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Ontogenetic Diet Shifts and Interrupted Piscivory in Introduced Largemouth Bass (*Micropterus salmoides*)

key words: exotic species, Centrarchidae, fish, Lake Banyoles, Spain

Abstract

The ecology of largemouth bass (*Micropterus salmoides*) is one of the best known for freshwater fish, though largely through studies within its native range (North America). I studied the habitat and diet of a bass population introduced into a Mediterranean lake. The bass displayed strong ontogenetic diet shifts as follows: young-of-the-year <25 mm fed on microcrustaceans; fish 25–75 mm, on amphipods and insects; fish 100–225 mm, on a freshwater shrimp, small fish and insects; fish 250–300 mm, on shrimp or crayfish; and fish >300 mm, on crayfish and large fish. The diet showed several differences from most previous studies: importance of freshwater shrimp instead of insects, low piscivory, and a delay in the ontogenetic shift to piscivory. Moreover, the ontogenetic shift to piscivory was interrupted at 250–300 mm, with consumption of shrimp and crayfish. This interruption of piscivory has been largely unreported and seems a consequence of the size-structure and species composition of the fish assemblage. A review of the literature suggests that piscivory by largemouth bass might be generally lower in populations introduced outside North America.

1. Introduction

The largemouth bass (*Micropterus salmoides*) is the principal piscivorous fish of North American fresh waters, one of the most important freshwater game fish (HEIDINGER, 1975; CARLANDER, 1977), and hence has been introduced to many countries worldwide (the fifth most frequently introduced inland fish according to WELCOMME, 1992). In many ecosystems, it co-occurs with one or more species of sunfish (*Lepomis* spp.) and the bass-sunfish system of North American lakes is among the best studied freshwater fish assemblages (see WERNER, 1977; WERNER *et al.*, 1977; TURNER and MITTELBACH, 1990; PHILLIPS *et al.*, 1995; OLSON, 1996; and references therein). Nonetheless, studies of populations introduced outside North America are much less common. The small young-of-the-year (YOY) bass prey on zooplankton, typically shifting to insects as they grow and then to fish very early (KEAST and WEBB, 1966; HEIDINGER, 1975; KEAST, 1985; PHILLIPS *et al.*, 1995). The ontogenetic shift to piscivory usually begins at 50–70 mm standard length (SL) (PHILLIPS *et al.*, 1995; OLSON, 1996) and generally bass are almost exclusively piscivores at 80–100 mm (CARLANDER, 1977; WERNER *et al.*, 1977; KEAST, 1985).

In this paper, I describe several divergences from this general pattern for a population of bass introduced into Lake Banyoles. Lake Banyoles is the second largest lake in the Iberian Peninsula and its limnology is well known. This study is part of a comprehensive research on the feeding ecology of the entire fish assemblage (GARCÍA-BERTHOU, 1999*a*, 1999*b*, 2001; GARCÍA-BERTHOU and MORENO-AMICH 2000*b*, 2000*c*). The lake is dominated by exotic species, particularly largemouth bass, pumpkinseed sunfish (*Lepomis gibbosus*),

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and roach (*Rutilus rutilus*) (García-Berthou and Moreno-Amich 2000*a*). I analyse the habitat and diet of this well-established introduced population of bass and discuss patterns that diverge from numerous previous studies, mostly conducted in North America.

2. Methods

2.1. Study Site

Lake Banyoles, situated at 42° 7′ N, 2° 45′ E and 172 m above sea level in Catalonia (Spain), consists of six basins and twelve bottom springs with suspended sediment (see bathymetric map in Moreno-Amich and García-Berthou, 1989). The mainly subterranean water sources and high calcium concentration restrict the lake's productivity. Although usually considered oligotrophic because of its low nutrient concentration and phytoplankton biomass, it is rather mesotrophic based on its primary production and benthic community. Information is available on its morphometry (Moreno-Amich and García-Berthou, 1989), hydrology (Casamitjana and Roget, 1993), bacterioplankton (Garcia-Gil *et al.*, 1996), phytoplankton (Planas, 1973), zooplankton (Miracle, 1976), and non-littoral zoobenthos (Rieradevall, 1991). Selected features of the lake are: surface area, 111.8 ha; mean depth, 14.8 m; water temperature, 7–26 °C; and conductivity, 0.9–2 mS cm^{-1}.

The history of fish introductions and the structure and habitat partitioning of the current assemblage is described by García-Berthou and Moreno-Amich (2000*a*). The littoral zone of Lake Banyoles is dominated in abundance by largemouth bass and pumpkinseed sunfish, and the rest of the lake by roach and common carp (*Cyprinus carpio*). Other exotic fish species such as mosquitofish (*Gambusia holbrooki*), rudd (*Scardinius erythrophthalmus*), and perch (*Perca fluviatilis*) are also present. The most common native species are the freshwater blenny (*Salaria (= Blennius) fluviatilis*) and chub (*Leuciscus cephalus*).

