

# Growth and diet of European catfish (*Silurus glanis*) in early and late invasion stages

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With 6 figures and 4 tables

**Abstract:** The ecological impact of many invasive species is usually unknown because of the absence of data before their introduction. We exemplify the usefulness of comparing early and late invasion stages to understand the ecological changes caused by invasive species, particularly concerning large species and large ecosystems, such as reservoirs, where experimental work is not easily carried out. We also report the first data on growth and diet for the European catfish (*Silurus glanis*) in the Iberian Peninsula and compare three populations in the Ebro River system, corresponding to the earliest introductions (> 30 years ago) with two recently introduced populations in reservoirs of the Ter River basin. The total length and age of the catfish varied significantly among populations and recent introductions consisted of smaller and younger catfish with significantly higher condition and size-specific growth rates compared to older (as well as native) populations. For example, 7+ old catfish were around 100 cm in the older populations and 150 cm in the more recent ones. Diet also depended on site and catfish size. Catfish measuring less than 30 cm consumed mostly invertebrates, thereafter shifting to red swamp crayfish *Procambarus clarkii* (old introductions) or fish (recent introductions). A number of fish species were present in stomachs but common carp (*Cyprinus carpio*) and birds were only present in very large fish (> 120 cm). The median length of common carp was significantly larger in reservoirs with late-stage catfish invasion. The abundance of waterbirds, particularly anatids, was significantly lower in reservoirs where catfish were present, suggesting a direct ecological impact, or else avoidance learning by the birds. Our results suggest that in the early stages of invasion, catfish display higher condition and growth rates by profiting from relatively unexploited resources (large fish and, secondarily, waterbirds), shifting to other prey (and thus reducing mean growth) in the late invasion stages.

**Key words:** ecological impact, introduced fish, invasive species, Iberian Peninsula, freshwater fish.

## Introduction

After habitat degradation, invasive species are the second leading cause of biodiversity loss, particularly in freshwater ecosystems (Moyle et al. 1986, Mack et al. 2000, Clavero & García-Berthou 2005). Non-native invasive species have caused enormous disruption to native ecosystems around the world. They generally affect native species by altering habitats, introducing diseases or parasites, hybridisation, predation or competition (Taylor et al. 1984, Williamson 1996). However, the effects of the vast majority of introduc-

tions have not been studied and their impact on the native biota are not known (Parker et al. 1999, García-Berthou 2007). Three main types of studies are used to reveal information about this ecological impact: laboratory experiments, field experiments and natural experiments (Diamond 1986). Laboratory and field experiments that manipulate the presence or density of invasive species can be informative of short-term, small-scale effects and are usually more conclusive and less prone to confounding effects than observational studies. However, such experiments are very difficult with large species and large ecosystems such as lakes

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or large rivers and are also problematic with regard to scaling up and generalisation (Diamond 1986, Lodge et al. 1998). Large fish such as Asian carps (*Ctenopharyngodon idella*, *Hypophthalmichthys molitrix*, *Aristichthys nobilis*) or the largemouth bass (*Microp-terus salmoides*) are among the ten most frequently introduced aquatic species in the world (García-Berthou et al. 2005) and many other large predatory fish are commonly introduced worldwide. The main approach to assess the impact of these large invaders is to view the introductions as “natural experiments” and to apply the best possible study design to them. An ideal study would be to follow an introduction in the recipient ecosystem and compare the temporal dynamics with nearby control sites. Unfortunately, baseline data from before the invasion are often unavailable (Parker et al. 1999) and such an ideal study design would also require long-term data, particularly since invasive species often display lag phases in their dynamics and their effects may take a long time to manifest (Mack et al. 2000). Alternatively, one could compare sites with recent and older introductions, within a limited region. This kind of study has the advantage of realism and the large temporal and spatial scales of “natural experiments” and does not require pre-invasion data.

The European catfish (*Silurus glanis*), also known as wels or sheatfish, is the largest European freshwater fish, being native to eastern Europe and western Asia and most abundant in the Danube and Volga river basins. *S. glanis* is now popular among European anglers and has been introduced into many European river basins, including some in Italy, the UK and the Iberian Peninsula (Elvira 2001, Elvira & Almodóvar 2001). The biology and ecology of these naturalised populations of European catfish in Western Europe is, however, poorly understood, probably because of the difficulty of sampling such a large species in large rivers and lentic ecosystems (Carol et al. 2007). Their ecological impact on native biota is therefore largely unknown (Copp et al. 2009), although the introduction of some parasites has been noted (Blanc 1997) and hy-

brids with *S. aristotelis*, endemic to Greece, have been observed (Paschos et al. 2004). The European catfish was first introduced to the Iberian Peninsula via the River Segre (Ebro River basin) around 1974, allegedly by a German biologist who illegally introduced 32 young specimens (Cabistañ 2003). Soon afterwards, catfish were also introduced for sport fishing into the lower Ebro River in the Mequinensa and Riba-roja reservoirs, where it is now abundant (Elvira 2001, Elvira & Almodóvar 2001). More recently, it has been recorded in a reservoir in the Tagus River basin (2002), in the Susqueda reservoir in the Ter River basin (Carol et al. 2003) and further upstream in the Sau reservoir, and also in La Baells reservoir in the Llobregat River basin (Benejam et al. 2007).

The main objectives of our paper are: (i) to report the first data on age, growth and diet of European catfish in the Iberian Peninsula, and (ii) to compare early and late stages of invasion by catfish in order to appraise their ecological impact on native biota. We compared growth and diet of European catfish at sites where they have been present for around 34 years (Ebro River basin), with sites where the species was introduced only a few years ago (Ter River basin) to examine early and late invasion stages and hence infer some of the impact of this large predatory fish on the recipient ecosystem. We hypothesised that in early invasion stages catfish would have higher growth rates because they benefited from underexploited resources (i.e., large fish), whereas in more advanced invasion stages, the growth rate should decrease after trophic restructuring of the invaded ecosystems.

