

Research Article

Colonization and plasticity in population traits of the invasive *Alburnus alburnus* along a longitudinal river gradient in a Mediterranean river basin

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Abstract

Identification of the most relevant habitat features necessary for the success of potential invaders, such as the bleak *Alburnus alburnus* with its high ecological risk, is fundamental for understanding the invasive process and, thus, for designing effective control programs. This study provides new insights into the residence time and variation of population traits of this species along a longitudinal gradient in one of the most regulated river basin in the Iberian Peninsula. Occurrence data collected from 25 sampling sites (three times in five years) along the Segura River Basin (SE Spain) showed that this species has spread rapidly and now inhabits more than 168 km of fluvial stretches (84.4% of the studied area). The captured individuals were four years old, although greater longevity and larger mature cohorts were more common in sites with longer residence times. Higher values in population abundance in the upstream part of the river basin were accompanied by increased growth rates and higher maximum sizes. The obtained results support the hypothesis that the wide plasticity of the population traits of *A. alburnus* plays an important role in its success in a highly regulated Mediterranean river basin, where this mechanism allows it to survive flow regulation events at various scales, as well as to resist the long-term environmental stress typical of Mediterranean-type rivers.

Key words: non-native, Cyprinids, Iberian Peninsula, life-history, phenotypic variability

Introduction

Biological invasions are considered one of the main threats to global biodiversity, with freshwater ecosystems and their native communities being particularly sensitive to invasive species (Clavero 2011). Invasive fish have been reported to alter aquatic communities by causing the decline, displacement and disappearance of native species, (Cucherousset and Olden 2011) and several studies have shown that they are a significant threat to Iberian native ichthyofauna (García-Berthou et al. 2007; Leunda 2010; Hermoso et al. 2011; Almeida et al. 2013; Fausch and García-Berthou 2013; García-Berthou et al. 2016). In spite of this, aspects about the establishment of invasive fish and their relationship to their biological traits are poorly understood.

The invasion success of fish introduced outside their native range is often explained by the expression of their life history traits that are strongly influenced by environmental conditions (Vila-Gispert et al. 2005; Ribeiro and Collares-Pereira 2010). In fact, the assessment of the growth and population structure provides ecological insights into how populations respond to abiotic and biotic factors (Ruiz-Navarro et al. 2013; Bergerot et al. 2015). Considerable intraspecific plasticity is often observed in the process of adaptation to a new environment (García-Berthou 2007; Ribeiro et al. 2008), and life history variability seems to play an important role in driving invasion success (Ribeiro and Collares-Pereira 2010; Almeida et al. 2014).

The bleak, *Alburnus alburnus* (Linnaeus, 1758) (Actinopterygii, Cyprinidae), is native to Europe, where it is widespread (most of Europe north of Caucasus, Pyrenees and Alps, eastward to Ural and Emba). It is naturally absent from the Italian Peninsula, Adriatic and Aegean drainages, and also the Iberian Peninsula (Froese and Pauly 2018) where it has behaved as a successful invader establishing populations in some basins (Vinyoles et al. 2007). Since its first record in the Ebro River Basin in 1992, it has been repeatedly introduced into reservoirs as a “forage fish” for non-native piscivorous predators and has rapidly spread through Iberian freshwaters as an invasive species (Elvira and Almodóvar 2001). Its impacts on Iberian native fish include competition, disease transmission, hybridization and habitat alteration (Leunda 2010; Almodóvar et al. 2012). Within its native distribution area, this species inhabits lentic habitats such as lakes and medium to large river sectors where it can form shoals reaching high densities (Freyhof and Kottelat 2008). *Alburnus alburnus* has several features that facilitate invasiveness and adaptability to new environments, such as high fecundity, the ability to feed on an extensive range of prey, and wide temperature tolerance (Chappaz et al. 1987; Latorre et al. 2016). Moreover, it has been suggested that *A. alburnus* shows higher spread in regulated rivers because there is a relationship between flow regulation impacts and their populations establishment (Vinyoles et al. 2007; Almeida et al. 2014). In fact, although Mediterranean flow regimes are considered to be leading factors in controlling fish population responses, the loss of natural regimes, together with the creation of lentic habitats related to flow regulation facilities (e.g. reservoirs and weirs) are encouraging the establishment of non-native fishes (Ribeiro and Collares-Pereira 2010; Clavero et al. 2013). However, no study has considered large longitudinal gradients in comparative approaches to intraspecific variations in the biological traits of *A. alburnus*. Except for a recent study which compared some of its growth and reproductive traits in five of the main Iberian watersheds (Latorre et al. 2018), studies of *A. alburnus* life history in Iberian non-native areas have mainly focused on man-made aquatic systems (Almeida et al. 2014, 2017) or local scales (Masó et al. 2016; Muñoz-Mas et al. 2016).

Increased knowledge of the phenotypic plasticity involved in the adaptation of invasive species to local conditions is necessary for management and control programs (Britton et al. 2011). Although biological plasticity of *A. alburnus* has been proposed as an important factor for its invasiveness (Almeida et al. 2014; Masó et al. 2016), there is a clear need for information on whether its population traits will change in invaded areas, as nothing is known about its intraspecific variability along longitudinal upstream-downstream gradients. Bearing in mind the scarcity of information about *A. alburnus* biology in non-native areas and, more specifically, in regulated watersheds, the principal purpose of the present study was to evaluate population features of this species along a longitudinal gradient in highly regulated Mediterranean streams in southeastern Spain (Segura River Basin). The hypothesis was that *A. alburnus* presents a high phenotypic plasticity which enables it to establish large populations in fluvial sectors of Mediterranean systems. Since the invasive success of *A. alburnus* seems to be favoured by flow regulation and the loss of natural flow regimes, understanding its biology in a highly regulated basin could have important implications for management and control programs.

Materials and methods

Study area

The Segura River Basin (drainage area of 18,870 km²) is an intensively regulated Mediterranean basin located in the southeast of the Iberian Peninsula. The climate of this basin is Mediterranean but with a strong climatic and altitudinal gradient; the area is characterized by a pronounced hydrological variability on both spatial and temporal scales. It is one of the most intensively regulated Mediterranean basins in Europe, where irrigation is responsible for the 90% of water demands and constitutes the main anthropogenic pressure on stream flows. The regulation capacity involving dams is equivalent to over 140% of the natural inputs and since the 1980s an inter-basin water transfer has operated from the Tagus River to the Mundo River (Grindlay et al. 2011). In fact, colonization of the Segura River by *A. alburnus* has been partially attributed to fish dispersion along that Tagus-Segura interbasin system (Andreu-Soler et al. 2004). The high degree of regulation is due to the huge demand for water for irrigation purposes and human supply, which entails profoundly altering the natural flow regimes (Belmar-Díaz et al. 2011).

