

Variability in feeding ecology of a South American cichlid: a reason for successful invasion in mediterranean-type rivers?

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Abstract – Ecological attributes behind the success of the South American cichlid *Australoheros facetus* in mediterranean-type rivers remain unclear. This study addresses this issue, by analysing its abundance and feeding patterns in the lower Guadiana drainage (Portugal), during the dry season of 2003. Despite slight spatial variations in abundance and individual size, *A. facetus* seemed well established in the Guadiana, Vascão and Ardila rivers. No seasonal or size-related changes in feeding intensity were found, but the diet changed across rivers, over time and throughout ontogeny. Feeding seemed highly generalist, with fish apparently reacting to both spatial and temporal changes in food supply and tending to use the most abundant and easily accessible food items. Overall prey breadth was broad relative to that of other native and non-native species. It is suggested that a generalist feeding strategy may play a significant role in the establishment of non-native fish in mediterranean-type rivers.

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Introduction

Non-native fish species have long been implicated in the decline and extinction of native freshwater biota, and are currently considered a major threat to conservation of freshwater diversity (Kolar & Lodge 2000; and references in Collares-Pereira et al. 2002). Nevertheless, the rate of fish introductions continues to increase worldwide (Welcomme 1992; Elvira & Almodóvar 2001), being often preceded by extensive habitat loss and degradation (Moyle & Marchetti 2006). In these circumstances, increased knowledge of biological attributes of successful non-native species is needed to improve our ability to predict their effects on natural biota as well as for developing management strategies, risk analyses and prevention and eradication measures (Moyle & Light 1996; Marchetti et al. 2004; Ribeiro et al., in press).

The chameleon fish *Australoheros* (= *Cichlasoma*) *facetus* (Jenyns 1842) is a South American cichlid, native to Paraguay, Uruguay, Argentina and Brazil (Řičan & Kullander 2006), that has been introduced

into the Iberian Peninsula since 1940 (Almaça 1995; Doadrio 2001). No exact reason is known for this introduction, although *A. facetus* is commonly used as an ornamental species (Lever 1996; Řičan & Kullander 2006). Presently, the species is established in several mediterranean-type (sensu Elron et al. 2006) drainages in both southern Portugal and Spain (Sado, Arade, Guadiana, Guadalquivir and possibly the Segura; Doadrio 2001; Collares-Pereira et al. 2000 and M.J. Collares-Pereira, J.A. Rodrigues, L. Rogado, & I.G. Cowx, unpublished data; C. Fernández-Delgado, personal communication), being particularly widespread and abundant in the lower Guadiana drainage (Collares-Pereira et al. 2000). Nevertheless, factors contributing to the invasiveness of *A. facetus* in mediterranean-type rivers remain unclear, and knowledge of its biological attributes is limited both outside and within the native range. Previous studies restricted to diet (Ruiz et al. 1992; Godinho & Portugal e Castro 1996; Yafe et al. 2002) and reproduction (Ruiz & Figueroa 2004), were developed in lacustrine environments and generally based on small sample sizes.

The invasive success of cichlid fishes has been attributed, at least in part, to their generalist diet (Arthington & Mitchell 1986; Galis 1998; Ruiz & Figueroa 2004; Bergmann & Motta 2005). This attribute may also be a key element in driving invasiveness in mediterranean-type rivers where food resources are strongly seasonal (Gasith & Resh 1999) and tend to greatly limit the foraging success of native fish (e.g., Magalhães 1993; Gomes-Ferreira et al. 2005). Mediterranean-type rivers are shaped by strongly seasonal flows, including both large winter floods and severe summer drying events (Gasith & Resh 1999). Drying is likely to be particularly significant to fish, as it results in major habitat contraction and loss of connectivity throughout the river network (see Magalhães et al. 2002). Fishes either die in areas that dry up or assemble at residual, permanent waters, where abiotic conditions tend to deteriorate as drying progresses (Gasith & Resh 1999). Moreover, as invertebrate communities shift from high to low abundance and diversity in the absence of flow (e.g., Pires et al. 2000), stranded fish can risk food starvation or at least raised competition for limited food resources. In these circumstances, diet generalists are likely to have a greater overall invasion success than diet specialists, although empirical evidence to corroborate this is still lacking.

The present study examined the extent of variability in the abundance and feeding patterns of *A. facetus* in the lower Guadiana drainage during the dry season, in an effort to better understand the mechanisms underlying its invasion success in mediterranean-type rivers. Specific objectives were to: (i) quantify the extent of spatial variability in population abundance, size structure and condition; (ii) identify the main food resource base potentially important to the species, and to quantify spatial, temporal and size-related changes in feeding activity, diet composition, diet breadth and diet overlap; and (iii) compare the diet breadth of *A. facetus* to other native and non-native species in the same drainage.

Methods

Study area

The Guadiana river drains about 66,960 km² and flows over 810 km, from the Ruidera lagoons (Spain) to the Atlantic Ocean in Vila Real de Santo António (Portugal). The study area was restricted to the lower Guadiana drainage (11,700 km²; Fig. 1). Drainage geology is complex with schist derivatives being the prevailing rocks; soils are highly impermeable and ground water is scarce. Climate is mediterranean, with a mean monthly temperature of 9.3 °C in the coldest month (January) and 24.5 °C in the hottest month (July). Mean annual rainfall is 598 mm, although

about 80% of the annual rainfall occurs during the wet semester (October–March) and virtually none in the hot dry summer (June–August). As a consequence of this climatic pattern and geological setting, flow regime is also highly seasonal, with zero flows prevailing in summer and large floods occurring in winter. However, this variation in flow tends to be strongly spatially structured, with smaller rivers being more temporally variable than larger ones.