## Methods

### Study area and sampling methods

We studied five catfish populations in the rivers Ebro and Ter in Catalonia, NE Spain (Table 1). In the Ebro River, catfish were caught in two neighbouring reservoirs (Flix and Riba-roja), about 70 km upstream from the river mouth, and in irrigation channels downstream. Flix is a small reservoir (300–400 m wide; maximum depth 9.5 m) which preserves most of its river

**Table 1.** Main features of the five European catfish sites and populations studied.

Population	Site code	River basin	Surface (ha)	Capacity (hm <sup>3</sup> )	Latitude	Longitude	Mean TL (mm)	TL range (mm)	<i>n</i>	Age range (years)
Flix reservoir	FLI	Ebro	320	11	41° 13' 60"	0° 32' 49"	1015	138–1990	55	0–17
Riba-roja reservoir	RIB	Ebro	2151	210	41° 14' 50"	0° 25' 34"	791	229–2100	22	0–17
Sau reservoir	SAU	Ter	570	169	41° 58' 05"	2° 24' 46"	781	338–1350	97	1–7
Susqueda reservoir	SUS	Ter	466	233	41° 58' 44"	2° 31' 36"	572	74–1040	15	0–4
Ebro channels	EBR	Ebro	–	–	40° 48' 13"	0° 30' 49"	501	171–1300	140	0–5

properties because of its very short residence time (0.15 days). The littoral area of the Flix reservoir presents a poor diversity of substrata and has some shallow slopes with reed beds (*Phragmites australis*). Riba-roja is a big reservoir (300–500 m wide; typical maximum depth 25 m) with more lentic properties, located immediately upstream from the Flix reservoir. The littoral area presents a diversity of substrata (rocks, stones and sand) and steep shore slopes, with vegetation only in specific zones. Catfish were also caught from four sites in large irrigation channels (Tortosa, Jesús, Tivenys and Deltebre), which divert water from the Ebro River (via the Xerta dam, about 50 km upstream from the river mouth) to rice crops in the Ebro Delta. The channels are drained each year, so the catfish caught there came from the river and had spent less than one year in the channels. In the River Ter basin, catfish were caught in the Sau and Susqueda reservoirs, approx. 60 km upstream from the river mouth. Both Sau and Susqueda are big reservoirs with widths ranging from 500–700 m and maximum depths of 35 m and > 100 m, respectively. The littoral areas present a diversity of substrata (rocks, stones and sand) and steep shore slopes, without vegetation.

In general, the fish assemblages of all four reservoirs were dominated, in terms of abundance, by introduced cyprinids (bleak *Alburnus alburnus*, roach *Rutilus rutilus*, rudd *Scardinius erythrophthalmus*, and common carp *Cyprinus carpio*) and two centrarchids (largemouth bass *Micropterus salmoides* and pumpkinseed *Lepomis gibbosus*) (see Carol et al. (2006) for further details on the limnology and fish assemblage of the four reservoirs). The irrigation channels were also dominated by the same introduced cyprinids, although centrarchids and percids were less abundant. A total of 329 catfish specimens were collected from March 2003 to June 2006 and frozen immediately. Most of them (220) were captured by electrofishing, by boat or wading in shallow sites, although 97 fish were caught with purse seines in the limnetic zone of the Sau reservoir during October and November 2005 (Benejam et al. 2008), 11 by angling and one with multimesh gillnets.

## Laboratory methods

The fish were measured and dissected in the laboratory. Total length was measured to the nearest millimetre and total, eviscerated and gonad weights to the nearest gram. Stomach contents

were preserved in 70 % ethanol until analysis and the first ray of the pectoral fin was removed for age estimation (Harka & Bíró 1990, Horoszewicz & Backiel 2003). A total of 324 specimens were used for the diet study. Prey organisms were sorted usually to the species or genus level, counted and weighed to the nearest milligram. For fish prey items in advanced stage of digestion, pharyngeal bones (cyprinids) and scales were used for identification. For cyprinid preys, the original lengths and weights were estimated using measurements of the pharyngeal bones and the regression conversions of Miranda & Escala (2002).

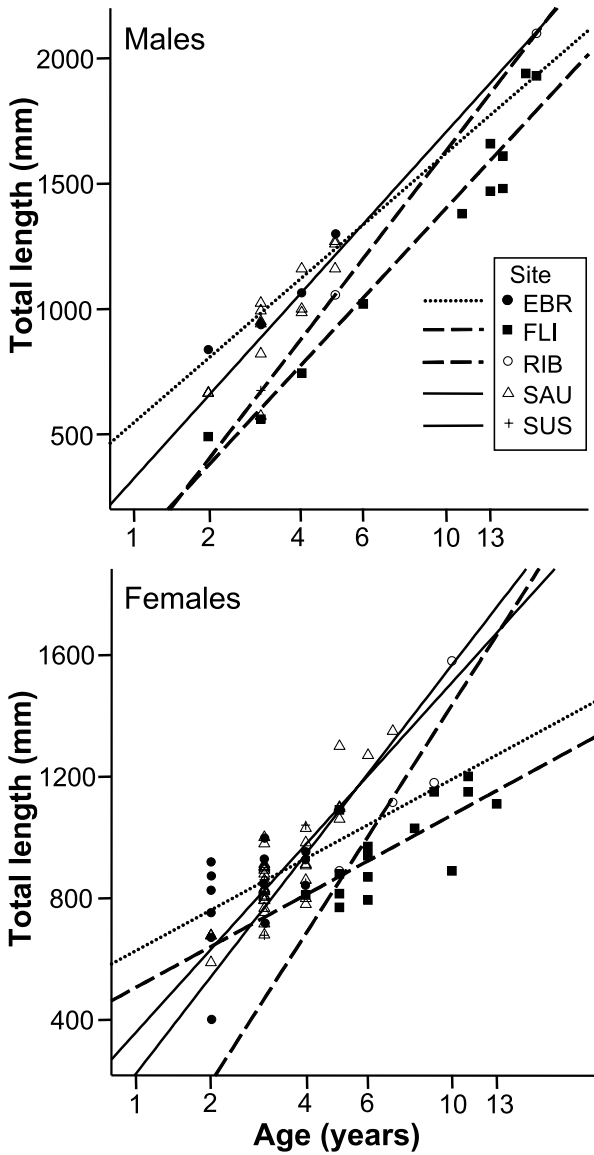
We estimated the age of 307 individuals of catfish and attempted to fit the growth data to the von Bertalanffy function (Ricker 1975):

$$L_t = L_\infty (1 - e^{-k(t-t_0)}),$$

where  $L_t$  is the length at age  $t$  (in years), and  $L_\infty$ ,  $k$  and  $t_0$  are the three parameters to be estimated. The aim of fitting this model was to assess its suitability for these data and enable us to compare it with previous literature; the suitability was judged by the adjusted coefficient of determination ( $R^2$ ) and the estimated  $L_\infty$ , which should be slightly above (ca. 105 %) the maximum observed length.

