FEEDING ECOLOGY OF NON-NATIVE CENTRARCHIDS (ACTINOPTERYGII: PERCIFORMES: CENTRARCHIDAE) IN TWO IBERIAN RESERVOIRS WITH CONTRASTING FOOD RESOURCES

Francisco N. GODINHO [1*] and Maria T. FERREIRA [2]

[1]*Conselho Nacional da Água, Lisbon, Portugal*

[2]*Centro de Estudos Florestais, Instituto Superior de Agronomia, University of Lisbon, Portugal*

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Background. Two North American fish species have been particularly successful in Iberian reservoirs, the largemouth black bass, *Micropterus salmoides* (Lacepède, 1802) and the pumpkinseed, *Lepomis gibbosus* (Linnaeus, 1758), but information on their ecology is still scarce, limiting their effective management and control. To increase the knowledge about the ecological mechanisms underlying bass and pumpkinseed invasion of freshwater systems, their feeding ecology and population descriptors are contrasted in two Iberian reservoirs differing in available resources.

Materials and methods. The studied reservoirs, situated in tributary streams of the Guadiana River, were sampled during the same months for a total of eight times, spanning two years. Fish samples were made by using electrofishing from a boat in the littoral area and trammel nets. Zooplankton and littoral benthic invertebrates were sampled concurrently with fish sampling. Fish diet was studied by examining individual stomach contents. The dominance of the different items in the diet of each species size-class was determined using the modified Costello diagram, diet overlap was estimated with Pianka's index and prey selection was assessed with the Manly-Chesson's alpha. Back-calculated length-at-age and body condition were also assessed for each fish.

Results. Invertebrates were dominant in the diet of pumpkinseed whereas invertebrates and pumpkinseed dominated the diet of bass. Both species demonstrated an overall dietary opportunism and a considerable food spectrum, with pumpkinseed eating fish and macrophytes. Feeding selectivity was observed that varied with species, size-class, reservoir and sampling period. Fish became the main prey for larger bass and the shift to piscivory was related to pumpkinseed availability. The dietary changes associated with pumpkinseed growth in native environments were not observed in the reservoirs. Dietary overlaps varied with sampling period, being frequently high. Differences in abundance, growth and body condition of bass and pumpkinseed were evident between reservoirs.

Conclusion. The ability to use several food items and to feed opportunistically likely facilitated the widespread success of the centrarchids in variable Iberian reservoirs. Moreover, our results seem to support the occurrence of resource competition between pumpkinseed size classes and between smaller bass and pumpkinseed.

Keywords: invasive, *Micropterus salmoides*, *Lepomis gibbosus*, ecology, diet, reservoirs, Iberia, biotic interactions

INTRODUCTION

Water availability is highly irregular in southern Iberia and, as a consequence, numerous dams have been built to store water from wet to dry periods, making riverine reservoirs (henceforth referred to simply as reservoirs) a conspicuous freshwater environment (Clavero et al. 2013). In a region almost devoid of natural lakes, reservoirs have offered new areas for native fluvial fish to colonise and promoted the naive introduction of several exotic fish, becoming some of the most heavily invaded systems in the world

(Hermoso et al. 2011). Two North American centrarchids have been particularly successful among the species introduced, the largemouth black bass, *Micropterus salmoides* (Lacepède, 1802), a primary piscivore, and the pumpkinseed sunfish, *Lepomis gibbosus* (Linnaeus, 1758), a specialised molluscivorous (Keast 1978). The sunfish was first introduced in the Spanish lake Banyoles around 1910 (García-Berthou and Moreno-Amich 2000b) but has spread westwards only in the 1970s. The bass was introduced to Portugal in 1952 and later to Spain (1955), and both cen-

* Correspondence: Dr. Francisco Godinho, Conselho Nacional da Água, Rua de O Século, 51, 2º. 1200-433 Lisboa, Portugal, phone: +351213231550; fax: +351213231523; e-mail: (FNG) *francisco.godinho@sg.maot.gov.pt* and *franciscogodinho111@gmail.com*; (MTF) *terferreira@isa.ulisboa.pt*.

trarchids presently co-occur in the majority of Iberian bodies of water, particularly in reservoirs. These same species were also introduced in many other world regions, becoming among the taxa most frequently established outside their natural ranges.

Scientists have long recognised the importance of feeding strategies in the ecological success of animal species, but, despite the importance of invasive bass and pumpkinseed as negative drivers of native fish assemblages (Clavero et al. 2013) and, in the case of bass, as a favoured angling species (Oliveira et al. 2009), available information about their feeding ecology in Iberia is still limited. Investigations conducted so far have addressed a single system (García-Berthou 2002), only one species (Zapata and Granado-Lorencio 1993) or a sole sampling period (Godinho et al. 1997), thus precluding a more comprehensive understanding of these species ecology in variable Iberian freshwater ecosystems.

In North America, the largemouth bass and *Lepomis* spp., particularly the bluegill, *Lepomis macrochirus* Rafinesque, 1819 (a sister species of the pumpkinseed sunfish not present in the Iberian Peninsula), are frequently sympatric in ponds and natural lakes (Shoup et al. 2007), and inter-specific interactions are often strong and dependent on size, since bass can use *Lepomis* spp. as prey but both taxa may share the same feeding resources at smaller sizes (Olson et al. 1995). Moreover, competitive interactions in juvenile *Lepomis* spp. are reportedly common in these taxa native habitats (Arendt and Wilson 1999).

To increase the knowledge about the ecological mechanisms underlying bass and pumpkinseed invasion of Iberian freshwater systems, in the presently reported study we contrast the feeding ecology and population descriptors of bass and pumpkinseed in two southern Iberian reservoirs with distinct available food resources. We were particularly interested in examining the ability of these introduced species to use the available resources, as well as to gain evidence on the occurrence of size-dependent biotic interactions in the bass-pumpkinseed association such as those reported for the bass-bluegill association in North America.

MATERIALS AND METHODS
Study sites and field sampling. Two warm-water reservoirs located in tributaries of the Guadiana River (southwest Iberia) were studied: the Monte Novo Reservoir (MN) and the Tapada Grande Reservoir (TG) (Table 1). Both reservoirs are distinct in some environmental conditions, noticeably in the resources available.

The reservoirs were sampled during the same months in consecutive weeks for a total of eight times, spanning two years (April, June, August, and November in 1992 and March, April, May, and November in 1993). Fish samples were made by using electrofishing from a boat in the littoral area (200 V, 3–6 A, DC) and nylon multi-mesh trammel nets (outer panel mesh: 25 cm; inner panel meshes: 25 and 50 mm) that were set overnight in non-littoral areas (i.e., limnetic and bottom).

After collection, bass and pumpkinseed were measured for total length (TL) to the nearest mm and weighed for total weight (TW) to the nearest 0.1 g. Scales were removed bellow the lateral line near the tip of the pectoral fin. Pumpkinseed and bass subsamples spanning available sizes were placed on ice after capture and deep-frozen within 4 h, being later taken to the laboratory.