2.2. Field and Laboratory Methods

Fish from Lake Banyoles were sampled in February, May, August, and November 1990. Sampling was by trammel nets (stretched mesh size: inner net, 2 cm; outer, 12.5 cm) and, in the littoral zone, by boat electrofishing. Constant sampling effort was used in different seasons, basins, and depths. Most of the largemouth bass were captured with electrofishing (see Results). Trammel net sizes were 6 × 2 m in the littoral (i.e. set 0–2 m deep) and 20 × 2.5 m in the rest of the lake. Trammel nets were placed at every 5 m of depth and set for 24 h on six consecutive days. We also captured small YOY fish at two littoral sites using dipnets. All captured fish were stored immediately on ice and later frozen.

Resource availability was not directly measured because the zooplankton (Miracle, 1976) and benthos (Rieradevall, 1991) had already been studied. Our sampling points (trammel nets) matched those of the previous benthos study and are detailed elsewhere (García-Berthou, 1999*a*).

In the laboratory, fish were measured (fork length to the nearest mm), eviscerated, and weighed (to the nearest 0.1 g). The stomach was preserved in 70% ethanol until analysis. The stomach contents of all largemouth bass ($n = 261$) were examined under a dissecting microscope. Prey were sorted usually to the species or genus level. Prey were counted and weighed to the nearest 0.1 mg after removing the excess moisture by blotting. The length of prey fish was also measured. The prey of small YOY fish were estimated volumetrically with a haemacytometer and converted to biomass data.

2.3. Data Analyses

Percent number (% number), percent biomass (% biomass), frequency of occurrence, and mean percentage of biomass were used to describe the importance of food categories. % 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 stomach contents of all fish. % biomass is the equivalent measure for biomass data.

Frequency of occurrence is the percentage 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.

Data analyses were performed with SPSS for Windows 7.5. Prey weight and fish length were log-transformed because homoscedasticity and linearity were clearly improved.

2.4. Literature Review

I reviewed the degree of piscivory reported in previous observational field studies. The large variety of ways in which data are reported difficults comparison and synthesis. For instance, fish length data may be reported as histograms, means, or medians, whereas diet data may be reported as frequency of occurrence, % number, % biomass, or mean percentage of biomass (or biovolume). I chose maximum length of fish analysed and frequency of occurrence of piscivory because they were the most commonly available in papers ($n = 13$). When a range of piscivory occurrence was reported (for several groups), I considered the midpoint of the range. I analysed these data with a multiple regression model of piscivory occurrence (dependent variable) as a function of maximum fish length, sample size (number of fish analysed) and geographical region (in or outside North America). Since geographical region was a categorical factor, this model is mathematically identical to an analysis of covariance.

3. Results

3.1. Size Structure and Habitat Use

Mean fork length (FL) of largemouth bass was 150.6 mm (SE = 4.2, range 11–519). There was seasonal variation in size structure of bass (ANOVA, $F_{3, 257} = 4.01$, $P = 0.008$): mean length was smaller in summer due to the abundance of YOY fish (length < 50 mm, Fig. 1). Most of the bass were captured at the surface with electrofishing (239 of 261) and only one bass was captured at depths of more than 2 m.

3.2. Ontogenetic and Seasonal Variation in Diet

The most important prey of largemouth bass were freshwater shrimp (*Atyaephyra desmaresti*), amphipods (*Echinogammarus* sp.), red swamp crayfish (*Procambarus clarkii*), and fish (Table 1). The freshwater shrimp dominated the diet by number and occurrence. Because of their much larger size, roach and crayfish were more important by biomass but were consumed by a few, large bass (Fig. 1).

The importance of these prey items was highly dependent on season and bass length (Fig. 1). Thus, freshwater shrimp was very dominant in diet in autumn and winter but barely consumed in summer, when it was replaced with insects (ephemeropteran nymphs and all stages of nematocerans) and small fish (mosquitofish and freshwater blenny).

The ontogenetic diet shifts were marked and can be summarised as follows (Fig. 1). YOY bass less than 25 mm long fed on microcrustaceans (mainly the cladocerans *Daphnia longispina* and *Ceriodaphnia reticulata*, and cyclopoid copepods); fish 25–75 mm, on amphipods and insects; fish 100–225 mm, on freshwater shrimp and, particularly in summer, small fish and insects; fish 250–300 mm, on shrimp or crayfish; and fish >300 mm, on crayfish and large fish (mostly roach 110–140 mm long).

There was a close relationship between the sizes of bass and their prey, and prey size changed by about 5–7 orders of magnitude over ontogeny (Fig. 2). This size-selectivity was even present within two prey (freshwater shrimp and crayfish) of bass (Fig. 3). The crayfish consumed by a given size of bass were much heavier than shrimps.