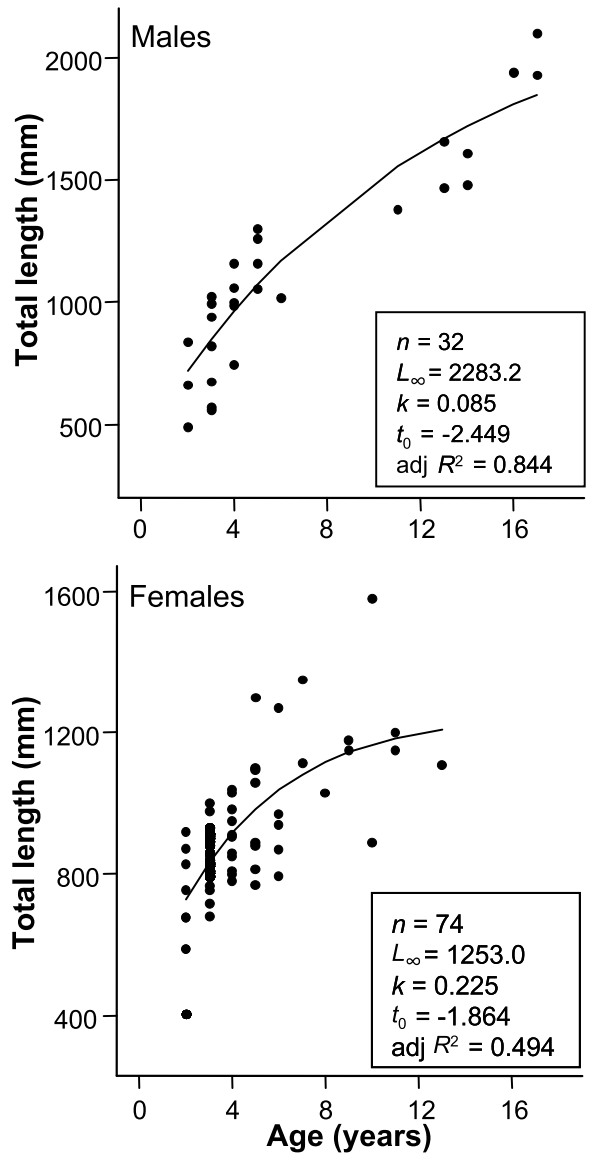
As with previous studies (Omarov & Popova 1984, Czarnecki et al. 2003), we observed some waterbirds in the diet of catfish. Therefore, to test for an effect of catfish invasion on waterbird population sizes, we compiled the data available (years 1999, 2001, 2002, 2003 and 2005) from the International Waterbird Census (<http://www.wetlands.org/>) for 22 Catalan reservoirs, considering only artificial reservoirs (like the four we studied) and excluding one natural lake and irrigation ponds. The International Waterbird Census consists of population size estimates derived from censuses made towards the end of the non-breeding season (January in Catalonia), when waterbird populations tend to be at their lowest and most stable (Delany & Scott 2006). We compared population size estimates of waterbirds (families Anatidae, Rallidae, and Podicipedidae) in three groups of Catalan reservoirs: those without catfish ( $n = 18$ ), those with early catfish invasion (Sau and Susqueda reservoirs), and those with late catfish invasion (Flix and Riba-roja reservoirs). For these reservoirs, we also considered, as potential confounding factors affecting waterbird population sizes, reservoir surface area, water capacity and altitude (obtained from the Catalan Water Agency, [\*\*Table 2.\*\* ANCOVAs of the life-history traits for males and females with total length as covariate. All quantitative variables were  \$\log\_{10}\$ -transformed. A measure of effect size \(partial  \$\eta^2\$ \) is also shown. Site  \$\times\$  month could not be computed in some cases because there were too many missing combinations. Significance levels: \\*  \$P \leq 0.05\$ ; \\*\\*  \$P \leq 0.01\$ ; \\*\\*\\*  \$P \leq 0.001\$ ;  \$a\$ :  \$P = 0.052\$ .](http://aca-</a></p>
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	Total weight			Eviscerated weight			Gonadal weight		
	d.f.	$F$	Partial $\eta^2$	d.f.	$F$	Partial $\eta^2$	d.f.	$F$	Partial $\eta^2$
<b>MALES</b>									
Length	1	1084.0***	0.97	1	869.97***	0.97	1	139.59***	0.84
Site	3	0.97	0.09	2	0.39	0.03	3	8.06***	0.48
Month	7	0.80	0.16	6	1.35	0.23	8	2.75*	0.46
Site $\times$ month	1	0.66	0.02						
Error	29			27			26		
<b>FEMALES</b>									
Length	1	1815.0***	0.97	1	1562.0***	0.96	1	80.26***	0.55
Site	3	5.02**	0.19	3	3.95*	0.15	3	0.18	0.01
Month	8	2.07 <sup>a</sup>	0.20	8	2.25*	0.22	8	2.53*	0.24
Error	65			65			66		



**Fig. 1.** Growth in five populations of European catfish (*Silurus glanis*) for males (top) and females (bottom). The linear regression functions are also shown for each population (continuous lines for recent introductions, discontinuous lines for old introductions; see Table 1 for site codes). Note the logarithmic scale for age to improve linearity and that only one male was caught in Susqueda (so no line is given).

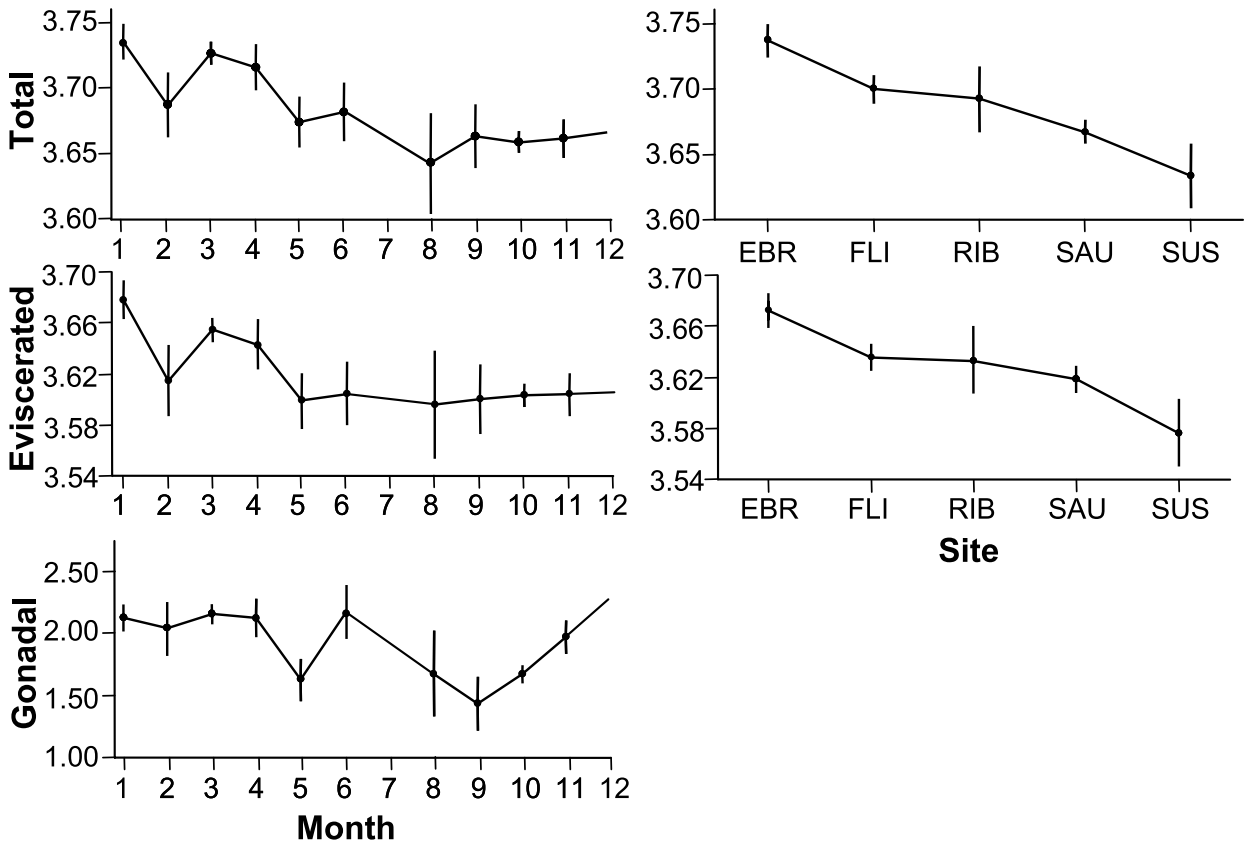
[web.gencat.cat/aca/](http://web.gencat.cat/aca/)), and chlorophyll-*a* concentration, conductivity, and Secchi depth from our previous survey in 2003 of 17 of these reservoirs (Carol et al. 2006). Similarly, we also analysed the length-frequency distribution of the common carp (*Cyprinus carpio*) sampled in 14 of these reservoirs during this survey (Carol et al. 2006), to compare prey size-structure at different stages of catfish invasion; common carp was the only fish preyed upon by catfish that was captured in all 14 reservoirs and was among the most abundant fish in these reservoirs.