Laboratory methods. In the laboratory, each fish was eviscerated, weighed (eviscerated weight, EW) and had its stomach content examined by using a binocular dissecting microscope, with food items identified to the lowest practical taxon and counted. In total, 355 pumpkinseed and 166 bass stomachs in TG reservoir, and 865 pumpkinseed and 146 bass stomachs in MN reservoir were examined for this study, with observations focusing on stomachs in which the prey could be clearly identified. Three size classes were established for each species to examine size-related diet shifts: small (<50 mm TL), intermediate (50–100 mm), and large (>100 mm) for pumpkinseed and: small (<100 mm TL), intermediate (100–200 mm), and large (>200 mm) for bass.

The age of each fish was determined by counting annuli from scale projections and the TL at age was back-calculated by using the Fraser–Lee method (Bagenal and Tesch 1978).

Data analysis. To evaluate the dietary importance of each food category, the frequency of occurrence (FO) and percent prey number (%N) were used. Percent number is the number of individuals of a prey category divided by the total number of individuals and expressed as a percentage, after pooling the stomach contents of all fish, whereas FO is the percentage of stomachs where a food category was present.

To describe the general prey importance and feeding strategy of each species size-class we used the modified Costello diagram (Costello 1990). The Costello diagram is based on a two-dimensional representation, where each point relates the occurrence of a prey item to its abundance (all in percent). Amundsen et al. (1996) modified the Costello diagram by replacing the abundance of a prey item by its prey-specific abundance, which equals:

$$P_i = 100(\sum S_i) \cdot (\sum S_{ti})^{-1}$$

where: P_i is the prey-specific abundance of prey i; S_i is the stomach content (number) comprised of prey i; and S_{ti} is the total stomach content in only those predators with prey i in their stomach. The dominant prey are closer to the top right corner, whereas the other diagonal corresponds to feeding strategy; prey with low occurrence but dominant by number correspond to individual specialisation and are closer to the top left corner.

Correspondence analysis (CA) was used to assess the main sources of diet variation in pumpkinseed and bass. CA is an ordination technique that reduces a species × samples matrix to a few dimensions explaining most of the variation and has been applied to dietary data (Marshall and Elliott 1997). The analysis was performed on matrices of diet categories × sample (each individual fish), with diet assessed as the numerical proportion of each food category. To increase the homogeneity in the

analysis, rare dietary items were grouped into an "other" dietary category and proportions were arcsine (square-root) transformed. Multivariate analysis of variance (MANOVA) of the sample (stomach) scores in the first two CA dimensions were used to interpret the pumpkinseed and bass dietary gradients according to fish length (size-class) and reservoir.

Temporal variation in the number of major prey categories eaten by size classes of largemouth bass and pumpkinseed was assessed with analysis of variance (ANOVA).

To evaluate prey selection (for macroinvertebrates and zooplankton), the Manly-Chesson's alpha (Chesson 1978, 1983) was determined in each sampling occasion with availability data and for each species size-class. The index

formula is:
$$\alpha = (r_i \times p_i^{-1}) \times [\textstyle\sum (r_j \times p_j^{-1})]^{-1}$$
where: r_i = the proportion of food item i in the diet ($i = 1, 2, \ldots, m$), p_i = the proportion of food item i in the environment and m = the number of food items in the environment (Chesson 1983). A value of a = ($1 \times m^{-1}$) occurs when a prey is consumed in proportion to its abundance, whereas values above ($1 \times m^{-1}$) indicate preference and values below ($1 \times m^{-1}$) indicate avoidance. The index was only calculated in sampling occasions with at least 5 bass or pumpkinseed with stomachs presenting well preserved food in a respective size-class and was separately determined for zooplankton and for benthic macroinvertebrates. To reduce some of the biases associated with selection indices (Chesson 1983) only prey with FO > 5 in

Table 1

Characteristics of Monte Novo and Tapada Grande reservoirs, Iberian Peninsula

	Tapada Grande 37°40′N, 7°30′W	Monte Novo 38°30′N, 4°42′W
Main use	Recreation/agriculture	Water supply/agriculture
Inundated area at pool level† [ha]	145	277
Mean depth [m]	4.2	5.5
Average annual air temp. [°C]†	17.4	16.7
Average annual rainfall [mm]†	563	693
Total phosphorous [mg·L⁻¹]†	0.08	0.10
Secchi transparency [m]	1.42	1.34
Conductivity [mS·cm⁻¹]†	265.4	404.8
Chlorophyll a [mg·L⁻¹]†	6.4	21.7
Number of benthic macroinvertebrates‡		
Decapoda	0.8 ± 0.1	1.5 ± 0.6
Diptera larvae§	13.8 ± 5.4	138.8 ± 35.2
Diptera pupae§	6.5 ± 4.2	12.4 ± 10.2
Ephemeroptera nymphs	112.3 ± 32.3	36.2 ± 14.5
Gastropoda	0.1 ± 0.1	1.9 ± 1.5
Heteroptera	30.5 ± 17.3	186.8 ± 100.9
Odonata nymphs	0.7 ± 0.3	3.0 ± 1.6
Terrestrial insects	0.2 ± 0.2	1.8 ± 1.8
Trichoptera larvae	0.3 ± 0.2	2.1 ± 1.1
Abundance of zooplankton in net samples [No. of individuals·L⁻¹]		
Bosmina	0.7 ± 0.6	0.3 ± 0.1
Calanoida	3.0 ± 0.6	2.2 ± 0.4
Chaoborus	<	<
Cladocera (other)	2.2 ± 0.9	5.6 ± 3.6
Cyclopoida	<	6.2 ± 3.3
Daphnia	0.7 ± 0.1	10.7 ± 2.0

Organisms' number and abundance given as mean ± standard error of the mean; †Data obtained from the Portuguese Information System on Water Resources (www.snirh.pt); other information was obtained during fish sampling and from bibliography; ‡Assessed concurrently with fish sampling on five occasions from three timed (5 min) kick samples using a hand net (400 mm frame, 550 µm mesh size); §Excluding *Chaoborus*; Zooplankton samples were taken near the dam on five occasions with a plankton net (200 mm diameter and 55 mm mesh size, three vertical hauls) and counted at the laboratory except the dominant rotifer; < Value below 0.01.

a particular centrarchid size-class were used in the evaluation of selection for that size-class.

Diet overlap (between different size-classes and species) was estimated in each reservoir and for each sampling period with Pianka's index (Pianka 1974). The index formula is:

$$O_{ij} = \sum_{k=1}^{n} P_{ik} \cdot P_{jk} \cdot \left(\sqrt{\sum_{k=1}^{n} P_{ik}^{2} + \sum_{k=1}^{n} P_{jk}^{2}} \right)^{-1}$$

where: O_{ij} is the resource overlap between species i and j, and P_{ik} and P_{jk} represent the proportions of the kth food category out of n such categories used by the ith and j^{th} species.

