



Food of introduced mosquitofish: ontogenetic diet shift and prey selection

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The mosquitofish *Gambusia holbrooki* of Lake Banyoles, Catalonia, Spain, were strictly littoral. Their population was dominated by females throughout the year, except in spring when males were more common. Their diet was based on littoral cladocerans, particularly *Chydorus sphaericus*, *Scapholeberis rammeri*, *Ceriodaphnia reticulata*, and *Pleuroxus laevis*, and nematoceran (basically chironomid) adults. There was a large variety of prey of terrestrial (collembolans, ants) or aquatic neustonic origin (*S. rammeri*, emerging nematoceran adults), showing the microhabitat of mosquitofish closely linked to the water surface. In contrast to other studies, terrestrial insects were not especially important in summer. In addition to seasonal and between-site variation, there was an ontogenetic diet shift from microcrustaceans, particularly cladocerans (smallest fish also using diatoms and copepod nauplii) to larger prey, namely nematoceran adults. However, there was an unusual, inverse relationship between fish length and the size of two prey (*S. rammeri* and the collembolan *Sminthurides* sp.), parallelling the overall increase in mean prey size.

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Key words: mosquitofish; *Gambusia holbrooki*; feeding; Lake Banyoles; Spain.

INTRODUCTION

Two species of mosquitofish *Gambusia affinis* (Baird & Girard) and *G. holbrooki* Girard have been introduced to 40 countries to control mosquitoes, a vector of malaria. Often they have been regarded as sub-species (*G. affinis affinis* and *G. affinis holbrooki*) but Wooten *et al.* (1988) proposed to return them to the original taxonomic designations as separate species and this change has been accepted widely. Although much of the literature refers to *G. affinis*, without specifying the sub-species, many populations are *G. holbrooki* (Wooten *et al.*, 1988; Haynes & Cashner, 1995). In area occupied, it is probably the most widely distributed freshwater fish (Krumholz, 1948; Murdoch & Bence, 1987), although it is native only to the United States and Mexico. However, little is known about their ecology (Hurlbert *et al.*, 1972; Hurlbert & Mulla, 1981; Meffe & Snelson, 1989). Research on mosquitofish feeding is particularly scarce although it is crucial to determine the impact of its introduction. The only published literature on mosquitofish diet in Europe seems to be Crivelli & Boy (1987) and that of a few individuals in Rodríguez-Jiménez (1989).

The present study investigated the feeding ecology of the fish assemblage of Lake Banyoles, the second largest lake in the Iberian peninsula. This lake is dominated by exotic species, including mosquitofish, roach *Rutilus rutilus* (L.),

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largemouth bass *Micropterus salmoides* (Lacépède), and pumpkinseed sunfish *Lepomis gibbosus* (L.). This paper describes the diet and feeding variation of mosquitofish introduced into a Mediterranean lake and compares them with previous studies, mostly from North America.

MATERIALS AND METHODS

STUDY AREA

Lake Banyoles, situated at 42°7' N, 2°45' E and 172 m above sea level in Catalonia (north-eastern Spain), is of mixed tectonic-karstic origin. The lake is structured in several basins with contrasting ecological features, containing bottom springs with suspended sediment (see bathymetric map in Moreno-Amich & García-Berthou, 1989). The mainly subterranean water sources and high calcium concentration restrict its 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 (García-Gil *et al.*, 1996), phytoplankton (Planas, 1973), zooplankton (Miracle, 1976), and non-littoral zoobenthos (Prat & Rieradevall, 1995). This paper is part of a comprehensive study on the feeding ecology of the entire fish assemblage (García-Berthou, 1994, 1999). The littoral of Lake Banyoles is dominated by largemouth bass and pumpkinseed sunfish and the rest by roach and common carp *Cyprinus carpio* L. Other exotic fish species such as rudd *Scardinius erythrophthalmus* (L.), and perch *Perca fluviatilis* L. are also present, while freshwater blenny *Blennius fluviatilis* Asso and chub *Leuciscus cephalus* (L.) are the most common native species.