**Fig. 2.** Relationship between total length and age for male and female European catfish in the five Iberian populations studied. The estimated von Bertalanffy growth function (see formula in the text) is also shown.

### Data analyses

Percent number (% number), percent biomass (% biomass), frequency of occurrence and mean percentage of biomass were used to estimate the dietary importance of the different food categories (see e.g., García-Berthou 2001, 2002). % number is the number of individuals of a prey type divided by the total number of individuals and expressed as a percentage, after pooling the gut contents of all fish. % biomass is the equivalent measure for biomass data. Frequency of occurrence is the per-



**Fig. 3.** ANCOVA-adjusted means of weights (total, eviscerated and gonadal,  $\log_{10}$ -transformed) of female catfish by site and month with total length ( $\log_{10}$ -transformed) as covariate. Bars are  $\pm 1$  SE.

centage of stomachs where a food category was present. Mean percentage of biomass was computed for pooled food categories as the percentage of stomach content for a certain food category averaged for all the fish in a size class.

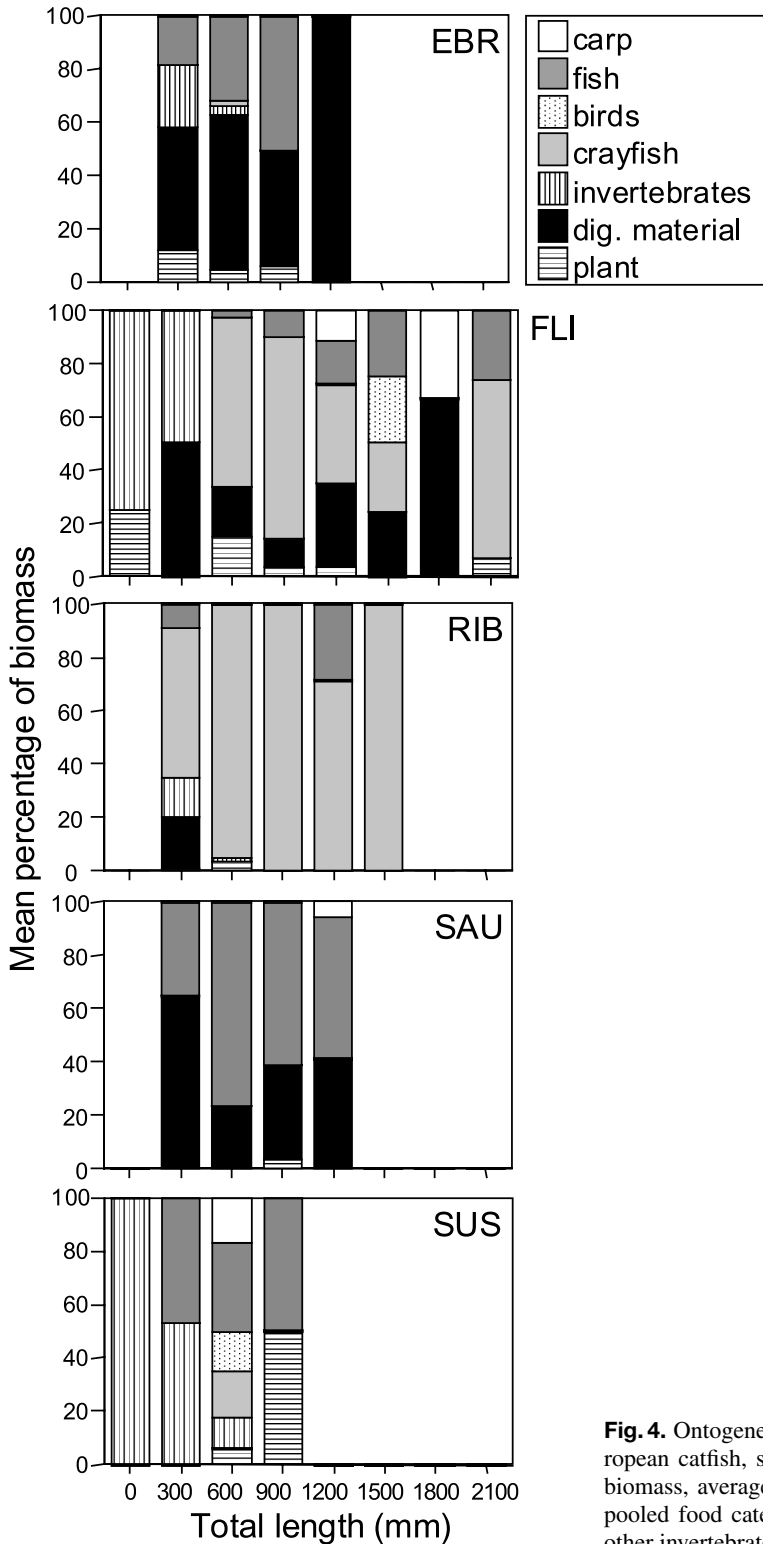
To compare growth among the different European catfish populations, the length-age relationship was compared with analysis of covariance (ANCOVA), after  $\log$ -transformation of age to linearise the relationship. ANCOVA was also used to compare variables (e.g. fish weight) among sex groups and sites, using fish length as the covariate. We first tested the assumption of homogeneity of slopes, with the covariate  $\times$  factor interaction; when this interaction was not significant ( $P > 0.10$ ; higher than the conventional 5% because this test is conservative and in order not to violate the assumption), it was removed from the model to increase statistical power, so the standard ANCOVA design was used (García-Berthou & Moreno-Amich 1993). The abundance of waterbirds was analysed with repeated measures analysis of variance (ANOVA) and regression analysis. Sex ratios were analysed with exact tests equivalent to  $\chi^2$  tests. Quantitative variables were  $\log$ -transformed for the analyses because homoscedasticity and linearity clearly improved. All factors were considered as of fixed effects. We used partial  $\eta^2$  (partial eta squared) as a measure of effect size (i.e. importance of factors). Similarly to  $r^2$ , partial  $\eta^2$  is the proportion of variation explained for a certain effect (effect SS / (effect SS + error SS)). Partial  $\eta^2$  has an advantage over  $\eta^2$  (effect SS/total SS) in that it does not depend on the number of sources variation in the