This index varies from 0, when there are no dietary items in common, to 1, when the diet is the same. The significance test of each Pianka's index was generated comparing the observed overlap value with a distribution of expected overlap values based on a null model generated from 1000 repetitions using the RA3 algorithm available in the EcoSimR software[*]. The values observed were considered statistically different from the values of the null distribution if they were higher or lower than 95% of the simulated indices. An observed value significantly lower than the simulated index suggests low resource overlap, whereas an observed value significantly higher than the simulated index suggests that there is strong resource competition (Gotelli and Graves 1996).

Analysis of covariance (ANCOVA) was used to compare eviscerated weight between reservoirs (fixed factor), using fish length as the covariate (García-Berthou and Moreno-Amich 1993). The relative weight W_R (Blackwell et al. 2000) was also determined to allow comparison of the fish condition in the studied reservoirs with the average condition of American populations of the same species. This index was developed in North America to compare the sampled fish weight to a standard weight (W_S), reflecting the weight of a well fed fish. We used the following formula:

$$W_R = 100 \text{TW} \times W_S^{-1}$$

where: W_R values between 95 and 105 indicating average body condition, whereas values above and below suggest, respectively, good and poor condition (Blackwell et al. 2000). W_S were derived for each fish following the standard weight equations derived for North American populations by Henson unpublished[**]), in the case of bass, and Liao et al. (1995), in the case of pumpkinseed. Minimum sizes used in calculations were 50 mm for pumpkinseed and 150 mm in bass.

Before analysis, quantitative variables (except proportions) were log-transformed to improve homoscedasticity and linearity. Data analyses were performed using specialized software such as: Statistica (StatSoft), Canoco (ver. 4), and R software[***].

All animal work was conducted according to Portuguese guidelines[****]. The necessary permits for fish sampling were obtained from the National Forest and Freshwater Fisheries Authority, Portuguese Ministry of Agriculture.

RESULTS

Fish collections. Pumpkinseed and bass accounted for the majority of fish collected in the littoral area of both reservoirs (proportion of each species in the total number of fish captured with electrofishing: in MN, pumpkinseed 87.4% and bass 12.5%; in TG, pumpkinseed 72.5% and bass 26.3%), whereas pumpkinseeds were also frequently captured in trammel nets (proportion of pumpkinseed in the total number of fish collected with nets: in MN 74.8% and in TG 46.2%). Also other species were captured but they were rare and basically restricted to non-littoral areas: *Cyprinus carpio* Linnaeus, 1758; *Luciobarbus comizo* (Steindachner, 1864); *Squalius pyrenaicus* (Günther, 1868); *Pseudochondrostoma willkommii* (Steindachner, 1866); *Cobitis paludica* (de Buen, 1930); *Gambusia holbrooki* Girard, 1859; and *Australoheros facetus* (Jenyns, 1842). Pumpkinseeds were found from 22 to 173 mm in TL, and from 24 to 146 mm in TL, respectively, in MN and TG reservoirs. For bass, specimens collected ranged from 65 to 475 mm in TL in MN, and from 71 to 385 mm in TL in TG.

Diets. Overall, pumpkinseed diet was dominated by benthic macroinvertebrates and zooplankton (Fig. 1). Piscivory was also observed as well as the consumption of pumpkinseed eggs, items related to the terrestrial environment (mainly Hymenoptera) and vegetation (FO ranging from 2.4 to 13.6 for pumpkinseeds > 50 mm in TL). The diet of bass included fish and invertebrates in both reservoirs. Fish consumed by bass were mostly pumpkinseed (97.2% of all fish prey in MN and 95.9% in TG), although bass and the native *C. paludica* and *S. pyrenaicus* were also found in stomach contents.

The graphical analysis exposed distinct feeding strategies between pumpkinseed size-classes. Diptera larvae, Ephemeroptera nymphs, and *Daphnia* were mostly eaten by fish > 50 mm, whereas the consumption of *Bosmina* and Copepoda was only important for smaller specimens. There was an increased specialisation of a few specimens on some prey (chiefly Cladocera), together with the generalised consumption of occasional prey by most pumpkinseeds. For largemouth, the graphical analysis depicted a clear specialisation for fish prey with increasing size, with larger specimens eating almost exclusively fish and Decapoda. Differences between reservoirs in the diet of bass and pumpkinseed size-classes were also depicted in the Costello diagrams. For example, Ephemeroptera
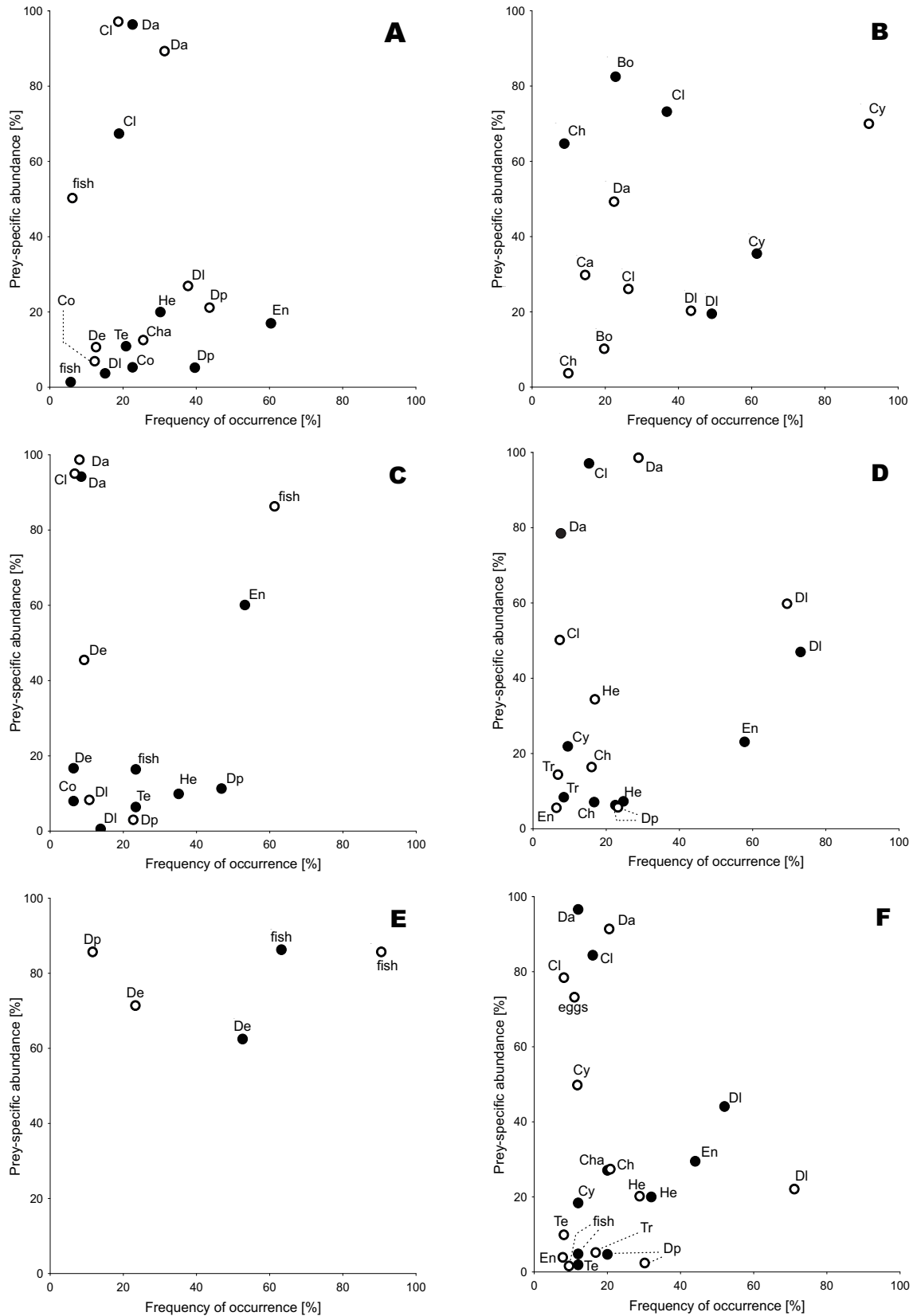
Fig. 1. Costello diagrams by species size-class and reservoir; Largemouth black bass, *Micropterus salmoides*: **A** small, **C** intermediate, **E** large; Pumpkinseed, *Lepomis gibbosus*: **B** small, **D** intermediate, **F** large; Black dot = Tapada Grande Reservoir, white dot = Monte Novo Reservoir; Prey codes: Bo = Bosmina, Ca = Calanoida, Ch = *Chydorus*, Cha = *Chaoborus*, Cl = other Cladocera, Co = Copepoda, Cy = Cyclopoida, Da =*Daphnia*, De = Decapoda, Dl = Diptera larvae (except *Chaoborus*), Dp = Diptera pupae (except *Chaoborus*), En = Ephemeroptera nymps, He = Heteroptera, Te = Terrestrial insects, Tr = Trichoptera larvae; Only prey with frequency of occurrence > 5.0% are depicted.

