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Food of introduced pumpkinseed sunfish: ontogenetic diet shift and seasonal variation

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The pumpkinseed sunfish *Lepomis gibbosus* introduced into Lake Banyoles (Spain) were predominantly littoral but there was a tendency of large fish to use deeper zones. Their diet was dominated by littoral macrobenthos, particularly amphipods (*Echinogammarus* sp.). There was ontogenetic variation in the diet, with small young-of-the-year (L_F<4 cm) feeding on several littoral microcrustaceans, especially the cladoceran *Ceriodaphnia reticulata*, whereas larger fish shifted to a freshwater shrimp (*Atyaephyra desmaresti*), snails and damselfly larvae. Seasonal variation in diet was linked to resource availability, with consumption of fish eggs and plant debris in spring and summer. In autumn, pumpkinseeds were partially zooplanktivores, preying on the cladoceran *Daphnia longispina*. The diet of pumpkinseeds in Lake Banyoles and other Iberian populations shows less molluscivory than North American populations. The potential ecological impact of this successful exotic species involves mainly predation on fish eggs and molluscs.

Key words: Centrarchidae; *Lepomis gibbosus*; exotic species; Iberian peninsula; Lake Banyoles.

INTRODUCTION

The pumpkinseed sunfish *Lepomis gibbosus* (L.) is a North American centrarchid fish that was introduced into Europe around 1880. It is among the most successful fish introduced into European countries (Holčík, 1991; Welcomme, 1991), particularly in reservoirs and coastal wetlands (Crivelli & Mestre, 1988; García de Jalón *et al.*, 1993). The largemouth bass *Micropterus salmoides* (Lacépède)–sunfish *Lepomis* spp. system of North American lakes is among the best known freshwater fish assemblages (Werner & Hall, 1979; Mittelbach *et al.*, 1992; Osenberg *et al.*, 1992). However, the only published literature on pumpkinseed sunfish diet in Europe is Zapata & Granado-Lorencio (1993), Godinho *et al.* (1997) (only summer data), and two reports of a few individuals (Brabrand & Saltveit, 1989, 35 fish from spring; Rodríguez-Jiménez, 1989, 48 fish from summer).

Introduction of pumpkinseed into the Iberian Peninsula dates back to 1910–1913, having started in Lake Banyoles, the basin studied in this paper (García-Berthou & Moreno-Amich, 2000). 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, 1994, 1999*a*,*b*). The lake is dominated by exotic species,

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particularly largemouth bass, pumpkinseed sunfish, and roach *Rutilus rutilus* (L.) (García-Berthou & Moreno-Amich, 2000). The research's goal is to assess the ecological role of the exotic species and their relationship with native species. In this paper, we analyse the habitat and diet of a well-established population of pumpkinseeds introduced into a Mediterranean lake and compare it with previous studies, mostly from North America. The potential ecological impact of pumpkinseed is also discussed.

METHODS

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 12 bottom springs with suspended sediment (see bathymetric map in Moreno-Amich & García-Berthou, 1989). The mainly subterranean water sources and high calcium concentration restrict the lake's productivity. Although usually considered oligotrophic because of the low nutrient concentration and phytoplankton biomass, it is rather mesotrophic based on its primary production and its benthic community. Information is available on its morphometry (Moreno-Amich & García-Berthou, 1989), hydrology (Casamitjana & Roget, 1993), bacterioplankton (Garcia-Gil *et al.*, 1996), phytoplankton (Planas, 1973), zooplankton (Miracle, 1976), and non-littoral zoobenthos (Rieradevall, 1991). The history of introductions and the structure and habitat partitioning of the current assemblage is described by García-Berthou & Moreno-Amich (2000). 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* L. Other exotic fish species such as mosquitofish *Gambusia holbrooki* Girard, rudd *Scardinius erythrophthalmus* (L.), and perch *Perca fluviatilis* L. are also present. The most common native species are the freshwater blenny *Blennius fluviatilis* Asso and chub *Leuciscus cephalus* (L.).