ANOVA design used, because it does not use the total sum-of-squares (SS) as the denominator (Tabachnick & Fidell 2001). All statistical analyses were performed using SPSS 15.

## Results

### Population structure and growth of catfish

The total length (TL) and age of European catfish varied significantly among the populations (two-way ANOVAs:  $F_{4, 328} = 34.7$ ,  $P < 0.001$  and  $F_{4, 306} = 60.4$ ,  $P < 0.001$ , respectively). The catfish were larger and much older in the Flix and Riba-roja reservoirs than in the Sau and Susqueda reservoirs (Table 1), confirming that the two latter populations are recent introductions (note particularly the maximum observed ages of 17 versus 7 years, respectively). The mean TL in the Ebro channels was also smaller than in the Ebro reservoirs (Table 1). This difference was due to a higher proportion of immature fish in the channels (86%) compared to the proportion in Flix (16%) and in the other populations (nearly 60%) ( $\chi^2_4 = 86.3$ , exact  $P < 0.0005$ ).



**Fig. 4.** Ontogenetic variation in diet of the five populations of European catfish, showing the mean percentage of stomach content biomass, averaged for 300 mm-length classes of catfish for seven pooled food categories (common carp, other fish, birds, crayfish, other invertebrates, digested material, and plant material).

TL depended significantly on sex (two-way ANOVA  $F_{2, 323} = 176.4, P < 0.001$ ): males (mean = 1114 mm, range 490–2100) were larger than females (mean = 911 mm, range 403–1580). Taking mature fish alone,

females were more abundant than males (80 versus 45; binomial test, exact  $P = 0.002$ ) and the sex-ratio appeared to vary among populations ( $\chi^2_4 = 7.85$ , exact  $P = 0.093$ ).

**Table 3.** Diet of European catfish: % number (N), % biomass (B), and frequency of occurrence (O) of the main food items in the five populations. See Table 1 for site code. Number of stomachs analysed = 324; total number of prey in the stomach contents = 925; total biomass = 10681.8 g.

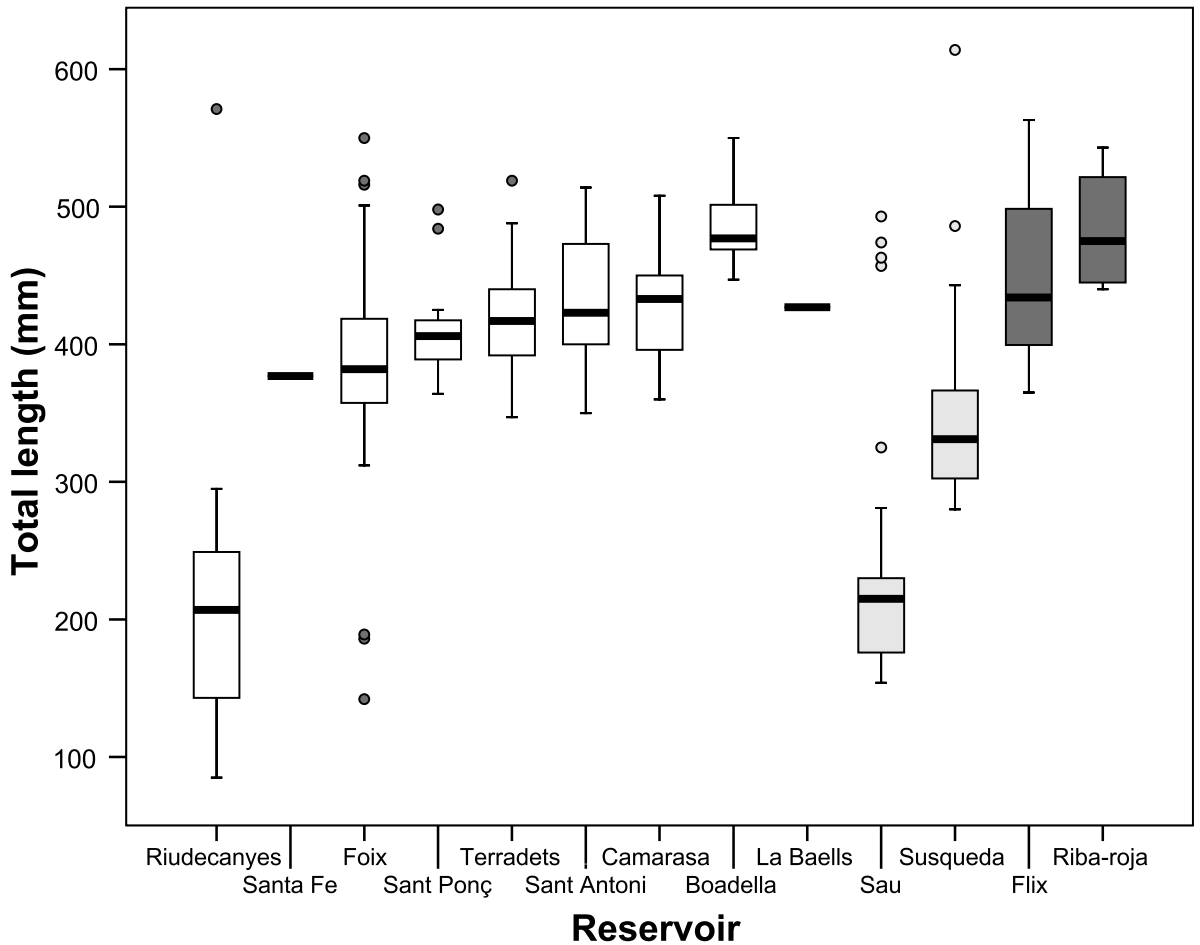
Food item	EBR			FLI			RIB			SAU			SUS		
	N	B	O	N	B	O	N	B	O	N	B	O	N	B	O
Plant material	-	0.44	23.2	-	1.83	62.8	-	0.70	33.3	-	0.08	8.54	-	0.46	26.7
Digested material	-	24.4	55.1	-	8.42	27.5	-	0.22	9.52	-	12.0	40.2	0	0	0
INVERTEBRATES	86.1	2.36	30.4	81.25	24.7	78.4	94.7	84.0	81.0	1.99	0.07	4.88	94.5	24.2	40.0
<i>Procambarus clarkii</i>	0.59	1.00	1.45	75.00	24.7	74.5	82.7	83.6	76.2	0.50	0.04	1.22	1.57	23.8	13.3
<i>Hydropsyche exocellata</i>	59.0	0.44	21.0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Atyaephyra desmaresti</i>	24.8	0.92	14.5	0	0	0	0	0	0	0	0	0	0	0	0
Ephemeroptera	0.59	0	1.45	0	0	0	0	0	0	0	0	0	0	0	0
Other invertebrates	1.18	0	2.17	6.25	0.03	11.8	12.0	0.41	19.1	1.49	0.03	3.66	87.4	0.20	13.3
FISH	13.9	72.8	28.3	18.18	64.1	33.3	5.33	15.1	19.1	98.0	87.9	59.8	5.51	0.16	26.7
<i>Alburnus alburnus</i>	2.36	11.3	5.80	6.25	0.75	9.80	0	0	0	0	0	0	0	0	0
<i>Luciobarbus graellsii</i>	7.96	43.1	15.2	0.57	0.43	1.96	0	0	0	0	0	0	0	0	0
<i>Cyprinus carpio</i>	0	0	0	1.14	57.9	3.92	0	0	0	0.50	2.35	1.22	0.79	29.3	6.67
<i>Rutilus rutilus</i>	0.29	3.10	0.72	1.70	3.49	5.88	1.33	14.5	4.76	96.5	81.7	59.8	-	-	-
Other fishes	3.24	15.4	7.25	8.52	1.56	13.7	4.00	0.68	14.3	1.00	3.86	2.44	3.94	22.0	33.3
BIRDS	0	0	0	0.57	0.88	1.96	0	0	0	0	0	0	0.79	24.1	6.67

