Ecology of Freshwater Fish 2009: 18: 15–23
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ECOLOGY OF
FRESHWATER FISH

Feeding tactics and body condition of two introduced populations of pumpkinseed *Lepomis gibbosus*: taking advantages of human disturbances?

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Abstract – Feeding tactics, body condition and size structure of two populations of pumpkinseed *Lepomis gibbosus* from Cabañeros National Park (Guadiana River basin, central Spain) were compared to provide insight into the ecological requirements favouring levels of success/failure in relation to human intervention. Habitat, benthic macroinvertebrates and pumpkinseed were quantified in Bullaque (regulated flow, affected by agricultural activities) and Estena (natural conditions) rivers, from May to September of 2005 and 2006. Significant differences were found in the limnological characteristics between the two rivers. Spatial and temporal variations in diet composition were likely related to opportunistic feeding and high foraging plasticity. Diet diversity was higher in Bullaque River. Electivity of benthic prey showed variation between sized individuals and populations. The body condition of pumpkinseed was better in Bullaque River. Current results show that this invasive species is favoured by human intervention in Bullaque River.

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Key words: invasive species; feeding tactics; prey selection; freshwater fishes

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Accepted for publication May 9, 2008

Introduction

Biological invasions induced by human activities have resulted in serious disturbances and deleterious effects of natural ecosystems all around the world (Money & Hobbs 2000). Actually, such invasions are one of the most important causes of biodiversity loss, particularly in aquatic ecosystems (Welcomme 1992). The growing concern about the impacts of non-native fish has led to the study of these species outside of their native ranges to improve our ability to predict their impact and to control the expansion of existing ones (Marchetti et al. 2004; García-Berthou 2007; Ribeiro et al. 2008). Nevertheless, despite intensive research, there is still an urgent need to increase our knowledge on the life history of non-native fish species (Wootton et al. 2000).

In Spain, more than 25 fish species have been introduced (Elvira 1995a; Elvira & Almodóvar 2001; Ribeiro et al. 2008). Available studies indicate that the impact of invaders upon native fish assemblages are due to habitat alteration (García-Berthou 2001), predation (Elvira et al. 1996; Nicola et al. 1996), trophic competition (García-Berthou 1999; Alcaraz & García-Berthou 2007) and hybridisation with native species (Elvira 1995b, 2001; Almodóvar et al. 2001, 2006).

The pumpkinseed *Lepomis gibbosus* (L.), a centrarchid fish native to eastern North America, was first introduced into the Iberian Peninsula (first time in Lake Banyoles, northeastern Spain) in 1910–1913 (Elvira & Almodóvar 2001) and was first recorded in the 1970s in the Guadiana River basin (Almaça 1995). The pumpkinseed is now widespread, particularly in reservoirs, and has been related to changes in native

doi: 10.1111/j.1600-0633.2008.00317.x

fish assemblages (Zapata & Granado-Lorencio 1993; Godinho & Ferreira 1998a; García-Berthou & Moreno-Amich 2000). Within its natural distributional range, pumpkinseed inhabits lentic environments such as lakes and ponds (Fox 1994; Robinson et al. 2000), where it chiefly feeds on zooplankton and benthic invertebrates (Scott & Crossman 1979; Deacon & Keast 1987).

The objective of this study was to compare auto-ecological features between two nearby pumpkinseed populations. More specifically this study compares diet, prey selection, body condition and size structure of pumpkinseed in two Spanish streams; namely in Bullaque and Estena rivers, within the Cabañeros National Park, central Spain, differing in the degree of human intervention.

Study area and fish fauna

Cabañeros National Park is a protected area of 408.56 km^2. Altitude ranges from 560 to 1448 m. This is characterised by a Mediterranean climate and comprises two main streams: Bullaque and Estena rivers (Guadiana River basin, central Spain), which run 84 and 61 km in length, respectively. Flow regime of Bullaque River is regulated by the Torre de Abraham reservoir, located nearby Cabañeros National Park (Fig. 1). This river runs next to the east borderline of the Park, where farming activities take place. Therefore, agricultural runoff (nutrients and organic matter resulting from cattle and farming activities) increases turbidity and organic pollutants promoting losses of water quality. In contrast, more natural conditions prevail in Estena River, i.e., higher water velocity and well developed riparian vegetation. During the study period, the limnological characteristics differed substantially between the two rivers (Table 1 and Fig. 2). Whilst the regulated water course of Bullaque River ensures a continuous flow during the rainless summer, isolated pools typify Estena River, a drought condition typical of small Mediterranean rivers.