The lower Guadiana drainage has a diverse and unique fish fauna comprising 11 primary species (Filipe et al. 2004), all but one are currently listed as threatened (Cabral et al. 2005). There are also 10 confirmed non-native species, seven of which have been introduced in the last 50 years (Filipe et al. 2004; Pérez-Bote et al. 2004). Presently, *A. facetus* may be found in the Guadiana mainstream and in twelve of its major tributaries (Caia, Degebe, Ardila, Marmelar, Odearce, Limas, Terges-Cobres, Oeiras, Carreiras, Chança, Vascão and Foupana; see Fig. 1).

Sampling sites

Sampling sites located in the Guadiana mainstream and in the Ardila and Vascão rivers (Fig. 1), and were selected to cover the range of flow variability in the drainage, and to support established populations of *A. facetus*. Specifically, higher discharges may be found in the Guadiana than in both the Ardila and Vascão rivers, with the latter generally presenting the lowest daily flow records (National Water Institute, <http://snirh.pt/>). Moreover, during the summer drought flow generally persist in both the Guadiana and Ardila rivers, whereas large sections of the Vascão river dry up completely or reduce to a series of isolated pools. Besides, sampling sites were similar in width (25–30 m), maximum depth (0.8–1.1 m) and annual water temperature range (8.1–34.8 °C) but concentration of chlorophyll *a* was much higher in the Ardila than in the remainder sites (9.7 ± 9.0 versus 0.8 ± 0.2 mg L⁻¹; Ribeiro F., unpublished data), reflecting the effects of increased agriculture run-off. Fish assemblages in the Vascão river are generally considered highly pristine, although species-rich assemblages may also be found in the Ardila and the Guadiana rivers (Collares-Pereira et al. 2000; Filipe et al. 2002, 2004). According to previous studies, *A. facetus* is widespread in the lower reaches of both the Ardila and Vascão rivers but less common in the Guadiana mainstream (M.J. Collares-Pereira, J.A. Rodrigues, L. Rogado & I.G. Cowx, unpublished data; Fig. 1).

Fish sampling

Fish sampling was conducted on a 3-week basis between April and September, 2003. At each site, a

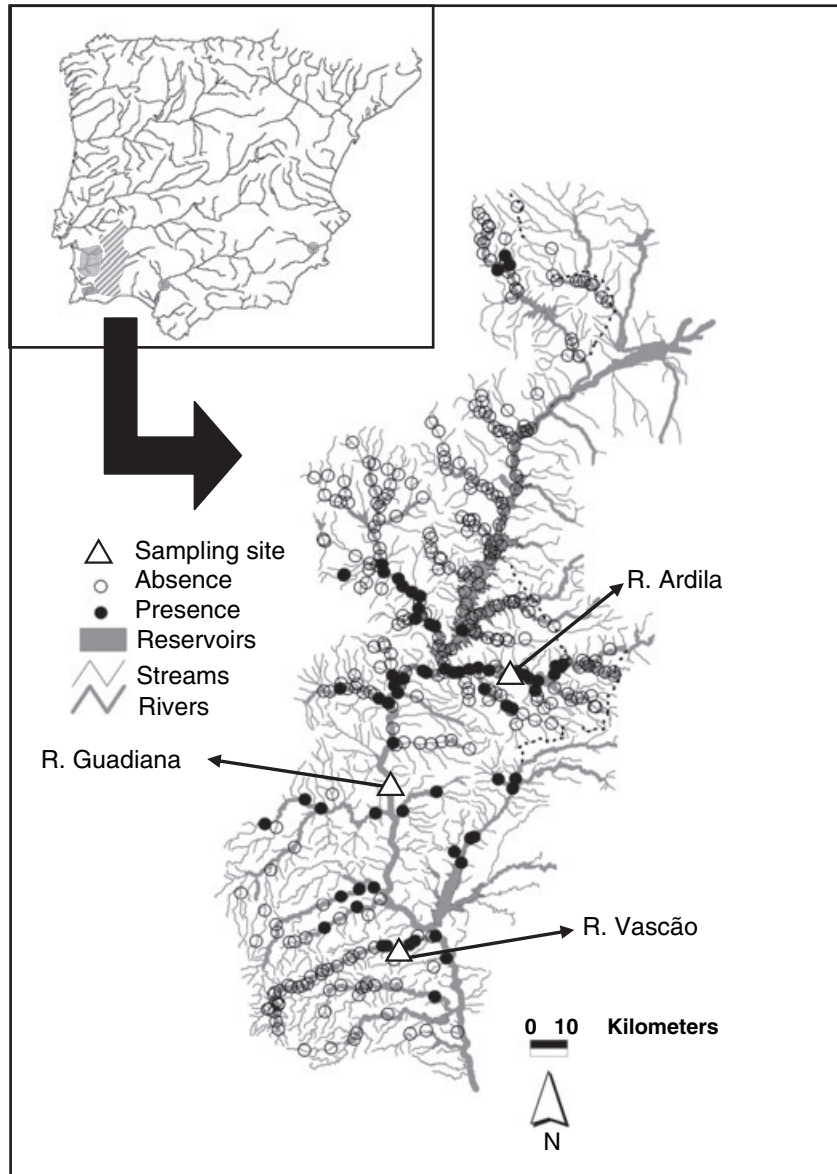


Fig. 1. Maps showing the distribution of *Australoheros facetus* in the Iberian Peninsula (grey area), and in the lower Guadiana drainage (diagonal bars) during 1998–2002 (M.J. Collares-Pereira, J.A. Rodrigues, L. Rogado, F. Ribeiro, A.F. Filipe, P. Tiago, L. Costa & I.G. Cowx unpublished data), and the location of sites sampled in the present study.

sample reach of 200 m was fished for 40 min, using a single anode electrofisher gear (300 V, 2–3 A, DC), always operated by the same person. Sample reaches were representative of the diversity of habitats, and their limits generally coincided with discontinuities in channel morphology or habitat change caused by water mills. Although capture-efficiency estimates are not available, previous experience in the Guadiana drainage indicated that this sampling effort is effective to capture most of the fish species, only missing a few rare species (Filipe et al. 2004). All the specimens collected were identified, counted and measured for standard length (SL, 1 mm) in the field, and returned back to the stream. Whenever possible, 30 individuals of *A. facetus*, representing the entire size range in each collection were retained for diet analysis, and immediately placed in ice before being deep-frozen at -20°C .