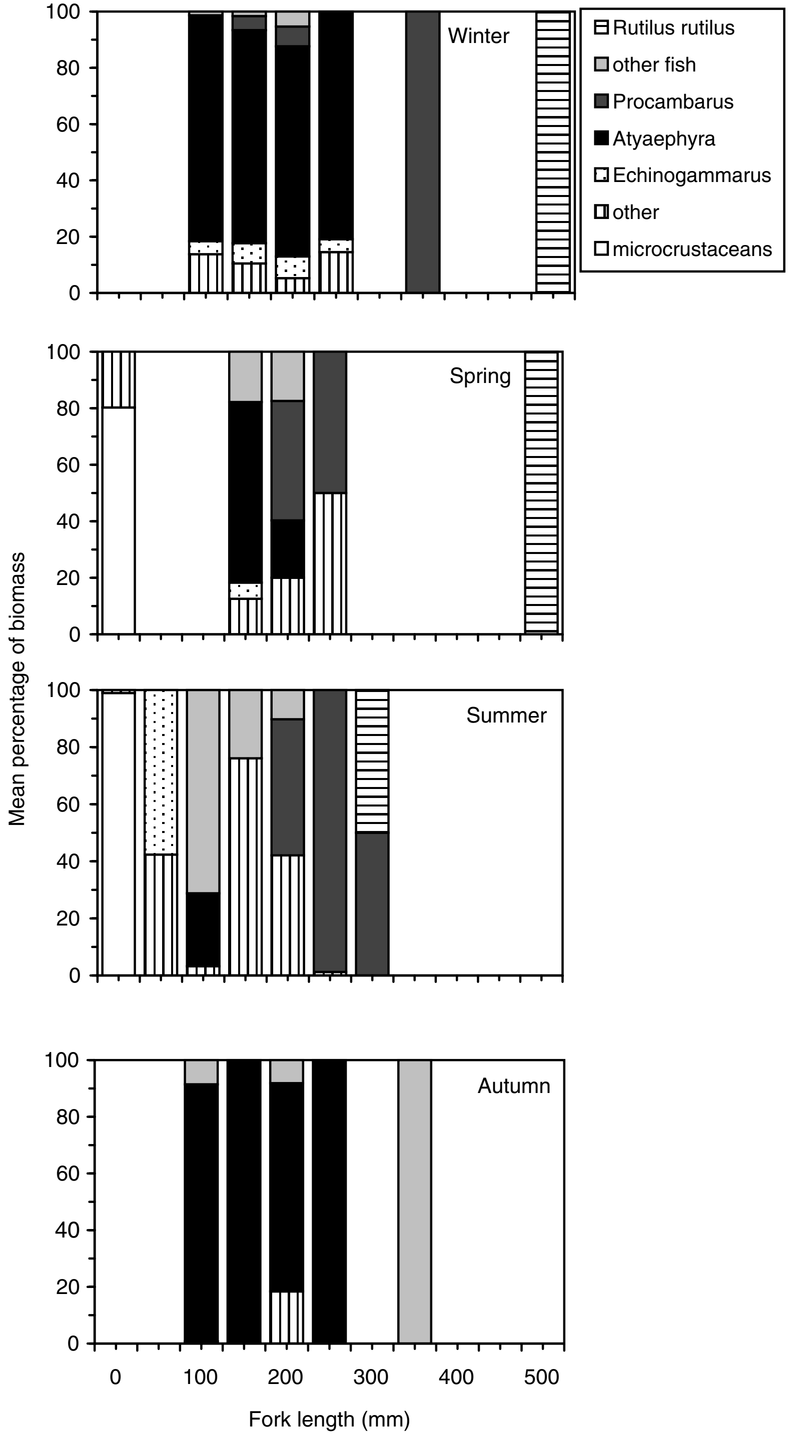

Figure 1. Ontogenetic and seasonal variation in the main food categories of largemouth bass in Lake Banyoles. Data are the percentage of stomach content biomass, averaged for 50 mm-length classes of bass.

Table 1. Diet of largemouth bass in Lake Banyoles: % number, % biomass, and frequency of occurrence of the main food components.

Food category	% number	% biomass	Frequency of occurrence
Algae and plant debris	0.34	0.05	14.2
Digested material	–	0.39	14.6
Cladocera and Copepoda	4.6	0.00	4.6
Echinogammarus sp.	14.5	0.24	36.4
Atyaephyra desmaresti	47.9	5.39	75.5
Procambarus clarkii	0.92	9.9	5.8
Nematocera larvae and pupae	5.2	0.01	11.9
Nematocera exuviae	5.0	0.00	4.2
Nematocera adults	7.2	0.02	19.5
Ephemeroptera	4.8	0.04	15.7
Other insecta	6.6	0.17	19.2
Other invertebrates	0.75	0.05	3.5
Rutilus rutilus	0.34	82.5	1.9
Other fish	1.8	1.2	6.5

Number of stomachs analysed = 261; total number of prey in the stomach contents = 1,740; total biomass = 278.4 g.