FIELD AND LABORATORY METHODS

Mosquitofish from Lake Banyoles were sampled quarterly from June 1990 to February 1991. Of 254 mosquitofish captured, 235 were caught by dipnets from two sites: (1) Tunes mouth, a small tributary of the lake dominated by cattail beds (*Typha angustifolia australis* and *Typha latifolia*) and leaf litter (mostly from *Platanus × hybrida* trees); and (2) Vilar channel, connecting Lake Banyoles and Lake Vilar and dominated by submerged macrophytes, particularly *Myriophyllum verticillatum*. Other mosquitofish (19) were captured by boat electrofishing in the littoral. All captured fish were stored immediately on ice and later frozen.

In the laboratory, fish were measured (total length, L_T , to the nearest 0.1 mm) and weighed (to the nearest 0.1 mg). The entire gut was preserved in 70% ethanol, sex was determined by gonad examination, and the eviscerated fish were weighed. The gut contents of all captured mosquitofish were examined under a dissecting microscope. Prey were sorted usually to the species or genus level. Prey were counted and the volume of food categories was estimated to the nearest 0.00025 mm³ with a Neubauer counting chamber (haemocytometer).

DATA ANALYSES

Per cent number, per cent biovolume, and frequency of occurrence were used to estimate the dietary importance of each food category. Per cent number is the number of individuals of a prey type divided by the total number of individuals and expressed as a percentage, after pooling the gut contents of all fish. Per cent biovolume is the equivalent measure for biovolume data. Frequency of occurrence is the percentage of guts where a food category was present. The graphical method of Costello (1990) was used to describe prey importance and feeding strategy. Diet diversity (for each fish) was measured with the complement of Simpson's index (D), calculated as

$$D = 1 - \sum_i \frac{n_i(n_i - 1)}{N(N - 1)}$$

where n_i is the number of individuals of prey type i , and N is the total number of prey (Hurlbert, 1971).

Correspondence analysis (CA) was used to describe the main sources of diet variation, separately for number and biovolume data. CA is an ordination technique that reduces a species \times sample matrix to a few dimensions explaining most of the variation. For community ecology data, CA generally performs better than principal component analysis (ter Braak, 1987). CA is better than the traditional procedure of *a priori* pooling food categories, which is based usually on taxonomic rather than on ecological criteria (Graham & Vrijenhoek, 1988). A few food categories were excluded from the CA because they dominated the first solutions as outliers due to very low occurrence but relatively high number or biovolume. Only the 235 fish from the two main sampling sites were used for CA in order to simplify analysis and interpretation. Correlation analysis and analysis of variance (ANOVA) of the sample (fish) scores were used to interpret the dimensions in terms of the measured features of the samples (fish length, sampling site, and season).

Dietary descriptors were analysed with analysis of covariance (ANCOVA) (García-Berthou & Moreno-Amich, 1993). Pillai's trace was preferred as a multivariate statistic because it is the most robust and powerful for most practical situations (Hand & Taylor, 1987). Most variables were log-transformed because homoscedasticity and linearity were clearly improved. All factors (e.g. season, basin) of linear models were considered as fixed effects (i.e. model I). All data analyses were performed with SPSS for Windows 6.0.

RESULTS

HABITAT USE AND POPULATION STRUCTURE

Mosquitofish were strictly littoral and only abundant in zones of the lake shore with dense cover, particularly the mouths of tributaries and inlets. The number captured (Fig. 1) was more constant in Vilar channel and lower in Tunes mouth in spring and summer (test of independence: $G_3=18.3$, $P=0.0004$), probably because of low water level of the latter. Females were much larger than males (three-way ANOVA of mosquitofish length: $F_{2,217}=31.7$; $P<0.0005$) and the two sites differed in size structure ($F_{1,217}=15.4$; $P<0.0005$) and its seasonal variation (season \times site: $F_{3,217}=11.8$; $P<0.0005$). The population was dominated by juvenile individuals during the reproductive season (spring and summer) but larger fish inhabited Tunes mouth (Fig. 1).