nymphs were mostly consumed in TG reservoir by both bass and pumpkinseed.

The first two dimensions of the correspondence analysis of prey proportions explained 23.7% and 25.2% of the dietary variance, respectively, for pumpkinseed and bass (Figs. 2 and 3). For pumpkinseed, the dietary gradients (stomach scores on the first two axes) varied with fish size (Wilk's Lambda = 0.73, $F_{4/2094}$ = 87.64, $P < 0.01$) and reservoir (Wilk's Lambda = 0.99, $F_{2/1047}$ = 5.38, $P < 0.01$). For bass, dietary variation was related to size-class (Wilk's Lambda = 0.88, $F_{4/620}$ = 8.27, $P < 0.01$) and reservoir (Wilk's Lambda = 0.94, $F_{2/310}$ = 8.38, $P < 0.01$). The interaction reservoir × size-class was also significant (Wilk's Lambda = 0.93, $F_{4/620}$ = 4.03, $P < 0.01$), reflecting different patterns of bass dietary variation with size in the two reservoirs.

The consumption of all major prey items by pumpkinseed changed significantly with sampling period in the two reservoirs (Table 2). The consumption of several food categories by bass also changed with sampling period, but some prey were eaten more regularly, namely fish by larger bass. Fish was also eaten more regularly by the intermediate-size bass in MN, but not in TG, where fish consumption was only important in the two last sampling periods.

The main invertebrates eaten by the pumpkinseeds were the most frequent and abundant and some of the diet differences between reservoirs could be related to variation in available prey (e.g., the distinct importance of Ephemeroptera nymphs, see Table 1). Despite the general relation between invertebrate abundance and importance in the diets, pumpkinseeds revealed variable selectivity for particular prey (Table 3). Diptera larvae were frequently preferred or eaten according to their abundance in the two reservoirs. When preference for Diptera larvae decreased, the preference for other prey increased.

The selection for invertebrates by bass varied with time and among reservoirs, with Diptera larvae being always avoided (Table 4). The importance of pumpkinseed in the diet of intermediate bass was strongly related with availability of pumpkinseed with vulnerable sizes in both reservoirs: Pearson's r between the number of pumpkinseeds per bass stomach and the (log-transformed) CPUE of pumpkinseed with vulnerable sizes (i.e., with a TL < 0.4 × the mean TL of bass, after Hoyle and Keast 1987) = 0.94, $P < 0.01$ in MN and 0.89, $P < 0.01$ in TG. This relation was, however, not observed for larger bass ($P > 0.10$).

Diet overlap among pumpkinseed size-classes varied with sampling period, but it was often high in the two reservoirs (Table 5). Diet overlap among pumpkinseed size-classes and bass (< 200 mm in TL) was sometimes high in both reservoirs.

Population descriptors. The catch rate of pumpkinseed was significantly higher in MN, particularly for larger fish, while catch rates of larger bass were higher in MN (Table 6). Bass grew slower in TG during the first years, but by age-3 length was comparable in the two reservoirs. Pumpkinseed grew significantly slower in TG.