The fish assemblage of Cabañeros National Park encompasses 14 species (Doadrio 1997, 2002, and authors' personal data). Eight species are endemic: *Anaecypris hispanica* (Steindachner), *Iberochondrostoma lemmingii* (Steindachner), *Luciobarbus comizo* (Steindachner), *Luciobarbus microcephalus* (Almaça), *Pseudochondrostoma willkommii* (Steindachner), *Squalius alburnoides* (Steindachner), *Squalius pyrenaicus* (Günther), and *Cobitis paludica* (De Buen). Other six accompanying species were introduced in nearby reservoirs, and have spread throughout. These species include: *Carassius auratus* (L.), *Cyprinus carpio* L., *Esox lucius* L., *Gambusia holbrooki* Girard, *Lepomis gibbosus* (L.) and *Micropterus salmoides* (Lacépède).

Materials and methods

Sampling and laboratory methods

Monthly samples of pumpkinseeds were conducted from May to September of 2005 and 2006 with electrofishing (2000 W DC generator at 200 V,

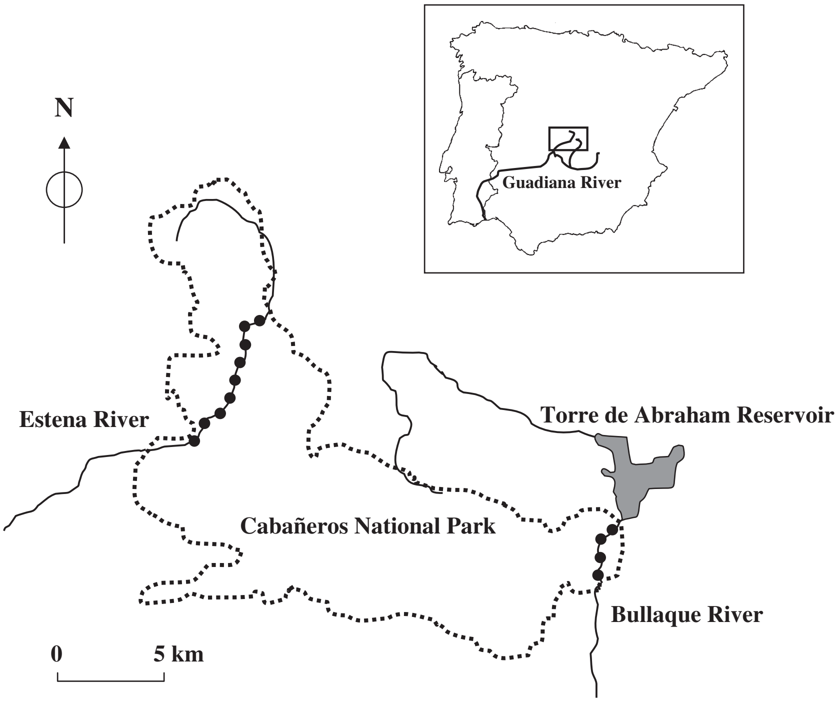

Fig. 1. Map of the study area. Dotted line marks the boundary of Cabañeros National Park. Sampling sites surveyed are marked as bold circles.

Table 1. Limnological features and macroinvertebrate abundances in the studied rivers for each sampling year.

	2005		2006	
	Bullaque River	Estena River	Bullaque River	Estena River
Limnological features				
Water velocity ($m{\cdot}s^{-1}$)	0.27 ± 0.07	0.06 ± 0.03	0.21 ± 0.06	0.05 ± 0.03
Depth (cm)	53.33 ± 2.12	27.08 ± 2.70	48.17 ± 3.03	31.83 ± 2.14
Aquatic vegetation (%)	27.41 ± 1.96	48.67 ± 2.38	30.63 ± 1.33	50.83 ± 2.77
Silt (<0.01 cm) (%)	26.84 ± 1.69	17.00 ± 2.86	29.37 ± 1.12	18.83 ± 2.92
Sand (0.01–0.5 cm) (%)	10.06 ± 1.50	8.07 ± 1.03	11.10 ± 2.35	10.25 ± 1.59
Gravel (0.5–7.6 cm) (%)	35.08 ± 5.33	34.92 ± 3.63	33.60 ± 3.24	36.57 ± 4.15
Pebble (7.6–30.5 cm) (%)	24.67 ± 5.17	33.77 ± 3.31	22.75 ± 5.04	29.75 ± 3.99
Block (>30.5 cm) (%)	3.34 ± 5.52	6.25 ± 3.31	3.18 ± 6.28	4.61 ± 2.47
Macroinvertebrates				
Density (1000 $ind.g{\cdot}m^{-2}$)	27.41 ± 4.68	5.90 ± 0.54	24.70 ± 3.41	7.29 ± 0.67
Biomass ($g{\cdot}m^{-2}$)	5.18 ± 0.33	1.12 ± 0.16	4.96 ± 0.54	1.09 ± 0.27

Results are means ± SE. Particle size classification is according to Platts et al. (1983).