FIELD AND LABORATORY METHODS

Fish from Lake Banyoles were sampled in February, May, August, and November 1991. Sampling was by boat electrofishing in the littoral zone and with trammel nets (stretched mesh size: inner net 2 cm; outer 12·5 cm). Constant sampling effort was used in different seasons and basins. Trammel net sizes were 6 × 2 m in the littoral (i.e. set at 0–2 m deep) and 20 × 2·5 m in the rest of the lake. Limnetic trammel nets were placed at 5, 10, and 15 m of depth and bottom trammel nets at 10 and 20 m (or 15 m for shallower basins). Nets were set for 24 h on six consecutive days. Young-of-the-year (YOY) fish were captured also at two littoral sites using dipnets. All captured fish were stored immediately on ice and later frozen.

Resource availability was not measured directly because the zooplankton (Miracle, 1976) and benthos (Rieradevall, 1991) had been studied already. The sampling points (limnetic and bottom trammel nets) matched those of the previous benthos study and are detailed elsewhere (García-Berthou, 1994, 1999*a*).

In the laboratory, fish were measured (fork length to the nearest mm), eviscerated, and weighed (to the nearest 0·1 g). The entire gut was preserved in 70% ethanol until analysis. The stomach contents of all pumpkinseeds ($n=384$) 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 prey of YOY fish were estimated volumetrically with an haemocytometer and converted to biomass data.

DATA ANALYSES

Per cent number (% number), per cent biomass (% biomass), and frequency of occurrence were used to estimate the dietary importance of each food category.

% 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. To describe prey importance and feeding strategy, Costello's (1990) graphical method was used, i.e. a plot of % number or % biomass with frequency of occurrence. The most important prey are closer to the top right corner. The other diagonal corresponds to feeding strategy; prey with low occurrence but dominant by number or biomass correspond to some sort of specialization and are closer to the top left corner. Mean percentage biomass was computed also for pooled food categories as the percentage of stomach content for a certain food category averaged for all the fish in a size class. Digested material was not considered for the computation of mean percentage biomass.

Detrended correspondence analysis (CA) was used to describe the main sources of diet variation (ter Braak, 1987). This technique has two main advantages over the conventional procedures of dietary data analysis: (1) instead of pooling food categories *a priori* (often according to taxonomic rather than to ecological criteria), CA groups similar food categories based on common occurrence (Graham & Vrijenhoek, 1988); and (2) relevant factors are not selected *a priori* by the researcher; instead, CA identifies the axes explaining the highest proportion of variation, including measured and unmeasured factors (García-Berthou, 1999*a*). Although it is not generally used for dietary data, CA is the standard method of data analysis in community ecology (ter Braak, 1987) and generally performs better than other ordination methods such as factor analysis (principal component analysis). CA was performed with MVSP 3.1 (Multi-Variate Statistical Package, Kovach Computing Services) on the prey number data. Correlation analysis and analysis of variance were used to interpret the axes in terms of the measured spatio-temporal coordinates of the fish samples. Empty guts are intrinsically excluded by CA.

Size structure and mean percentage of biomass were analysed by analysis of covariance, ANCOVA (García-Berthou & Moreno-Amich, 1993). Mean percentage biomass was arcsin-transformed and fish length was log-transformed because homoscedasticity and linearity were improved clearly. Data analyses were performed with SPSS for Windows 6.0.

RESULTS

SIZE STRUCTURE AND HABITAT USE

Mean length of pumpkinseeds was 119 mm (range 19–176). Though pumpkinseeds were predominantly littoral (Fig. 1), the few fish that inhabited deeper zones were large (standard design of ANCOVA of length with depth as covariate and season as factor, $F_{1,379}=30{\cdot}8$, $P<0{\cdot}0005$). This ontogenetic habitat shift did not vary with season (ANCOVA test of homogeneity of slopes, $F_{2,377}=0{\cdot}34$, $P=0{\cdot}71$), in spite of seasonal variation in mean size (standard design of ANCOVA, $F_{3,379}=7{\cdot}7$, $P<0{\cdot}0005$). Identical statistical conclusions were obtained when considering only trammel net data, so these patterns were not due to different sampling methods.