The condition of pumpkinseed was higher in MN (ANCOVA of EW with reservoir as fixed factor and length as the covariate, $F_{1/1052}$ = 7.87, $P < 0.01$). The condition of bass was also different between reservoirs (ANCOVA, $F_{1/287}$ = 50.12, $P < 0.01$), but only for smaller fish (reservoir × TL, $F_{1/287}$ = 50.12, $P < 0.01$). Based on W_R, the pumpkinseeds (> 50 mm) in the two reservoirs had a body condition lower than the average condition of American populations, whereas bass (>150 mm) condition was lower than the average American condition only in TG reservoir.
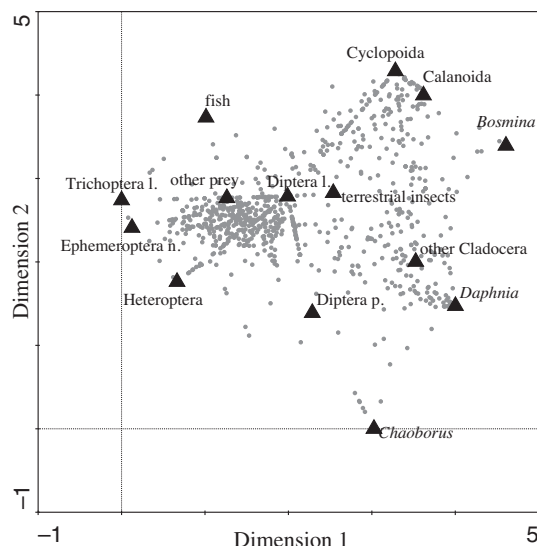
Fig. 2. Correspondence analysis biplot for the stomach contents (proportion prey number) of pumpkinseed, *Lepomis gibbosus* in Monte Novo and Tapada Grande reservoirs, Iberian Peninsula: food category and sample (stomachs) scores for the first and second dimensions
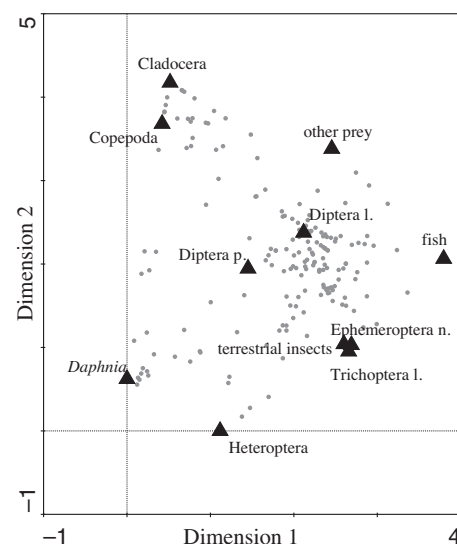

Fig. 3. Correspondence analysis biplot for the stomach contents (proportion prey number) largemouth black bass, *Micropterus salmoides* in Monte Novo and Tapada Grande reservoirs, Iberian Peninsula: food category and sample (stomachs) scores for the first and second dimensions

DISCUSSION

Diets of pumpkinseed and bass in the reservoirs included some of the food items commonly eaten in their native and acclimatised ranges (Keast 1978, Hoyle and Keast 1987, Zapata and Granado-Lorencio 1993, García-Berthou and Moreno-Amich 2000a, García-Berthou 2002, Almeida et al. 2009, Brown 2009). Notwithstanding, the sporadic consumption of fish by the pumpkinseeds has been rarely reported elsewhere (Rezsu and Specziár 2006). Note that we found entire fish in stomach contents and not fish remains, such as scales, whose ingestion could be independent of piscivory. In addition, the presence of macrophytes in pumpkinseed stomach contents was abnormally frequent in our study reservoirs, as other studies have reported much lower frequencies of occurrence (e.g., <2%, Bonar et al. 2004).

The increase in fish consumption and the corresponding decline of the invertebrate food component observed in the diet of bass with increasing body size parallel the dietary changes described in other studies (Brown 2009). In contrast, the typical dietary shifts associated with pumpkinseed growth in native environments (i.e., a rapid replacement of zooplankton by benthic macroinvertebrates as increasing size permits the handling of bigger, more profitable prey; Werner 1974) were unclear in the studied reservoirs, as zooplankton consumption remained high for a few larger specimens. The relevant consumption of gastropods by pumpkinseeds above 80 mm often described in native environments (Keast 1978, Mittelbach et al. 1992) was also not observed in the reservoirs, but it was likely related to the low abundance of this prey.

Table 2

Temporal variation in the mean number of prey/stomach for pumpkinseed, *Lepomis gibbosus*, and largemouth bass, *Micropterus salmoides*, in Monte Novo and Tapada Grande reservoirs, Iberian Peninsula