The sex ratio varied seasonally (heterogeneity test, $P<0.05$). The sex ratio always differed significantly from 1:1 (G tests, $P<0.05$) except in autumn. Females were generally more abundant, except in spring when males were more common (Fig. 1).

MOSQUITOFISH FOOD

The main mosquitofish prey were littoral cladocerans, particularly *C. sphaericus*, *S. ramneri*, *C. reticulata*, and *P. laevis*, and nematoceran (largely chironomids and *Chaoborus flavicans*) adults (Table I, Fig. 2). Many prey were: (1) from terrestrial origin (i.e. mostly captured at the water surface), such as spiders, collembolans (*Anurophorus* sp., *Lepidocyrtus* sp., *Odontella* sp., and *Dicyrtomina* sp.), Mallophaga, Aphidoidea, unidentified homopterans, Thysanoptera (*L. cerealium*, *T. angusticeps*), ants (*T. pygmaeum*, *H. eduardi*, *Lasius* sp., and *L. niger*), unidentified Hymenoptera, and Brachycera adults; and (2) aquatic neuston, such as *Sminthurides* sp. (Collembola), heteropterans (*M.*

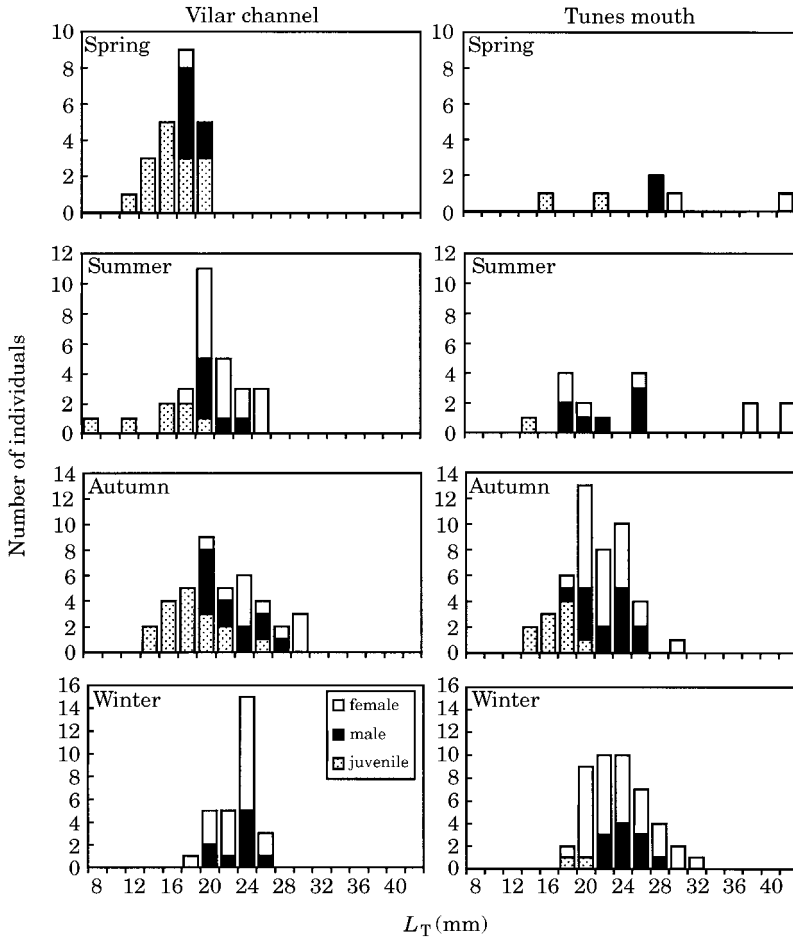


FIG. 1. Length-frequency distribution of mosquitofish by season and sex category at the two main sampling sites (Vilar channel and Tunes mouth).

meridionalis, unidentified Gerromorpha, *M. vittigera*, and *M. pygmaea*), nematoceran adults (important in diet), cladoceran ephippia, and *S. ramneri* (the most important cladoceran in the diet).