PUMPKINSEED FOOD

Amphipods (*Echinogammarus* sp.) were by far the most important prey for pumpkinseeds (Fig. 2; Table I). Less notable food were plant debris and several littoral macroinvertebrates, namely *Microtendipes* sp. (Chironomidae), trichopterans (*Ecnomus* sp. and Leptoceridae), and *Micronecta meridionalis* (Heteroptera).

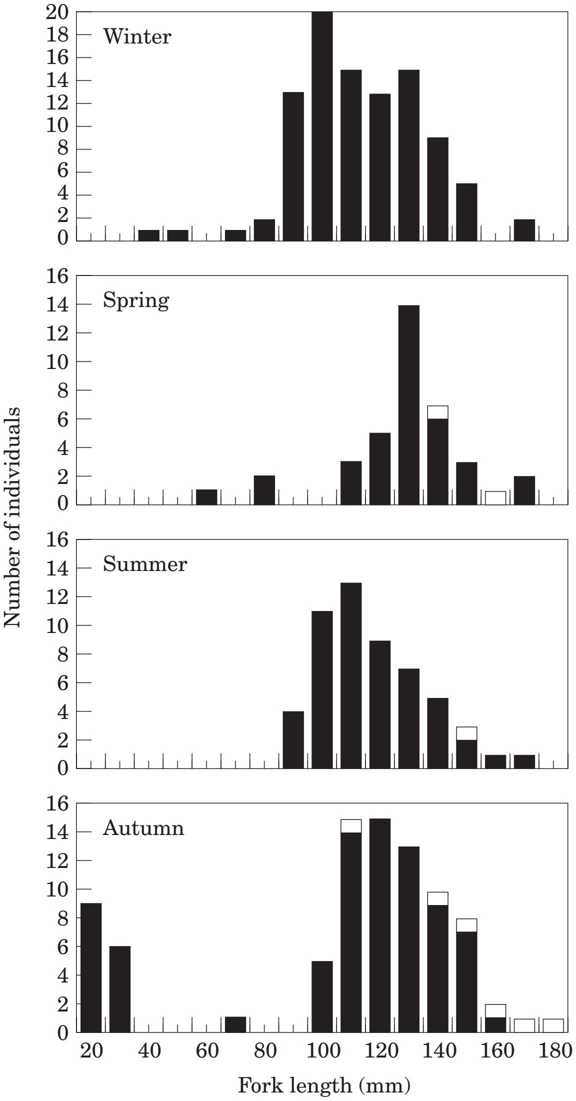

FIG. 1. Length-frequency distribution of pumpkinseeds of Lake Banyoles by season and depth (■, 0–2 m; □, 10–15 m).

The relationship among number, biomass, and occurrence (Fig. 2) already pointed to some feeding variation among individuals, which was confirmed by other methods (see below). First, some prey (e.g. the cladocerans *Ceriodaphnia reticulata* and *Daphnia longispina*, the cyclopoid copepod *Tropocyclops prasinus*, and plant seeds) were very important by number but not by occurrence (i.e. consumed by few individuals). *Ceriodaphnia reticulata* and *T. prasinus* were littoral zooplankton, mostly consumed by YOY pumpkinseeds. Other food categories were important by biomass but with low occurrence, such as the freshwater shrimp *Atyaephyra desmaresti*, the larvae of the damselfly