The relationship between TL and the age of the catfish (hereafter, growth rates) varied significantly between mature females and males (ANCOVA: sex × age,  $F_{1, 102} = 25.6, P < 0.0005$ ; sex,  $F_{1, 102} = 14.9, P < 0.0005$ ), with males having higher growth rates (Fig. 1). Therefore, we analyzed the relationship between TL and age separately for males and females in subsequent analyses. Growth rates also varied significantly among populations for both males (ANCOVA,  $F_{4, 26} = 9.0, P < 0.0005$ ) and females (ANCOVA: population × age,  $F_{4, 64} = 3.4, P = 0.014$ ; population,  $F_{4, 64} = 2.6, P = 0.045$ ). These among-population differences in growth rates between earlier and more recent introductions were also significant for males (ANCOVA,  $F_{1, 25} = 14.8, P = 0.001$ ) and females (ANCOVA: population × age,  $F_{1, 70} = 15.1, P < 0.0005$ ; population,  $F_{1, 70} = 12.3, P = 0.001$ ), with growth rates higher in the recently introduced populations (Sau and Susqueda) (Fig. 1). The estimated TL of 7+ catfish was about 1500 mm in the Sau and Susqueda reservoirs whereas it was only about 1000 mm in Flix and Riba-roja. The lower adjusted  $R^2$  and the low estimated  $L_\infty$  (much lower than the maximum length of the fish observed) show that, in contrast to males, females did not fit the von Bertalanffy growth function well (Fig. 2).

With regard to the life-history traits, we found significant differences among sites and months (after accounting for fish size with ANCOVA) for several variables of both sexes (Table 2), although less for males because of the lower sample size. The partial  $\eta^2$  revealed that fish size was the most important source of variation, generally followed by month and finally by among-site variation. Total and eviscerated weights varied significantly among sites for females (Table 2) and their adjusted means were higher in the Ebro populations than in the Ter populations (Fig. 3). The three variables for females and the gonadal weight for males varied significantly among months (Table 2), with a clear decrease of all these variables in May (Fig. 3) after the reproduction period in April.

**Ontogenetic and site variation in catfish diet**

The most important prey of catfish were red swamp crayfish (*Procambarus clarkii*) and cyprinid fishes (Table 3). Because of their smaller size, a few other invertebrates were also important in number but only in the Ebro channels (the trichopteran *Hydropsyche exocellata*, and the freshwater shrimp *Atyaephyra desmaresti*) and the Susqueda reservoir (ephemeropterans). Among the fish preyed on by catfish, we found mosquitofish *Gambusia holbrooki*, pike *Esox lucius*,