Diet analysis

In the laboratory, individuals of *A. facetus* were measured for standard length (SL, 1 mm), and weighted before and after removing their gonads and stomachs (TW and EW, to 0.01 g). Stomach fullness was assessed by visual inspection and categorised from 0 (empty) to 10 (full) as the presence of large amounts of mucous prevented an efficient volumetric estimation. Presence of plant material, isolated fish scales and inorganic material was recorded. Isolated scales, with no other fish remains, were considered without energetic value and to have been ingested accidentally or as a result of a territorial behaviour (see Ruiz et al. 1992). Animal prey remains were identified to the lowest readily recognisable taxon (usually family) and counted. Identifications followed Tachet

Table 1. Variation of the numeric abundance (A_N , %) and frequency of occurrence (F_O , %) of food items found in the stomachs of *Australoheros facetus* in the Guadiana, Ardila and Vascão rivers.

Food category		River						H	P	Dunn's test
		Guadiana (N = 93)		Ardila (N = 83)		Vascão (N = 112)				
		A_N (%)	F_O (%)	A_N (%)	F_O (%)	A_N (%)	F_O (%)			
Plant material			77.4		73.5		94.6			
Inorganic material			73.1		59.0		68.8			
Teleostei scales			40.9		30.1		36.6			
Insecta										
Ephemeroptera	Baetidae, Caenidae, Polymitarcyidae	10.2	60.2	2.3	38.6	30.0	84.9	84.9	***	V ^a G ^b A ^c
Odonata	Gomphidae, Aeshnidae	0.2	7.5	0.3	18.1	0.3	5.5	5.5	n.s.	
Heteroptera	Corixidae	44.9	82.8	11.5	59.0	2.8	95.2	95.2	***	G ^a A ^b V ^c
Diptera larvae	Chironomidae	22.7	87.1	71.7	97.6	30.0	99.3	99.3	***	A ^a V ^b G ^b
	Simuliidae, Limoniidae, Ceratopogonidae	0.3	12.9	0.3	19.3	2.6	12.6	12.4	**	V ^a G ^b A ^b
Diptera adults		0.1	3.2	0.8	22.9	0.4	23.1	23.1	***	A ^a V ^b G ^b
Coleoptera	Helmidae, Dytiscidae, Adephaga, Dryopidae, Curculionidae	0.8	15.1	0.4	16.9	1.2	0.5	0.5	n.s.	
Trichoptera	Hydroptilidae, Leptoceridae, Hydropsychidae	1.2	21.5	0.5	16.9	3.4	23.2	23.2	***	V ^a G ^b A ^b
Mollusca	Gastropoda (Planorbidae)	1.4	28.0	0.2	8.4	0.2	23.6	26.6	***	G ^a A ^b V ^b
Bivalvia		0.5	20.4	0.2	9.6	0.9	6.6	6.6	*	V ^a G ^{ab} A ^b
Chelicerata	Acari, Hydracarina, Oribatei	1.9	37.6	1.3	28.9	18.0	56.6	56.6	***	V ^a G ^b A ^b
Crustacea	Ostracoda	14.2	64.5	8.7	48.2	3.2	45.8	45.8	***	G ^a A ^b V ^c
Cladocera		0.1	5.4	0.2	8.4	1.1	2.1	2.1	n.s.	
Teleostei	Cyprinidae, Centrarchidae, Blenniidae	0.1	6.5	0.2	9.6	1.9	10.6	10.6	**	V ^a A ^{ab} G ^b
Other prey	Plecoptera (Perlodidae), Heteroptera (Pleidae, Micronecta, Naucoridae, Gerridae), Formicidae, Rotifera, unidentified prey items	1.3	32.3	1.5	33.7	3.9	0.1	0.1	n.s.	

Statistical differences among rivers were obtained by Kruskal–Wallis tests (H). Results of a *posteriori* Dunn's test are indicated by superscript letters; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

et al. (2000) for invertebrates and Prenda et al. (1997) for fish remains. For a further analysis, animal prey items were categorised into 15 items according to number, habitat and systematic criteria (Table 1).

Data analysis

Analyses focused on quantifying population attributes and feeding patterns of *A. facetus* in each sampling site, and in comparing its frequency of consumption of plant material and animal prey breadth to those of co-existing native and non-native species. Analyses were carried using EXCEL 2003 and STATISTICA 7.0.

Species abundance, size distribution and condition

Because sampling effort (i.e., sampling time, site length and procedures) was similar among sites and sampling dates, counts of individual fish species were directly used in the analyses. Overall abundance for each species (number of fish per 100 m²) at each site was calculated by averaging data across sampling dates. Total catches were used for deriving length distributions for *A. facetus*. Variation in body condition was analysed using linear regression models to relate the eviscerated weight (as log₁₀) of individual fish collected for diet analysis to its standard length (as log₁₀). Among-river variation in weight–length relationships was tested with ANCOVA (Zar 1999).

Feeding patterns of *A. facetus*

Temporal variation in feeding was assessed by categorising samples into months, considering the April and May samples together due to their small sizes. To identify size-related feeding shifts, fish were grouped into four arbitrary standard length classes: I ≤ 30 mm; II = 31–60 mm; III = 61–90 mm; IV ≥ 91 mm.

Relative importance of food categories was evaluated by calculating the percentage occurrence of all food categories (F_O , %) and the numeric abundance of each animal prey category (A_N , %). Empty guts were omitted in calculating frequency occurrence and numeric abundance was based on the total number of prey in each sample (Hyslop 1980).