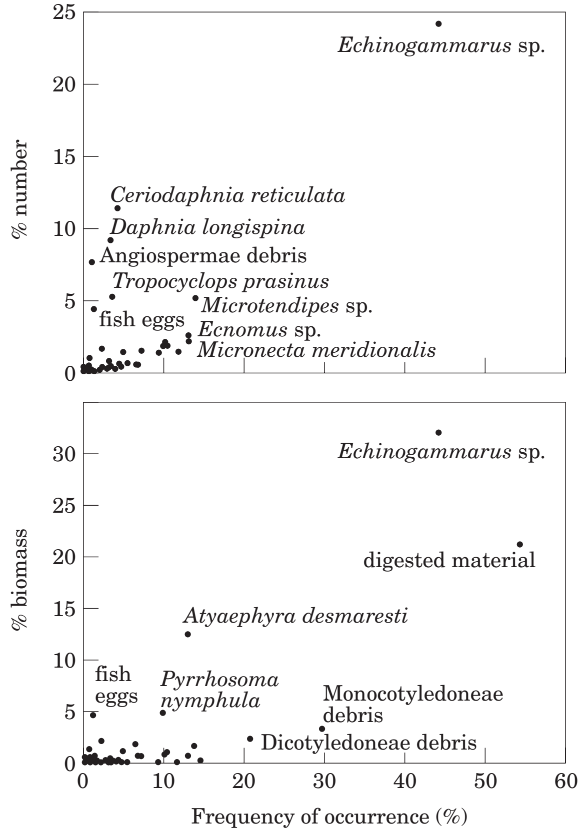

FIG. 2. Relationship among % number, % biomass, and frequency of occurrence of the food categories in pumpkinseed diet. Plots based on Costello's (1990) method. The most important food categories are detailed.

Pyrrhosoma nymphula, and fish eggs. These three food categories and *D. longispina* show seasonal variation in pumpkinseed diet (see below).

DIET VARIATION

For detrended correspondence analysis of prey number, the first two axes explained globally 24% of the variance (eigenvalues=0·872 and 0·465). The first axis (hereafter *CA1*) distinguished on the left the smallest prey species, basically littoral microcrustaceans such as copepods (*T. prasinus*) and especially cladocerans (*C. reticulata*, *Chydorus sphaericus*, *Scapholeberis rammneri*, *Alonella exigua*, *Bosmina longirostris*, and *Pleuroxus laevis*) (Fig. 3). On the right of *CA1* the largest prey were distinguished, such as amphipods, the freshwater shrimp, and other macroinvertebrates. *CA1* fish scores were correlated significantly with fork length ($r=0{\cdot}48$, $n=275$, $P<0{\cdot}0005$) because the microcrustaceans dominated the stomachs of the smallest pumpkinseeds (15 YOY of length <4 cm), whereas the consumption of the largest prey increased with fish size (see also Fig. 4).

The second axis (hereafter *CA2*) distinguished the freshwater shrimp and snails (*Acroloxus lacustris*, *Mercuria confusa*, and *Physella acuta*) on top and several insect species on the bottom (Fig. 3). *CA2* fish scores varied significantly with

TABLE I. Diet of pumpkinseed sunfish in Lake Banyoles: % number, % biomass, and frequency of occurrence of the main food components

Food category	% number	% biomass	Frequency of occurrence
Algae	0·4	1·5	3·1
Plant debris	—	5·9	39·8
Plant seeds	7·8	0·1	1·8
Digested material	—	21·2	54·2
Ceriodaphnia reticulata	11·4	0·1	4·2
Daphnia longispina	9·3	0·5	3·4
Echinogammarus sp.	24·4	31·9	44·0
Atyaephyra desmaresti	2·2	12·4	13·0
Other Crustacea	7·8	0·1	9·4
Odonata nymphs	2·9	6·5	18·2
Ephemeroptera	4·6	1·7	17·5
Trichoptera	5·1	1·8	21·9
Nematocera	13·4	5·3	33·9
Other Insecta	2·3	1·1	18·5
Mollusca	3·3	3·8	18·5
Other invertebrates	0·3	0·7	3·4
Fish	0·1	0·8	1·3
Fish eggs	4·5	4·7	1·3

Number of stomachs analysed=384; total number of prey in the stomach contents=5728; total biomass=12·3 g.

season (ANOVA, $F_{3,271}=9{\cdot}7$, $P<0{\cdot}0005$) and were not correlated with fish length ($r=-0{\cdot}08$, $n=275$, $P=0{\cdot}20$). Mean *CA2* fish scores by season (Fig. 3) indicate that the freshwater shrimp and snails were consumed more in winter, whereas insects were more important in summer.