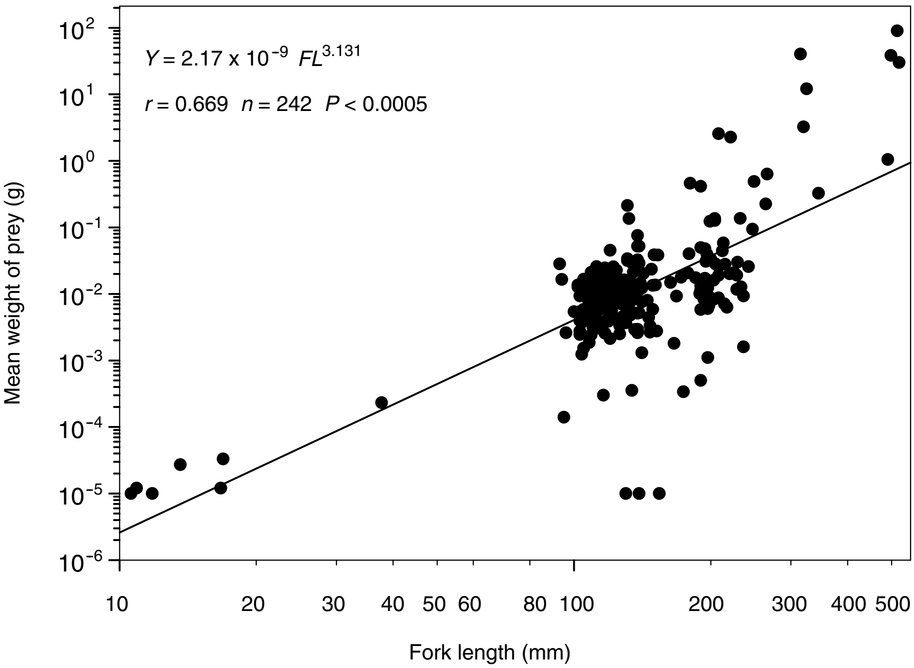

Figure 2. Relationship between mean weight of prey and length of largemouth bass.

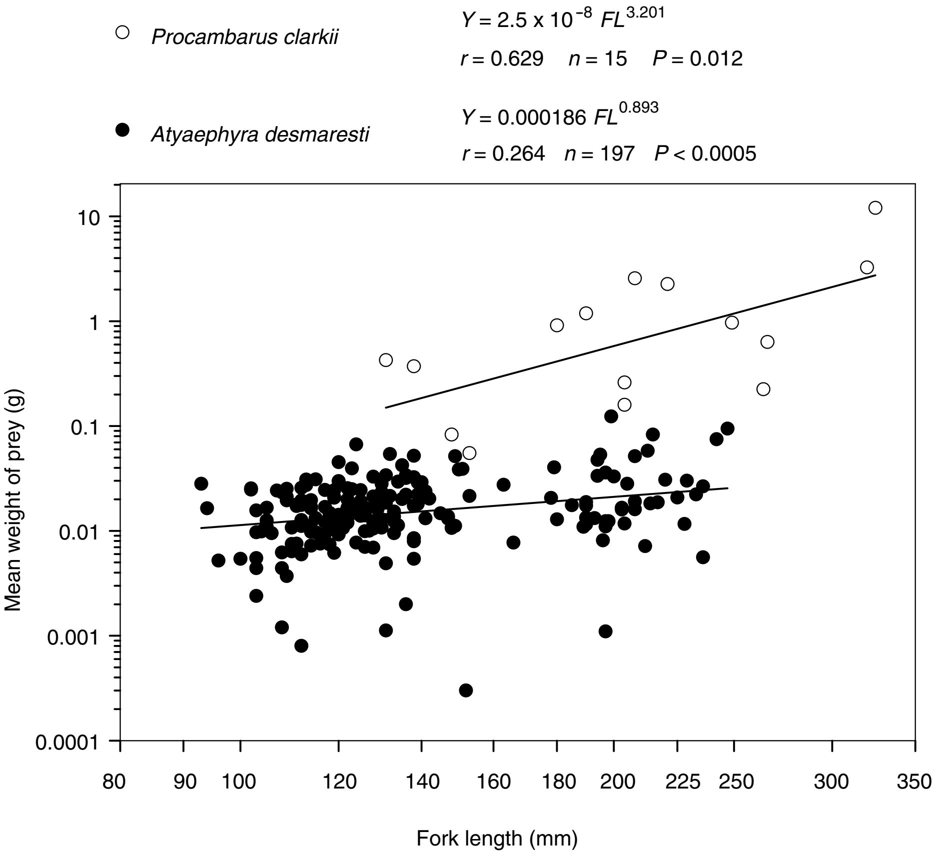

Figure 3. Relationship between the length of largemouth bass and the size of two prey (*A. desmaresti* and *P. clarkii*).

Among the fish captured by bass, I found mosquitofish, blenny, and roach. No bass or pumpkinseed sunfish were detected in bass diet although they were abundant in the lake (Fig. 4) and dominant in the littoral (GARCÍA-BERTHOU and MORENO-AMICH, 2000*a*). Interestingly, there were two stages of piscivory: mosquitofish and blenny (8–39 mm long) were found in bass ranging 110–212 mm in length and roach were eaten by 315–519 mm bass. At 250–300 mm, bass preyed on shrimp (in autumn and winter) or crayfish (Fig. 1). Although bass were more piscivorous in summer, this interruption of piscivory took place in all seasons (Fig. 5).

