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Trophic plasticity of invasive juvenile largemouth bass *Micropterus salmoides* in Iberian streams

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ABSTRACT

Biological invasions are a major factor for biodiversity loss, particularly in freshwater environments. Largemouth bass *Micropterus salmoides* is native to North America and is invasive on the Iberian Peninsula, primarily to provide angling opportunities in reservoirs. However, this species is a threat to the endemic Iberian fauna via predation and competition. Currently, there is little information on largemouth bass in European streams. Thus, we assessed the trophic plasticity and body condition of young largemouth bass in both invasive (the regulated Bullaque River) and native (Murray Creek) streams. Abundance of juvenile largemouth bass, percentage of full stomachs and body condition were higher in Bullaque River. Largemouth bass preyed on benthic invertebrates much more heavily in the Bullaque River, whereas fishes were the most important prey in Murray Creek. Prey richness, diet diversity and trophic niche breadth were higher in the Bullaque River population. Largemouth bass preferred water-column fishes as prey and avoided consuming benthic fishes in Murray Creek, whereas water-column fishes were avoided in Bullaque River. These results demonstrate that largemouth bass display substantial trophic plasticity which possibly facilitates its success as invasive species. Regulated Iberian streams may provide both suitable food and habitat resources with minimal predation pressure, and hence may serve as recruitment sources for this invasive fish.

1. Introduction

Invasive species have strong negative effects on ecosystems (Genovesi, 2005). Furthermore, the introduction of invasive species into freshwater ecosystems is regarded as one of the main drivers of biodiversity loss (Clavero and García-Berthou, 2006; Jelks et al., 2008; Rahel, 2002). Not surprisingly, fishes are the most common invasive species in inland waters (Cowx, 1998; Ribeiro et al., 2008; Welcomme, 1998). Invasive fishes have a variety of adverse impacts on native species and habitats, such as hybridization (Madeira et al., 2005; Sanz et al., 2006), as a vector of diseases (Gozlan et al., 2005), food web alteration (Almeida et al., 2009; Blanco-Garrido et al., 2008), habitat degradation (García-Berthou, 2001), interspecific competition (Hazelton and Grossman, 2009a,b; Keller and Brown, 2008) and predation (Pearson and Goater, 2009; Schilling et al., 2009). Of these effects, predation is particularly important in the Iberian Peninsula (Carol et al., 2009; García-Berthou, 2002; Godinho and Ferreira, 1998). Consequently, studies detailing how invasive predators forage are of great interest to the field of invasion biology in this region, especially to those examining trophic plasticity (e.g. Almeida et al., 2009; García-Berthou, 2002; Leunda et al., 2008). Knowledge of this ecological trait would greatly aid managers in predicting the impacts of invasive species in aquatic environments (García-Berthou, 2007; Marchetti et al., 2004; Ribeiro et al., 2008; Vila-Gispert and Moreno-Amich, 2002; Wootton et al., 2000).

The native range of largemouth bass *Micropterus salmoides* (Lacépède) includes drainages in eastern North America from the St. Lawrence – Great Lakes, Hudson Bay (Red River), through the Mississippi drainage and south to northern Mexico. This species chiefly inhabits warm water lakes and rivers, where it is a major piscivore (Marcy et al., 2005). However, largemouth bass display ontogenetic shifts in diet, feeding on zooplankton and insects while young, shifting to larger prey as they grow (e.g. crayfish, amphibians and fish) (Hodgson and Hansen, 2005; Olsen and Young, 2003). Largemouth bass have been stocked for angling in reservoirs on the Iberian Peninsula since 1950s (Leunda, 2010). Given that there were no native warm-water piscivores in this region, the native fauna evolved with few defensive adaptations to predators such as largemouth bass. Consequently, this predator has become a major threat

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to the native fishes on the Iberian Peninsula (Elvira, 1990, 1995a,b; Elvira and Almodóvar, 2001; Leunda, 2010; Nicola et al., 1996). The voracious predatory behavior of largemouth bass, together with its limnophilic habits, have been the basis for several studies of trophic ecology in Iberian lentic environments including lakes (García-Berthou, 2002), lagoons (Nicola et al., 1996), reservoirs (Godinho and Ferreira, 1994) and highly regulated water courses (Godinho et al., 1997; Godinho and Ferreira, 1998). However, little information on the foraging biology of this species in lotic environments (i.e. streams) exists. Streams may furthermore represent nursery areas for largemouth bass (D. Almeida, unpubl. data), which could yield insights into factors affecting recruitment of this species.