As a part of a larger study to examine the ecological status of fish communities and populations, a total of 25 sampling sites in a stretch of river were located along upstream-downstream gradients, from the Upper Mundo river to the Mundo-Segura rivers confluence (52.2 km long) and from the Upper Segura river to Middle Segura (158 km) (Figure 1). Each site was sampled by electrofishing three times in five years (during autumn

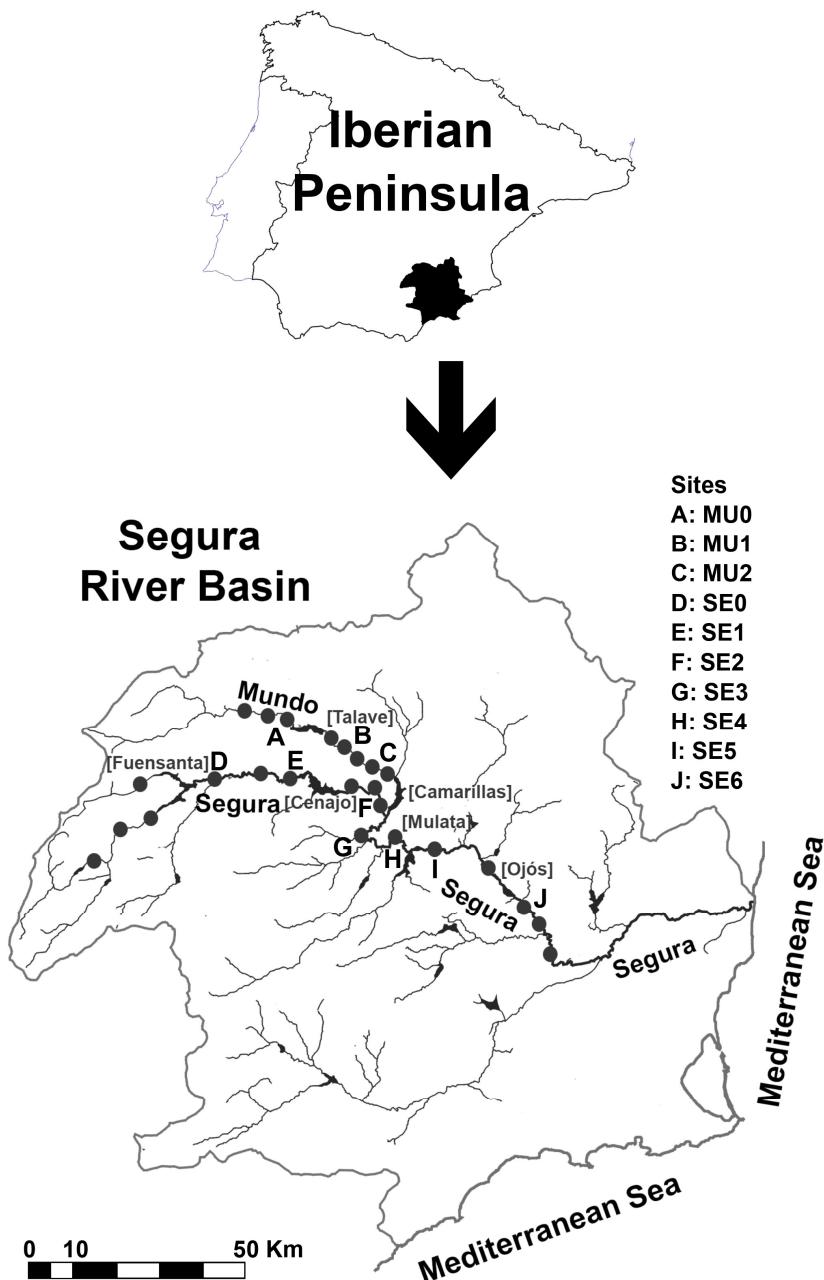


Figure 1. Location of the Segura River Basin (SE Iberian Peninsula) and the 25 sampling sites (black points) where *Alburnus alburnus* occurrences were sampled (2005–2010). A–J: sampling sites for the study of biological traits at population level (autumn 2010). See Supplementary Table S1 to sampling sites geo-reference information.

of 2005, 2008 and 2010). The altitude range of the localities is 90–860 m.a.s.l., water conductivity varies between 364 and 1303 $\mu\text{s cm}^{-1}$, and the average annual water temperatures ranges between 13.9 °C in the upper stretches and 16.9 °C in the lower stretches.

Fish assemblage in the Segura River Basin is composed of both native and non-native species, but is dominated by the latter (Oliva-Paterna et al. 2014). In the middle reaches where *A. alburnus* inhabited, the ichthyophagous species northern pike *Esox lucius* Linnaeus, 1758, pike-perch *Sander lucioperca* (Linnaeus, 1758) and largemouth black bass *Micropterus salmoides* (Lacépède,

Table 1. Habitat variable values of each sampling site where *Alburnus alburnus* populations were assessed: altitude (meters above sea level, m.a.s.l.), ecological status (categories: 1 = very good; 2 = good; 3 = moderate; 4 = deficient); water conductivity ($\pm 0.1 \mu\text{s cm}^{-1}$); water temperature ($^{\circ}\text{C}$); mean daily flow (Mdf, $\text{m}^3 \text{s}^{-1}$) and flow variability Q_{10%}–Q_{90%} (Fv) from the period 2009–2010.

Sampling site	Code	Altitude (m.a.s.l.)	Ecological status	Cond. ($\mu\text{s cm}^{-1}$)	Temp. ($^{\circ}\text{C}$)	Mdf ($\text{m}^3 \text{s}^{-1}$)	Fv
Cola Talave	MU0	540	2	619.3	13.87	5.11	-2.84
Puente Isso	MU1	460	3	674.3	14.10	13.84	-1.61
Blas García	MU2	430	3	687.7	14.10	13.84	-1.61
Bajo Fuensanta	SE0	470	1	340.0	14.67	10.20	-3.89
El Gallego	SE1	452	1	401.0	14.72	9.95	-1.57
Las Minas	SE2	306	2	579.3	14.28	5.18	-6.53
Cañaverosa	SE3	290	2	755.7	15.39	19.41	-1.16
El Esparragal	SE4	260	3	803.0	15.69	19.38	-1.15
Rio Muerto	SE5	200	2	860.7	16.43	19.07	-1.12
Azud de Ulea	SE6	112	4	1157.3	16.87	4.40	-1.59

1802) are also present. Along the river, *A. alburnus* shares resources and habitat with native cyprinids, such as the Southern Iberian barbel *Luciobarbus sclateri* (Günther, 1868) and Southern Iberian chub *Squalius pyrenaicus* (Günther, 1868), and with several abundant non-native species, including pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758), pyrenean gudgeon *Gobio lozanoi* Doadrio and Madeira, 2004, common carp *Cyprinus carpio* (Linnaeus, 1758), and Iberian straight-mouth nase *Pseudochondrostoma polylepis* (Steindachner, 1864).

Field sampling and laboratory procedures

To study biological traits at population level, specimens from 10 sampling sites (Figure 1, Table 1, Supplementary material Table S1) were captured by electrofishing following standard protocols (CEN 2003) during autumn 2010 (mainly November). Sampling during this period avoided the capture of pre-spawning and spawning fish, and ensured that any variations in body condition were unaffected by gonad development. In order to obtain representative samples from each site in relation to the types of meso and microhabitats, the minimum wadeable sections covered at each sampling site were approximately 100 metres long. Fish collected at each sampling site were considered as independent populations for several reasons: the minimum distance along the river course between sampling sites exceeded 15 km and the main channels have several small weirs restricting fish movements. However, both the existence of a high population connection between individuals caught in the sampling sites of the same fluvial sector separated by large physical barriers (reservoirs), and a low connection between fish caught in adjacent fluvial sectors were assumed.