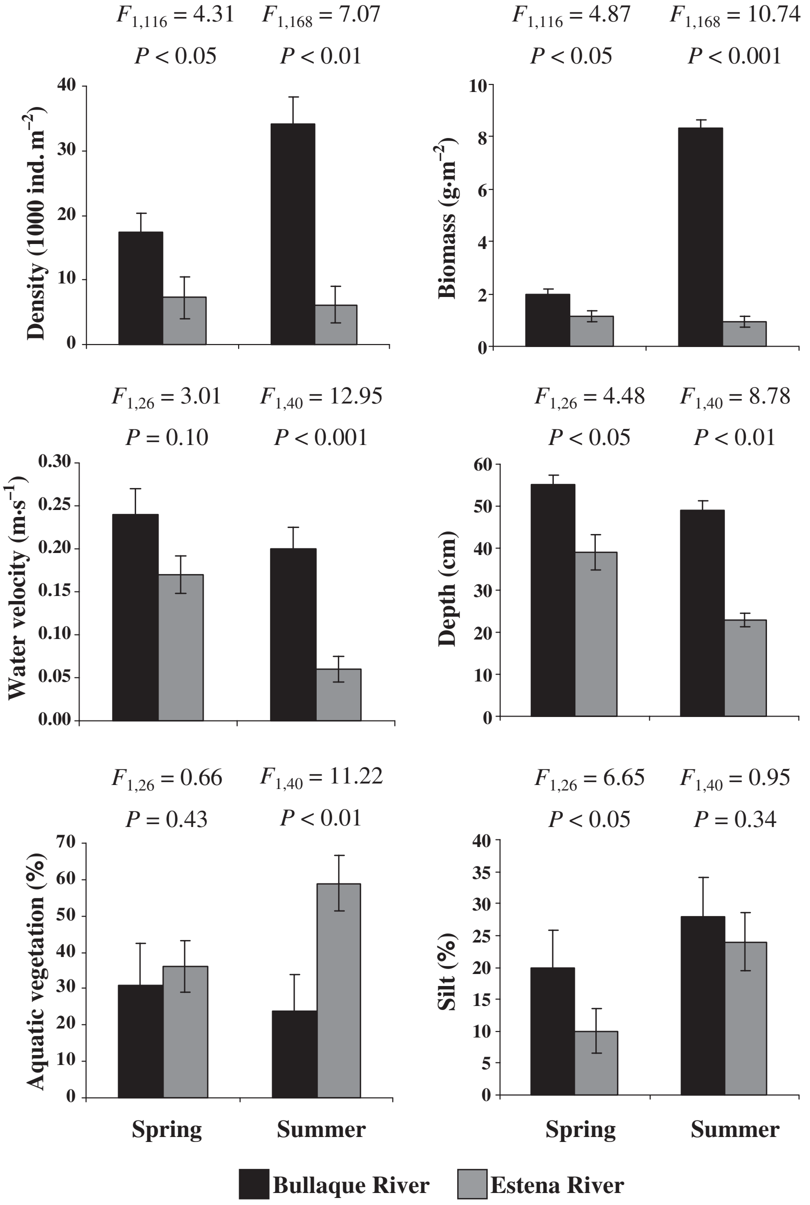

Fig. 2. Significant differences found in macroinvertebrates abundances (densities and biomasses) and habitat characteristics between rivers for each sampling season. Results are means ± SE. *F*-values and significance levels after ANOVA are indicated.

1–2 A). Sampling sites were located along 4 km in Bullaque River and 10 km in Estena River (Fig. 1). These sites (one site per two kilometres, 25–30 m long, sampling time 30–40 min) comprised different mesohabitats (run, riffle, pool) to include the existing environmental variability. Benthic macroinvertebrates were sampled on the same sites and dates (3–5 three-minute replicates) and mesohabitats using a cylinder core-type sampler (Edmondson & Winberg 1971) (55 cm height, 35 cm diameter and 250-μm-mesh net) The fishes and macroinvertebrates were preserved in 8% Formalin.

At each sample site, water velocity, depth, aquatic vegetation, and substrate composition were quantified (Table 1). Water velocity and depth were measured with a graduated current meter; aquatic vegetation as percentage of submerged macrophytes cover on the wetted area and substrate categories were visually determined (Platts et al. 1983). In the laboratory, all fish were measured for fork length (±1 mm) and eviscerated weight (±1 g). The stomachs contents of 69 and 125 pumpkinseeds from Bullaque and Estena rivers, respectively, were examined. Prey were identified to the lowest possible taxonomic level, counted, and weighed (wet weight ± 0.01 g). Macroinvertebrates were identified at the same taxonomic level than diet, counted, and weighed.