In this paper we assess aspects of the trophic plasticity of juvenile largemouth bass in Iberian streams. To do that, we carried out a comparative analysis of feeding habits and physical condition between a small Spanish stream (Bullaque River) and a native population from the middle Savannah River basin (Murray Creek, Southeastern USA). Specifically, we compared a residual index of body mass, diet, dietary diversity and prey electivity between study areas.

2. Materials and methods

2.1. Study area

The feeding habits of invasive largemouth bass were characterized in the Bullaque River (Guadiana River basin, central Spain), a small water course (wetted width range = 3–10 m; water depth range = 0.2–0.9 m), regulated by the Torre Abraham dam. The region is characterized by a Mediterranean climate with cold, rainy autumns and winters, and hot, dry summers, though water regulation in Bullaque River ensures stable flows throughout the year (annual range = 0.2–0.3 $m^3 s^{-1}$). The fish assemblage of Bullaque River consists of 13 species, seven of which are Iberian endemics: *Iberochondrostoma lemmingii* (Steindachner), *Luciobarbus comizo* (Steindachner), *Luciobarbus microcephalus* (Almaça), *Pseudochondrostoma willkommii* (Steindachner), *Squalius alburnoides* (Steindachner), *Squalius pyrenaicus* (Günther) and *Cobitis paludica* (de Buen). The other six species, goldfish *Carassius auratus* (L.), common carp *Cyprinus carpio* L., pike *Esox lucius* L., mosquitofish *Gambusia holbrooki* Girard, pumpkinseed *Lepomis gibbosus* (L.) and largemouth bass, were initially introduced in Torre Abraham Reservoir (built in 1974), but have spread successfully downstream in the Bullaque. Typically, the vast majority of largemouth bass residing in the Bullaque are juveniles probably because of a lack of suitable habitat for adults (i.e. deep, structurally complex habitat) (Almeida, 2008). Both biotic and abiotic characteristics of this area have been described previously by Almeida (2008) and Almeida et al. (2009).

Limnological and biological characteristics of the middle Savannah River basin were described in Marcy et al. (2005). In particular, Murray Creek is a small unregulated water course (wetted width range = 2–7 m; water depth range = 0.2–1.1 m; annual discharge = 0.1–0.6 $m^3 s^{-1}$). The region is characterized by an Atlantic and subtropical climate with temperate, rainy autumns and winters, and hot, humid summers. The fish assemblage showed a high variety (e.g. Table 1).

2.2. Fish sampling and laboratory procedures

Juvenile largemouth bass (fork length range = 20–127 mm, n = 47) were captured from the Bullaque River in July 2006. In the Savannah River basin, largemouth bass were captured from Murray Creek in August 2007, since the limnological and hydrological conditions of this water course at that moment were very similar to those in Bullaque River. Moreover, 2006 and 2007 were hydrologically average years for each study water course, respectively (Ministry of Environment Spain, 2011; USGS, 2011), which avoids the effects of particular dry or wet years. In the Murray Creek, we focused on a fish size range and a sampling size (fork length range = 50–118 mm, n = 58) similar to those collected in Bullaque River for comparisons. In both study areas, sampling sites were isolated with block nets and fish were captured by electrofishing (2000 W DC generator at 200–250 V, 2–3 A) in order to estimate fish abundances, following the removal sampling without replacement or Zippin's method (1956). Sampling points were selected to include all mesohabitats present (run, riffle, pool). After capture, largemouth bass were immediately preserved in 8% formalin. All field procedures were complied with animal use and care regulations of Spain and USA. Summer was chosen as sampling season because of low discharge, high temperature and high fish density which potentially accentuate biotic interactions between largemouth bass and native species (Godinho et al., 1997).

In the laboratory, all fish were measured by means of a measuring board (fork length ±1 mm) and eviscerated weight was taken

Table 1
Comparison of fish assemblages between study areas. Results are mean ± SE. *F* values and significance levels of ANOVA are indicated.