In accordance with administrative permits, total captures were sacrificed in an overdose solution of anaesthetic (1:10 solution of clove oil dissolved in ethanol 70%) and stored on ice before preserved in 10% buffer formaldehyde solution for later processing in the laboratory. A total of 1285 *A. alburnus* were measured (Fork length; $L_F \pm 1 \text{ mm}$) and a sample of 474 individuals was processed to obtain the eviscerated mass ($M_E \pm 0.1 \text{ g}$) and organ

masses (hepatic and gonad mass, M_H and $M_G \pm 0.001$ g). Sex was determined by gonad examination, and age class using scales from the left side of the body of a total of 335 specimens. A Leica MZ 9.5 stereomicroscope coupled with a digital camera (Leica DFZ 295) was used for counting annuli and LAS software version 3.5.0 to measure distances from focus to each annulus and scale radius length.

Populations were analysed at site and fluvial sector level along the longitudinal gradient from the upper part to the middle of the Segura River Basin in order to assess the intraspecific variability of the population traits. The fish parameters studied were: abundance (CPUE: Catch Per Unit Effort – number of fish caught per hour assuming a standardised sample area), size and age structure (by length-frequency distribution and back-length tables), growth rate (b-growth and growth index GI), somatic condition, hepatic condition and reproductive investment.

Each sampling site was characterized by the following six environmental variables: altitude (meters above sea level), ecological state according to data from the General Survey on the Segura River Basin, water conductivity ($\mu\text{s cm}^{-1}$), mean monthly temperature ($^{\circ}\text{C}$), mean daily flow ($\text{m}^3 \text{s}^{-1}$) and flow variability ($Q_{10\%}-Q_{90\%}$) (Table 1). The last three were calculated from a time series data of the 2009–2010 hydrological cycle obtained from the official monitoring service of the administrative Institution of the Segura River Basin. These six selected environmental variables are among the ecological drivers that play a significant role in the biological invasion of Mediterranean-climate rivers (Ilhéu et al. 2014).

Statistical analyses

Statistical analyses carried out to compare fish condition and reproductive investment included the application of analyses of covariance (ANCOVA) using M_E , M_H and M_G as dependent variables, L_F as the covariate (log-transformation data), and maturity (mature, immature) and sex (male, female) as factors. Mature individuals are longer than 80 mm of standard length *sensu* Almeida et al. (2014). Differences between dependent-covariate relationships were tested verifying that the covariate by-factor interaction (homogeneity of slopes) was significant ($p < 0.05$). If the covariate by-factor interaction was not significant, standard ANCOVA was applied to obtain predicted values. Variation in somatic condition, hepatic condition and reproductive investment (only in mature fish) were studied by using the predicted values of M_E , M_H and M_G testing differences with an analysis of variance (ANOVA, Tukey's HSD post hoc tests) as proposed by García-Berthou and Moreno-Amich (1993).

Back-calculated lengths were obtained separately for each population according to the Fraser-Lee equation:

$$L_F n = [(Rn / R_T) (L_F - a)] + a$$

where L_F is the length at the capture time, L_{Fn} is L_F at age n , Rn is the scale radius at age n and a is the intercept of the linear relationship between the scale's total radius (R_T) and L_F . Differences between males and females in R_T-L_F regressions were tested by ANCOVA and a t-Student test was used to test differences between males and females for the back-calculated lengths.

Relative growth rates of each population were estimated by the mean of growth index (GI) following the method used in previous studies that dealt with the same species (Masó et al. 2016; Latorre et al. 2018). For comparison of growth trajectories, the linearity in the relationships between ages and back-calculated L_F for each population was analysed at site level. The homogeneity of the regression coefficients was tested (parallelism as the assumption of equal slopes) with an ANCOVA design that analyzed the pooled covariate-by-factor interaction followed by an ANCOVA using sex and sampling sites as factors. Non-equal slopes indicate significant differences in the growth trajectories among populations.

The natural complexity of the habitat must be taken into account in studies similar to the present one, since many interacting variables may be involved simultaneously in the ecological variations along longitudinal gradients. This situation is best analyzed by multivariate statistics. In this study, a Principal Component Analysis (PCA) was applied with the varimax rotation method to the environmental variable matrix (ln or arcsin-transformed data) in order to extract independent principal components (henceforth PCs), which could be interpreted as gradients describing patterns in habitat variation along the longitudinal gradient of the rivers. To assess the usefulness of the PCA the Kaiser-Meyer-Olkin's measure (KMO) of sampling adequacy was used (values above 0.5). To explore patterns of association between the habitat gradients (scores of the selected habitat gradient (PCs) (Clavero et al. 2009)) and population traits regression models were used. Due to our fluvial context in longitudinal gradients and the relatively small number of sampling sites to study biological traits at population level ($n = 10$), linear and non-linear expected models (curve estimation) were chosen to explain relationships between habitat gradients and population traits. The final selected models were those with highest r^2 values. In addition, a linear regression model was used to analyse abundance and downstream distance to the closest lentic habitat (weir or reservoir). Statistical analyses were performed with the SPSS® software package v. 15.0 and a significance level of 0.05 was accepted.

Results

Abundance and occurrence

Since 2010, *A. alburnus* has been found along 35.4 km stretching from the Upper Mundo river to the Mundo-Segura rivers confluence (67.8% of the studied section) (Figures 1, 2). According to its frequency of occurrence in

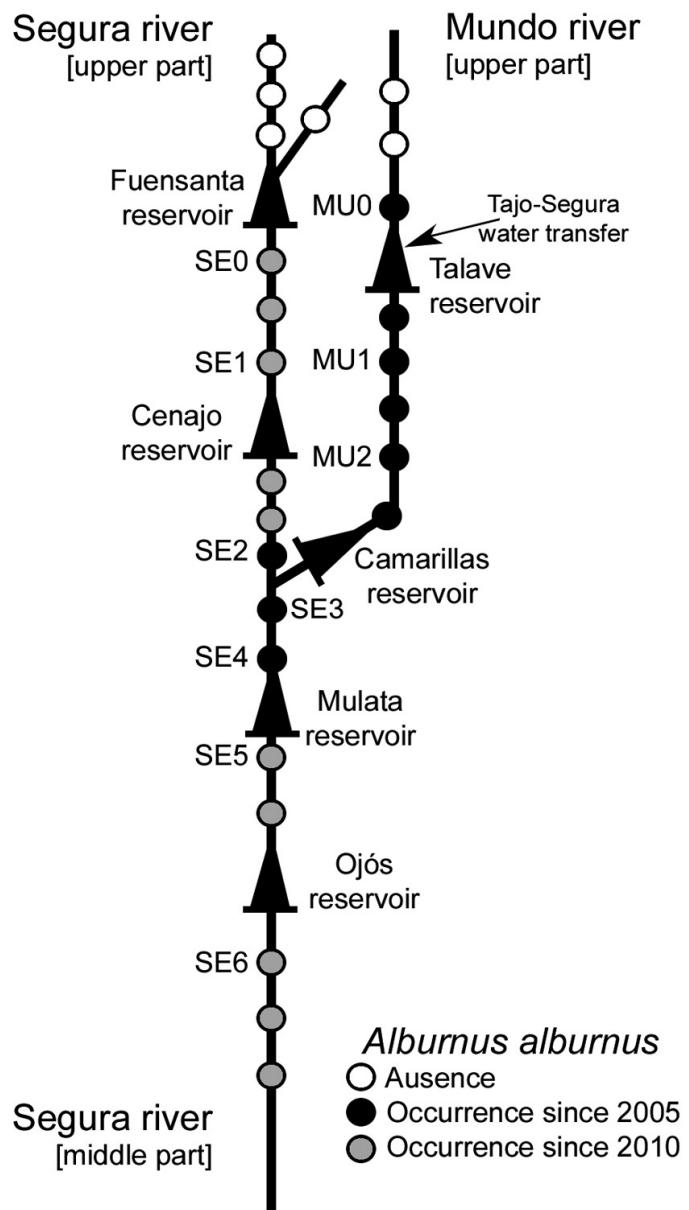


Figure 2. Diagram of the Segura and Mundo rivers axes and the 25 sampling sites (white, black and grey points) where *Alburnus alburnus* occurrences were sampled (2005–2010). MU0 to MU2, and SE0 to SE6 are sites selected to the study of biological traits at population level. The main physical barriers (principal dams) are marked (black triangles). White points mark sites where the species is absent, black and grey points indicate species presence since 2005 and 2010 respectively. See Supplementary Table S1 to sampling sites geo-reference information.

