

Variability in the growth rate of chub *Leuciscus cephalus* along a longitudinal river gradient

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An increase in individual growth rate of chub *Leuciscus cephalus* along a longitudinal river gradient of the Rhône River basin was observed and supported by significant differences between mean growth rates of successive river size groups. The potential implications of the results for studies on species traits variability along large-scale environmental gradients are discussed.

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Within a particular species-specific genetic component, growth rate is a highly plastic character in fishes, depending on various environmental factors. Water temperature is among the most important (Mann, 1976), although further insights showed that growth rate is related to the overall environmental structure involving flow fluctuations, food supply, population density, insurmountable barriers and microhabitats (Copp *et al.*, 1991; Grossman & De Sostoa, 1994; Bouchard *et al.*, 1998). Because riverine fish species often have particular habitat requirements (Buisson *et al.*, 2008), restricting their distribution within rivers, variability in fish growth has usually been the focus of local-scale studies (Abdoli *et al.*, 2007). At large spatial scales and except for latitudinal studies (Heibo *et al.*, 2005; Blanck & Lamouroux, 2007), very few papers have considered large environmental gradients in comparative approaches of intraspecific variation in growth rates (Przybylski, 1996; Pegg & Pierce, 2001).

Although the longitudinal upstream–downstream gradient can be considered as the most well-known pattern in stream fish assemblage structure, accounting for a wide range of environmental factors (Matthews, 1998; Buisson *et al.*, 2008), little is known about the intraspecific variability of species traits along this gradient. Here the focus is on the growth pattern of a widely distributed

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species, *Leuciscus cephalus* (L.), along an extensive river size gradient of the Rhône River drainage (France). The great ecological amplitude of *L. cephalus* colonizing a large number of habitats with different environmental conditions at the drainage scale, offers the possibility to explore the variability of growth rate in contrasting situations. Large longitudinal river gradients produce important gradual changes in the physical and biological factors affecting fish growth rates. Decreasing elevation (inversely related to temperature) and flow constraints combined with increasing habitat dimensions and nutrient availability going downstream (Allan, 1995) are expected to positively influence the growth patterns of this ubiquitous species.

Sixteen *L. cephalus* populations were sampled by electrofishing from 1993 to 1994. From 20 to 30 individuals were collected by site (*i.e.* population) leading to 418 individuals. Sites were located over an upstream–downstream gradient, from the Grosne River to the Lower Rhône River (Fig. 1). All individuals were measured (total length, L_T to the nearest mm), and scale samples were collected from the first two rows between the lateral line and the dorsal fin (Spillmann, 1961). Three scales per individual were read, and the measurement described below were averaged to partially clear out the potential intra-individual variability. Backcalculation (Ricker, 1992) of L_T [a method validated for *L. cephalus* by a mark–recapture study by Le Louarn & Baglinière (1997)] was estimated from the radius of successive annuli and from the linear regression between L_T (in mm) and total radius (R in mm) of the scale: $L_T = 48.87R + 48.94$ ($r^2 = 0.96$, $n = 418$). Individual growth rate g (in mm year⁻¹) was computed by averaging the growth over the ages 1 (L_{T1})–3 (L_{T3}) years as $0.5(L_{T3} - L_{T1})$ to avoid possible differences in growth rate observed between mature males and females (Le Louarn *et al.*, 1997), and differences in fish age among populations (Zivkov *et al.*, 1999). In return, growth rate was computed for 381 individuals, ranging from 12 to 33 individuals per site. Excluding mature individuals also allows circumventing a potential confounding effect of spawning migrations (Fredrich *et al.*, 2003), home-range movements being negligible at the scale studied (*c.* 500 m; Allouche *et al.*, 1999).

Four descriptors of the position of each site along the longitudinal river gradient were used: (1) distance from the headwater source D_S (km), (2) surface area of the drainage basin above the sampling site A_S (km²), (3) elevation E (m) and (4) river width W (m). The first three variables were derived from topographic maps and the last from aerial photographs. The first axis of a principal component analysis (PCA) based on these ln-transformed variables was used to compute a synthetic index (I_{LRG}) describing the position along the longitudinal gradient. The first axis accounted for 88% of the variability and was positively related to D_S , A_S and W and negatively to E . Accordingly, high I_{LRG} values corresponded to the most downstream sites.

Growth rate data from Przybylski (1996) and Larno *et al.* (2001) computed as described above were used to check if the present results were commensurated, and if the growth rate–longitudinal gradient relationship was confirmed. These authors worked on *L. cephalus* growth over a large longitudinal river gradient of the Warta and the Rhône River drainages, respectively, but only studied three sites each. The position in the longitudinal gradient of these sites was estimated as described above.