Variation among sites, months and size-classes in the frequency of occurrence of plant material and in numeric prey abundance was assessed using chi-squared tests of independence and Kruskal–Wallis tests (Zar 1999), respectively. In the latter case, when significant differences were found, the Dunn's *post hoc* test was applied. The same procedure was used in assessing variation in stomach fullness. Because unbalanced designs and pooling of data and time and size factors may result in misleading patterns (Zar 1999), analyses of temporal variation in numeric prey abundance were carried separately for small (classes I and II) and large fish (classes III and IV), thus providing some insights into the extent of interaction between factors.

Animal prey breadth and overlap were calculated by the Shannon–Wiener (SW) and Schoener formulae, respectively (Krebs 1989). The SW measure ranges from 0 to ∞ , with increasing values generally indicating broader diets. SW estimates were improved using jackknife procedures following Magurran (2004), and the 95% confidence intervals of jackknifed estimates were further compared among sites, months and size-classes. The Schoener measure ranges between zero and one and values higher than 0.6 were generally regarded as high (Zaret & Rand 1971).

Comparison of feeding patterns among species

Data on the diet of native and non-native species co-existing with *A. facetus* in the lower Guadiana drainage were obtained from published and grey literature (Table 3). Gathered data included the frequency of occurrence of plant material and the numerical abundance of animal prey items consumed during the dry season (July to September). Animal prey breadth for each species was assessed using the SW formulae. Prior to the analysis, prey items were categorised according to number, habitat and systematic criteria as used for *A. facetus*, thus avoiding over-representation of minor prey items in the analysis and assuring direct comparability of results among species. Estimates obtained from the literature were then analysed in relation to the 95% confidence intervals of the jackknifed estimates for *A. facetus*. Comparisons were made within rivers, to account for spatial variation in food supply. Because variation in sample size may also result in misleading patterns, diet breadth of *A. facetus* was assessed from both the full sample and a random sub-sample of individuals, with the same size of that for the least numerous co-occurring species.

Results

Species abundance, size distribution and condition

There was considerable spatial variation in fish species composition and abundance (Fig. 2a), with *A. facetus* being more abundant in the Ardila (19.0 individuals per 100 m²) and Vascão (13.0 individuals per 100 m²) rivers than in the Guadiana mainstream (4.4 individuals per 100 m²). In the later, assemblages were dominated by the non-native *Lepomis gibbosus* (112.0 individuals per 100 m²) whereas native barbels were the most abundant in the Ardila (67.2 individuals per 100 m²) and Vascão (45.5 individuals per 100 m²). Moreover, *L. gibbosus* was also much more abundant in the Ardila than in the Vascão (24.0 vs. 0.1 individuals per 100 m²), where *A. facetus* was the most numerous non-native species. Spatial variation in length distributions was also evident for *A. facetus*,

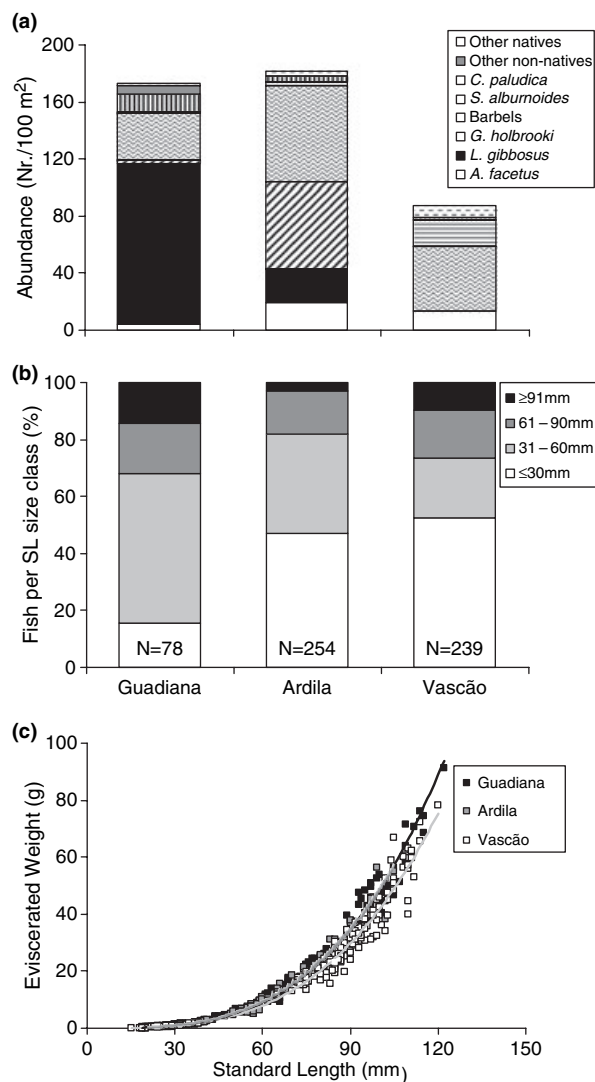


Fig. 2. Population attributes of *Australoheros facetus* in the Guadiana, Ardila and Vascão rivers; (a) variation in mean fish abundance (Nr. individuals per 100 m²) and local assemblage composition, (b) variation in length distribution and (c) variation in body condition (Guadiana river – black line; Ardila river – dark grey line; Vascão river – light grey line).

with fish smaller than 60 mm SL occurring in all rivers, but small specimens (SL ≤ 30 mm) being less numerous in the Guadiana and large specimens (SL ≥ 91 mm) being rare in the Ardila (Fig. 2b). Individual condition showed no significant variation among rivers (ANCOVA, $F = 2.83$; $P > 0.05$, d.f. 2, 484; Fig. 2c).