2005 and 2010 throughout the sampled section from the Upper Segura river to Middle Segura river, this species showed a fast colonization rate, with 24.8% (39.2 km long) of the section occupied in 2005 and 84.4% (133.4 km long) in 2010 (Figures 1, 2).

CPUE estimates for *A. alburnus* showed a high degree of spatial variation (Table 2), the highest relative abundances being found in the upper fluvial sectors above 400 m.a.s.l.. Maximum values occurred in SE0 (320 fish per 100 m per hour) and SE1 (226.5 fish per 100 m per hour), located in the upper fluvial sector of the Segura River. Values were lower in

Table 2. Population traits of *Alburnus alburnus* in sampling sites: abundance (CPUE: Catch Per Unit Effort), mean fork length in cm (L_F), somatic condition, hepatic condition and reproductive investment (mean values of measured M_E , M_H and M_G , g). (Immat.): immature individuals; and (Mat.): mature individuals. For sampling site location please see Figure 1.

Sampling site	Abundance (CPUE)	L_F Mean	Mean values M_E Immat.	Mean values M_H Mat.	Mean values M_G Immat.	Mean values M_G Mat.	female	male
MU0	198	12.5	4.95	22.17	0.07	0.31	0.91	0.31
MU1	121.5	9.5	3.61	16.73	0.06	0.27	0.14	0.17
MU2	106	10.3	3.70	15.40	0.07	0.33	0.52	0.16
SE0	320	10.4	4.40	18.48	0.06	0.25	0.44	0.17
SE1	226.5	8.7	3.57	12.38	0.04	0.19	0.40	0.07
SE2	30.67	8.4	3.45	8.71	0.04	0.17	0.06	0.14
SE3	29.45	8.7	3.23	19.99	0.08	0.52	1.29	0.26
SE4	50	12.2	4.05	15.66	0.06	0.22	0.86	0.18
SE5	71	8.1	2.76	9.42	0.05	0.11	0.22	0.08
SE6	55	7.5	2.26	7.64	0.05	0.12	0.22	0.05

sampling sites from the middle part of the basin with minimum values (SE2 and SE3) in the fluvial sector immediately below the largest reservoir of the Basin (Cenajo reservoir; 437 hm³ of storage volume) (Figure 2, Table 2). Moreover, lentic stretches created by weirs or reservoirs probably act as shelter habitats because *A. alburnus* abundance and downstream distance to the closest lentic habitat (weir or reservoir) showed a negative relationship (Linear regression, b-slope = -0.35, $r^2 = 0.43$, $P = 0.04$).

Population traits

Size population structure differed among sampling sites although a bimodal distribution pattern was evident in most sampling sites along the longitudinal gradient (Figure 3). MU0 and SE4 sampling sites located just above Talave and Mulata reservoirs, respectively (Figures 1, 2), were the only sites without individuals measuring less than 8 cm L_F , but clear modals of young of the year (0+) were not observed in any sampling sites.

When age was determined by scales, five groups (0+ to 4+) were identified for both sexes, although only one male (caught in MU1) presented the age of 4+. Populations (site level) showed older females (4+) only in sampling sites where the species had inhabited since 2005 (Figure 2), while in the more recently invaded areas the oldest captures were individuals from the 3+ age group (Table 3). *Alburnus alburnus* individuals ranged from 3.5 cm to a maximum L_F of 16.9 cm, and males ($L_F 10.9 \pm 0.3$ cm) were significantly longer than females ($L_F 10.1 \pm 0.4$ cm) (ANOVA $F_{(1, 397)} = 9.15$, $P = 0.003$). Significant spatial effects (at site level) were detected (ANCOVA $F_{(1, 9, 397)} = 2.97$, $P = 0.002$; sex × site interaction), with a decrease in the average L_F in populations along the longitudinal gradient; larger sizes (> 13 cm L_F) were not captured at lower sampling sites (Figures 3, 4).

Back-calculated lengths, the slopes of the back-calculated L_F – age relationships and growth index at sampling site level are presented in Table 3. The sex factor had no significant effect on back-calculated lengths (ANOVA $F_{(1, 578)} = 2.27$, $P = 0.132$) or on the relationships (ANCOVA $F_{(1, 9, 578)} = 0.30$,