The relationship among dietary descriptors (Fig. 2) suggested some feeding variation. Some prey, such as diatoms, *S. ramneri*, and *C. reticulata* were more important by number than by occurrence (i.e. consumed by few individuals). *Scapholeberis ramneri*, *C. reticulata*, and also nematoceran adults were more important by biovolume than by occurrence. These four prey taxa were also distinguished by the correspondence analysis (see Diet Variation, below).

DIET VARIATION

From the correspondence analysis of prey number, the first two dimensions (Fig. 3) explained 11% of the variance. The first dimension (hereafter, *D1*) was related significantly to fish length ($r=0.16$; $n=215$; $P=0.02$). There was a significant site effect (two-way ANOVA: $F_{1,207}=29.0$; $P<0.0005$) and

TABLE I. Diet of mosquitofish in Lake Banyoles: % number, % biovolume, and frequency of occurrence of the main food components

Food category	% number	% biovolume	Frequency of occurrence
Algae	47.2	0.18	18.9
Plant debris	—	0.27	6.3
Digested material	—	46.6	76.0
Nematoda	5.35	0.16	18.1
<i>Ceriodaphnia reticulata</i>	5.50	4.37	15.0
<i>Scapholeberis ramneri</i>	8.87	6.02	20.1
<i>Daphnia longispina</i>	1.45	1.90	3.5
<i>Pleuroxus laevis</i>	3.85	2.48	8.3
<i>Alonella exigua</i>	1.46	0.35	13.0
<i>Chydorus sphaericus</i>	6.51	2.71	30.3
Other Cladocera	1.33	0.73	10.6
Copepoda	7.63	4.67	46.1
Other Crustacea	0.27	2.17	4.3
Collembola	1.31	1.11	15.7
Chironomidae larvae	0.53	0.51	9.8
Nematocera adults	3.75	15.3	36.6
Other Diptera	0.58	1.81	11.0
Other Insecta	2.46	8.11	31.5
Other invertebrates	1.93	0.55	17.3

Number of guts analysed=254; total number of prey in the gut contents=6023; total biovolume=184.5 mm³.

site \times season interaction ($F_{3,207}=8.3$; $P<0.0005$) on $D1$ scores but not a significant season effect ($F_{3,207}=1.2$; $P=0.33$). Of the 24 fish with lowest $D1$ scores, which were smaller than 26 mm, 17 were from Tunes mouth and only seven from Vilar. The food of those small fish from Tunes mouth consisted of small items (diatoms and copepod nauplii) and cladocerans (*D. longispina* and *A. rectangula*) (Fig. 3).

The second dimension ($D2$) was not related significantly to length ($r=0.13$; $n=215$; $P=0.07$) but to season (ANOVA, $F_{3,207}=58.7$; $P<0.0005$), site ($F_{1,207}=7.4$; $P=0.007$), and their interaction ($F_{3,207}=12.1$; $P<0.0005$). Fish with high $D2$ were individuals captured during autumn and winter particularly at Tunes mouth, and had consumed chydorid cladocerans such as *P. laevis* (only at Vilar), *C. sphaericus*, and *A. exigua* and other prey such as cyclopoid copepods (undetermined and *Eucyclops* sp.) (Fig. 3). Fish with low $D2$ were from Vilar channel and spring (or some from autumn) and consumed prey common in the littoral such as *S. ramneri* and *C. reticulata* and, secondarily, rotifers (*K. quadrata quadrata* and *L. quadridentata*).

The results of CA for biovolume data were quite similar and thus are not shown here. They distinguished (1) fish from Vilar in summer, feeding on *D. longispina* and diatoms, (2) small fish from Vilar in autumn and spring, feeding on *S. ramneri*, *C. reticulata*, and rotifers.