Feeding patterns of *A. facetus*

Overall diet

Altogether, stomachs of 288 *A. facetus* specimens (range 15–122 mm SL) were analysed yielding a total of 17,957 prey items. A broad spectrum of food

categories was identified although a smaller subset composed the main forage base (Table 1). Plant material occurred in 83% of the stomachs, while animal prey items were found in all of them. Chironomidae larvae were the most prevalent prey accounting for 44.4% of animal prey and being found in 86.1% of the fish. Corixidae were the second most abundant preys, making up 23.0% of prey numbers and being present in 52.8% of the stomachs. Ephemeroptera nymphs were also frequent (63.2%) but less important numerically (11.0%), whereas Cladocera, Odonata and Pisces were only rarely consumed. 'Other prey' included minor animal prey ($A_N < 0.2\%$) but also some unidentified prey items. The percentage of fishes with inorganic material and isolated fish scales in their stomachs was high ($F_O = 62.8\%$ and 33.7% , respectively).

Spatial feeding variability

Stomach fullness showed significant variation among rivers ($H = 21.3$, d.f. = 2, $P < 0.01$), being higher in the Vascão river (mean: 5.5 vs. 4.1–4.6). There was also considerable variation in diet composition between rivers (Table 1). Plant material was more frequently consumed in the Vascão and less commonly in the Ardila ($\chi^2 = 35.5$, $P < 0.001$, d.f. = 2). Eleven of the 15 prey categories displayed significant spatial variation in numerical abundance (Kruskal–Wallis, $P < 0.01$), reflecting considerable shifts in the main prey base. Corixidae, Chironomidae larvae, Ostracoda and Ephemeroptera nymphs were abundant in the diet in the Guadiana river, whereas distribution of prey categories was highly uneven in the Ardila river, where Chironomidae larvae were the staple food. In the Vascão river, fishes fed chiefly on Ephemeroptera nymphs, Chironomidae larvae and Hydracarina, but predation on Trichoptera, Diptera larvae and Pisces was higher compared with the remaining rivers (Table 1).

Overall, *A. facetus* tended to exhibit a generalist feeding strategy in the Guadiana and Vascão rivers, with most prey categories being eaten by more than half of the fish, although their average contribution to the stomach contents of these fishes was consistently low (Table 1). Conversely, a tendency for a specialisation towards the Chironomidae larvae was found in the Ardila, with all individuals tending to feed on this prey item. Indeed, animal prey breadth tended to be much narrower in the Ardila river fish than in both Guadiana and Vascão rivers (Table 2).

Temporal feeding variability

Stomach fullness showed little temporal variation, with significant fluctuations restricted to the Guadiana river ($H = 13.8$, d.f. = 4, $P < 0.01$) where fullness increased in September (mean: 5.7 vs. 3.9–4.6). By contrast, diet composition showed considerable temporal variation

Table 2. Variation of prey breadth (jackknife estimate and 95% confidence interval) and prey overlap (median and quartile range) along months and across size-classes of *Australoheros facetus* in the Guadiana, Ardila and Vascão rivers.

	Guadiana	Ardila	Vascão
Overall	1.91 (1.79–2.03)	1.15 (0.98–1.31)	1.89 (1.80–1.98)
Months			
April/May	1.62 (1.39–1.84)	1.35 (1.08–1.62)	1.75 (1.51–1.98)
June	1.83 (1.57–2.09)	0.51 (0.16–0.87)	1.76 (1.46–2.05)
July	1.36 (0.87–1.85)	1.13 (0.57–1.70)	1.69 (1.52–1.87)
August	1.75 (1.35–2.14)	1.14 (1.00–1.29)	1.90 (1.66–2.13)
September	1.68 (1.41–1.95)	0.74 (0.43–1.04)	1.91 (1.74–2.08)
Overlap	0.55 (0.48–0.62)	0.73 (0.68–0.78)	0.67 (0.60–0.74)
Size classes			
I ≤ 30 mm	1.66 (1.27–2.05)	0.98 (0.55–1.40)	1.75 (1.53–1.97)
II = 31–60 mm	1.73 (1.46–2.00)	0.90 (0.68–1.11)	1.84 (1.62–2.06)
III = 61–90 mm	1.78 (1.61–1.95)	1.29 (1.08–1.51)	1.73 (1.56–1.91)
IV ≥ 91 mm	2.08 (1.87–2.29)	1.63 (0.93–2.34)	1.95 (1.73–2.16)
Overlap	0.73 (0.69–0.78)	0.79 (0.73–0.85)	0.70 (0.61–0.79)

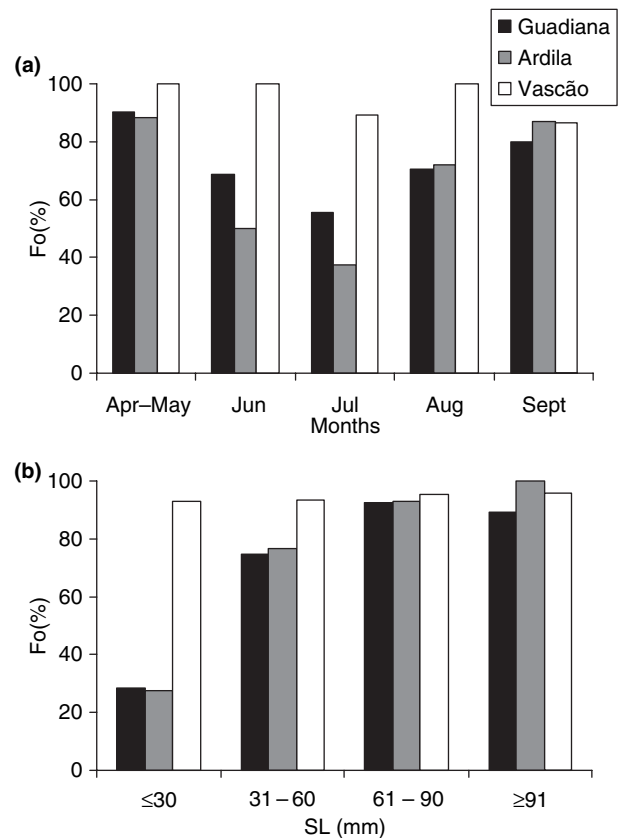


Fig. 3. Frequency of occurrence (F_O , %) of plant material in the diet of *Australoheros facetus* in the rivers Guadiana, Ardila and Vascão; (a) variation over months, (b) variation across length classes.