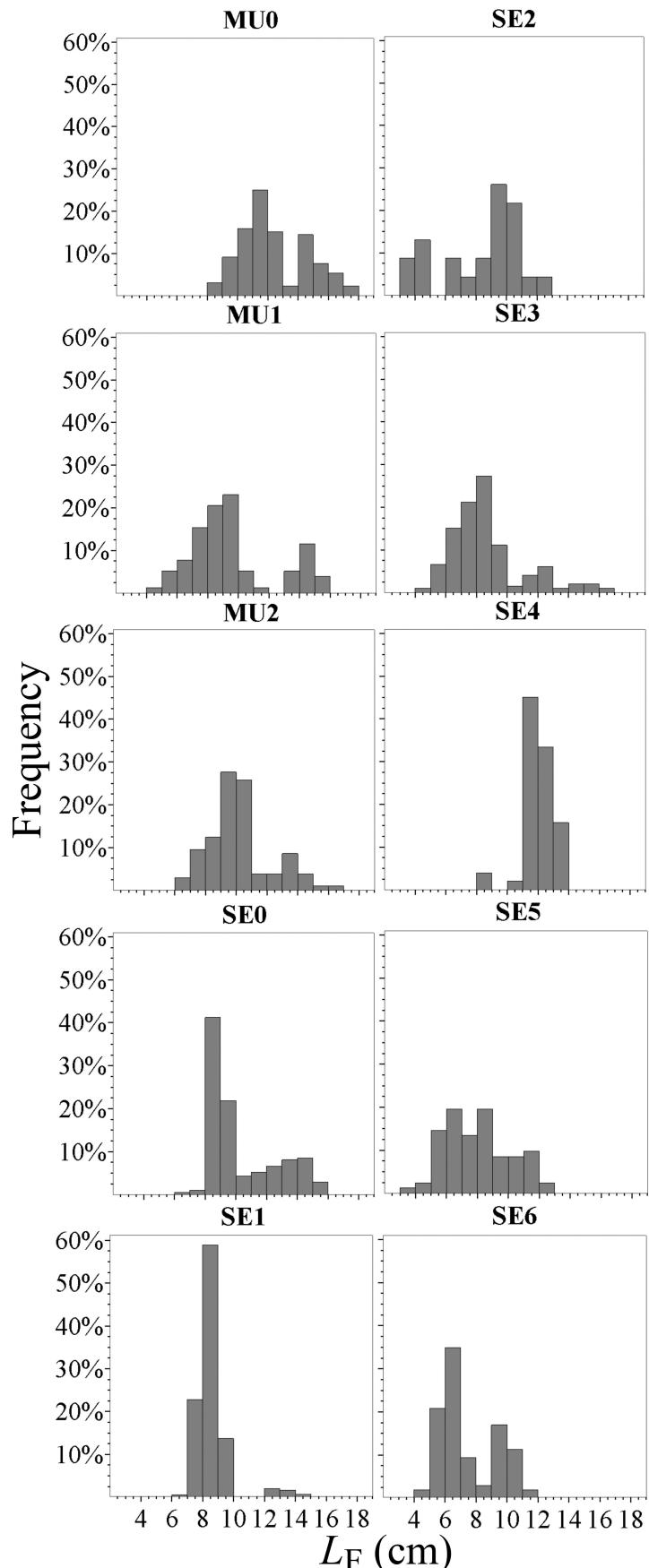


Figure 3. Fork length (L_F ; 1 cm length groups) frequency distribution of *Alburnus alburnus* in the sampling sites (MU0 to MU2 and SE0 to SE6) selected for the study of biological traits at population level.

Table 3. Population traits of *Alburnus alburnus* at sampling sites. Mean back-calculated fork length (cm) at ages L_F (n), slopes of L_F – Age relationships (b-growth), growth index (GI, % ± IC 95%) and the sex-ratio (males: females). (*: Significant differences from 1:1; $P < 0.05$). For sampling site location please see Figure 1.

Sampling site	L_F (1+)	L_F (2+)	L_F (3+)	L_F (4+)	b-growth	GI	Sex-ratio
MU0	5.8	8.2	10.7	13.5	24.6	116.0 ± 15.5	0.85
MU1	5.5	7.8	10.8	12.9	25.6	114.5 ± 9.5	0.57*
MU2	5.6	8.0	10.7	13.5	25.3	114.1 ± 15.7	0.59*
SE0	6.0	8.6	12.1	–	28.8	122.4 ± 7.9	0.67
SE1	6.1	8.4	11.4	–	25.7	120.7 ± 11.9	0.48*
SE2	5.3	7.4	9.0	–	19.1	104.3 ± 15.7	1.29
SE3	5.6	8.1	10.8	11.4	24.2	116.8 ± 11.1	0.86
SE4	5.9	8.4	10.3	–	23.1	116.3 ± 18.0	1.44
SE5	5.4	8.0	9.5	–	23.5	109.1 ± 8.7	0.67
SE6	5.7	7.7	9.5	–	19.5	111.1 ± 4.0	0.78

$P = 0.974$; sex × site interaction). There were significant differences among sampling sites on slopes (b-growth parameter) of the relationships (ANCOVA $F_{(1,9,638)} = 3.65$, $P < 0.001$ for slope). *Alburnus alburnus* grew faster and with higher GI in populations of the upstream sector of the Segura river (SE0 and SE1) (Table 3).

The overall sex-ratio (171 males, 227 females) was significantly skewed towards females ($\chi^2 = 7.88$, $P = 0.005$), although only in three sampling sites from the upper sectors (MU1, MU2 and SE1 sampling sites) females were significantly dominant (Table 3). Maturity had a significant effect on the organosomatic indices and sex only significantly affected the reproductive investment values (ANCOVA tests, $P < 0.05$; Table 4). Indeed, the ANCOVA analysis (initial or final design in Table 4) pointed to significant differences in estimated marginal values of M_E , M_H and M_G (Table 3). Patterns of variation in relation to the environmental gradients are shown in Figures 4 and 5.

Relationship between population traits and environmental variables

Information on habitat characteristics was summarised in the PCA ($KMO = 0.60$), wherein the first two axis (PC1 and PC2) with eigenvalues > 1 and explaining 82.3% of total variance were retrieved (Table 1). PC1 described a gradient from the upper sampling sites (higher altitude) (Correlation coefficient $r = -0.86$; $P = 0.001$) to sites of poorer ecological status ($r = 0.84$; $P = 0.002$), higher water conductivity values ($r = 0.98$; $P < 0.001$) and higher monthly temperatures ($r = 0.90$; $P < 0.001$), i.e. a habitat quality deterioration trend correlated to the longitudinal gradient in the basin. PC2, which was positively associated with mean daily flows ($r = 0.89$; $P = 0.001$) and flow variability ($r = 0.88$; $P = 0.001$), explained 24.9% of the variation.

Alburnus alburnus abundance was significantly correlated to both PC1 and PC2 (Figure 4). CPUEs at site level showed a significant decreasing relationship with positive values in PC1, and a unimodal response with the flow gradient (PC2) in which abundance peaks were showed at intermediate values. PC1 gradient had a quadratic negative effect on maximum captured