	Apr 92	Jun 92	Aug 92	Nov 92	Mar 93	Apr 93	May 93	Nov 93	ANOVA
Monte Novo PUMPKINSEED >100 mm in TL									
Diptera larvae	6.3 ± 1.2	6.2 ± 0.7	20.2 ± 3.5	15.8 ± 3.1	9.0 ± 2.3	7.0 ± 1.3	9.0 ± 3.4	1.8 ± 0.5	$F_{7/521} = 5.13$
Heteroptera	0.8 ± 0.2	7.5 ± 4.3	6.1 ± 2.5	<	2.9 ± 1.7	7.0 ± 1.9	9.4 ± 6.3	0	$F_{7/521} = 11.78$
Daphnia	314.6 ± 79.2	11.2 ± 8.6	87.6 ± 43.2	69.0 ± 26.4	0.3 ± 0.2	208.5 ± 40.1	105.2 ± 51.2	0.5 ± 0.4	$F_{7/521} = 11.21$
Cladocera (other)	8.9 ± 3.2	4.0 ± 2.3	32.6 ± 21.2	32.3 ± 15.1	3.4 ± 1.7	0	1.6 ± 0.7	0	$F_{7/521} = 4.47$
Copepoda	4.7 ± 2.3	4.1 ± 3.0	<	32.5 ± 16.2	5.2 ± 3.3	0.8 ± 0.3	0.6 ± 0.4	2.3 ± 1.5	$F_{7/521} = 6.79$
Fish	<	<	0.3 ± 0.1	<	0	0	0	0.3 ± 0.1	$F_{7/521} = 5.18$
Monte Novo PUMPKINSEED 50–100 mm in TL									
Diptera larvae	12.3 ± 1.7	13.3 ± 3.1	30.0 ± 6.9	2.3 ± 0.6	0.5 ± 0.4	11.2 ± 4.1	23.2 ± 3.5	0.6 ± 0.4	$F_{7/243} = 11.31$
Heteroptera	0	3.0 ± 1.5	0.3 ± 0.3	0	0	3.3 ± 1.0	3.5 ± 1.2	0	$F_{7/243} = 8.82$
Daphnia	115.2 ± 72.1	0	26.7 ± 20.5	0	0	0.2 ± 0.2	1.7 ± 0.7	0	$F_{7/243} = 2.38$
Cladocera (other)	0.7 ± 0.3	0	0.1 ± 0.1	10.1 ± 5.3	0	0	0	1.3 ± 0.9	$F_{7/243} = 4.56$
Copepoda	3.8 ± 1.2	0	5.7 ± 4.5	2.1 ± 1.0	0	<	<	21.9 ± 11.3	$F_{7/243} = 3.31$
Tapada Grande PUMPKINSEED 50–100 mm in TL									
Diptera larvae	1.6 ± 0.5	5.3 ± 1.0	0.8 ± 0.3	2.2 ± 1.8	16.5 ± 2.9	18.2 ± 3.4	12.0 ± 2.2	5.4 ± 1.6	$F_{7/316} = 13.80$
Ephemeroptera nymph	0.9 ± 0.6	3.4 ± 0.4	3.8 ± 1.2	1.2 ± 0.8	2.7 ± 0.6	9.0 ± 1.7	2.3 ± 0.3	0.1 ± 0.1	$F_{7/316} = 11.24$
Daphnia	9.0 ± 6.3	2.2 ± 1.8	21.7 ± 9.3	101.0 ± 53.2	3.1 ± 2.7	0	0.9 ± 0.8	1.9 ± 1.7	$F_{7/316} = 5.27$
Cladocera (other)	133.0 ± 76.7	1.9 ± 0.6	73.9 ± 26.7	160.0 ± 137.0	0.2 ± 0.1	6.8 ± 0.1	0	59.0 ± 15.0	$F_{7/316} = 7.64$
Copepoda	4.5 ± 2.7	0.6 ± 0.3	1.7 ± 1.3	0	0.4 ± 0.2	0.2 ± 0.2	0	14.4 ± 5.2	$F_{7/316} = 10.65$
Monte Novo LARGEMOUTH BASS >200 mm in TL									
Fish	0.5 ± 0.2	1.0 ± 0.2	2.0 ± 0.3	1.1 ± 0.1	0.6 ± 0.2	0.6 ± 0.2	1.1 ± 0.4	1.7 ± 0.3	$F_{7/48} = 2.10$, n.s.
Decapoda	0.7 ± 0.3	0	0	0	0	0.4 ± 0.2	0.3 ± 0.2	0	$F_{7/48} = 1.09$, n.s.
Monte Novo LARGEMOUTH BASS 100–200 mm in TL									
Fish	—	0.6 ± 0.5	1.0 ± 0.8	0.2 ± 0.3	0.1 ± 0.2	1.0 ± 1.0	0.8 ± 0.6	1.3 ± 0.5	$F_{7/71} = 19.01$
Diptera pupae	—	3.5 ± 3.2	0.8 ± 0.9	1.0 ± 1.1	4.1 ± 1.2	1.7 ± 1.9	0	0	$F_{7/71} = 7.55$
Cladocera	—	126.6 ± 115.6	0	6.3 ± 8.2	226.5 ± 210.5	0	75.0 ± 68.2	0	$F_{7/71} = 25.72$
Tapada Grande LARGEMOUTH BASS >200 mm in TL									
Fish	2.0 ± 0.7	1.0 ± 0.1	—	—	1.0 ± 0.1	0.6 ± 0.2	1.0 ± 0.1	1.1 ± 0.3	$F_{7/32} = 1.74$, n.s.
Decapoda	0.5 ± 0.2	0	—	—	0.2 ± 0.1	0.3 ± 0.1	1.0 ± 0.2	0.6 ± 0.1	$F_{7/32} = 3.81$
Tapada Grande LARGEMOUTH BASS 100–200 mm in TL									
Fish	0	<	0.1 ± 0.1	0.1 ± 0.1	0	0	0.9 ± 0.3	1.0 ± 0.2	$F_{7/102} = 24.17$
Ephemeroptera nymph	0.2 ± 0.2	2.1 ± 1.3	1.1 ± 0.9	1.4 ± 1.3	13.0 ± 11.2	76.4 ± 31.3	12.1 ± 8.7	0	$F_{7/102} = 2.75$
Diptera pupae	0	3.0 ± 1.2	0.1 ± 0.5	1.3 ± 0.4	1.7 ± 0.6	4.0 ± 81.0	0.8 ± 1.2	0	$F_{7/102} = 1.61$, n.s.
Heteroptera	0	<	0.5 ± 0.2	0.9 ± 0.7	3.9 ± 1.0	2.8 ± 0.8	0.4 ± 0.2	0	$F_{7/102} = 12.27$
Terrestrial insects	0	0.2 ± 0.2	3.7 ± 2.1	0.4 ± 0.3	0.2 ± 0.1	0.9 ± 0.8	0.3 ± 0.2	0	$F_{7/102} = 0.97$, n.s.
Cladocera	0	190.6 ± 75.6	72.4 ± 41.1	2.4 ± 5.6	0	0	0	0	$F_{7/102} = 4.20$

ANOVA results comparing temporal variation in the number of prey/stomach are given; All significant (*P* < 0.01), except were noticed (non-significant, n.s.). Only the dominant size-classes and primary prey are presented; < value below 0.1.

Table 3

Manly–Chesson (a) for size-classes of pumpkinseed, *Lepomis gibbosus*, feeding on benthic macroinvertebrates and zooplankton in Monte Novo and Tapada Grande reservoirs, Iberian Peninsula

	Aug 92	Nov 92	Feb 93	May 93	Nov 93
MONTE NOVO Pumpkinseed >100 mm in TL					
m^{-1}	0.14	0.13	0.17	0.14	0.25
Decapoda	<	0	0		
Diptera larvae	0.15	0.09	0.27	0.35	0.85
Diptera pupae	0.04	0.08	0.27	0.31	<
Heteroptera	0.58	<	0.12	<	0
Ephemerotera nymph	<	0	0.07	0.14	
Trichoptera larvae	0.02	0.77	0.27	0.02	0
Gastropoda		0.04		0	
Terrestrial insects	0.20	0		0.18	
m^{-1}		0.20	0.20	0.25	0.20
Daphnia		0.04	0.67	0.96	0.10
Cladocera (other)		0.04	0.18	0	0
Cyclops		0.02	0.05	0.04	0.86
Calanoida		<	<	<	0.04
Chaoborus		0.89	0.09		0
MONTE NOVO Pumpkinseed 50–100 mm in TL					
m^{-1}	0.20	0.20	0.20	0.25	0.20
Diptera larvae	0.35	0.15	0.08	0.35	0.07
Diptera pupae	0.44	0.03	0.60	0.08	<
Heteroptera	0.18	0	0	<	0
Ephemerotera nymph	0	0	0.32	0.57	0.01
Trichoptera larvae	0	0.92	0		<
m^{-1}		0.20	0.20		0.20
Daphnia		0	0.68		0
Cladocera (other)		0.16	0		0.59
Cyclops		0.02	0.04		0.41
Calanoida		0.49	0		<
Chaoborus		0.32	0		0
TAPADA GRANDE Pumpkinseed > 50 mm in TL					
m^{-1}	0.20	0.17	0.25	0.20	0.33
Diptera larvae	0.19	0.29	0.85	0.62	0.82
Diptera pupae	0.04	0.30	0.03	0.02	0.17
Heteroptera	0.17	0.31	<	0.02	
Ephemeroptera nymph	0.05	0.01	0.11	0.14	0.01
Trichoptera larvae	0.47	0			
Terrestrial insects		0		0.16	
m^{-1}		0.17	0.25	0.17	0.20
Daphnia		0.17	0.58	0	0.01
Bosmina		0		0	0.28
Cladocera†		0.79	0	<	0.08
Cyclops		0	0.41	<	0.51
Calanoida		0	0.01	<	0.12
Chaoborus		0.03		0.99	

The index was determined for size-classes with at least five specimens in a particular size-class/sampling occasion; The reciprocal of the (m) number of prey in each sampling location/date (m^{-1}) represents neutral selection Values > m^{-1} indicate positive selection and values < m^{-1} indicate avoidance; < a value below 0.01.