	Fish abundances (ind. ha^{-1})	
	Murray Creek	Bullaque River
Alosa aestivalis (Mitchill)	3 ± 1	–
Dorosoma cepedianum (Lesueur)	98 ± 19	–
Dorosoma petenense (Günther)	626 ± 162	–
Esox niger Lesueur	68 ± 10	–
Cyprinus carpio	1 ± 0.3	–
Cyprinella nivea (Cope)	9 ± 4	–
Notemigonus crysoleucas (Mitchill)	8 ± 3	–
Notropis hudsonius (Clinton)	574 ± 192	–
Iberochondrostoma lemmingii	–	354 ± 24
Squalius alburnoides	–	2293 ± 377
Squalius pyrenaicus	–	116 ± 17
Carpiodes carpio (Rafinesque)	13 ± 5	–
Carpiodes cyprinus (Lesueur)	1 ± 1	–
Hypentelium nigricans (Lesueur)	1 ± 1	–
Minytrema melanops (Rafinesque)	26 ± 9	–
Moxostoma anisurum (Rafinesque)	3 ± 1	–
Cobitis paludica	–	1098 ± 186
Fundulus diaphanus (Lesueur)	110 ± 43	–
Gambusia holbrooki	158 ± 27	3284 ± 808
Ameiurus natalis (Lesueur)	1 ± 0.3	–
Ameiurus nebulosus (Lesueur)	2 ± 1	–
Ameiurus platycephalus (Girard)	1 ± 1	–
Ictalurus punctatus (Rafinesque)	9 ± 1	–
Noturus gyrinus (Mitchill)	35 ± 6	–
Pylodictis olivaris (Rafinesque)	3 ± 1	–
Perca flavescens (Mitchill)	205 ± 31	–
Etheostoma fusiforme (Girard)	96 ± 3	–
Etheostoma olmstedi Storer	1 ± 1	–
Lepomis auritus (L.)	206 ± 47	–
Lepomis cyanellus Rafinesque	274 ± 54	–
Lepomis gibbosus	18 ± 7	1203 ± 123
Lepomis gulosus (Cuvier)	732 ± 165	–
Lepomis macrochirus	13,799 ± 2058	–
Lepomis microlophus (Günter)	1330 ± 353	–
Pomoxis nigromaculatus (Lesueur)	95 ± 27	–
Micropterus salmoides	159 ± 49	298 ± 34
White perch *Morone americana* (Gmelin)	22 ± 5	–
Morone Chrysops (Rafinesque)	2 ± 1	–

Assemblage parameters	Murray Creek	Bullaque River	$F_{1,29}$
Species richness	24.33 ± 0.78	4.43 ± 0.32	65.53***
Total fish abundance	18,690 ± 663	8646 ± 224	6.41*
Largemouth bass abundance (<130 mm)	93 ± 25	298 ± 34	5.14*

* P < 0.05.
*** P < 0.001.

by means of an electronic balance (wet weight within 1 g). Stomach contents were examined and different food categories were identified to the lowest possible taxonomic level using a binocular microscope. Prey species and genus were achieved for fishes, order for insects and class for other invertebrates. Prey were counted using a binocular microscope and weighed using an electronic balance (wet weight to within 0.1 mg). The minimum number of individuals of each prey was estimated by the number of diagnostic parts (e.g. mouth bones for fish, heads and thorax for insects, carapaces for crustaceans, and clitella for earthworms).

2.3. Data analyses

The effect of body size was controlled for statistical analyses by means of analyses of covariance (ANCOVA), using the ln-transformed fork length as the covariate.

Species richness, total fish abundance and juvenile largemouth bass abundance were compared between native and non-native habitats using one-way analysis of variance (ANOVA). We used Chi-square to test for significant differences in the frequency of empty stomachs between areas. Body condition of largemouth bass was quantified using residuals from a linear regression between ln eviscerated somatic mass and ln fork length for all pooled samples (Jakob et al., 1996). This index controls for body size and provides biologically meaningful results (i.e. negative values indicate poor condition and positive represent good condition). We tested for differences in the residual index between areas using ANOVA. Dietary data were analysed using percentage of occurrence, omitting empty stomachs, and mass (expressed as a percentage of the total ingested mass) of each food category. Examination of both of the metrics indicate how commonly a given prey is eaten within the population, and how important energetically the prey type is to the population. Furthermore, several diet parameters were measured for each fish such as percentage of ingested mass for four different prey classes (see below), prey richness, dietary diversity, niche breadth and prey selection. Four prey classes were examined for comparison of ingested mass between areas, based on habitat use: (1) water-column invertebrates, (2) benthic invertebrates, (3) water-column fishes, and (4) benthic fishes. Dietary diversity was measured using the Shannon–Weaver's index (H') and trophic niche breadth was estimated by measuring standardised Levin's index (B). Both indices were calculated as follows:

$$H' = -\sum_{i=1}^{n} p_i \log_2 p_i$$

$$B = \frac{1}{\sum_{i=1}^{n} p_i^2}$$

where p_i is the proportional abundance of prey i and n is the number of prey for each fish. To further evaluate the type of piscivory displayed in both populations, we classified fish prey by their habitat: water-column and benthic fishes. Prey selection was measured with Vanderploeg and Scavia's (1979) relativised electivity index (ε_i), using the following equations:

$$\varepsilon_i = \frac{\alpha_i - (1/n)}{\alpha_i + (1/n)}, \quad \text{where} \quad \alpha_i = \frac{r_i/p_i}{\sum_{i=1}^{n}(r_i/p_i)}$$

r_i is the proportional abundance of prey i in the diet, p_i is the proportional abundance of prey i in the environment, n is the number of prey included in the analysis and α is the Manly–Chesson's alpha (Chesson, 1978). Fish abundances were used to estimate prey availabilities. The electivity value ranges from −1 (avoidance) to 1 (selection), with zero indicating no selection. There are many electivity indices, but Lechowicz (1982) showed that Vanderploeg and Scavia's index best represented the properties of true selection. Hypothesis tests were performed to evaluate electivities with a null hypothesis of the mean equalling zero. All variables were ln-transformed prior to statistical testing, except for the electivity index, which was arcsine-transformed (arcsine $\sqrt{[(\varepsilon_i + 1)/2]}$). Assumptions of normality of distributions and homogeneity of variances were verified through Shapiro–Wilk and Levene's tests, respectively. All statistical analyses were performed with STATISTICA 6.0 for Windows. The significance level was set at $\alpha = 0.05$.

Table 2
Diet composition of largemouth bass from Murray Creek and Bullaque River. Percentages of occurrence (oc.) and mass are shown.

Food category	Murray		Bullaque	
	oc.	Mass	oc.	Mass
Algae and plant debris	–	–	13	[a]
Oligochaeta	–	–	3	[a]
Acari	–	–	3	[a]
Planktonic Crustacea	38	[a]	39	[a]
Insecta				
Odonata nymphs	9	1	45	48
Ephemeroptera and Plecoptera nymphs	3	[a]	95	25
Diptera larvae	21	[a]	87	4
Trichoptera larvae	–	–	8	[a]
Heteroptera and Coleoptera adults	24	12	16	2
Flying insects (Lepidoptera and Hymenoptera)	6	6	5	[a]
Fishes				
Dorosoma spp. (Clupeidae)	3	3	–	–
Notropis spp. (Cyprinidae)	9	13	–	–
C. paludica (Cobitidae)	–	–	13	8
G. holbrooki (Poeciliidae)	3	1	16	12
Etheostoma spp. (Percidae)	3	4	–	–
Lepomis spp. (Centrarchidae)	53	59	–	–

[a] Percentage < 1.

3. Results

Fish species richness was much higher in the Murray Creek relative to Bullaque River (Table 1). Total fish abundance was also higher in the Murray Creek (almost 19,000 ind. ha^{-1}), although young largemouth bass were more abundant in Bullaque River (almost 300 ind. ha^{-1}) (Table 1).

Largemouth bass from Bullaque River showed a significant lower frequency ($\chi^2 = 4.97$, $P < 0.05$) of empty stomachs (19.14%) than conspecifics did from the Murray Creek (41.38%). The relationship between body length and body weight [ln(eviscerated weight) = −11.36 + 3.01 ln(fork length)] was strong and highly significant ($r^2 = 0.99$, $F_{1,103} = 12{,}860.64$, $P < 0.001$). Condition index value was significantly greater ($F_{1,103} = 22.94$, $P < 0.001$) in the Bullaque river (residual index = 0.064, SE = 0.020) than in Murray Creek (residual index = −0.052, SE = 0.014).

Diet composition of largemouth bass in Bullaque River is shown in Table 2. Ephemeroptera and Plecoptera nymphs were the most common prey in occurrence, followed by Diptera larvae, Odonata nymphs and planktonic Crustacea (Cladocera and Copepoda). Gravimetric analyses indicated that Odonata nymphs were the most important prey as ingested mass, followed by Ephemeroptera and Plecoptera nymphs and fishes. In native largemouth bass, the analysis of diet composition showed that fish of genus *Lepomis* were the most significant prey in occurrence (more than 50%). Planktonic Crustacea was also a common food category, followed by water striders (Heteroptera) and Diptera larvae. However, gravimetric analyses showed that fishes were the dominant prey, representing approximately 80% of ingested mass, followed by Heteroptera (12%) and flying insects (6%) (Table 2).