4. Discussion

4.1. Degree of Piscivory and Species-Specific Vulnerability to Predation

The diet of largemouth bass in Lake Banyoles showed several differences from most other populations previously studied. First, the usual ontogenetic diet shift is zooplankton – in-

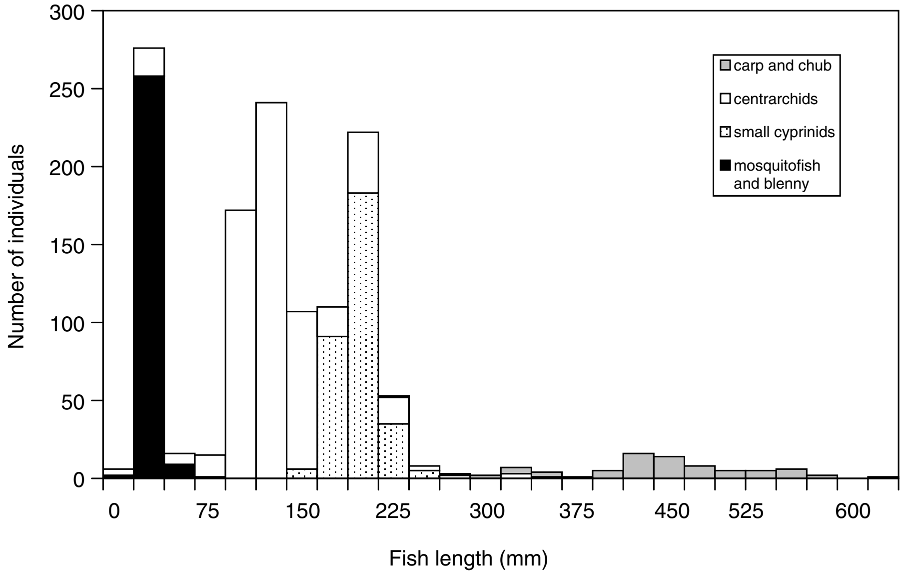

Figure 4. Size structure of the fish assemblage of Lake Banyoles (data from GARCÍA-BERTHOU and MORENO-AMICH 2000*a*). The total number of fish captured by species group from February 1990 to November 1991 is shown. The centrarchids are largemouth bass and pumpkinseed sunfish; small cyprinids are roach and rudd. Length data are fork length, except for mosquitofish and freshwater blenny (total length). Three rare fish species are not included.

sects and small fish – crayfish and fish (KEAST and WEBB, 1966; HEIDINGER, 1975; KEAST, 1985; PHILLIPS *et al.*, 1995), whereas in Lake Banyoles a freshwater shrimp was very important and largely replaced insects. This shrimp was hardly consumed by other fish species in the lake (GARCÍA-BERTHOU, 1999*a*, 1999*b*; GARCÍA-BERTHOU and MORENO-AMICH, 2000*b*, 2000*c*), probably because of its relatively large size, and thus represents a competitive refuge for bass.

Another peculiarity is the low degree of piscivory by bass in Lake Banyoles. The occurrence of piscivory in the lake (8.4%) was much lower than in most other field studies that included large bass (Fig. 6). A multiple regression analysis of the literature data (Fig. 6) showed a significant positive effect of maximum length of the fish analysed ($P = 0.009$), whereas sample size ($P = 0.42$) and geographical region ($P = 0.40$) were not significant. The dependency of piscivory on maximum length is a bit disturbing because it might be due to an interesting pattern (greater piscivory in populations dominated by larger individuals) and/or to sampling efficiency (low piscivory in studies that mostly captured small fish). Although geographical region was not significant (probably due to few studies outside North America), the effect of length was only significant for studies in North America, where piscivory was higher.

The low piscivory in Lake Banyoles seems clearly related to the low availability of suitable prey fish in the lake, as it was in another exotic population (HICKLEY *et al.*, 1994). This low availability is likely due to the low productivity of Lake Banyoles and to the species composition of the fish assemblage. Thus, among the fish captured by bass, I found mosquitofish, blenny, and roach. Although bass and pumpkinseed sunfish are the most common