Data analyses

Habitat condition and macroinvertebrate abundance were not significantly different between years (Table 1), and as a consequence, data were pooled and we compared spring (the beginning of the dry period, May to June) and summer (strong drought, July to September) samples.

Three arbitrary size intervals of pumpkinseed were considered for diet analyses: <40, 40–80 and >80 mm. Frequency of occurrence (Fq.) was determined, omitting empty stomachs. Numerical frequency (No.) of each prey category was also calculated, and together with the weight (Wt) was expressed as a percentage. The relative importance index (RI) was calculated excluding weight from plant material (Hyslop 1980; Elvira et al. 1996; Nicola et al. 1996). Diet diversity for single individuals was measured using the Shannon's index (H'). To evaluate prey selection, the Vanderploeg & Scavia's (1979) relativised electivity index (ε_i) was calculated for benthic prey (non-benthic prey were excluded from diet and environment). The electivity value ranges from -1 to 1, where 1 indicates positive selection for a prey item, -1 indicates an avoidance of a prey item and zero implies neutral selection. Body condition of pumpkinseeds was calculated for the ln-transformed eviscerated somatic weight and ln-transformed fork length.

Assumptions of normality of distributions and homogeneity of variance were verified through Shapiro-Wilk and Levene's tests, respectively. Comparisons among macroinvertebrate abundance, habitat characteristics, and pumpkinseed abundance, fork length and body condition between populations were examined by standard analysis of the variance (ANOVA, Zar 1996). A chi-square test, with Yates' correction, was used to compare the frequency of empty stomachs between rivers. All statistical analyses were performed with STATISTICA 6.0. The significance level was set at $\alpha = 0.05$.

Results

Higher water velocity and depth characterise Bullaque River (Table 1) except for aquatic vegetation in the summer (Fig. 2). In this river, macroinvertebrate abundance was greater, especially in summer (Table 2). Ephemeroptera and Plecoptera nymphs, Diptera larvae and Oligochaeta were the most abundant groups.

Pumpkinseed abundance (fish m^{-2}) was significantly higher in Bullaque River (mean = 0.12, SE = 0.01) than in Estena River (mean = 0.09, SE = 0.01) ($F_{1,68} = 4.14$, $P < 0.05$). Fish were larger in Estena River (mean = 69.10, SE = 1.96, range 24–118) than in Bullaque River (mean = 57.58, SE = 2.05, range 34–109) ($F_{1,192} = 14.27$, $P < 0.001$). The pumpkinseed population structure also showed significant differences between rivers (Fig. 3).

In the Estena River, pumpkinseed displayed a higher frequency of empty stomachs, 20.0%, relative to 4.4% in Bullaque River ($\chi^2 = 7.60$, $P < 0.01$). Overall, the diet of pumpkinseed comprised 25 food categories (Table 3): Diptera larvae (chiefly Chironomidae and Simuliidae) were the most important prey followed by Ephemeroptera nymphs, and Cladocera and Trichoptera larvae (Table 3).

Table 2. Relative densities (%) of benthic macroinvertebrates used as prey by sampling season in Bullaque and Estena rivers.

	Spring		Summer	
Benthic group	Bullaque River	Estena River	Bullaque River	Estena River
Oligochaeta	29.16	35.31	10.85	55.46
Mollusca	1.07	0.13	0.85	0.50
Odonata nymphs	0.15	0.04	0.92	0.17
Nymphs*	8.30	7.67	3.28	16.97
Heteroptera	0.10	0.09	0.02	0.50
Diptera larvae	60.41	56.64	83.06	25.89
Trichoptera larvae	0.76	0.09	0.63	0.34
Other larvae	0.05	0.03	0.39	0.17

*Ephemeroptera and Plecoptera.

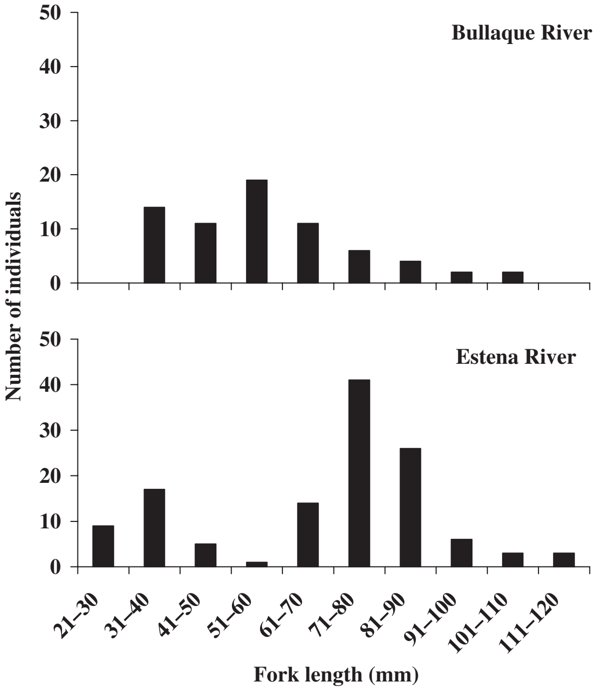

Fig. 3. Length–frequency distribution of pumpkinseeds in Cabañeros National Park by river.