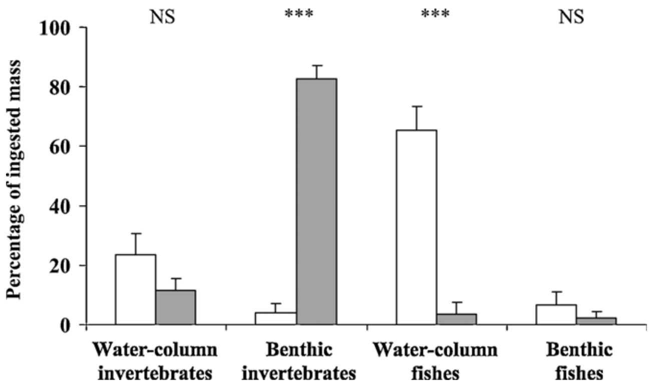

Fig. 1. Percentage of ingested mass for different prey groups. Results are adjusted means ± SE after, ANCOVA (ln fork length as the covariate). White, Murray Creek; grey, Bullaque River. NS: $P > 0.05$; ***$P < 0.001$.

Furthermore, the use of habitat-prey type also varied between study rivers (Fig. 1). Although the mean in percentage of ingested mass for water-column invertebrates and benthic fish did not show significant differences ($F_{1,69} = 0.01$, $P = 0.92$; $F_{1,69} = 0.65$, $P = 0.42$; respectively), differences were highly significant for the other two prey groups. Thus, benthic invertebrates were more important for largemouth bass in the Bullaque River (mean > 80%) ($F_{1,69} = 314.30$, $P < 0.001$), whereas in the Murray Creek water-column fishes dominated the diet (≈65%) ($F_{1,69} = 42.16$, $P < 0.001$).

Dietary summary statistics for largemouth bass differed between study areas (Fig. 2). Fish from the Bullaque River presented higher values of prey richness ($F_{1,69} = 70.20$, $P < 0.001$), diet diversity ($F_{1,69} = 137.27$, $P < 0.001$) and trophic niche breadth ($F_{1,69} = 197.44$, $P < 0.001$) than fish from the Murray Creek. Almost three different prey in average were found in stomachs from Bullaque River, whereas only one was observed in the Murray Creek. Differences in Shannon and Levin indexes between areas were even much higher (Fig. 2).

Prey selection was different between study areas for the two considered fish-habitat types (Fig. 3). Largemouth bass from Bullaque River avoided water-column fishes ($t = 22.79$, $P < 0.001$), whereas these prey were positively selected in the Murray Creek ($t = 3.00$, $P < 0.01$) ($F_{1,69} = 56.98$, $P < 0.001$). Electivity index in Bullaque River showed no selection for benthic fishes ($t = 1.93$, $P = 0.06$), whereas the mean value for Murray Creek was clearly negative ($t = 9.02$, $P < 0.001$) ($F_{1,69} = 5.18$, $P < 0.001$).

4. Discussion

Dietary patterns of largemouth bass differed between native and non-native habitats on both qualitative and quantitative levels. One unusual difference was that 13% of largemouth bass in the Bullaque River consumed plant material, although given its low volume it is likely that this material was consumed incidentally while pursuing macroinvertebrate prey such as Odonata. By contrast, plant material was not observed in the stomachs of largemouth bass from the native habitat. Nonetheless, García-Berthou (2002) and Blanco et al. (2003) also detected plant material in the diet of largemouth bass from Spanish lakes. Largemouth bass in their native habitat preyed extensively on surface-dwelling invertebrates such as water striders, as well as terrestrial insects such as Lepidoptera and Hymenoptera. In the native habitat, largemouth bass were primarily piscivorous particularly on small *Lepomis* spp. The *Micropterus*–*Lepomis* predator–prey relationship has been well studied in North America (Olsen and Young, 2003; Olson, 1996; Phillips et al., 1995; Turner and Mittelbach, 1990). Sunfishes dominated the fish fauna in Murray Creek, with bluegill