in all study rivers (Figs 3 and 4). Plant material consumption displayed significant variation in the Ardila ($\chi^2 = 13.9$, $P < 0.01$, d.f. = 4), being less frequent in the diet in June and July (Fig. 3). Significant variations in prey abundance were found in all

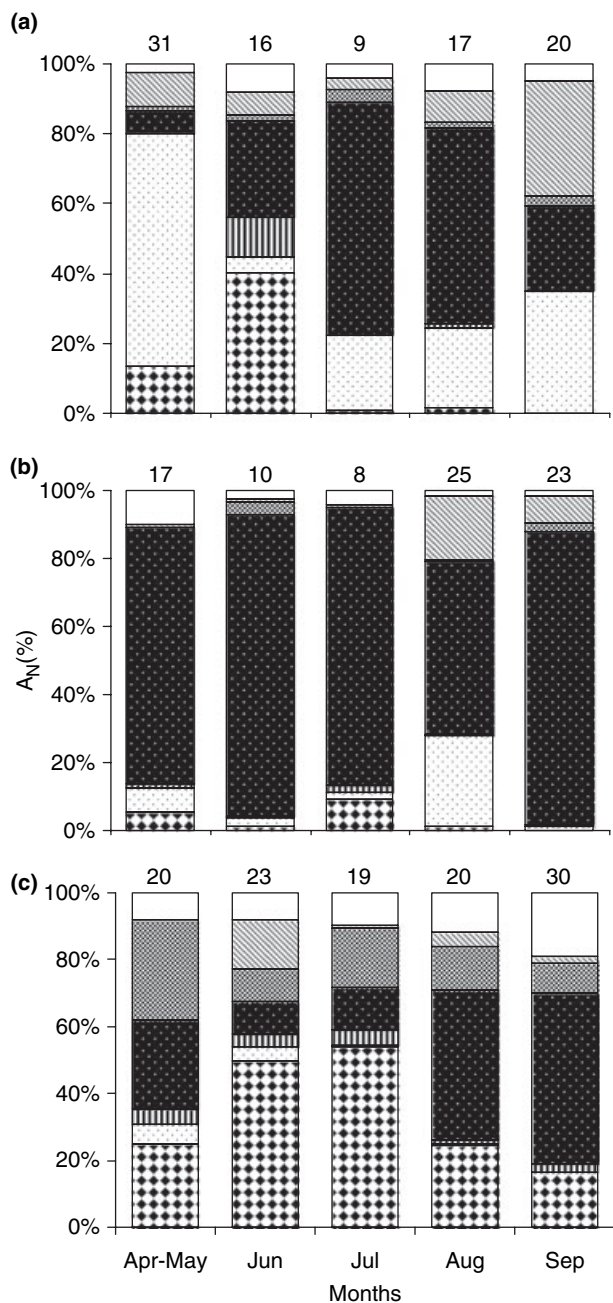


Fig. 4. Temporal variation of the numeric abundance (A_N , %) of animal prey items in the diet of *Australoheros facetus* in the rivers Guadiana (a), Ardila (b) and Vascão (c). The numbers above each column represent sample size (■, Ephemeroptera; □, Corixidae; ▨, Trichoptera; ■, Chironomidae; ●, Hydracarina; ▩, Ostracoda; □, Other prey).

study rivers (Kruskal–Wallis, $P < 0.01$), although they were more marked in the Guadiana and Vascão than in the Ardila (Fig. 4). In the former rivers, more Ephemeroptera nymphs were eaten in June and July whereas consumption of Chironomidae larvae and Ostracoda increased in July and August (Fig. 4). Conversely, in the Ardila, Chironomidae larvae remained the staple prey over all months, although a slightly increased

predation on Ostracoda and Corixidae was found in July. Similar results were obtained in analyses restricted to small or large fish, indicating that the perceived temporal patterns of prey consumption were little affected by time–size interactions.

Animal prey breadth showed little temporal variation in the Guadiana and Vascão rivers (Table 2). However, marked fluctuations were found in the Ardila, reflecting the increased consumption of Chironomidae larvae in June (89%), and September (86%). Animal prey overlap between months was higher in the Ardila, although values over 0.6 were also recorded in the Vascão. In the Guadiana, overlap values were generally lower than 0.6 (Table 2).

Size-related feeding variability

Stomach fullness tended to increase with fish size in both the Ardila ($H = 11.9$, d.f. = 3, $P < 0.01$) and the Vascão ($H = 11.2$, d.f. = 3, $P < 0.01$) rivers, with class IV (SL ≥ 91 mm) presenting particularly full stomachs (mean: 6.6 vs. 4.7–5.9). Considerable size-related variation in diet composition was found in all the study rivers (Figs 3 and 5). Consumption of plant material tended to increase with fish length in both the Guadiana ($\chi^2 = 29.6$, d.f. = 3, $P < 0.001$) and the Ardila rivers ($\chi^2 = 40.1$, d.f. = 3, $P < 0.001$), but was fairly common in the diet of all size-classes in the Vascão (Fig. 3). Significant size-related variations in prey abundance were found in all the study rivers (Kruskal–Wallis, $P < 0.01$), although they were more conspicuous in the Guadiana and Vascão than in the Ardila (Fig. 5). Generally, in the former rivers, smaller fish (SL ≤ 30 mm) tended to prey more Chironomidae larvae and Ostracoda, while large fish (SL ≥ 61 mm) evidenced an increase in the consumption of Corixidae and Ephemeroptera nymphs (Fig. 5). In the Ardila, Chironomidae remained the staple prey for all size-classes, although the abundance of Corixidae greatly increased in the diet of large fish. The item Pisces was only found in the diet of size-classes III and IV (SL ≥ 61 mm).