Table 3. Diet composition of 166 pumpkinseed from Cabañeros National Park. Frequency of occurrence (Fq.), number (No.), wet weight (Wt) and relative importance index (RI) for each prey category are indicated.

Food category	Fq. (%)	No. (%)	Wt (%)	RI
Algae and plant debris	21.08	–	2.78	–
Oligochaeta	1.81	0.12	3.84	1.36
Mollusca	4.82	0.23	0.34	1.28
Acari	3.01	0.12	0.05	0.75
Araneae	0.60	0.02	0.11	0.17
Crustacea				
Cladocera	16.27	33.82	0.67	11.96
Copepoda	3.01	2.02	0.05	1.20
Atyaephyra desmaresti	3.01	0.14	2.99	1.45
Insecta				
Anisoptera (nymphs)	1.20	0.08	0.53	0.43
Zygoptera (nymphs)	1.20	0.04	0.43	0.39
Odonata undet.	1.81	0.06	0.43	0.54
Ephemeroptera (nymphs)	41.57	8.03	14.05	15.00
Plecoptera (nymphs)	2.41	0.08	0.14	0.62
Nymphs undet.*	18.67	8.86	10.69	9.01
Heteroptera (adults)	12.05	0.50	1.47	3.31
Orthoptera (adults)	0.60	0.02	0.11	0.17
Megaloptera (larvae)	1.81	0.06	1.71	0.84
Coleoptera (adults)	1.81	0.06	1.07	0.69
Coleoptera (larvae)	1.81	0.06	1.71	0.84
Formicidae (adults)	1.20	0.04	0.27	0.36
Diptera (adults)	0.60	0.04	0.64	0.30
Diptera (larvae and pupae)	75.90	41.03	46.32	38.47
Trichoptera (larvae)	22.29	3.54	3.07	6.81
Fishes				
Fish eggs	4.22	0.84	0.12	1.22
Gambusia holbrooki	5.42	0.19	6.41	2.83

*Ephemeroptera and Plecoptera.

The relative importance index varied across sizes and between populations for each season (Fig. 4). Planktonic crustaceans (Cladocera and Copepoda) had greater contribution for smaller individuals. The index of these prey decreased with increased size in Bullaque River during spring (Fig. 4a). Diptera larvae had a similar contribution for each of the three size intervals, however they were dominant in Estena River. The relative contribution of nymphs increased with fish size and was higher for pumpkinseed from Bullaque River. In summer, Heteroptera showed a consistent pattern to increase with fish size in Bullaque River (Fig. 4b). The percentage of plant biomass in pumpkinseed diet decreased from smaller to larger fish. Contribution of plant material in spring was 0.80%, 0.13%, and 0.00% for <40, 40–80 and >80 mm individuals, respectively, for Bullaque pumpkinseed, and 14.93%, 2.42%, and 0.91% for the individuals in the same size intervals for Estena pumpkinseed. In summer, however, the contribution of plant material declined to 11.92%, 10.69% and 10.10% for Bullaque, and 3.79%, 1.07% and 0.15% for Estena pumpkinseed.

Prey diversity was higher in both seasons in Bullaque (spring: mean $H' = 1.08$; summer: mean $H' = 0.93$) than in Estena pumpkinseed (spring: mean $H' = 0.59$; summer: mean $H' = 0.41$) (ANOVA, $F_{1,85} = 6.43$, $P < 0.05$ in spring; $F_{1,75} = 12.33$, $P < 0.001$ in summer), but similar across sized individuals for each season (ANOVA, $F_{1,85} = 0.15$, $P > 0.05$ in spring; $F_{1,75} = 1.19$, $P > 0.05$ in summer).

Eight categories of benthic prey were detected in the diet of pumpkinseed (Table 2 and Fig. 5). Electivity index varied between seasons and fish size. In spring (Fig. 5a), fishes from both rivers showed positive electivity for Trichoptera larvae. Heteroptera and other larvae were also positively selected but only in Estena. In summer (Fig. 5b), Trichoptera larvae and Heteroptera were also positively selected in both rivers. In addition, positive values were also detected for nymphs, Diptera, and other larvae in Estena.