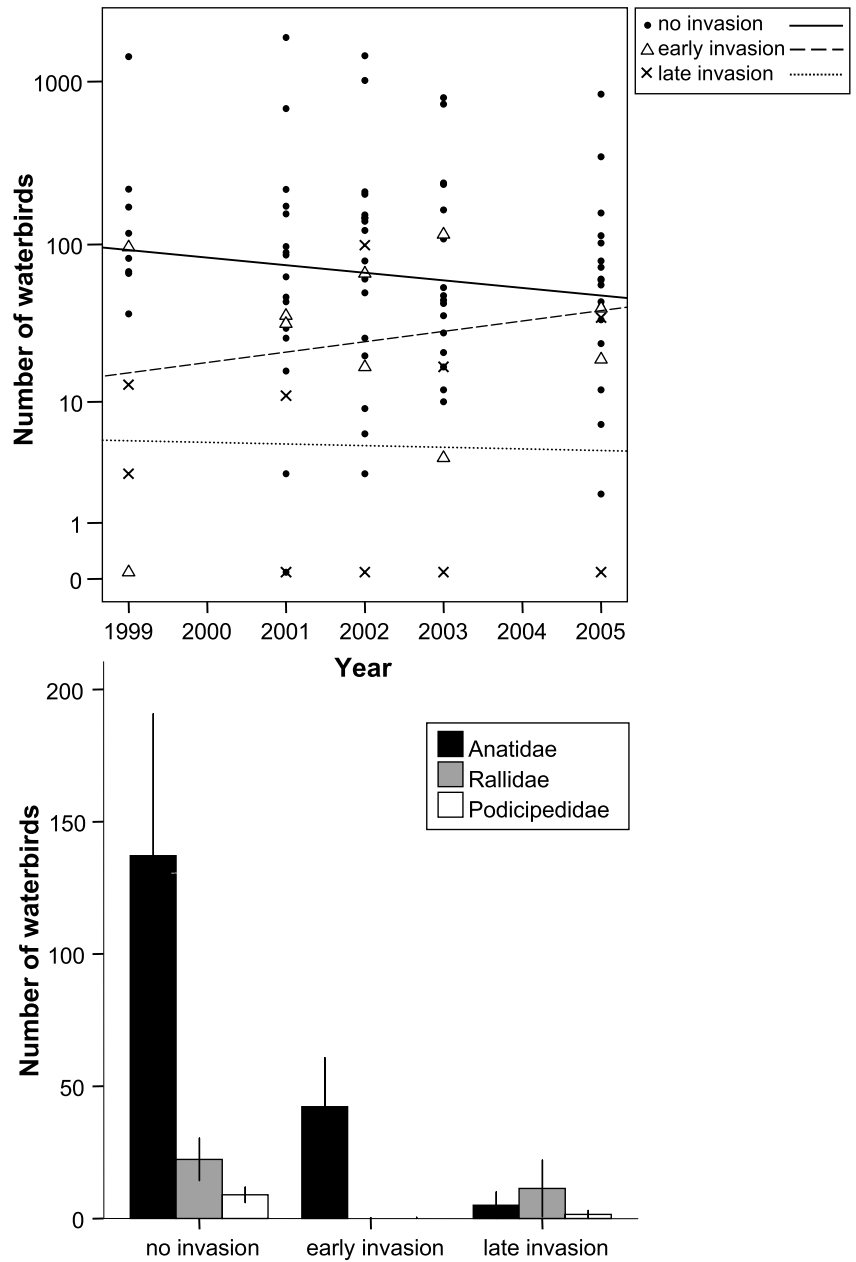
**Fig. 5.** Length-frequency distribution (box-plots) of common carp (*Cyprinus carpio*) in 13 Catalan reservoirs sampled from February to May 2003 (see Carol et al. (2006) for location and further data). Open bars (the first eight reservoirs) represent locations where catfish have not been detected; light grey shading: early stage invasion and dark shading: advanced stage invasions (the last two reservoirs). The box (rectangle) corresponds to the 25–75th percentiles, the dark line inside the box represents the median total length, and error bars are the minima and maxima excepting outliers (represented by circles).

pumpkinseed, mullet *Liza* sp., and mainly cyprinid species such as common carp, Ebro barbel *Luciobarbus graellsii*, bleak, roach and rudd. Interestingly, birds were also detected in two catfish stomachs, a passeriform species in Susqueda and a moorhen *Gallinula chloropus* in Flix.

The dietary importance of prey items (mean percentage of biomass) was highly dependent on site (MANCOVA: Wilk's  $\lambda$ ,  $F_{6,295} = 13.98$ ,  $P < 0.0001$ ) and catfish TL (Wilk's  $\lambda$ ,  $F_{6,295} = 8.40$ ,  $P < 0.0001$ ) (Fig. 4). The percentages of crayfish and fish in diet both depended on site and catfish TL ( $P < 0.05$ ) but partial  $\eta^2$  showed that site was more important than fish size, whereas invertebrates were more dependent on catfish TL. In contrast, the importance of plants did not depend on site or size ( $P > 0.22$ ). The ontogenetic diet shifts were marked (Fig. 4) and can be summarised as

follows: catfish generally consumed invertebrates and plant material until they grew to 300 mm, when there was an ontogenetic diet shift to crayfish or fish depending on site. In older populations (Flix and Riba-roja reservoirs) the main prey of catfish larger than 300 mm TL was crayfish, which amounted to > 60% of percent biomass, occurrence and mean percentage of biomass (Table 3, Fig. 4). In contrast, among recent introductions (Susqueda and Sau reservoirs), the shift was to fish, which were dominant in occurrence and biomass. This difference in fish consumption between early and late invasion stages was greater in catfish ranging from 300–900 mm long, which barely consumed fish in Flix and Riba-roja in contrast to the rest of the sites (Fig. 4). Accordingly, common carp (the largest cyprinid in Catalan reservoirs) were consumed by small catfish in early invasion stage reservoirs but was not in Riba-roja





**Fig. 6.** (Top) total population size estimates of waterbirds during 1999–2005 and (bottom) five-year mean per reservoir for three waterbird families (Podicipedidae, Anatidae and Rallidae) in 22 Catalan reservoirs with no, early-stage and advanced-stage catfish invasion. The regression functions for the three reservoir types are not significant, implying no significant temporal trend.

(despite being present) and were only eaten in Flix by catfish that were > 1200 mm long (e.g. a carp estimated to be ca. 500 mm long and 2000 g of weight) (Fig. 4).

**Resource availability in Catalan reservoirs**

Among the 14 reservoirs sampled in 2003, the two reservoirs with late stage catfish invasion (Flix and Riba-roja) had common carp with the second and third largest median (and mean) TL (Fig. 5). These two reservoirs had carp mean lengths (Welch  $F_{1, 8.3} = 9.3$ ,  $P = 0.015$ ) and median lengths (Welch  $F_{1, 5.6} = 6.0$ ,  $P =$

0.053) that were significantly larger than those of the other reservoirs.

The abundance of waterbirds in reservoirs did not vary significantly among years (repeated-measures ANOVA, Huynh-Feldt corrections: year,  $F_{2,9, 23.1} = 0.34$ ,  $P = 0.79$ ; year  $\times$  catfish,  $F_{5.8, 23.1} = 0.74$ ,  $P = 0.62$ ) but was significantly lower in reservoirs with both early and late stage catfish invasion compared to reservoirs with no catfish at all (ANOVA,  $F_{2,8} = 4.86$ ,  $P = 0.042$ ) (Fig. 6). This decrease in waterbird abundance was mostly due to the Anatidae family (rm-ANOVA,  $F_{2,8} = 6.24$ ,  $P = 0.023$ ), which was the most

**Table 4.** Correlation matrix of waterbird abundance (number, log-transformed) and catfish invasion stage (coded 0 to 2, from no invasion to advanced invasion) with selected abiotic variables in 22 Catalan reservoirs. Below diagonal, Pearson's correlation coefficient; above diagonal, sample size (limnological data was unavailable for five reservoirs). Significance levels: \*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ .