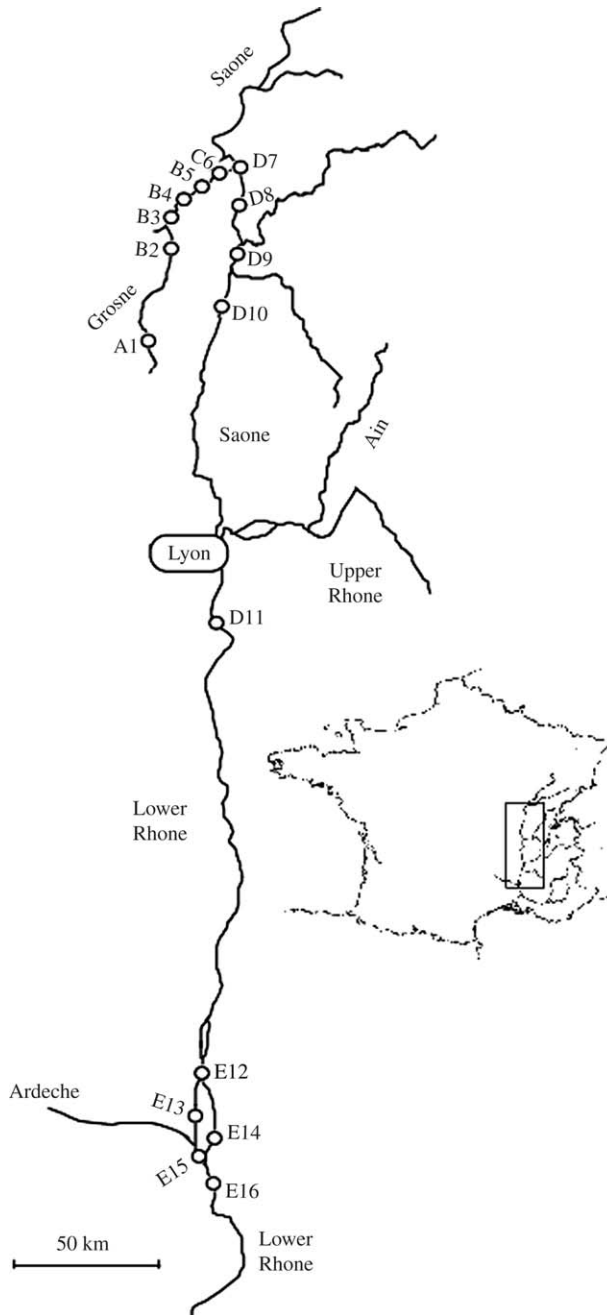


FIG. 1. Location of *Leuciscus cephalus* sampling sites (A1–E16) along the Rhône River drainage basin.

To visualize the growth rate–longitudinal gradient relationship, mean growth rates of each population were plotted as a function of I_{LRG} . To test for differences between growth rates accounting for the redundancy in the positioning of sampling

sites along the gradient, a cluster ordination was applied on the PCA results in order to determine groups of similar longitudinal gradient characteristics (from A to E; Table I and Fig. 1). One-way ANOVA was then applied to these groups.

The mean g rate estimated over the 381 individuals ($53.5 \text{ mm year}^{-1}$) was similar to most of other European temperate water bodies (Mann, 1976; Hickley & Bailey, 1982; Przybylski, 1996; Le Louarn *et al.*, 1997), although differences exist within populations inhabiting extreme northern or southern rivers of the species latitudinal range (Känno, 1969; Vitali & Braghieri, 1984). A positive growth rate–longitudinal river gradient relationship was observed when comparing mean values by site (Fig. 2). The positive trend and the magnitude of the observed values were commensurate with standardized data from Przybylski (1996) and Larno *et al.* (2001). Significant differences were found when comparing mean g of successive river size groups (from A to E; Fig. 2) supporting the observed gradual increase in growth along the river gradient ($A \cong B < C < D \cong E$; $F_{4,396}$, $P < 0.001$).

The growth pattern of *L. cephalus* was expected to reflect differences in habitat conditions as going downstream. Przybylski (1996) and Mann (1997) studied the variation in fish growth characteristics along a river course and found a growth pattern in accordance with the present results, although they did not explicitly relate the finding to the longitudinal river continuum. A longitudinal river size increase may go along with an increase in water temperature. Unfortunately, temperature data of the growing periods prior to sampling (*e.g.* years 1988–1993 for a 5 year-old individual) were not available for the sampling sites. As a rough indication to discuss the observed growth pattern, water temperature measured on 15 and 16 June 1993 by the French Agency for Water (<http://www.rhone-mediterranee.eaufrance.fr/>) from localities in close proximity to some of the present sampling sites display a positive relationship with growth rates ($r^2 = 0.48$, $n = 13$, $P < 0.01$; no temperature data were found for sites E14, E15 and E16). This temperature measurement was significantly correlated to the longitudinal river gradient (Pearson's correlation between I_{LRG} and water temperature; $r = 0.65$, $n = 13$, $P < 0.05$) and was not significant in explaining growth rate after accounting for I_{LRG} . Although simplifying the high variability of temperature to a single value is inappropriate, these trends show that summer temperature may be involved to some extent, though cannot be conclusive. Temperature is the main factor determining the metabolic rate in fishes, influencing a variety of physiological and external variables such as feeding and digestion rates (Elliott, 1976; Hofmann & Fischer, 2003), and food availability (Jones, 1986), ultimately affecting growth rate. Since the longitudinal river gradient is related to daily and seasonal variability in temperature, it is difficult to disentangle between the relative effects of temperature and habitat. Bouchard *et al.* (1998) suggested that deep-water areas with low current speed constitute some sort of hydraulic refuges, where low energy consumption associated with movements enhances growth rates. In natural water courses, the frequency of calm deep habitats increases progressively downstream, in accordance with the observed increase in growth.