An exploration into the food selection for the three mayor benthic prey groups showed that in the two populations in spring and summer, Diptera larvae and Ephemeroptera and Plecoptera nymphs were negatively selected for whereas Trichoptera larvae were positively selected for in Bullaque River (Fig. 6a) and scarcely represented in spring and negatively selected for during summer in Estena (Fig. 6b).

Discussion

Mediterranean-type streams typically show wide fluctuations in the flow regime over an annual cycle (Gasith & Resh 1999). Bullaque lost that seasonal

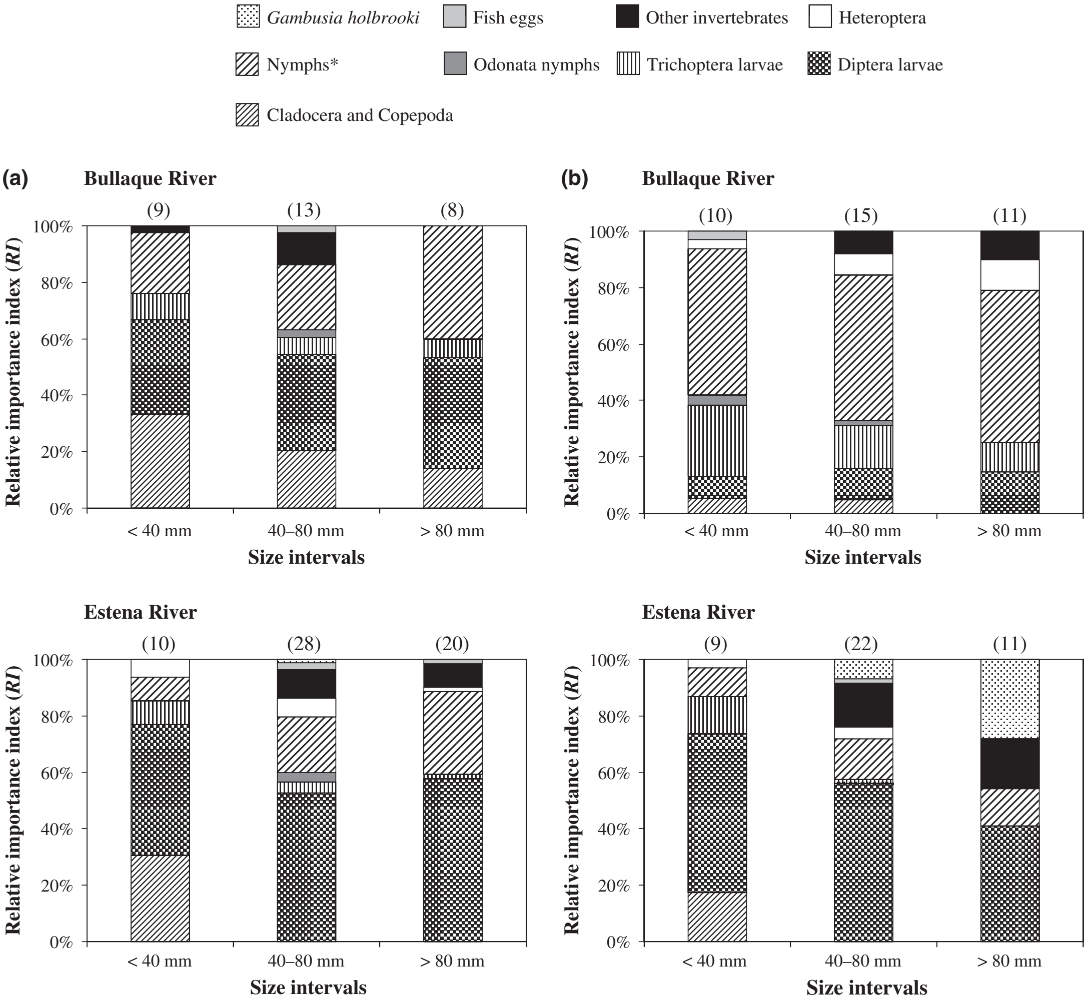

Fig. 4. Relative importance index (*RI*) of prey groups by size intervals of pumpkinseed in Bullaque and Estena rivers. (a) Spring; (b) Summer. Numbers in brackets are individuals for every size interval. *Ephemeroptera and Plecoptera.

variation since a dam was built in 1974, and this stream now presents a continuous flow from Torre de Abraham reservoir, with small variations in water level all the year long. That explains the strong differences between biotic and abiotic characteristics between the two rivers. Discharge in non-regulated Mediterranean streams may also vary from year to year, but relatively long-term dry and wet cycles (>10 years) are common (Gasith & Resh 1999). Apparently, the study period was included within a long-term dry cycle.

