, suggesting decreased mortality rates (Beverton 1987). In the case of growth, the decreasing trends with latitude reflected the observed patterns in the climate-related global growth rates (see *Growth patterns*), even though the latter did not support the presence of differences in body size (i.e. equal FL_{∞} across climate classes). However, given that the VBGF typically models asymptotic growth rather than growth at a certain age, the validity of the findings is maintained.

When accounting for confidence intervals, the estimated thresholds for the two life-history parameters for roach investigated in the present study encompassed the 50°N latitude breakpoint in absolute fecundity, VBGF parameters and reproductive life-span identified by Lappalainen et al. (2008) for this species. In that study, non-linear relationships with latitude were modelled and an argument was made that decreased growth patterns near the southern limits of the species' distributional range might be linked to temperatures exceeding optimal levels for efficient growth. In the present study, there was evidence for a decreasing trend in growth as described by FL_{Age4}, and this could be explained in accordance with Lappalainen et al. (2008) in terms of thermal stress experienced by roach at the high water temperatures of lotic water bodies in its southern range of distribution during the summer months (see 'hypoxia argument': Bajer and Sorensen 2010). Whereas, the lack of statistical significance in a trend for GI at latitudes below 48°N would indicate the presence of a plateau but also of water body-specific a/biotic factors acting upon the species' 'genetically-programmed' growth capacity (Lappalainen et al. 2008).

Countergradient growth variation

Growing degree days varied largely from northernmost to southernmost water bodies, indicating the extent of the distributional range of roach as a eurythermal generalist fish species. At all age classes (i.e. 1+ to 10+) for which representative sample sizes

Table 2 Piecewise regression relationship for two life-history parameters for roach along its latitudinal gradient of distribution

Parameter	Absolute latitude				Source	Estimate	SE	t	P
	Mean	LCI	UCI	Threshold					
GI	48.08	37.28	59.26	<48°N	Intercept	278.83	79.57	3.50	
					Latitude	−3.54	1.82	−1.94	0.059
				≥48°N	Intercept	226.65	24.94	9.09	
					Latitude	−2.47	0.46	−5.42	**<0.001**
FL_{Age4}	54.43	41.40	62.95	<54°N	Intercept	308.83	37.82	8.17	
					Latitude	−2.90	0.76	−3.81	**<0.001**
				≥54°N	Intercept	383.24	68.31	5.61	
					Latitude	−4.29	1.16	−3.71	**<0.001**

The threshold absolute latitude (with 95 % lower and upper confidence intervals LCI and UCI, respectively; 1000 bootstrap iterations) is provided at which a shift in the trend is estimated to occur. Statistically significant tests (in bold) are Bonferroni-corrected at $\alpha = 0.05/2 = 0.025$ because of fitting two models to the same dataset. See also Fig. 3

Table 3 Fixed and random effects coefficients for a linear mixed effect model (Eq. 8) describing countergradient growth variation in roach (growth rate G in mm GDD^{-1}: Eq. 6) across all ages and separately for ages 1 through to 10 (see also Fig. 4)

Age	Fixed effects			Random effects
	Intercept	Latitude	Altitude	
All	−0.09181	0.00249	0.00006	–
1	−0.06288	0.00249	0.00006	0.02855
2	−0.07687	0.00249	0.00006	0.01453
3	−0.08397	0.00249	0.00006	0.00764
4	−0.08980	0.00249	0.00006	0.00217
5	−0.09423	0.00249	0.00006	−0.00225
6	−0.09718	0.00249	0.00006	−0.00506
7	−0.10084	0.00249	0.00006	−0.00854
8	−0.10298	0.00249	0.00006	−0.01094
9	−0.10319	0.00249	0.00006	−0.01153
10	−0.10615	0.00249	0.00006	−0.01457

for CGV computation were available, there was a strong indication of countergradient effects. These results are in line with studies on other fishes (e.g. Conover and Present 1990; Conover et al. 1997; Power and McKinley 1997; Rypel 2012a, b, 2014) and in the present context indicate that roach populations at higher latitudes would compensate for the shorter seasonal 'window of opportunity' for growth by growing faster at virtually all ages. Also, the inclusion of altitude as a covariate in the models was critical to adjust for the potential spurious effects of water temperature conditions in water bodies located in mountainous regions (e.g. Batak Reservoir, Dospat Reservoir and Lake Sayram, all above 1000 m a.s.l.; see Appendix Table S2 in Electronic Supplementary Material). It is therefore argued that this modelling improvement should not be overlooked in further studies on CGV.