Table 4

Manly–Chesson (a) for size-classes of largemouth bass, *Micropterus salmoides*, feeding on benthic macroinvertebrates and zooplankton in Monte Novo and Tapada Grande reservoirs, Iberian Peninsula

	Aug 92	Nov 92	Feb 93	May 93	Nov 93
MONTE NOVO Largemouth bass 100–200 mm in TL					
m^{-1}	—	0.14	0.17	0.17	—
Decapoda	—	0.62	0.70	0	—
Diptera larvae	—	0.01	<	0	—
Diptera pupae	—	0.36	0.10	0.14	—
Heteroptera	—	0	0	<	—
Ephemeroptera nymph	—	0	0	0.43	—
Terrestrial insects	—	0		0.43	—
Odonata nymph	—	0	0.20		—
m^{-1}	—	0.33	0.33	0.33	—
Daphnia	—	0	0.99	0	—
Cladocera (other)	—	0.73	0	0	—
Chaoborus	—	0.27	<	0	—
MONTE NOVO Largemouth bass < 100 mm in TL					
m^{-1}	—	0.20	0.17	—	—
Decapoda	—	0.04	0	—	—
Diptera larvae	—	<	0.06	—	—
Diptera pupae	—	0.96	0.46	—	—
Heteroptera	—	<	0	—	—
Ephemeroptera nymph	—	0	0.07	—	—
Trichoptera larvae	—		0.41	—	—
m^{-1}	—	0.25	0.25	—	—
Daphnia	—	0.39	0	—	—
Cladocera (other)	—	0.32	0	—	—
Cyclops	—	<	0	—	—
Chaoborus	—	0.26	0	—	—
TAPADA GRANDE Largemouth bass 100–200 mm in TL					
m^{-1}	0.13	0.13	0.14	0.14	0.25
Decapoda	0	0.02	0	0.01	1.00
Diptera larvae	0.01	0	0.04	<	0
Diptera pupae	0.02	0.07	0.11	0.06	0
Heteroptera	0.04	0.07	0.03	<	
Ephemeroptera nymph	0	<	0.42	0.30	0
Trichoptera larvae	0	0.09	0.02	0	
Terrestrial insects	0.92	0.09	0.12	0.57	
Odonata nymph	0	0.65			
m^{-1}		0.33	0.33	0.33	0.33
Daphnia		0	0	0	0
Cladocera (other)		1.00	0	0	0
Cyclops		0	0	0	0
TAPADA GRANDE Largemouth bass < 100 mm in TL					
m^{-1}	0.17	—	0.17	—	—
Decapoda	0	—	0.16	—	—
Diptera larvae	0.06	—	0	—	—
Diptera pupae	0	—	0.14	—	—
Heteroptera	0	—	0.03	—	—
Ephemeroptera nymph	<	—	0.68	—	—
Trichoptera larvae	0.93	—	0	—	—

The index was determined for size-classes with at least five specimens in a particular size-class/sampling occasion; The reciprocal of the (m) number of prey in a particular sampling location/date (m^{-1}) represents neutral selection; Values > L × m^{-1} indicate positive selection and values < L × m^{-1} indicate avoidance; < a value below 0.01.

Constrained by each species morphology (bass is a swift-striking predator more adapted to water column and surface prey whereas pumpkinseed is adapted to feeding on the bottom), both pumpkinseed and bass demonstrated an overall dietary opportunism, feeding on the most frequent and abundant prey in each reservoir and changing prey according to availability and vulnerability. For example, Diptera larvae were likely more vulnerable to pumpkinseed than other benthic prey, like the active swimmers Heteroptera, whereas Diptera pupae and terrestrial insects could have been more accessible to bass.

Table 5

Piankas's index of overlap for size-classes of largemouth bass, *Micropterus salmoides* and the pumpkinseed, *Lepomis gibbosus* sampled in Monte Novo and Tapada Grande reservoirs, Iberian Peninsula

Date	MN pumpkinseed size-classes	MN pumpkinseed–bass (<200 mm)	TG pumpkinseed size-classes	TG pumpkinseed–bass (<200 mm)
April 92	0.97>	0.98>	0.95>	0.81>
June 92	0.51>	0.40>	0.37>	0.60>
August 92	0.29>	0.39>	†	0.96>
November 92	0.36>	0.59>	0.34>	n.s.
March 93	0.34>	0.30>	0.76>	0.35>
April 93	0.06<	n.s.	0.53>	0.46>
May 93	0.82>	n.s.	0.94>	0.36>
November 93	0.89>	0.46>	0.83>	0.28>

MN = Monte Novo, TG = Tapada Grande; > value significantly higher than the value obtained under a full model ($P < 0.05$); < value significantly lower than the value obtained under a full model ($P < 0.05$); n.s. = non-significant overlap value; †A single size-class sampled.

Table 6

Characteristics of the largemouth black bass, *Micropterus salmoides,* and the pumpkinseed, *Lepomis gibbosus*, populations sampled in Monte Novo and Tapada Grande reservoirs, Iberian Peninsula

		Tapada Grande	Monte Novo	ANOVA
Abundance	Catch E bass	0.32 ± 0.09 (8)	0.33 ± 0.11 (8)	$F_{1/14} = 0.03$
	Catch E pumpkinseed	1.23 ± 0.34 (8)	2.81 ± 1.12 (8)	$F_{1/14} = 9.05$†
	Catch E bass > 200 mm	0.03 ± 0.01 (8)	0.11 ± 0.05 (8)	$F_{1/14} = 4.91$††
	Catch E bass ≤ 200 mm	0.29 ± 0.12 (8)	0.22 ± 0.05 (8)	$F_{1/14} = 0.38$
	Catch E for pumpkinseed > 100 mm	0.08 ± 0.03 (8)	1.65 ± 0.32 (8)	$F_{1/14} = 9.97$†
	Catch E for pumpkinseed 50–100 mm	0.82 ± 0.19 (8)	0.40 ± 0.11 (8)	$F_{1/14} = 3.04$
	Catch E pumpkinseed ≤ 50 mm	0.33 ± 0.24 (8)	0.76 ± 0.56 (8)	$F_{1/14} = 2.97$
	Catch N bass	0.07 ± 0.06 (8)	0.30 ± 0.11 (8)	$F_{1/14} = 2.86$
	Catch N pumpkinseed	2.32 ± 1.22 (8)	6.34 ± 1.05 (8)	$F_{1/14} = 4.92$††
Growth	Bass TL age 1 [mm]	128.6 ± 2.12 (98)	161.2 ± 4.11 (91)	$F_{1/187} = 78.51$†
	Bass TL age 2 [mm]	206.9 ± 9.81 (158)	248.0 ± 7.76 (113)	$F_{1/269} = 64.38$†
	Bass TL age 3 [mm]	358.3 ± 10.2 (12)	339.6 ± 8.7 (24)	$F_{1/34} = 3.49$
	Bass TL age 4 [mm]	405.0 ± 6.0 (6)	400.1 ± 4.0 (9)	$F_{1/13} = 2.18$
	Pumpkinseed TL age 1 [mm]	60.0 ± 1.27 (236)	73.1 ± 3.82 (258)	$F_{1/492} = 17.86$†
	Pumpkinseed TL age 2 [mm]	81.1 ± 0.99 (82)	103.5 ± 1.18 (73)	$F_{1/153} = 69.13$†
	Pumpkinseed TL age 3 [mm]	94.0 ± 1.02 (67)	121.4 ± 1.54 (85)	$F_{1/150} = 71.05$†
	Pumpkinseed TL age 4 [mm]	102.3 ± 1.56 (26)	134.0 ± 1.35 (40)	$F_{1/64} = 92.15$†
BC	W_R for bass > 150 mm	91.90 ± 0.63 (152)	111.27 ± 0.71 (137)	$F_{1/287} = 7.71$†
	W_R for pumpkinseed > 50 mm	80.50 ± 0.69 (289)	87.98 ± 0.48 (765)	$F_{1/1052} = 11.15$†