Godinho & Ferreira (1998a) observed that pumpkinseed selected lentic habitats and stable hydrological conditions in the highly regulated Guadiana River. In addition, Pérez-Bote et al. (2001) found that this species selected fine substrates with low amounts of aquatic vegetation for nesting and moderate water velocity and depth. These features can be currently found in Bullaque River below the dam. Estena River, in contrast, shows markedly severe seasonal floods (autumn and winter) and summer droughts. Such regime generates a decline in the availability of suitable refuges that may hamper the spread and colonisation of pumpkinseed. The major differences detected between the two populations of pumpkinseed include fish abundance and body condition. These may probably be linked to the higher food availability as result of nutrient loads from agricultural activities in Bullaque River. Important issued to deal with in further studies concern the opportunistic trophic behaviour of pumpkinseed in Bullaque River. So that, it may contribute to the decline of native fish species at this river or alternatively whether native species may also behave opportunistically, that is to say, growing larger and having higher abundances when compared with populations as those from Estena River.

Prey categories in the diet of pumpkinseed were similar to those found in its native distribution (Mittelbach 1984; Mittelbach et al. 1992; Osenberg et al. 1992) and in previous studies from the Iberian Peninsula (Godinho et al. 1997; Godinho & Ferreira

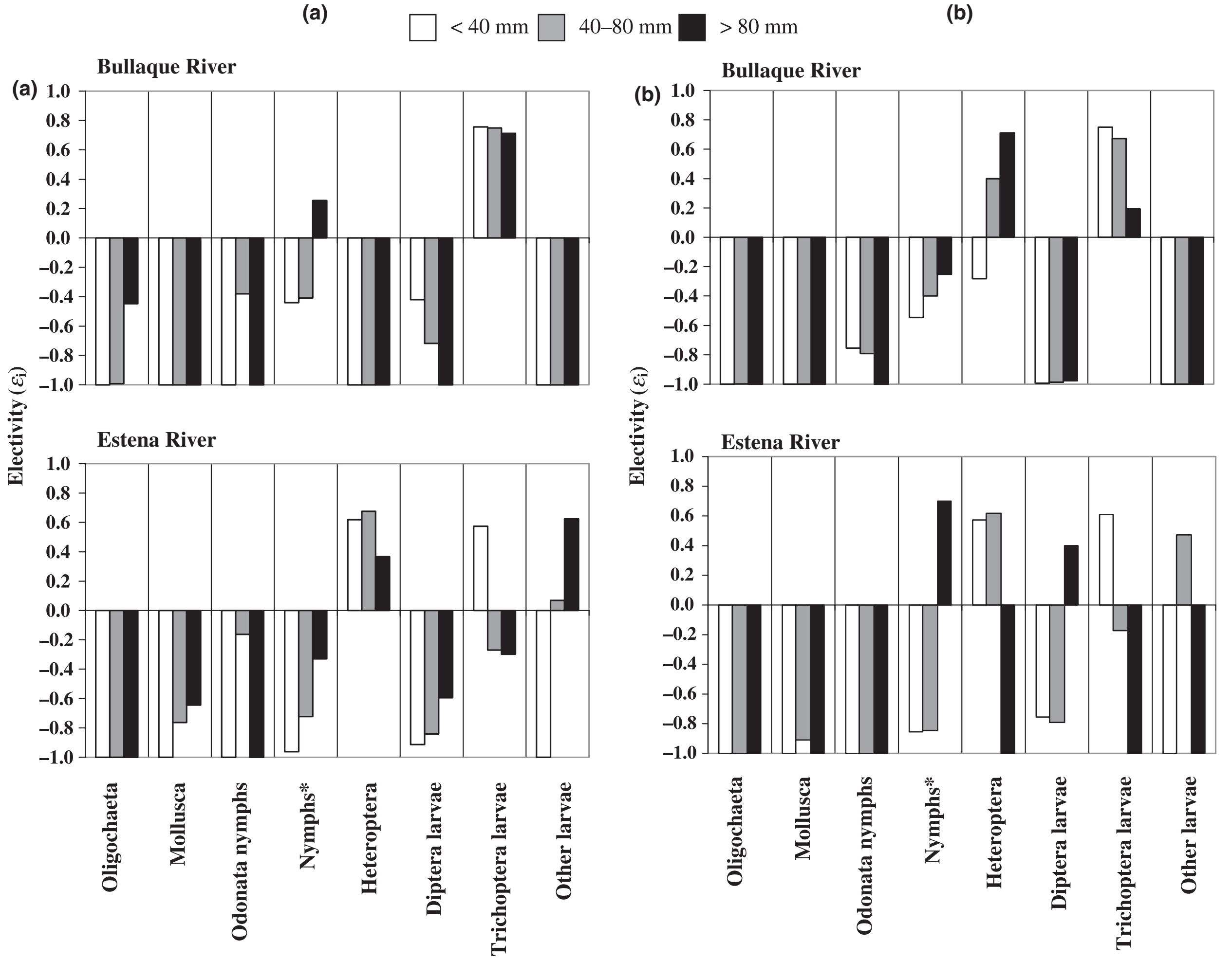

Fig. 5. Electivity index (ε_i) of benthic prey by size interval of pumpkinseed in Bullaque and Estena rivers. (a) Spring; (b) Summer. *Ephemeroptera and Plecoptera.

1998b; García-Berthou & Moreno-Amich 2000; Blanco et al. 2003). The consumption of plant material was previously reported by García-Berthou & Moreno-Amich (2000) and Blanco et al. (2003) in Mediterranean lagoons and by Godinho et al. (1997) in the lower Guadiana River basin (Portugal) during the dry season.

Diet shifts with increased fish size have been related to resource partitioning with other species of *Lepomis* (Osenberg et al. 1992). Mittelbach (1988) showed that ontogenetic shifts in diet include replacement of planktonic prey by a higher consumption of macroinvertebrates, which is consistent with our observations in Bullaque River.