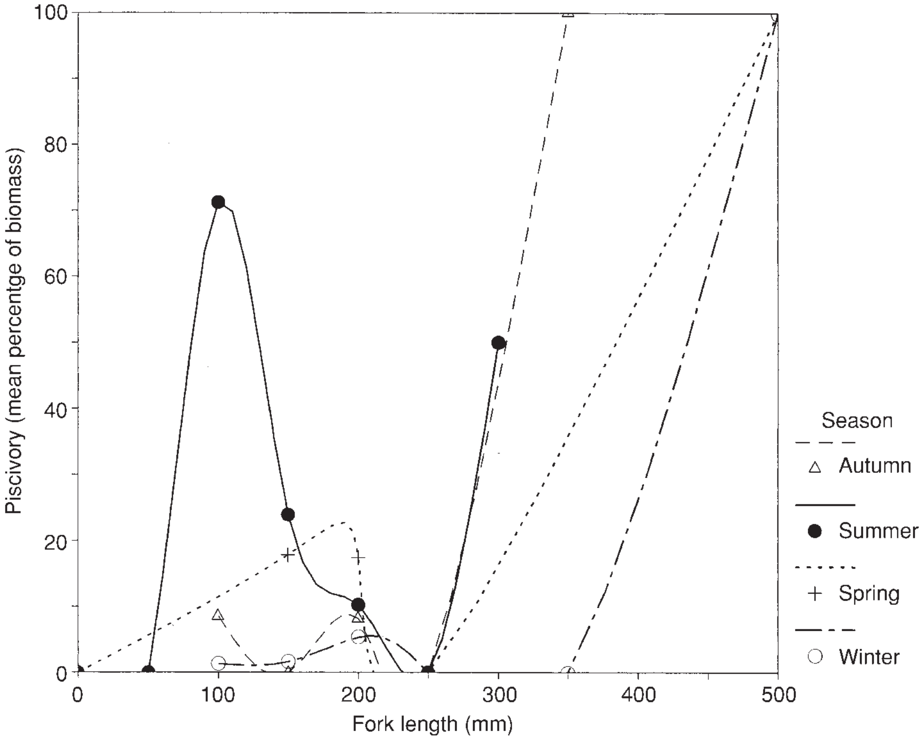

Figure 5. Ontogenetic and seasonal variation in piscivory by largemouth bass. Data are based on Fig. 1, pooling "other fish" and roach.

fish in the littoral of the lake (GARCÍA-BERTHOU and MORENO-AMICH, 2000*a*), they were not detected in bass diet. Sunfish species are less vulnerable to predation by bass than medium-sized cyprinids (such as roach) and other species (such as mosquitofish or blenny) because of: their anti-predator behaviour; large body depth; and spiny rays in dorsal and anal fins, which increase the cost of capture, apparent size, and the possibility of injuries during ingestion (HOYLE and KEAST, 1987; SAVINO and STEIN, 1989; HAMBRIGHT, 1991). The much larger mean size of cyprinids than of pumpkinseed in the lake (Fig. 4) reflects this greater vulnerability of small cyprinids, suggesting stronger predation pressure on them by large bass. The size structure of the pumpkinseed sunfish population (Fig. 4; see also GARCÍA-BERTHOU and MORENO-AMICH, 2000*b*) is also consistent with the fact that the vulnerability of bluegill (*L. macrochirus*), a congener similar in morphology, is very low above 75 mm SL (WERNER and HALL, 1988), implying a size refuge (SAVINO and STEIN, 1989; TURNER and MITTELBACH, 1990; HAMBRIGHT *et al.*, 1991). The maximum size of pumpkinseeds ingested by large bass (275 mm SL) was 75 mm SL in feeding trials (HAMBRIGHT, 1991), whereas mean size of pumpkinseed in Lake Banyoles was 119 mm FL (GARCÍA-BERTHOU and MORENO-AMICH, 2000*b*).

As in HICKLEY *et al.* (1994), the low piscivory was associated with a delay in the shift to piscivory. The most pronounced shift to piscivory usually occurs in YOY bass of 50–70 mm SL (PHILLIPS *et al.*, 1995; OLSON, 1996) and bass are almost exclusively piscivores at 80–100 mm (CARLANDER, 1977; WERNER *et al.*, 1977; KEAST, 1985). In contrast, the smallest piscivorous bass in Lake Banyoles was 106 mm FL.

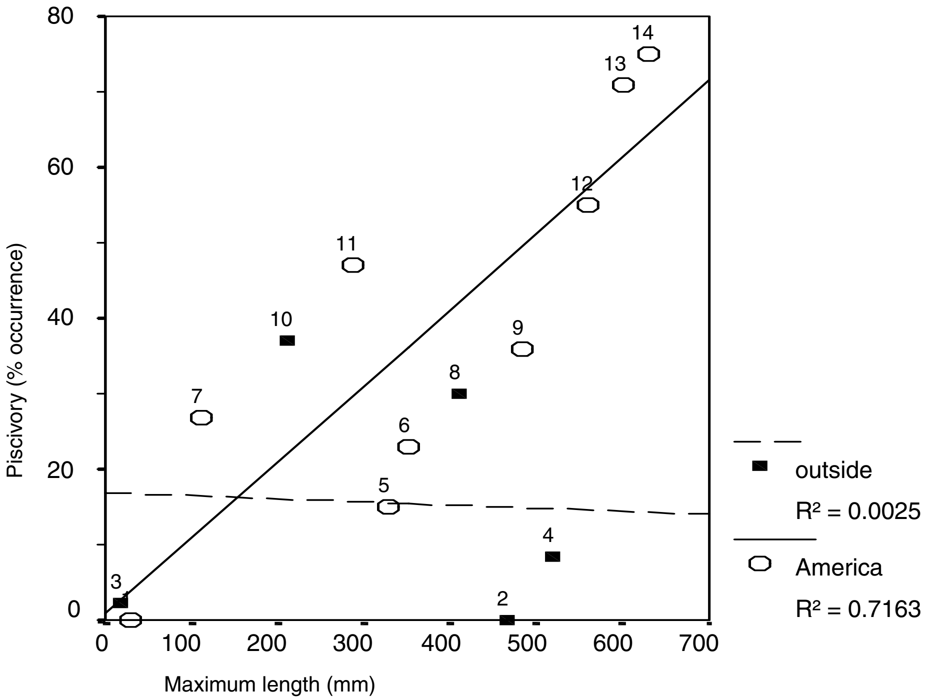

Figure 6. Dependence of piscivory on size structure (maximum length of fish analysed) in previous field studies of largemouth bass diet. Studies in and outside North America are distinguished. The figure above the point indicates the study number: 1 = ELLIOTT (1976), 2 = HICKLEY *et al.* (1994), 3 = RODRÍGUEZ-JIMÉNEZ (1989), 4 = this study, 5 = HODGSON and KITCHELL (1987), 6 = GODINHO and FERREIRA (1998), 7 = HAMILTON and POWLES (1979), 8 = NICOLA *et al.* (1996), 9 = LEWIS *et al.* (1974), 10 = PRENDA and MELLADO (1993), 11 = WERNER (1977), 12 = MINCKLEY (1982), 13 = GILLILAND and CLADY (1981), 14 = GODINHO and FERREIRA (1994).