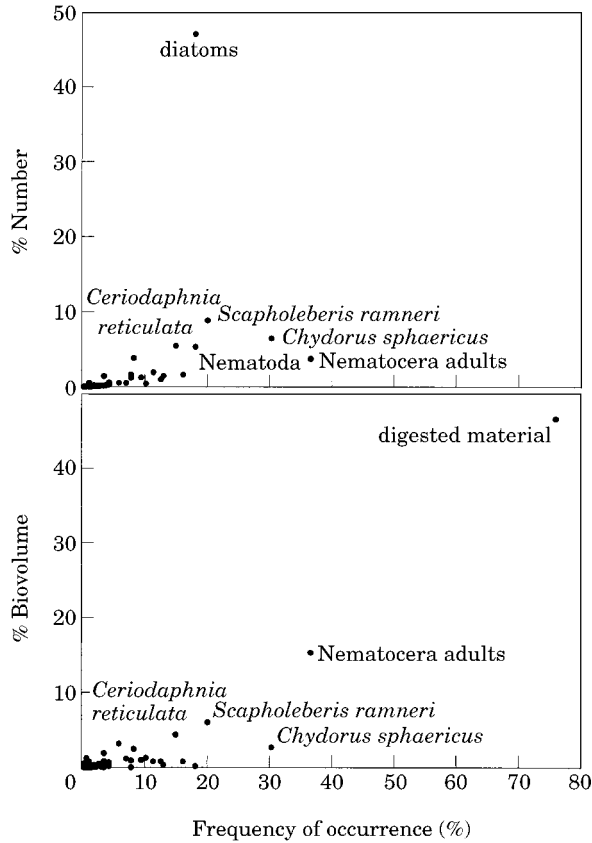


FIG. 2. Relationship among % number, % biovolume, and frequency of occurrence of the main components of mosquitofish diet. Plots based on Costello's method. Detailed food categories are the most important dietary items.

ONTOGENETIC SHIFT AND SEASONAL VARIATION IN DIET

Additional insight into the relative contribution of ontogeny and season to variation in diet was obtained with some simple descriptors (Table II). The parallelism assumption, i.e. homogeneity of slopes (García-Berthou & Moreno-Amich, 1993), was satisfied for the multivariate test and all variables ($P > 0.10$, length \times season interaction), so the standard ANCOVA design (Table II) was appropriate. Although multivariate tests were significant, total number of prey and diversity showed no significant variation, suggesting that these variables were not relevant to the diet of this mosquitofish population. Total biovolume increased significantly with length (Table II, Fig. 4) but showed no seasonal variation. Mean volume of prey also increased with length but also showed seasonal variation, prey size being largest in summer and smallest in winter. Number of food categories was not related significantly to length but varied seasonally and decreased from spring (mean = 5.2) to winter (mean = 3.5).

In the analysis of the relationship between mean prey volume and mosquitofish length independently for each prey category, only two neustonic prey showed significant correlations (Fig. 5). Surprisingly, these two prey

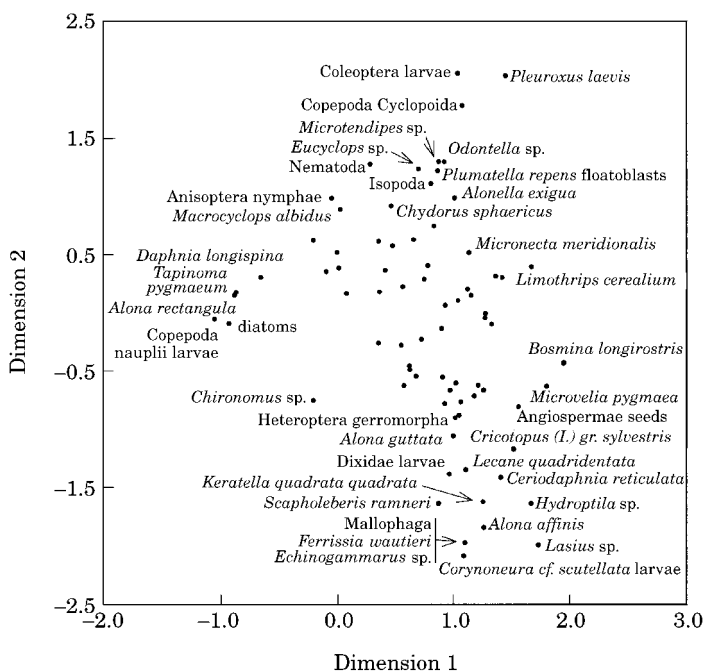


FIG. 3. Correspondence analysis of gut contents (prey number) of mosquitofish: food category scores for the first and second dimensions.

showed a negative correlation, corresponding with fish mainly from Vilar channel and spring or autumn. Therefore, these data imply that the overall positive correlation reported above between mean volume of prey and mosquitofish length is largely interspecific; i.e. the ontogenetic shift to larger prey involves a change in prey categories.