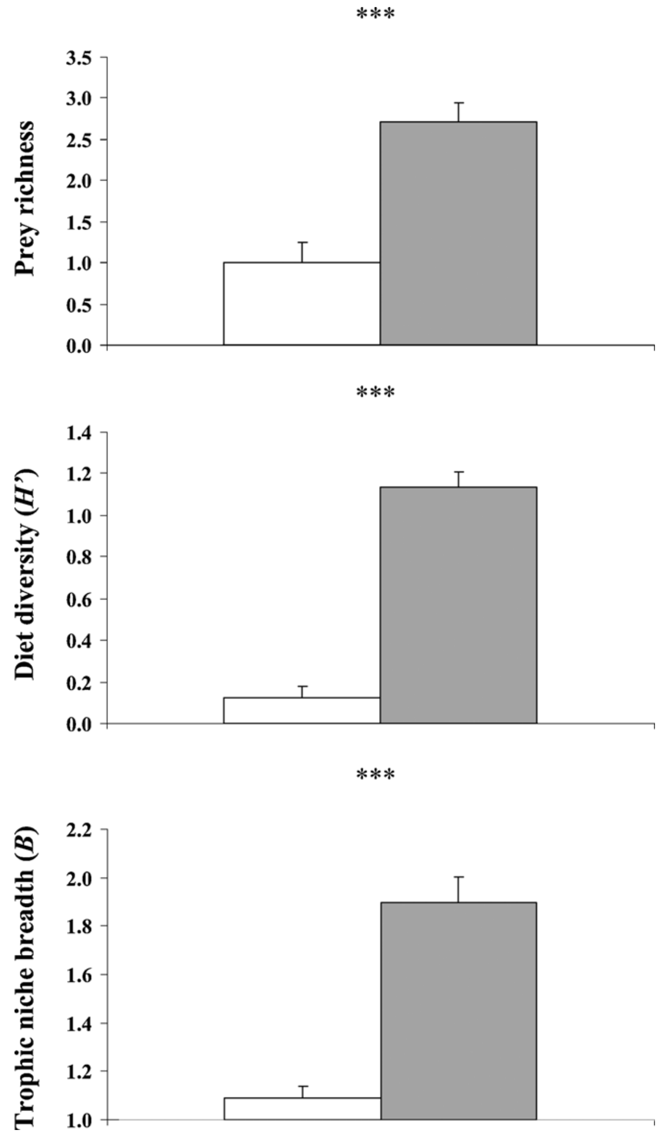

Fig. 2. Comparison of three diet parameters between study areas. Results are adjusted means ± SE, after ANCOVA (ln fork length as the covariate). White, Murray Creek; grey, Bullaque River. ***$P < 0.001$.

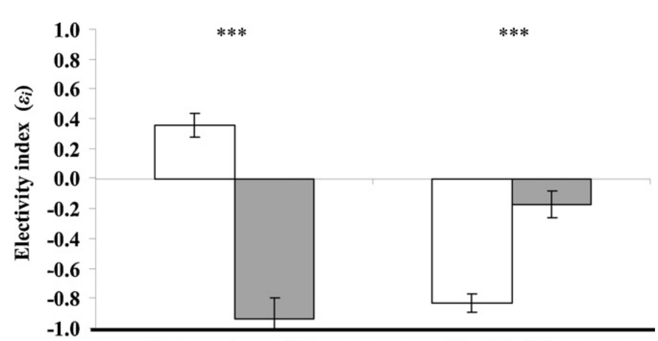

Fig. 3. Electivity index (ε_i) for fish prey groups between study areas. Results are adjusted means ± SE, after ANCOVA (ln fork length as the covariate). White, Murray Creek; grey, Bullaque River. ***$P < 0.001$.

Lepomis macrochirus Rafinesque being most abundant (almost 13,800 ind. ha^{-1}) (Table 1). Sunfish are not absent from the Bullaque River and the invasive pumpkinseed is abundant (more than 1200 ind. ha^{-1}) (Table 1), although it was absent from largemouth bass diet in this river. Perhaps it was too energetically costly to capture in comparison to abundant invertebrate prey (e.g. Hambright et al., 1991). Indeed, we observed negative electivities for all water-column fishes in the Bullaque River. Moreover, electivity analyses also indicated no selection for benthic fishes, which were consumed in proportion to their abundance in the environment. In Banyoles Lake (north eastern Spain), García-Berthou (2002) also observed low rates of piscivory in invasive largemouth bass, probably related to the low abundance of native fishes (Aparicio et al., 2000). In this system, small largemouth bass also consumed large numbers of a limnetic invertebrate, the freshwater shrimp *Atyaephyra desmaresti* (Millet) (>75% frequency of occurence and almost 6% dietary mass). These results document the opportunistic foraging behavior of largemouth bass which can be a surface, mid-water or bottom feeder depending on prey availability.