4.2. The Interruption of the Ontogenetic Shift to Piscivory

Another singularity of bass in Lake Banyoles was that the ontogenetic shift to piscivory was interrupted at 250–300 mm, with consumption of shrimp (in autumn and winter) or crayfish. 110–212 mm bass preyed on mosquitofish and blenny (8–39 mm long), whereas bass >300 mm preyed on 110–140 mm roach. This interruption of piscivory coincides with the dominance of centrarchids among fish 75–150 mm in size (Fig. 4) and supports the low availability of suitable prey fish. Although less marked, a similar pattern is also observable in the data on Lake Naivasha (HICKLEY *et al.*, 1994) but has been previously unnoticed. Lake Naivasha and Lake Banyoles share a low richness of fish species, which might explain this pattern that contrasts with previous studies in North America. Bass grows much faster after switching to piscivory and the timing of this shift thus affects survival and recruitment rates (CARLANDER, 1977; PHILLIPS *et al.*, 1995; OLSON, 1996). Predation on crayfish instead of fish probably implies also a change to a more benthic microhabitat and different foraging behaviour. The numerous singularities observed in this bass population and in Lake Naivasha suggest that the feeding ecology of introduced populations of bass partially differs from that in North America and deserves further attention.

The low, delayed, and interrupted piscivory of introduced bass does not imply a negligible impact on native fish populations, since piscivory was probably much stronger in the initial stages of introduction. Moreover, complex interactions among bass, small fish and crayfish have been shown to mediate the behaviour and vulnerability of small fish (RAHEL and STEIN, 1988).

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6. References

CARLANDER, K. D., 1977: Handbook of freshwater fishery biology. 2. Life history data on centrarchid fishes of the United States and Canada. – Iowa State University Press, Ames, Iowa.

CASAMITJANA, X. and E. ROGET, 1993: Resuspension of sediment by focused groundwater in Lake Banyoles. – Limnol. Oceanogr. **38**: 643–656.

ELLIOTT, G. V., 1976: Diel activity and feeding of schooled largemouth bass fry. – Trans. Amer. Fish. Soc. **105**: 624–627.

GARCÍA-BERTHOU, E., 1999*a*: Spatial heterogeneity in roach (*Rutilus rutilus*) diet among contrasting basins within a lake. – Arch. Hydrobiol. **146**: 239–256.

GARCÍA-BERTHOU, E., 1999*b*: Food of introduced mosquitofish: ontogenetic diet shift and prey selection. – J. Fish. Biol. **55**: 135–147.

GARCÍA-BERTHOU, E. and R. MORENO-AMICH, 2000*a*: Introduction of exotic fish into a Mediterranean lake over a 90-year period. – Arch. Hydrobiol. **149**: 271–284.

GARCÍA-BERTHOU, E. and R. MORENO-AMICH, 2000*b*: Food of introduced pumpkinseed sunfish: ontogenetic diet shift and seasonal variation. – J. Fish. Biol. **57**: 29–40.

GARCÍA-BERTHOU, E. and R. MORENO-AMICH, 2000*c*: Rudd (*Scardinius erythrophthalmus*) introduced to the Iberian peninsula: feeding ecology in Lake Banyoles. – Hydrobiologia **436**: 159–164.

GARCÍA-BERTHOU, E., 2001: Size- and depth-dependent variation in habitat and diet of the common carp (*Cyprinus carpio*). – Aquat. Sci. **63**: 466–476.

GARCIA-GIL, L. J., X. CASAMITJANA and C. A. ABELLA, 1996: Comparative study of two meromictic basins of Lake Banyoles (Spain) with sulphur phototrophic bacteria. – Hydrobiologia **319**: 203–211.

GILLILAND, E. R. and M. D. CLADY, 1981: Diet overlap of striped bass X whitebass hybrids and largemouth bass in Sooner Lake Oklahoma. – Proceedings of the Annual Conference of the Southeastearn Association of Fish and Wildlife Agencies **35**: 317–330.

GODINHO, F. N. and M. T. FERREIRA, 1994: Diet composition of largemouth black bass, *Micropterus salmoides* (Lacépède), in southern Portuguese reservoirs: its relation to habitat characteristics. – Fisheries Management and Ecology **1**: 129–137.

GODINHO, F. N. and M. T. FERREIRA, 1998: Spatial variation in diet composition of pumpkinseed sunfish, *Lepomis gibbosus*, and largemouth bass, *Micropterus salmoides,* from a Portuguese stream. – Folia Zoologica **47**: 205–213.