Since growth is related to fish size, which in turn is related to several other life-history traits (Peters, 1983), the present results have clear consequences for future large-scale comparative studies, particularly those focusing on latitudinal

TABLE 1. Mean \pm s.d. values of environmental characteristics and *Leuciscus cephalus* growth rates. For each cluster ordination group (A–E) produced by the principal component analysis describing the position along the longitudinal gradient of each sampling site (Fig. 1)

	D_s (km)	A_s (km ²)	E (m)	W (m)	I_{LRG}	g (mm year ⁻¹)	n
A	20.00 \pm 0.00	100.00 \pm 0.00	356.00 \pm 0.00	8.00 \pm 0.00	-3.75 \pm 0.00	39.34	27
B	66.25 \pm 11.79	650.00 \pm 216.02	191.00 \pm 9.20	20.00 \pm 4.40	-1.94 \pm 0.29	35.10	98
C	96.00 \pm 0.00	1000.00 \pm 0.00	171.00 \pm 0.00	55.00 \pm 0.00	-1.13 \pm 0.00	50.26	21
D	407.40 \pm 66.26	34484.00 \pm 15495.36	166.80 \pm 4.92	211.00 \pm 18.84	0.97 \pm 0.14	66.08	100
E	679.40 \pm 12.09	74986.00 \pm 1350.36	46.80 \pm 9.88	231.00 \pm 118.02	2.32 \pm 0.29	66.53	135

A_s , surface area of the drainage basin above the sampling site; D_s , distance from the headwater source; E , elevation; g , growth rate; n , number of individuals; W , river width.

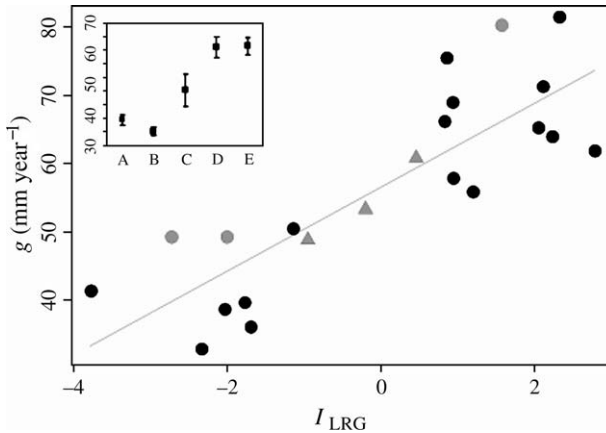


FIG. 2. Mean values of *Leuciscus cephalus* growth rates (g) by sampling site (●, present results; ●, Larno *et al.*, 2001 and ▲, Przybylski, 1996) as a function of the longitudinal position along the river gradient (I_{LRG}). A linear regression including data from Przybylski (1996) and Larno *et al.* (2001) is shown ($y = 6.14x + 56.57$ $r^2 = 0.70$, $n = 22$). The inserted plot shows mean g values by successive river size groups (from A to E; Fig. 1 and Table I) and their CI limits ($\alpha = 0.95$). Data from Przybylski (1996) are mean g values of three distinct river zones of the Warta River (Poland), while data from Larno *et al.* (2001) are mean values of three localities within the Rhône River drainage (France).

variability in freshwater fish species traits (Lobón-Cerviá *et al.*, 1996; Pegg & Pierce, 2001; Heibo *et al.*, 2005; Blanck & Lamouroux, 2007; Lappalainen & Tarkan, 2007). Authors comparing freshwater fish populations from different drainages often use data from the literature and try to reach a whole species distribution range but without accounting for local habitat characteristics. From the present results, factoring out the position in the longitudinal river gradient of the compared populations seems necessary to accurately test patterns relating to latitude, and hence temperature and length of growing period, to life-history traits. Furthermore, a latitudinal study controlling for longitudinal position of populations would help to distinguish between temperature and river size effects on freshwater fish trait variability.

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