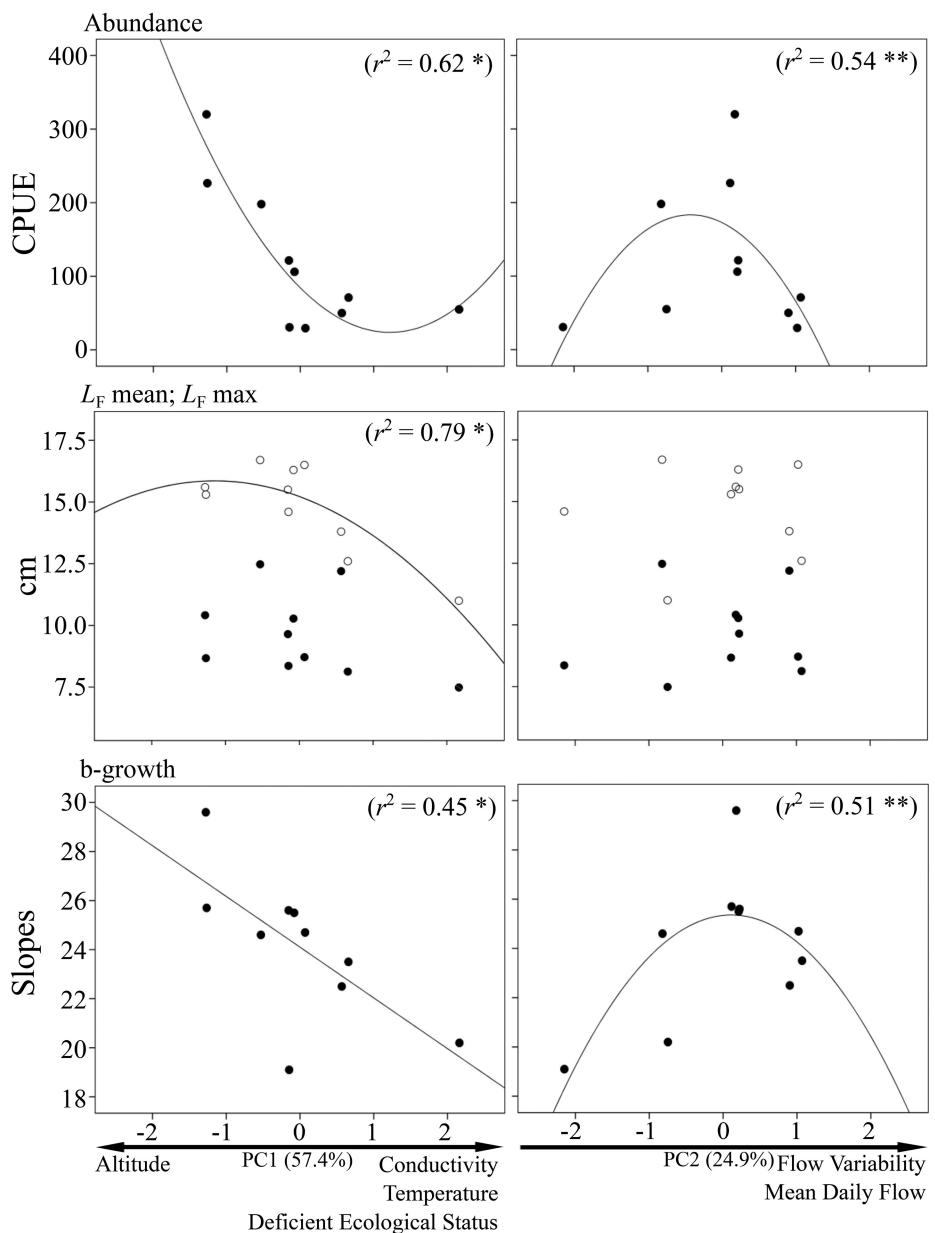


Figure 4. Relationship between *Alburnus alburnus* abundance, mean and maximum fork length (black and white points respectively) and b-growth at population level and principal components (PC1 and PC2). Explained variance of each PC is presented and the interpretation of PCs is based on the significantly correlated original variables. Significant relationships (linear or quadratic) are marked with continuous lines (*: significance level $P < 0.05$; **: marginal significance level $P < 0.1$).

sizes at each site (L_F max), but no effects on mean L_F (Figure 4). The parameter (b-growth) was negatively related to the longitudinal gradient (PC1) and showed also a unimodal response with flow gradient (PC2), presenting higher values in the middle part of the gradient (Figure 4). GI showed a similar pattern although it did not present significant levels.

All the organosomatic indices depended significantly on L_F (Table 4) and, after accounting for this, the somatic condition, hepatic condition and reproductive investment significantly differed among populations (sampling sites). However, only the somatic condition of juveniles (estimated M_E values) showed a significant linear relationship with PC1 (Figure 5).

Table 4. Results of ANCOVA analyses of population traits of *Alburnus alburnus*. Fork length is the covariate, and maturity, sex and sampling site are the factors. Degrees of freedom, *F*-statistics and *P* values (significant effects in bold) are presented.

Source	Dependent variables											
	Eviscerated mass			Hepatic mass			Gonadal mass					
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>		<i>P</i>		
All individuals												
Length	1	14444.9	<0.001	1	419.17	<0.001	1	432.39		<0.001		
Maturity	1	33.97	<0.001	1	8.27	0.004	1	8.23		0.004		
Length × maturity	1	36.15	<0.001	1	10.16	0.002	1	10.02		0.002		
Mature individuals												
Length	1	11411.6	<0.001	1	501.93	<0.001	1	854.73		<0.001		
Sex	1	0.74	0.389	1	0.01	0.908	1	5.91		0.016		
Length × sex	1	1.25	0.265	1	0.001	0.990	1	10.35		0.001		
Immature individuals												
Length	1	1025.44	<0.001	1	15.13	<0.001	1	66.25		<0.001		
Sex	1	0.12	0.723	1	0.002	0.96	1	13.18		<0.001		
Length × sex	1	0.16	0.689	1	0.001	0.97	1	11.08		<0.001		
Mature individuals												
Males												
Length	1	4054.10	<0.001	1	230.90	<0.001	1	111.3	<0.001	1	15.03	<0.001
Sampling site	9	1.58	0.122	9	2.54	0.008	9	1.40	0.194	9	2.93	0.004
Length × Sampling site	9	1.33	0.224	9	2.14	0.027	9	1.56	0.134	9	3.03	0.003
Females												
Final design (no interaction)												
Length	1	12241.7	<0.001				1	344.9	<0.001			
Sampling site	9	15.62	<0.001				9	3.77	<0.001			
Immature individuals												
Length	1	1356.9	<0.001	1	9.55	0.003						
Sampling site	7	4.07	0.001	7	2.33	0.030						
Length × Sampling site	7	4.25	<0.001	7	2.57	0.018						

Discussion

Since its first record in the upper part of the Segura River Basin in 2004 (Andreu-Soler et al. 2004), the rapid and wide establishment of *A. alburnus* along most of this basin is a further evidence of its invasive potential in Mediterranean-type rivers. Despite its ecological requirements—inhabiting open waters of lakes and medium-large rivers in its native range—, previous studies on Iberian populations have displayed the ability of *A. alburnus* to inhabit small Mediterranean streams (Almeida et al. 2014; Masó et al. 2016; Almeida et al. 2017). In the present study, the rapid establishment of *A. alburnus* populations along more than 168.8 km (133.4 km of the Segura river, 35.4 km of the Mundo river) of one of the most regulated Iberian river basins and in lotic environments is confirmed. In fact, our results show that *A. alburnus* can reach high abundances in a variety of habitat conditions, although they were significantly related to habitat quality deterioration and flow gradients. In agreement with Almeida et al. (2014), although *A. alburnus* is considered a limnophilic species, the high occurrence and abundance data obtained in fluvial stretches sampled in our study confirm its wide phenotypic plasticity as regards habitat requirements, which certainly contributes to its high invasiveness (Sakai et al. 2001).