A more conventional way of analysing diet variation (Fig. 4) agrees with the results of CA. The use of amphipods and snails increased significantly and microcrustaceans decreased significantly with ontogeny (ANCOVA of the percentage of biomass with length and season as sources of variation, $P<0{\cdot}05$). All food categories except snails and fish eggs varied significantly with season (ANCOVA, $P<0{\cdot}0005$). The shrimp was more important in winter, amphipods more important in autumn and less in summer, plant material more important in summer and less in autumn, and the other category (mostly insects) dominated in summer (Fig. 4). Adult pumpkinseeds only consumed microcrustaceans (zooplanktonic *D. longispina*) in autumn.

DISCUSSION

SEASONAL VARIATION AND RESOURCE AVAILABILITY

The diet of pumpkinseeds in Lake Banyoles, based on littoral macrobenthos, was similar to those of North American populations (Keast, 1978; Laughlin & Werner, 1980; Mittelbach, 1984; Fox & Keast, 1990; Mittelbach *et al.*, 1992; Osenberg *et al.*, 1992). In Lake Banyoles, however, some pumpkinseeds were

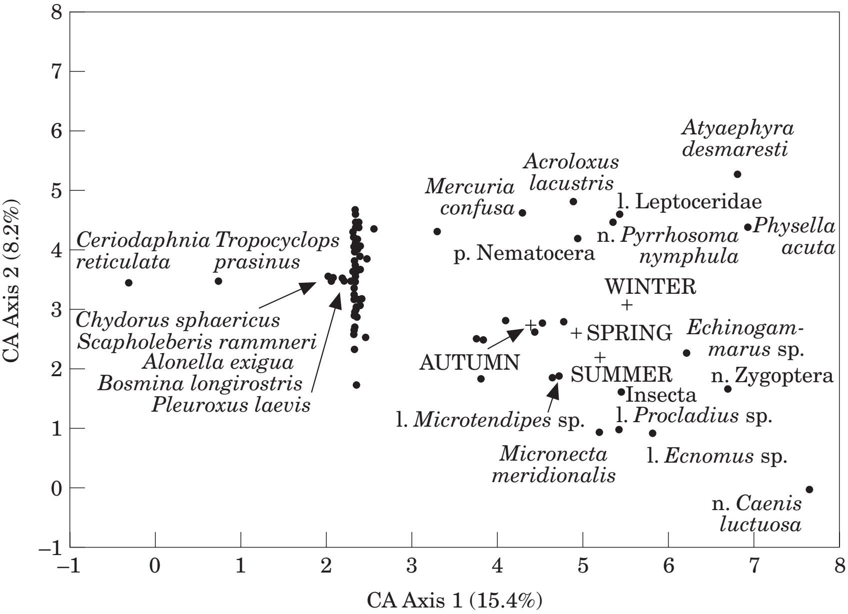

FIG. 3. Detrended correspondence analysis of stomach contents (prey number) of pumpkinseeds: food category scores (●) for the first and second axes and mean fish scores (+) by season. l, larvae; n, nymphs; p, pupae.

zooplanktivores in autumn, feeding on *D. longispina*. This cladoceran is more abundant in the lake in autumn (Miracle, 1976) and, thus, the seasonal variation in diet is related to resource availability. The spring diet of pumpkinseeds in Portuguese reservoirs consisted of zooplankton also, mostly *Daphnia* sp. (Brabrand & Saltveit, 1989). The dominance of large cladocerans in the zooplanktivorous diet is common (Werner & Hall, 1979; Mittelbach, 1984). Pumpkinseeds are less efficient zooplanktivores than bluegill sunfish *Lepomis macrochirus* Rafinesque and most other sunfish species besides the bluegill rarely feed on zooplankton (Werner & Hall, 1979). In the absence of bluegill, pumpkinseeds assume greater zooplanktivory (Robinson *et al.*, 1993). However, in Lake Banyoles roach fed more on zooplankton (García-Berthou, 1999*a*) than did pumpkinseed, suggesting the former species is a more efficient zooplanktivore.