HAMBRIGHT, K. D., 1991: Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. – Trans. Amer. Fish. Soc. **120**: 500–508.

HAMBRIGHT, K. D., R. W. DRENNER, S. R. MCCOMAS and N. G. JR. HAIRSTON, 1991: Gape-limited piscivores, planktivore size refuges, and the trophic cascade hypothesis. – Arch. Hydrobiol. **121**: 389–404.

HAMILTON, J. G. and P. M. POWLES, 1979: Feeding habits and growth of young-of-the-year largemouth bass (*Micropterus salmoides*) near its northern limit, Nogies Creek, Ontario. – Can. J. Zool. **57**: 1431–1437.

HEIDINGER, R. C., 1975: Life history and biology of the largemouth bass. – *In*: STROUD, R. H. and CLEPPER, H. (ed.). Black bass biology and management. Sport Fishing Institute, Washington, D. C.: 11–20.

HICKLEY, P., R. NORTH, S. M. MUCHIRI and D. M. HARPER, 1994: The diet of largemouth bass, *Micropterus salmoides*, in Lake Naivasha, Kenya. – J. Fish. Biol. **44**: 607–619.

HODGSON, J. R. and J. F. KITCHELL, 1987: Opportunistic foraging by largemouth bass (*Micropterus salmoides*). – Am. Midl. Nat. **118**: 323–336.

HOYLE, J. A. and A. KEAST, 1987: The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). – Can. J. Zool. **65**: 1972–1977.

KEAST, A. and D. WEBB, 1966: Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. – Journal of the Fisheries Research Board of Canada **23**: 1845–1874.

KEAST, A., 1985: The piscivore feeding guild of fishes in small freshwater ecosystems. – Environmental Biology of Fishes **12**: 119–129.

LEWIS, W. M., R. HEIDINGER, W. KIRK, W. CHAPMAN and D. JOHNSON, 1974: Food intake of the largemouth bass. – Trans. Amer. Fish. Soc. **103**: 277–280.

MINCKLEY, W. L., 1982: Trophic interrelations among introduced fishes in the lower Colorado River, southwestern United States. – California Fish and Game **68**: 78–89.

MIRACLE, M. R., 1976: Distribución en el espacio y en el tiempo de las especies del zooplancton del lago de Banyoles. – Monografías ICONA **5**: 1–270.

MORENO-AMICH, R. and E. GARCÍA-BERTHOU, 1989: A new bathymetric map based on echo-sounding and morphometrical characterization of the Lake of Banyoles (NE-Spain). – Hydrobiologia **185**: 83–90.

NICOLA, G. G., A. ALMODÓVAR and B. ELVIRA, 1996: The diet of introduced largemouth bass, *Micropterus salmoides*, in the Natural Park of the Ruidera Lakes, Central Spain. – Polskie Archiwum Hydrobiologii **43**: 179–184.

OLSON, M. H., 1996: Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. – Ecology **77**: 179–190.

PHILLIPS, J. M., J. R. JACKSON and R. L. NOBLE, 1995: Hatching date influence on age-specific diet and growth of age-0 largemouth bass. – Trans. Amer. Fish. Soc. **124**: 370–379.

PLANAS, D., 1973: Composición, ciclo y productividad del fitoplancton del lago de Banyoles. – Oecologia **1**: 1–106.

PRENDA, J. and E. MELLADO, 1993: Características biológicas y espectro trófico durante el otoño de dos poblaciones simpátricas de *Blennius fluviatilis* y *Micropterus salmoides* en un embalse pequeño. – Limnética **9**: 107–115.

RAHEL, F. J. and R. A. STEIN, 1988: Complex predator-prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. – Oecologia **75**: 94–98.

RIERADEVALL, M., 1991: Ecologia i producció del bentos del llac de Banyoles. – Ph.D. dissertation, University of Barcelona, Barcelona, Spain.

RODRÍGUEZ-JIMÉNEZ, A. J., 1989: Hábitos alimenticios de *Micropterus salmoides* (Pisces: Centrarchidae), *Lepomis gibbosus* (Pisces: Centrarchidae) y *Gambusia affinis* (Pisces: Poeciliidae) en las orillas del embalse de Proserpina (Extremadura, España). – Limnética **5**: 13–20.

SAVINO, J. F. and R. A. STEIN, 1989: Behavioural interactions between fish predators and their prey: effects of plant density. – Anim. Behav. **37**: 311–321.

TURNER, A. M. and G. G. MITTELBACH, 1990: Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. – Ecology **71**: 2241–2254.

WELCOMME, R. L., 1992: A history of international introductions of inland aquatic species. – ICES mar. Sci. symp. **194**: 3–14.

WERNER, E. E., 1977: Species packing and niche complementarity in three sunfishes. – Am. Nat. **111**: 553–578.

WERNER, E. E., D. J. HALL, D. R. LAUGHLIN, D. J. WAGNER, L. A. WILSMANN and F. C. FUNCK, 1977: Habitat partitioning in a freshwater fish community. – J. Fish. Res. Bd Can. **34**: 360–370.

WERNER, E. E. and D. J. HALL, 1988: Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. – Ecology **69**: 1352–1366.

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