Phenotypic and ecological plasticity are common traits displayed by successful invaders in novel habitats (Agrawal, 2001). In particular, largemouth bass show a wide range of variation in population parameters correlated with the local non-native environment (e.g. Scalici et al., 2009). Largemouth bass also display very flexible foraging behavior in native areas as described by the fact they are strongly influenced by local food availability (Huskey and Turingan, 2001). Thus, largemouth bass in the non-native habitat had higher prey richness, dietary diversity and trophic niche breadth than in the native habitat, which corresponds to a shift from a specialist to a generalist strategy between study areas. Our results may provide insight into one factor (i.e. trophic plasticity at juvenile stages) affecting the successful invasion of largemouth bass in other regions including multiple Iberian streams. Furthermore, the fact our sampling occurred in years with hydrologic regimes close to long-term averages (Ministry of Environment Spain, 2011; USGS, 2011) renders our findings more general despite the short term nature of the sampling.

The frequency of full stomachs, body condition and abundance of young largemouth bass all being greater in the Bullaque River compared to the Murray Creek suggests that some Iberian streams provide suitable habitat for this species. Nonetheless, most Iberian streams and rivers have a Mediterranean climate, with flooding events during autumn and winter, and low flows during summer (Gasith and Resh, 1999). This variability in flow may hamper the establishment and spread of invasive largemouth bass in Mediterranean rivers (Bernardo et al., 2003), although other centrarchids, such as pumpkinseed are widely distributed throughout both Spain and Portugal. Nonetheless, invasive species that are used to more stable hydrographs (e.g. largemouth bass) may persist in habitats where flow variation is damped such as reservoirs and regulated rivers such as the Bullaque. Almeida et al. (2009) demonstrated that anthropogenically altered flow regime in this stream favoured another invasive centrarchid, the pumpkinseed. By contrast, alteration of natural flow patterns may negatively affect fishes in many fluvial ecosystems, which disturbs native fish faunas and their habitats (Brown and Ford, 2002; Murchie et al., 2008; Wang et al., 2011), especially Iberian fish assemblages with a high degree of endemicity (Clavero et al., 2004; Santos et al., 2004). Invasive largemouth bass also may be able to fulfil their ecological requirements in Iberian waters because of a lack of predators in most riverine systems (Elvira and Almodóvar, 2001; Leunda, 2010). Although both pike and adult largemouth bass prey upon juvenile largemouth bass (Elvira et al., 1996; Nicola et al., 1996), neither are particularly abundant in Iberian streams. Cannibalism was present in adult largemouth bass (>220 mm fork length) in the native habitat, Murray Creek (D. Almeida, unpubl. data), but these large individuals are uncommon in the Bullaque River (Almeida, 2008). Therefore, the success of largemouth bass in both the Bullaque River and other Iberian streams may be a function of (1) damped flow variation, (2) naive prey, and (3) low predation pressure. It is likely that the success of largemouth bass in the Bullaque River is at least partially a result of the presence of Torre Abraham Reservoir upstream of the study site. Reservoirs may serve as sources for invasive species on the Iberian Pensinsula, because these artificial environments may simulate natural habitat for lentic species (Almeida, 2008; Elvira, 1995b; Godinho et al., 1998). In fact, Clark et al. (1998) observed that the banks of reservoirs provided nesting habitat for the ecologically similar smallmouth bass *Micropterus dolomieu* Lacépède, as long as water fluctuations were not high. Furthermore, given that Torre Abraham Reservoir is used as a water supply reservoir rather than for power generation, its water level fluctuations are low and as a consequence so are those in the downstream Bullaque River (Almeida, 2008). This facilitates development of riparian vegetation and the establishment of complex and abundant benthic macroinvertebrate communities (Flory and Milner, 1999; Prus et al., 1999), which serve as both habitat and prey respectively for juvenile largemouth bass (i.e. "nursery" area). To summarize, a constellation of anthropogenically–linked factors including altered flows, an ample and naive prey base, coupled with low predation pressure, contribute to the success of invasive largemouth bass in the Bullaque River and likely in other streams in the Iberian Peninsula.

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