Whilst all age-related relationships between growth rate and latitude were statistically significant, the lack of differences between slopes also was in line with previous findings. Thus, Rypel (2012a) found a significant exponential decline in the regression slopes for growth rate in all age classes of striped bass *Morone saxatilis* (Walbaum, 1792), even though the slopes amongst the corresponding regression lines did not

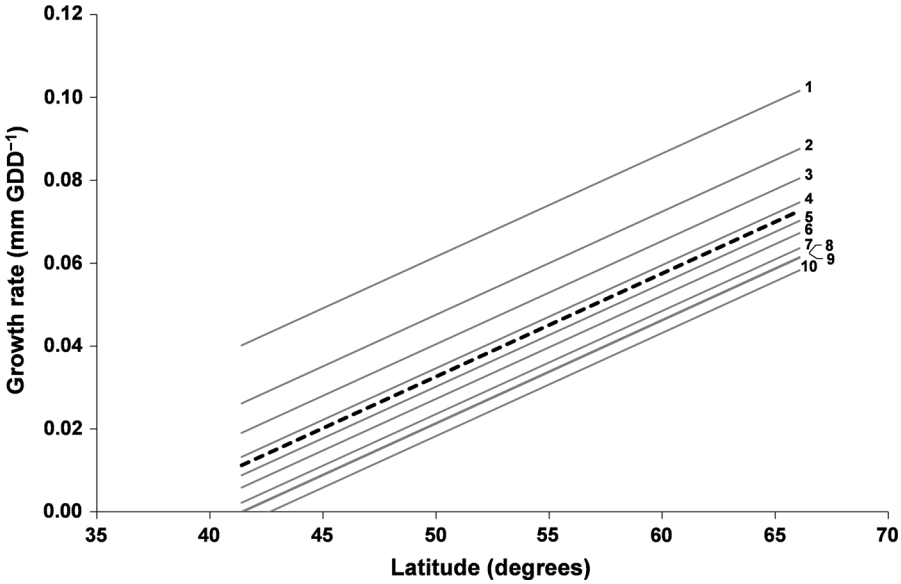

Fig. 4 Countergradient growth variation in roach at ages 1–10. For each age, the fitted linear relationship between growth rate (GDD = growth degree days) and absolute latitude according to a mixed effects model (parameters in Table 3) is indicated together with the overall relationship across all ages (*hatched line*)

differ significantly. This was also the case for the present study, in which fitting common slope regression lines by mixed effects modelling provided for a robust and statistically valid description of the relationships.

Implications for further dispersal and climate change predictions

As a result of the documented impacts on other species in its non-native areas of introduction, roach is currently listed as a 'potential pest' (Froese and Pauly 2014), and in a recent assessment of its potential further spread across the Iberian Peninsula was categorised as a 'high risk' species (Almeida et al. 2013). In the present review, no published age-growth data were available for roach from the Iberian Peninsula, nor were mean LAA data available with which to model GI-based relationships for the two introduced populations of Lake Maggiore (Volta and Jepsen 2008) and Lake Piediluco (Giannetto et al. 2014) in the Italian Peninsula. Regardless, in those studies growth rates of roach were reported to be higher compared to other European waters. However, this contention was not supported by the current global evaluation, nor was the case for the semi-naturalised populations from Ireland and the translocated population from China. On the other hand, should further dispersal by introduction and/or translocation occur at the southernmost limits of the species' range of distribution, water body-specific biotic factors are likely to come into play as main drivers for growth rate in roach, as observed in the present study for the translocated populations in Seyhan and Porsuk reservoirs.

Regardless of the ongoing tension between denialism versus catastrophism (Costello et al. 2011), should climate change predictions for warmer conditions across the species' distributional range prove valid, then based on the present findings a northern shift in the identified thresholds for growth may be postulated. This would result in faster growth rates, increased mortality and decreased longevity at latitudes higher than those currently identified, even though water body-specific a/biotic factors are likely to dampen such effects. Given its eurythermal preferences, roach is likely to adapt quite rapidly to altered climates, with warmer water temperatures increasing the scope for recruitment, although within the local constraints indicated above (Graham and Harrod 2009). However, given the geography of the Eurasian landmass causing latitudinal temperature gradients to be comparatively less pronounced compared to e.g. those for North America (e.g. Rypel 2012b), the effect of increased water temperatures may not be as exacerbated at least in northwest and central Europe. On the other hand, a

west–east (i.e. longitudinal) effect may become more evident in continental Eurasia with a shrinkage in the range of cold climates. Inter-continentally, a decrease in the species' range would result following increased annual average temperatures because of thermal stress (Lappalainen and Tarkan 2007; Lappalainen et al. 2008). It is therefore argued that further dispersal of roach aided by increased temperatures because of changed climate conditions may 'homogenise' the population dynamics of this species, which may respond to increased thermal stress and unpredictability of environmental conditions through a shift toward more 'altricial' (i.e. less specialised and more adaptable) life-history characteristics (e.g. Kováč et al. 2009; Vilizzi and Kováč 2014).

Acknowledgments We are grateful to Bořek Drozd (University of South Bohemia, Czech Republic), Gordon H. Copp and Phil Davison (Cefas, UK), Hui Wei (Chinese Academy of Fishery Sciences, China), Riikka Puntila (University of Helsinki, Finland) and Tamsin Vicary (Freshwater Biological Association, UK) for contributing key references towards the literature review. Contribution to this study by LV was through a 2221 Fellowship Programme granted by The Scientific & Technological Research Council of Turkey (TÜBİTAK) and The Department of Science Fellowships & Grant Programs (BİDEB).

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