Amphipods in the sublittoral zone (5–7 m deep) of Lake Banyoles are more abundant in June and November and less in August (Rieradevall, 1991). This explains the higher consumption of amphipods by pumpkinseed in November and lower in August.

In many temperate lakes, there is more use of non-animal food (i.e. plant debris, vegetation, and detritus) by roach in summer due to increased resource limitation (Persson, 1983; Persson & Greenberg, 1990). The same tendency was observed for both roach (García-Berthou, 1999*a*) and pumpkinseeds in Lake Banyoles. Resource availability is a crucial factor in fish foraging and probably the rest of seasonal variation in Lake Banyoles also corresponds to resource availability.

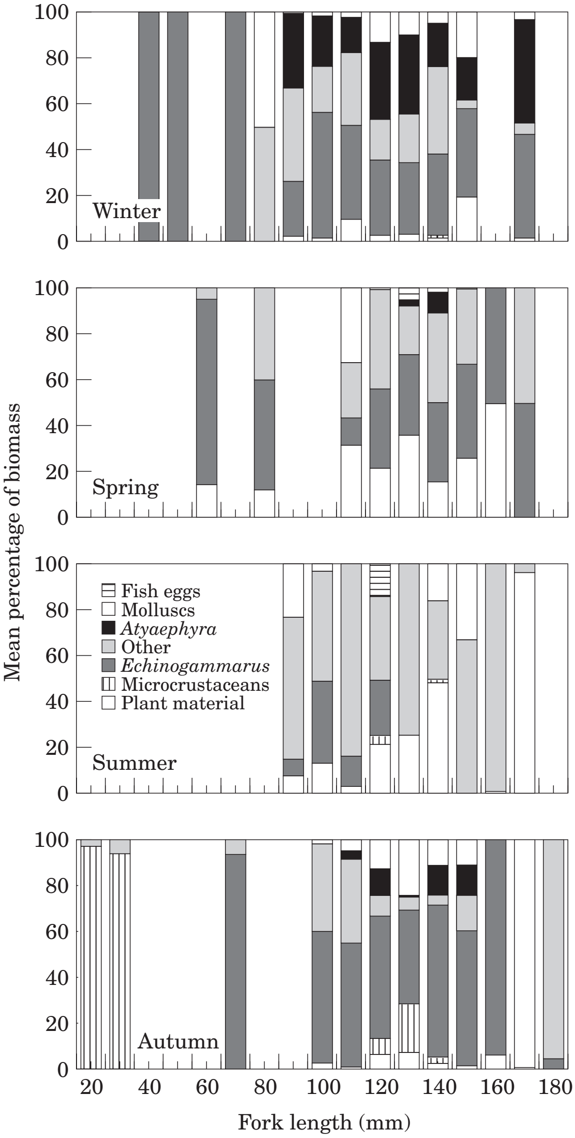

FIG. 4. Ontogenetic and seasonal variation in the main food categories of pumpkinseed diet. Data are the percentage of stomach content biomass, averaged for 10 mm length classes of pumpkinseed.