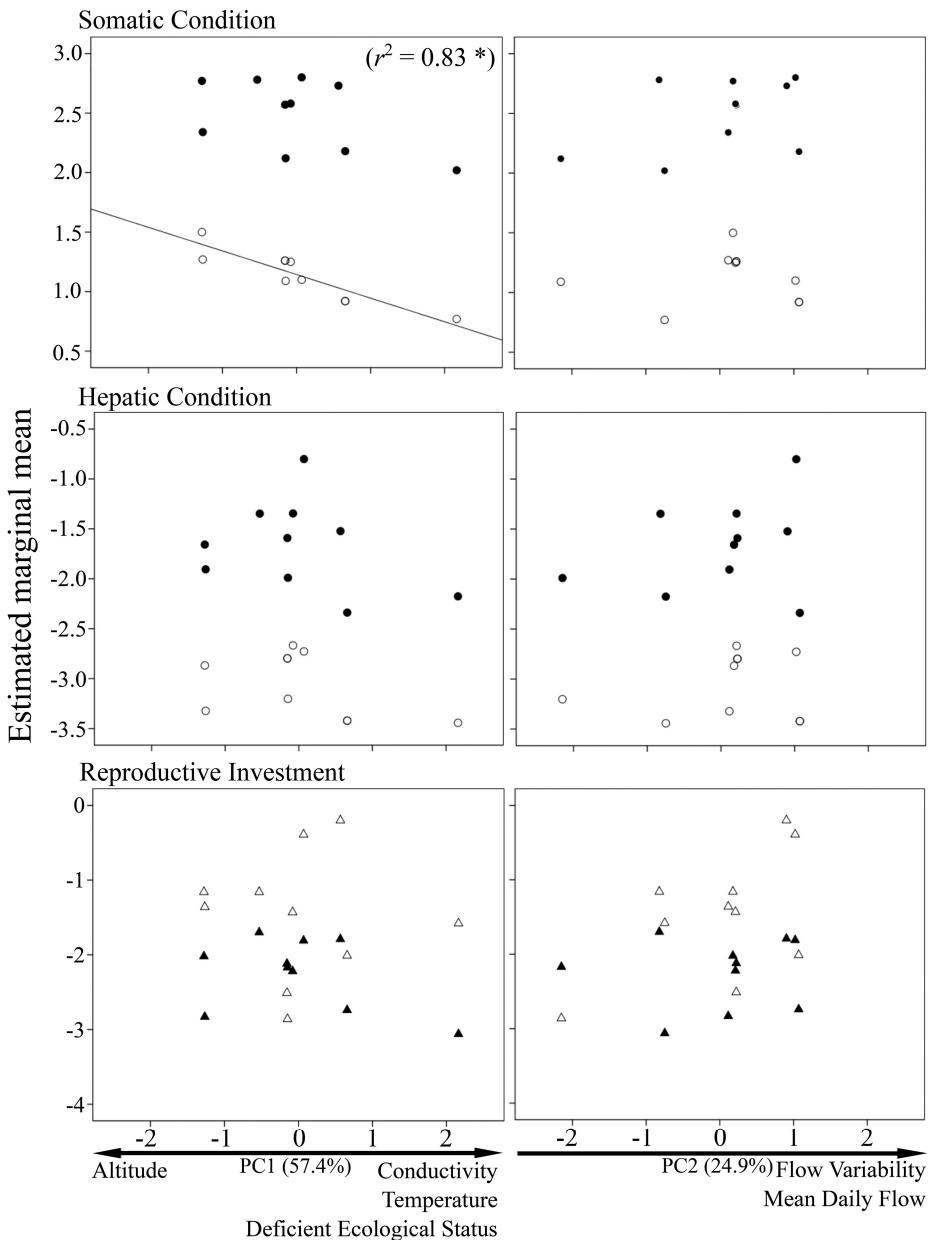


Figure 5. Relationship between *Alburnus alburnus* somatic condition, hepatic condition, and reproductive investment (estimated marginal means of M_E , M_H and M_G) at population level and principal components (PC1 and PC2). Explained variance of each PC is presented and the interpretation of PCs is based on the significantly correlated original variables. Mature and immature individuals are coded with black and white points, respectively. Black and white triangles indicated male and female values respectively. Significant relationships (linear or quadratic) are marked with continuous lines (*: significance level $P < 0.05$; **: marginal significance level $P < 0.1$).

Frequently, reservoirs have been used to introduce non-native fish species (Elvira and Almodóvar 2001; Clavero et al. 2013). In the case of the Iberian population of *A. alburnus*, a positive correlation was established between its dispersion and regulated rivers because large reservoirs seemed to be acting as source populations to colonize river stretches (Vinyoles et al. 2007). In the Segura River Basin, its colonization has been attributed to fish dispersion along an interbasin system that flows into the Talave reservoir (Figure 2), or to its deliberate or accidental introduction by

anglers since sport fishing is popular in reservoirs of the upper part of the basin (Andreu-Soler et al. 2004). The dispersion process in its distribution range through the rest of the Segura Basin could be explained at three different levels: (1) upstream and downstream movements within fluvial sectors (i.e. dispersion process in sector *Seg3*, Figure 2); (2) invading interconnected fluvial sectors from passive movements through dams located upstream (i.e. colonization or dispersion process to sectors *Mun2*, *Seg3*, *Seg4* and *Seg5*, starting from its arrival at *Mun1*, Figure 2); and (3) dispersion related to human intervention or deliberate introductions, which is the only factor to explain up movement through large dams (i.e. colonization of sector *Seg2* in the Segura Basin, Figure 2). Our findings showed that the sector *Seg1* was the only fluvial sector where this species does not occur, probably because it has not yet been introduced into the Fuensanta reservoir (Figure 2). However, strong seasonal flows from the upper part of the basin may be also preventing its expansion though this river sector. Moreover, higher abundances of *A. alburnus* were detected in fluvial sectors of the upper part of the basin located between the largest reservoirs where natural flow regimes are highly affected (Belmar-Díaz et al. 2011). Longitudinal connectivity is also highly affected by the presence of small longitudinal barriers (e.g. weirs), which implies an increase in lentic and homogeneous environments that favour the expansion of introduced limnophilic species (Clavero et al. 2013). In the Segura River Basin, lentic stretches created by weirs also probably act as shelter habitats for *A. alburnus* populations because a negative relationship was found between *A. alburnus* abundance and downstream distance to the closest lentic habitat. This could be indicating that river damming and flow regulation act as stepping stones for the spread and colonisation of *A. alburnus* throughout Iberian waters, as it has been noticed in the establishment of other non-native fishes (Ribeiro and Collares-Pereira 2010; Clavero et al. 2013).

Size population structure showed two mature cohorts along the whole longitudinal gradient. This bimodal pattern has been found in previous studies on this species in both non-native regions (population in rivers and reservoirs in the Iberian Peninsula) (Almeida et al. 2014) and native regions (such as populations in Hungary) (Bíró and Muskó 1995). In a similar way, the age structure of *A. alburnus* specimens caught in the Segura River Basin (from 0+ to 4+ age groups) did not differ from that observed in other Iberian studies (Almeida et al. 2014; Latorre et al. 2016, 2018), but showed a significant contrast with some native areas, e.g. some native populations show up to ten age classes (9+) (Bíró and Muskó 1995). Moreover, higher longevity and larger size cohorts were more common in fluvial sectors first colonized by the species (Mundo river). These results could be related with earlier stages of invasiveness of the species in fluvial

sectors where the residence time is shorter. A higher reproductive effort in newly invaded sectors where this species is not fully adapted probably triggered higher mortality in larger individuals. A similar result was not obtained in the reproductive investment indicator probably because autumn data outside the reproductive period of the species are not the most suitable for such an assessment.

Population dynamics in the early stage of invasiveness present different life strategies compared to well-established populations (Ribeiro et al. 2008). For instance, Bøhn et al. (2004) found higher growth rates for invasive fishes during the initial invasion stages compared with sites where there were fish populations in establishment phases. In the early stages of the establishment process, with low densities and weak intra-specific competition, *A. alburnus* would be expected to present high growth rates and a high reproductive investment. Accordingly, in the present study, two sampling sites (SE0 and SE1), associated with the group with shorter residence time, and located in the upper part of the basin, showed the highest mean back-calculated lengths at age and, also, the fastest growth (Table 3). However, fish in another two sites where the species also showed short residence times, but located in the lowest part of the longitudinal gradient and also in fluvial sectors with a poorer ecological status (SE5 and SE6), showed lower back-calculated lengths and lower growth rates. Mean back-calculated lengths calculated in the present study were higher for younger individuals (1+ and 2+) than was found in a previous study in the same basin, but similar to the older fish (Latorre et al. 2018). Moreover, the GI values estimated in the present study were also higher than those obtained in Latorre et al. (2018) for the same basin and for other rivers of the Iberian Peninsula (Masó et al. 2016).