Pumpkinseed display an opportunistic feeding behaviour, which is consistent with observations on its life history traits (Fox et al. 2007). Also, pumpkinseed exhibit preferences or avoidances to certain prey, irrespective of their abundance. For instance, Heteroptera adults (mainly Corixidae) were positively selected, with the exception of Bullaque River in the spring, as well as Trichoptera larvae, even when these groups do not accomplish 1% of the total benthic abundance. Diptera larvae were the most abundant benthic prey when its electivity was highest, whereas Oligochaeta were refused in spite of being the second benthic group with higher relative abundance.

Differences between the two populations in the relative importance of Diptera larvae, Ephemeroptera and Plecoptera nymphs and exotic *G. holbrooki*, were remarkably greater during the summer drought. It is hypothesised that such variations in diet composition among populations and seasons reflect not only variations in food supply but also a high foraging plasticity that enables the great invasive capacity of this species.

In conclusion, habitat alteration caused by human activities on Mediterranean-type streams may be responsible for the establishment of this invasive fish, as denoted by the higher abundance, better body condition, and broad feeding habits exhibited by pumpkinseed in Bullaque River.

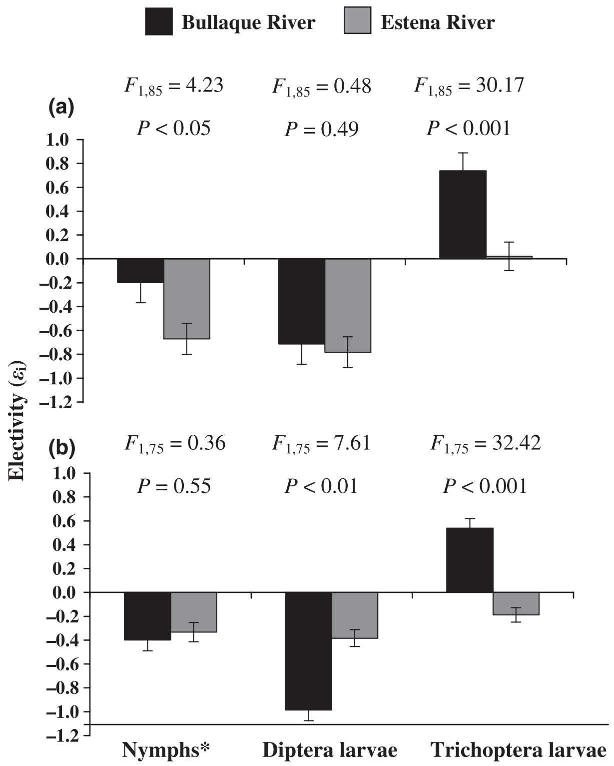

Fig. 6. Electivity index (ε_i) for the main benthic prey in Bullaque and Estena rivers. (a) Spring; (b) Summer. Results are means ± SE. *F* values and significance levels after ANOVA are indicated. *Ephemeroptera and Plecoptera.

Acknowledgements

This research was supported by the Spanish Ministry of Environment through a research project 104A/2002. D. Almeida held a postgraduate fellowship (FPI 2004–2008) from Complutense University of Madrid. We are grateful to I. Doadrio, National Museum of Natural Sciences of Madrid (CSIC), for helping us during the field work. Moreover, we would like to thank the comments of the associated editor and two anonymous reviewers that considerably improved the manuscript.

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