ONTOGENETIC DIET SHIFT AND MOLLUSCIVORY

This study has demonstrated ontogenetic variation in the pumpkinseed sunfish diet. Small YOY fish preyed on littoral microcrustaceans, while most of the population fed on littoral macrobenthos, particularly amphipods, and the largest individuals shifted to larger prey, especially a freshwater shrimp, snails and damselfly larvae. Ontogenetic variation in diet is common for pumpkinseeds (Keast, 1978), though generally they change from soft-bodied (fish <4·5 cm L_S) to hard-bodied invertebrates, basically snails (fish >7·5 cm L_S). In our study, molluscs appeared in the diet also at this fish size (Fig. 4). This food shift almost parallels sexual maturation and allows consideration of the adult as a molluscivore, particularly of snails (Mittelbach *et al.*, 1992; Osenberg *et al.*, 1992). Mean percentage biomass of molluscs in diet of pumpkinseeds is often >70% (Keast, 1978; Laughlin & Werner, 1980; Osenberg & Mittelbach, 1989; Fox & Keast, 1990; Osenberg *et al.*, 1992). This ontogenetic diet shift allows a resource partitioning with other species and generates higher growth rates (Osenberg *et al.*, 1992). Thus snails are a competitive refuge for adult pumpkinseeds (Laughlin & Werner, 1980; Mittelbach, 1984).

The ontogenetic variation in this study lake was related only weakly to the use of molluscs, which were not as important overall in the pumpkinseed diet (Table I). Molluscs were even less important in the pumpkinseeds of the Guadiana river (Godinho *et al.*, 1997) and Spanish reservoirs (Rodríguez-Jiménez, 1989; Zapata & Granado-Lorencio, 1993). Molluscs are not abundant in Lake Banyoles (Rieradevall, 1991) because macrophytes are scarce due to scarcity of shallow habitat. Calcium concentration, which is high in the lake, and vegetation are essential factors for snails (Mittelbach *et al.*, 1992; Osenberg *et al.*, 1992). Comparative studies of lakes in Michigan and Wisconsin (Mittelbach *et al.*, 1992) have shown that the importance of molluscs in the diet is correlated strongly with their availability.

However, less is known on pumpkinseed foraging when snails are scarce (Osenberg *et al.*, 1992). Snails are not the preferred prey of adult pumpkinseeds in absolute terms, but a food item consumed less by other predators and thus valuable when resources are more limited. For example, pumpkinseeds preferred odonate larvae or a cladoceran (*Simocephalus* sp.) in rich ponds (Laughlin & Werner, 1980).

THE POTENTIAL IMPACT OF PUMPKINSEED INTRODUCTION

The actual impact of exotic species is generally impossible to ascertain because precise data before the introduction are usually lacking (Taylor *et al.*, 1984; Ross, 1991). This is true for most introduced species and populations, including Lake Banyoles, which was the first site on the Iberian peninsula where pumpkinseed sunfish was introduced. The pumpkinseed is now common and widespread in the Iberian peninsula, particularly in reservoirs and coastal wetlands. The most obvious potential impact of pumpkinseed introduction involves egg predation and molluscivory. The consumption of fish eggs by pumpkinseeds is a popular concern (García de Jalón *et al.*, 1993). In Lake Banyoles the use of fish eggs was considerable by number and biomass (Table I). The low occurrence is due to its limitation to the spawning season, i.e. spring or early summer for all fish species in the lake. Of the five pumpkinseeds with fish eggs in the stomach, four were caught in August, when only pumpkinseed was spawning in the lake (Vila-Gispert & Moreno-Amich, 1998). Therefore, pumpkinseed predation on fish eggs was intraspecific. As is the case for mosquitofish piscivory (Meffe, 1985), the importance of egg predation is probably underestimated because of rapid digestion and strong effects even at low predation rates.

Another obvious potential impact of pumpkinseeds is on molluscs. It has been demonstrated experimentally and by historical and comparative data that pumpkinseed predation controls and reduces snail abundance (Osenberg *et al.*, 1992). Pumpkinseeds can also change the morphology and life history traits of some snails (DeWitt, 1998). This impact could be particularly dramatic in Lake Banyoles, where some endemic mollusc subspecies exist (Altaba, 1992), and less severe in reservoirs, where snails are generally scarce because of poor development of vegetation due to water level fluctuation. However, the low molluscivory detected for Iberian populations of pumpkinseed suggests that the high success of this exotic species does not depend on molluscivory.

The actual impact of pumpkinseed sunfish remains uncertain. Nonetheless, the abundance and widespread distribution of pumpkinseed suggest that studies documenting European freshwater ecosystems before and after the introduction of this species are urgently needed.

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