Animal prey breadth showed a marked increase with fish length in both the Guadiana and the Ardila rivers, evidencing that larger fish tend to eat a broader array of prey items than small-sized fish (Table 2). No similar trend was found in the Vascão river, where animal prey breadth was generally high in all size-classes. Animal prey overlap among size-classes was high in all the study rivers. Nevertheless, the highest and lowest overlap values were found in the Ardila and Vascão rivers, respectively (Table 2).

Comparison of feeding patterns among species

Australoheros facetus consumed plant material more frequently than any other species (Table 3). Indeed, plant material was virtually absent in the diet of

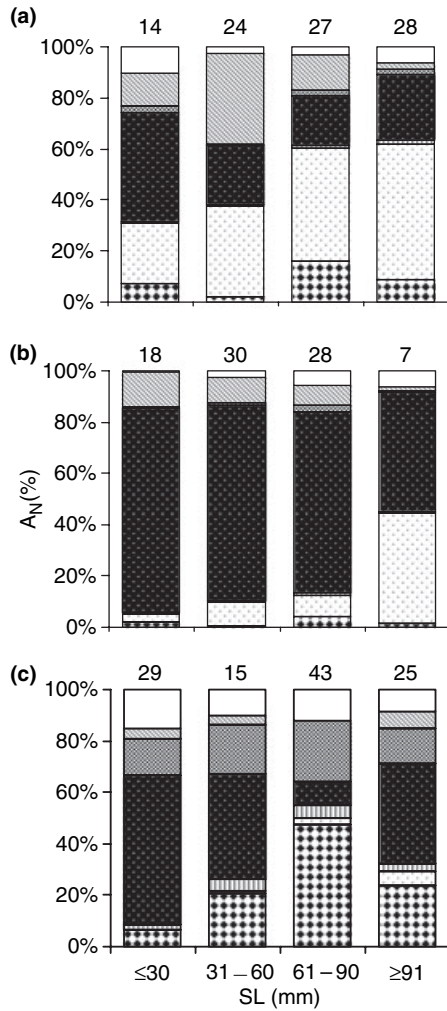


Fig 5. Size-related variation of the numeric abundance (A_N , %) of animal prey items in the diet of *Australoheros facetus* in the rivers Guadiana (a), Ardila (b) and Vascão (c). The numbers above each column represent sample size (▣, Ephemeroptera; □, Corixidae; ▤, Trichoptera; ■, Chironomidae; ▨, Hydracarina; ▩, Ostracoda; □, Other prey).

non-native *L. gibbosus* and *Micropterus salmoides*, and was much less common in the diet of all native species, and particularly of *Salaria fluviatilis*.

A considerable among-species variation in animal prey breadth was observed (Table 3). Animal prey breadth for *A. facetus* tended to be higher than those obtained for both non-native species across the all Guadiana drainage and native species in the Ardila river and its tributaries only. Similar, but less marked patterns, were obtained when the analysis restricted to a sub-sample of *A. facetus* ($SW = 0.71-1.12$). Animal prey breadth for native species in Ardila river was virtually constant.

Discussion

The results of this study indicate that *A. facetus* is established and tends to display a generalist and highly flexible feeding in the lower Guadiana drainage. The main forage base showed marked shifts among rivers and considerable, although less pronounced, temporal and size-related fluctuations in food resource use were also found. Perceived feeding patterns denoted an opportunistic ability to use locally abundant food resources, which seems to result in a broader diet breadth relative to both non-native and native, co-occurring species.

Conducting the study in the dry season only, despite the marked seasonality of mediterranean-type rivers may be considered a potential shortcoming. However, this will probably have no other effects in the results than minimising the perceived extent of variability in the abundance and feeding patterns of *A. facetus*, given fish generally display marked fluctuations in space and food resource use between the wet and the dry season (e.g., Magalhães 1993; Pires et al. 1999; Filipe et al. 2002; Gomes Ferreira et al. 2005). A potentially more serious problem concerns the data used to assess among-species variation in feeding patterns. These data were assembled from the literature, covered different years and rivers and are likely dependent on sampling conditions and author's skills. Consequently, the approach used herein must be considered as a first insight into this issue of interest,

Table 3. Variation in plant material consumption and animal prey breadth among native and non-native species co-occurring in the lower Guadiana drainage, during the dry season (July to September).

Species	Rivers	N	SW	F_0 (%)	Reference
Non-natives					
<i>A. facetus</i> (Jenyns 1842)	Guadiana, Ardila, Vascão	171	1.85 (1.70–2.01)	83.0	Present paper
<i>Lepomis gibbosus</i> (L. 1758)	Guadiana and tributaries	468	1.61	–	Godinho et al. (1997)
<i>Micropterus salmoides</i> (Lacépède 1802)	Guadiana and tributaries	115	1.63	–	Godinho et al. (1997)
<i>A. facetus</i> (Jenyns 1842)	Ardila	56	1.08 (0.90–1.32)	73.5	Present paper
Natives					
<i>Squalius alburnoides</i> (Steindachner 1866)		30	0.92	36.7	Gomes-Ferreira et al. 2005
<i>Barbus microcephalus</i> Almaça 1967		44	0.91	50.0	M.J. Collares-Pereira, C.L. Mieiro,
<i>Barbus steindachneri</i> Almaça 1967	Ardila and tributaries	63	0.95	23.8	P. Tiago, F. Ribeiro & S. Botelho
<i>Salaria fluviatilis</i> (Asso 1801)		81	0.93	4.9	unpublished data

Values are the frequency of occurrence of plant material (F_0 %) and the Shannon–Wiener (SW) estimates of animal prey breadth. For *Australoheros facetus* 95% confidence intervals of jackknifed estimates are presented (in parenthesis). N = sample size.

although considerable improvements were introduced in the analytical design to support the current findings.