The growth traits pattern of *A. alburnus* populations would be expected to reflect differences in habitat condition along the longitudinal gradient. In fact, decreasing altitude and flow constraints combined with increasing water temperature and with increased nutrient availability downstream were expected to positively influence the growth rates of this species, as was observed in other Cyprinids (Tedesco et al. 2009). Moreover, the higher occurrence of deep-water areas, as a sort of hydraulic refuge (Bouchard et al. 1998), in the middle part of the basin could also positively affect the growth of this species. Conversely, abundance, maximum length and growth in *A. alburnus* populations showed a negative significant relationship with the longitudinal gradient (PC1; Figure 4) from the sites located in the upper part of the Segura River Basin to those in the middle part with their higher water temperatures, higher water conductivity values and poorer ecological status. These findings could be related with residence time of the studied populations but also, probably, with increased environmental stress along the longitudinal gradient. In fact, agrochemical

and nutrient inputs (via run-off) are high in the fluvial sectors invaded by *A. alburnus* because the middle part of the Segura River Basin is one of the most important irrigated agricultural areas of the Iberian Peninsula (Grindlay et al. 2011).

Despite being considered as a limnophilic fish (Harby et al. 2007), *A. alburnus* has been categorized as eurytopic and preferably dwelling in run-type habitats in others studies in Mediterranean streams (Muñoz-Mas et al. 2016), which would also explain better the rapid spread of *A. alburnus* in the Iberian systems (Vinyoles et al. 2007). Certainly, flow regime is one of the fundamental attributes of lotic ecosystems, and has profound effects on physical, chemical and biological characteristics, which promotes significant changes among population traits (Wootton 1998). In *A. alburnus* populations of the Segura River Basin, abundance and growth parameters were significantly dependent on the ecological variables related to water flow (Figure 4). Sampling sites with medium values of flow variability and mean daily flow were related to the highest fish density and growth rates. This flow effect would also partially explain the lack of homogeneity observed for growth among populations with similar residence times, as previously mentioned. Nevertheless, the results presented here are the first approach to assessing the life-history variability of *A. alburnus* populations under different flow regulation conditions, while further research should include additional approaches to relate such variability with regulation types or seasonal variation effects. Piscivorous species may exert a strong predatory pressure on *A. alburnus* populations (Almeida and Grossman 2014), thus acting as a leading factor influencing in traits. A similar predatory pressure among the studied populations was assumed because of the similarity in the fish community composition (Oliva-Paterna et al. 2014). However, community effects should be more closely investigated.

Almeida et al. (2014) found a seasonal effect on the sex-ratio, with females being predominant in lotic habitats during autumn. Our findings are fairly similar to that work because the sex-ratio of *A. alburnus* in the Segura River Basin as a whole was significantly skewed towards females, although seven of the studied populations showed an equal sex-ratio. Proportion of sexes is strongly influenced by environmental factors and seasonality, as observed for some introduced *A. alburnus* populations (Fouzia and Abdeslem 2012). In the Iberian Peninsula, other studies on this species have frequently pointed to a predominance of males, although many of them considered spring data (Masó et al. 2016; Latorre et al. 2018), which are not comparable with those of the present study.

The somatic and hepatic condition, and also the reproductive investment, differed substantially between the populations studied. Differences in the estimated values of M_E , M_H and M_G were probably caused by differences in habitat conditions, but little or nothing correlated

with the longitudinal gradient. The short sampling period in November prevented the capture of prespawning and spawning fish and thus ensured that the variability of the estimated values was not related to seasonal variations in the conditions of *A. alburnus* (Almeida et al. 2014). However, it also meant that the data estimated for M_G are not suitable for evaluating reproductive investment. Changes in the ecological status, water conductivity and temperature along the longitudinal gradient probably affect *A. alburnus* condition, as observed for other fish species (De Miguel et al. 2013). Other studies in the same river basin showed that ecological features that accounted for most of the variation in fish condition were variables related to flow and water conductivity (Oliva-Paterna et al. 2003). The results concerning the somatic and hepatic condition of *A. alburnus* showed no relationships with flow characteristics. Moreover, the high variability observed at site level in fish condition metrics suggests high phenotypic plasticity at population level, reflecting previous findings (Alemida et al. 2014; Masó et al. 2016; Latorre et al. 2018).

In agreement with Tedesco et al. (2009), the results of the present study have clear consequences for the interpretation of large-scale comparative studies, particularly those focusing on latitudinal variability in invasive freshwater fishes. In general, studies comparing invasive fish populations from different basins, including the only study of this type with *A. alburnus* (Latorre et al. 2018), often use data obtained from the literature or from sampling designs without accounting for position in the longitudinal river gradient (e.g. Cucherousset et al. 2008).

Understanding the factors promoting successful invasions of freshwater fish such as *A. alburnus* is of great conceptual and practical importance. From a practical point of view, it should help to prevent future invasions and to mitigate any effects of recent invaders through their early detection and prioritization of management measures (Ilhéu et al. 2014). According to Bøhn et al. (2004), the success of an invasive species is probably related with the high variability of their population traits, so a knowledge of any such plasticity in population traits may contribute to manage and control their spread throughout new environments (Britton et al. 2011). *Alburnus alburnus* has rapidly spread through Iberian freshwaters (Vinyoles et al. 2007), so a risk-based programme of sustainable control must be considered as a measure to manage their increasing distribution (Britton et al. 2010). In this context, management and control programmes should be addressed to preventing the species' secondary introduction into tributaries or aquatic systems where it is not yet present. Initiatives based on the management of flow discharges and to prevent colonization through river channels or damming should also be considered. Due to its wide distribution throughout the watershed, its establishment in reservoirs and its high phenotypic plasticity, the eradication of *A. alburnus* from the Segura River

Basin seems improbable. However, the recommended actions could help control or eradication of this species in specific areas or isolated aquatic systems, being piscicide application the most effective method, which has already been demonstrated for other small invasive Cyprinids, even at higher population densities (Allen et al. 2006; Britton et al. 2008; Eilers et al. 2011).

The rapid spread and establishment of *A. alburnus* in highly regulated Mediterranean basins can be attributed, in part, to their adaptive capacity to change population traits in response to environmental condition but also to the lentic shelter habitats created by the impact of flow regulation (e.g. weirs, small impoundments, reservoirs, etc.) although this subject needs to be more closely investigated. Non-native fish species of lower trophic positions are more efficient at obtaining energy from basal trophic groups (Gido and Franssen 2007). Moreover, *A. alburnus* shows wide trophic plasticity (Almeida et al. 2014, 2017; Latorre et al. 2018), which concurs with the success of this species in the Segura River Basin. In summary, the results support the hypothesis that the wide phenotypic variability in population traits previously described for *A. alburnus* (Almeida et al. 2014, Masó et al. 2016) plays an important role in its success in highly regulated Mediterranean-type rivers. This phenotypic plasticity, which has also been observed in other invasive species inhabiting Iberian aquatic systems (e.g. Almeida et al. 2009; Ribeiro and Collares-Pereira 2010), seems to be an important factor in the invasion process. However, the variations found in its biological traits is related to a suite of factors that act both together and separately, such as habitat conditions along the longitudinal river gradient, flow regulation effects, and different stages of the invasion along the basin.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Geo-referenced information on sampling sites where *Alburnus alburnus* is present: location name, code of sampling site on the map, latitude and longitude degrees and sampling date.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2019/Supplements/AI_2019_Amat-Trigo_et_al_Table_S1.xlsx