Catch E = catch per min of electrofishing; Catch N = catch per 100 m² non-littoral trammel net; BC = Body condition; Fish age in years; W_R = Relative Weight; Values are mean ± standard error of the mean (number); ANOVA results are comparisons between the two reservoirs; †$P < 0.01$, ††$P < 0.05$.

The abundance of fish with vulnerable dimensions strongly conditioned the diet of largemouth bass. In particular, intermediate-size bass took fish (mostly pumpkinseed) if available in vulnerable sizes and used other, smaller prey, more frequently where and when fish were less numerous. In contrast, the higher and more constant availability of vulnerable pumpkinseeds found by larger bass in the reservoirs may have resulted in the lack of relation between the abundance of pumpkinseed and its consumption by bass above 200 mm. The other fish species present in the reservoirs with some importance, i.e., large-sized cyprinids *Luciobarbus comizo* and *Pseudochondrostoma willkommii*, were not vulnerable to bass since their populations are composed of relatively large individuals that reproduce outside the reservoirs in tributary streams (Godinho unpublished). Nevertheless, two native species were found in bass stomach contents, including the endangered small-sized cyprinid *Squalius* spp. Other investigations have shown bass to prefer Iberian native soft-bodied cyprinids to *Lepomis* spp. (Godinho and Ferreira 2006) and have related its introduction to the collapse of native fish assemblages in some of the few natural lakes in the Iberian Peninsula (García-Berthou and Moreno-Amich 2000b). Small-sized cyprinids were found to be absent or rare in the presence of both bass and pumpkinseed in a set of Iberian reservoirs (Clavero et al. 2013), but no data on the fish assemblages of the two studied reservoirs was available before the present investigation to allow a clearer assessment of the effect of the introduction of the two centrarchids on the MN and TG fish assemblages.

In the absence of preferred prey several fish species take less profitable food and the maintenance of zooplankton in the diet of larger pumpkinseeds, but also of other uncommon prey like fish, could have represented the most profitable feeding strategy available in the reservoirs, as frequent water level fluctuations should constrain the overall availability of littoral benthic prey, including gastropods (Fontoura and Paw 1991). Although experimental studies suggest that pumpkinseed above 80 mm use *Daphnia* with less profitability than other prey, such as gastropods (Mittelbach 1984), some investigations conducted in North America have showed that adult pumpkinseeds can eat large quantities of zooplankon in lakes without the bluegill or other zooplanktivorous species, sometimes developing a pelagic morphotype (Robinson et al. 1993, 2000). The adult bluegill is morphologically better adapted than the pumpkinseed to eat zooplankton and when the two species are sympatric the former usually precludes the utilisation of zooplankton by the pumpkinseed (Osenberg et al. 1988, 1992, Mittelbach et al. 1992). Interestingly, the phenotypic plasticity observed in some American pumpkinseed populations (littoral and pelagic morphotypes) has been found in some Iberian reservoirs (Bhagat et al. 2006, Vila-Gispert et al. 2007) and could be related to the patterns of zooplankton use observed in this study. In the studied reservoirs as in the majority of Iberian environments the absence of other zoo-

planktivorous species may facilitate the use of zooplankton by the pumpkinseeds (Braband and Saltveit 1989).

The inclusion of zooplankton in the diet of larger pumpkinseed likely contributed to the maintenance of abundant populations in the reservoirs; catch rates were comparable to catch rates reported for bluegill (the more abundant *Lepomis* species due to its zooplankton utilization) in American lakes and reservoirs (Gabelhouse 1987, Hardin and Connor 1992, Dumont and Dennis 1997). The high pumpkinseed abundance was, however, linked to low individual growth of larger individuals, when compared with the growth described for several American populations (Fox et al. 2007), and poor condition, particularly in the reservoir with few resources. Conversely, pumpkinseed growth at ages 1 and 2 years was fast and comparable to the growth reported for some American populations living in warmer waters (Fox et al. 2007), suggesting that limitations in profitable food resources could have been more pronounced for larger pumpkinseeds than for smaller ones.

For bass, growth in the reservoirs was comparable to the growth reported at similar latitudes in North America (Beamesderfer and North 1995) but body condition was lower for smaller individuals in the reservoir with lower resources. The delayed transition to piscivory registered in TG may have constrained the survival of bigger individuals, as the littoral catch rate for larger specimens was lower than most catch rates reported in North America (Gabelhouse 1987, Hardin and Connor 1992, Dumont and Dennis 1997).

High resource overlap could be indicative of exploitative competition in animal communities when associated with measurable consequences at the individual and population levels, such as reductions in growth and abundance (Hodgson et al. 1991, He et al. 1994). Although resource overlap was frequently high in the two reservoirs between bass and pumpkinseed and between different pumpkinseed size-classes, the contrasting population characteristics were observed in the two reservoirs, i.e., in TG (lower food availability) vs. MN (higher food availability):
• The lower growth and worst condition of smaller bass and all pumpkinseeds;
• The lower abundance of pumpkinseed and larger bass.
The above characteristics seem to support the occurrence of food competition between pumpkinseed size classes and between smaller bass and pumpkinseed, somewhat mirroring to biotic relations reported for the bass/bluegill association in American ponds and small reservoirs.

Reservoirs present higher environmental variability than natural lakes (Wetzel 1990), something that should limit the overall importance of biotic interactions (Wahl et al. 1995), but the characteristics of studied reservoirs (and of southern Iberian reservoirs in general), with high temperatures (high fish metabolism), presence of simple fish communities without typical zooplanktivores (leaving the pelagic habitat empty) and limitations in littoral invertebrates abundance (related to the water level fluctuations due to reservoir water use), likely contributed to the observed patterns in resource use and overlap.

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