Although *A. facetus* seemed to be well established in the lower Guadiana drainage, there seemed to be considerable heterogeneity in its local success. Indeed, *A. facetus* tended to be less abundant in the Guadiana than in both the Vascão and Ardila rivers, where juveniles were more prevalent. Variation in habitat use and spatial size-related segregation in stream fish usually reflect changes in stream size, flow regime, and local habitats, but also in competition and predation risks (e.g., Matthews 1998). This is probably also the case in here, given for instance, competition risks may be enhanced in the Guadiana river, due to the high abundance of *L. gibbosus*, a species highly similar to *A. facetus* in both body morphology and habitat use (see Doadrio 2001). However, individuals were generally in good condition, suggesting that other local factors may favour species establishment. Detailed data on environmental and biotic influences on species distribution and abundance are thus needed to sort out their specific roles in driving invasiveness.

Despite the diet of *A. facetus* displayed considerable variability, the main forage base used in the lower Guadiana drainage was much similar to that used in lacustrine systems, both within (Yafe et al. 2002) and outside the species native range (Ruiz et al. 1992; Godinho & Portugal e Castro 1996). This result is in line with previous evidence for similarity in the diet of other cichlid fish living in native and invaded areas, pointing to the use of the same general suite of food items over broad geographic ranges (Bergmann & Motta 2005).

The marked dietary shifts found among rivers probably reflect the use of locally abundant food resources. A particularly striking feature was the apparent specialisation in Chironomidae larvae in the Ardila river and the use of broad prey bases in both the Vascão and Guadiana rivers. The Ardila river tends to be heavily loaded with agriculture nutrients, that are likely to considerably reduce water quality, and may thus promote decreased macro-invertebrate diversity and favour tolerant taxa, such as Chironomidae larvae (Pires et al. 2000). Conversely, the Vascão river drains a largely pristine valley, with little land use and human occupation, where invertebrates requiring high-quality waters, such as Ephemeroptera nymphs and Trichoptera larvae, are likely found (Pires et al. 2000; Tachet et al. 2000). Likewise, the Guadiana river is expected to encompass more heterogeneous habitats and increased macro-invertebrate diversity relative to its tributaries (Cortes et al. 1998), with, for example, predation on Corixidae and Trichoptera suggesting the use of both still, shallow and flowing habitats, respectively (Thorp & Covich 1991).

Feeding seemed nearly continuous throughout the dry season, with perceived within river variations apparently reflecting fluctuations in the availability and diversity of local food supply. Specifically, prevalence of Ephemeroptera nymphs in the diet in late Spring probably concurred with abundance peaks (Pires et al. 2000), whereas prominence of Ostracoda towards the end of the dry season, seemed to reflect increased confinement to shallower habitats due to water receding (Thorp & Covich 1991). Nevertheless, prey breadths were largely stable and overlaps remained generally high throughout the season. The only exception to this pattern was found in the Guadiana mainstream, probably reflecting the higher diversity in local food supply (Cortes et al. 1998).

Ontogenetic variation in feeding was characterised by both an increase in the consumption of plant material and an increase of prey spectrum, which was associated with a shifting tendency from small, soft-bodied to large, hard-shelled, preys. Three primary factors are probably involved in producing this feeding pattern. First, diet may be shaped by morphologically based limitations, with gape size, pharyngeal jaw strength, and gut length, probably constraining the use of large Ephemeroptera nymphs, hard-shelled Corixidae and plant material by small fish, respectively (see Werner 1974; Junger et al. 1989; Bergmann & Motta 2005). Second, feeding changes may reflect a dynamic trade-off between the expense of prey capture and the energy benefit of prey intake, with individuals facing increasing energetic demands, and thereby shifting to larger, more profitable preys such as fish as they grow (Persson 1991). Third, transition from narrow to broader diets may coincide with size-related changes in habitat preferences, as previously recorded for native species in mediterranean-type rivers (e.g., Magalhães 1993; Gomes-Ferreira et al. 2005). Nevertheless, in spite of diet and prey breadth variations, all size-classes exploited essentially the same prey base, showing consistently high overlaps.

Overall, *A. facetus* displayed a largely generalist feeding relative to co-occurring species. Although the significance of diet breadth as a correlate of invasion success has mixed support (see Rehage et al. 2005), generalist diets are generally considered advantageous in favouring the establishment of non-native species (Ehrlich 1989; Grabowska & Grabowski 2005), and in determining its spread and abundance in invaded watersheds (Marchetti et al. 2004). This appears also to be the case herein, as prey breadths of *A. facetus* and the well-established *L. gibbosus* and *M. salmoides* seemed to be broader than those of co-occurring native species, and non-native species with specialised diets, such as *Esox lucius* L. 1758, tend to remain both sparse and rare in the Guadiana drainage (Pires et al. 1999). Moreover, consumption of plant material by

A. facetus may also play greatly contribute to the outcome of invasive processes, given shifts to this alternative, less profitable but abundant, and easily accessible food may be an efficient buffer strategy if and when prey become scarce (Persson 1991; Magalhães 1993).

Despite some similarity in forage bases between *A. facetus* and native species may be perceived no evidence of dietary competition should be drawn from the current study. Likewise, present information is insufficient to evaluate predation risks for native species, although fish were seldom found in the diet. Indeed, further analyses on the patterns of habitat and food resource availability, use and partitioning are needed to clarify how the *A. facetus* interacts with both non-native (e.g., *L. gibbosus*) and highly endangered native species, and may thus impact local fish assemblage structure.

Taken together, results from the present study suggest that the generalist feeding displayed by *A. facetus* may play a key role in driving its establishment in mediterranean-type rivers. However, other ecological attributes besides generalist feeding may also contribute to the invasive success of *A. facetus*. For instance, this species is recognised to have a high physiological tolerance (e.g., Lever 1996) and to display parental care behaviour (Ruiz et al. 1992), attributes that may have strong invasive advantages (Moyle & Marchetti 2006; Ribeiro et al., in press). Searching for the specific relevance of different ecological attributes on the distribution, abundance and invasive ability of *A. facetus* are thus worthy subjects to advance our knowledge on processes driving non-native fish success in mediterranean-type rivers.

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