	Waterbird abundance	Catfish invasion	Chlorophyll (mg m <sup>-3</sup> )	Conductivity (µS cm <sup>-1</sup> )	Secchi depth (cm)	Reservoir surface (ha)	Water capacity (hm <sup>3</sup> )	Altitude (m)
Waterbird abundance		22	17	17	17	22	22	22
Catfish invasion	-0.435*		17	17	17	22	22	22
Chlorophyll	0.103	-0.054		17	17	17	17	17
Conductivity	-0.400	0.552*	0.705**		17	17	17	17
Secchi depth	-0.253	0.233	-0.381	-0.162		17	17	17
Reservoir surface	-0.261	0.472*	-0.231	0.012	0.343		22	22
Water capacity	0.011	0.186	-0.200	-0.298	0.442	0.789**		22
Altitude	-0.005	-0.383	-0.329	-0.572*	0.519*	-0.205	0.024	

abundant (yearly mean of 136 birds per reservoir, consisting mostly of mallards *Anas platyrhynchos*), and was not completely significant in Rallidae (ANOVA,  $F_{2,8} = 3.77$ ,  $P = 0.070$ ) and Podicipedidae (ANOVA,  $F_{2,8} = 2.41$ ,  $P = 0.15$ ), which were much less common (15 and 9 birds per reservoir, respectively) (Fig. 6). Although several physical and chemical features of the reservoirs were intercorrelated and catfish have been introduced preferentially in large reservoirs at low altitude (i.e. high water conductivity), waterbird abundance was not significantly related to any variable (such as reservoir surface, altitude, or trophic state, as measured for instance with chlorophyll-*a*) except catfish invasion stage (Table 4). A multiple regression analysis (stepwise procedure) of waterbird abundance with the seven factors only selected catfish invasion as a predictor, confirming the absence of confounding effects of the other six abiotic and trophic variables.

## Discussion

### Comparison with growth and diet in previous studies

European catfish growth has been studied mostly in their native area in Eastern Europe (Harka 1984, Harka & Bíró 1990, Horoszewicz & Backiel 2003), although it has also been studied in Italy, France and the UK (Rossi et al. 1991, Haffray et al. 1998). This is the first study of age, growth and diet of catfish in the Iberian Peninsula. Male catfish were significantly larger than females, as in Haffray et al. (1998), where males grew from 2 to 15% faster than females; our data (Fig. 2) also agree with the observation that female catfish are larger than males before age 2+ but smaller afterwards (Planche 1987). The estimated total length of a 7+ cat-

fish in our study was ca. 1100 mm (Figs 1 and 2), which is similar to data reported in native areas: 703 mm in the Vag River, Slovakia; 894 mm in the Tisza River, Hungary; 1020 mm in the Danube River, Serbia and 1285 mm in the Don River, Russia (Harka 1984).

The diet in the populations studied was based mostly on crayfish and cyprinid fishes (Fig. 4). This is also similar to previous studies, which have found that catfish mostly feed on fish species but also on other vertebrates such as frogs, birds and rodents, and invertebrates including crayfish (Orlova & Popova 1975, Omarov & Popova 1984, Adámek et al. 1999, Czarnecki et al. 2003, Dogan Bora & Gül 2004, Wysujack & Mehner 2005). For instance in Italy (Rossi et al. 1991), catfish less than 300 mm long also consumed mainly invertebrates and plant material, shifting to prey upon cyprinids at larger sizes.

### Early and late stages of catfish invasion

Our age and length data for European catfish confirmed that Ebro populations are much older introductions ( $\geq 34$  years) than the Ter populations ( $< 10$  years). We also observed that growth rates were significantly higher in recently introduced populations than in populations at a more advanced invasion stage. While the estimated total length of 7+ catfish in Sau and Susqueda was around 1500 mm, in Flix and Ribarroja it was only around 1000 mm. Comparison with published length-at-age data revealed a high growth rate in the Ter River similar to those also introduced into the Po River (Rossi et al. 1991), while growth in the Ebro River was similar to that of native populations and those of the UK (Harka 1984). Accordingly, the condition (weight-length relationship) was also significantly higher in recently introduced populations.

These differences in condition and growth rates between recent and older introductions may be related to diet. In early stage invasion sites (Sau and Susqueda reservoirs), catfish mainly consumed fish because of a high abundance of small cyprinid species, such as roach and bleak (Carol et al. 2006). In contrast, crayfish was the main prey of catfish in advanced stage invasion sites (Ebro reservoirs) and the ontogenetic shift to piscivory was delayed until the catfish grew larger. Accordingly, these advanced stage invasion reservoirs had size structures dominated by larger sizes of common carp. Although further data are needed to see how frequent these patterns are, our results strongly suggest that at the early stages of invasion, catfish grow faster and are in better condition because they prey more on fish. As invasion proceeds, however, the catfish reduce fish numbers, particularly of smaller fish, indirectly favouring crayfish and eventually resulting in their own reduced growth rates. Further data are needed to clarify the specific mechanisms for the relative replacement of fish with crayfish, but our results are in line with the lower caloric content of the latter (Pope et al. 2001, Eggleton & Schramm 2004) and the frequently reported negative correlations in abundances of crayfish and freshwater fish, including common carp (Hinojosa-Garro & Zambrano 2004, Hein et al. 2007).

In addition to fish prey, another likely ecological impact of catfish is on some groups of waterbirds, especially in the Anatidae family. We observed a few birds in the catfish stomach contents, as in previous studies (Omarov & Popova 1984, Czarnecki et al. 2003). We also found that waterbird abundance, made up mostly of anatids which were largely dominated in abundance by the mallards *Anas platyrhynchos*, varied significantly with the invasion sequence (no catfish, early, and late invasion stages) and this was not due to correlation or confounding with abiotic factors (e.g. reservoir size, altitude or trophic state). Among 22 reservoirs, the two with advance-stage invasions (Riba-roja and Flix) were the first and eighth reservoirs with the lowest abundance of waterbirds, despite the Riba-roja being the one with the largest surface area and Flix having more extensive reed beds (an excellent habitat for waterbirds) compared to most other reservoirs. The anatids of the reservoirs are particularly dominated in number by the mallard *Anas platyrhynchos*, which is mostly sedentary in this region. Anecdotal local information suggests that ducks in these reservoirs sometimes detect and escape from approaching catfish and thus learn to avoid them. Therefore, the significantly lower abundance of waterbirds in reservoirs with catfish could be due to either a direct ecological impact

by catfish and/or to avoidance behaviour by waterbirds to reduce predation risk. It would be interesting to analyse whether behaviour and habitat use of waterbirds differs in nearby reservoirs with and without catfish and particularly to monitor waterbirds where catfish have been recently introduced.

Overall, our study exemplifies that comparing early and late invasion stages in similar sites within a region might provide a cost-effective study design to appraise the effects of invasive species, particularly in the case of very large predators in very large ecosystems, which are not easily amenable to realistic experimentation.

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