When applying CA to spring data from Vilar channel, the first two dimensions explained 35% of the variance. The first dimension was related significantly to fish length ($r=0.57$; $n=23$; $P=0.005$), in contrast to the second dimension ($r=-0.11$; $n=23$; $P=0.63$). Thus this analysis differentiated, in a single sample, smaller mosquitofish preying on cladocerans, particularly *S. ramneri*, nematoceran larvae (*Chironomus* sp., Dixidae, Ceratopogonidae), diatoms, and a collembolan (*Sminthurides* sp.) from larger mosquitofish feeding on nematoceran adults.

DISCUSSION

POPULATION STRUCTURE OF MOSQUITOFISH

Many poeciliids are sexually dimorphic, with females larger, hardier, and longer-lived than males, this producing biased adult sex ratios (Haynes & Cashner, 1995). The life history of mosquitofish in Lake Banyoles was similar to other populations of *G. holbrooki* in the Iberian Peninsula (Fernández-Delgado, 1989; Vargas & Sostoa, 1996), as well as to the western mosquitofish *G. affinis* (Krumholz, 1948; Haynes & Cashner, 1995). The largest individuals (mostly

TABLE II. ANCOVA of the dietary descriptors of mosquitofish

Variable (adjusted r^2) Source of variation	F	d.f.	P
Multivariate			
Length	15.5	5229	<0.0005
Season	3.2	15693	<0.0005
Total number of prey (0.00)			
Length	0.6	1233	0.44
Season	0.4	3233	0.72
Total biovolume (0.14)			
Length	35.7	1249	<0.0005
Season	2.0	3249	0.12
Mean volume of prey (0.13)			
Length	17.8	1233	<0.0005
Season	8.6	3233	<0.0005
Number of food categories (0.07)			
Length	1.2	1249	0.28
Season	7.7	3249	<0.0005
Diversity (0.00)			
Length	0.2	1233	0.63
Season	1.0	3233	0.39

All dependent variables (total number of prey, total biovolume, mean prey volume, number of food categories, and diversity) and covariate (total length) were log-transformed [$\log(D+1)$ for Simpson's index of diversity (D)].

Multivariate F statistics correspond to Pillai's trace.

1+ females) disappeared in autumn, after the reproductive season. Females dominated, except in spring when males were more common. In contrast, other populations showed different patterns of sex ratio variation (Barney & Anson, 1921; Britton & Moser, 1982; Fernández-Delgado & Rossomanno 1997). Vargas & Sostoa (1996) attributed the male-biased sex ratio to differential predation but alternative explanations such as maturation patterns (Barney & Anson, 1921; Snelson, 1989) are also possible.

DIET OF MOSQUITOFISH

Nematoceran adults were common in the food of mosquitofish in Lake Banyoles but cladocerans were more important, particularly by number and occurrence. Although mosquitofish are used commonly for mosquito control (Krumholz, 1948; Bence, 1988; Linden & Cech, 1990), they are considered generalist predators with no preference for mosquitoes (Miura *et al.*, 1979; Farley, 1980). In most habitats, the basis of their diet is zooplankton, namely cladocerans, ostracods, and copepods (Bence & Murdoch, 1986; Bence, 1988; Soto & Hurlbert, 1991), with a preference for cladocerans in many systems, such as rice fields (Farley, 1980; Blaustein & Karban, 1990), seminatural ponds (Miura *et al.*, 1979), and drainage canals (Crivelli & Boy, 1987).

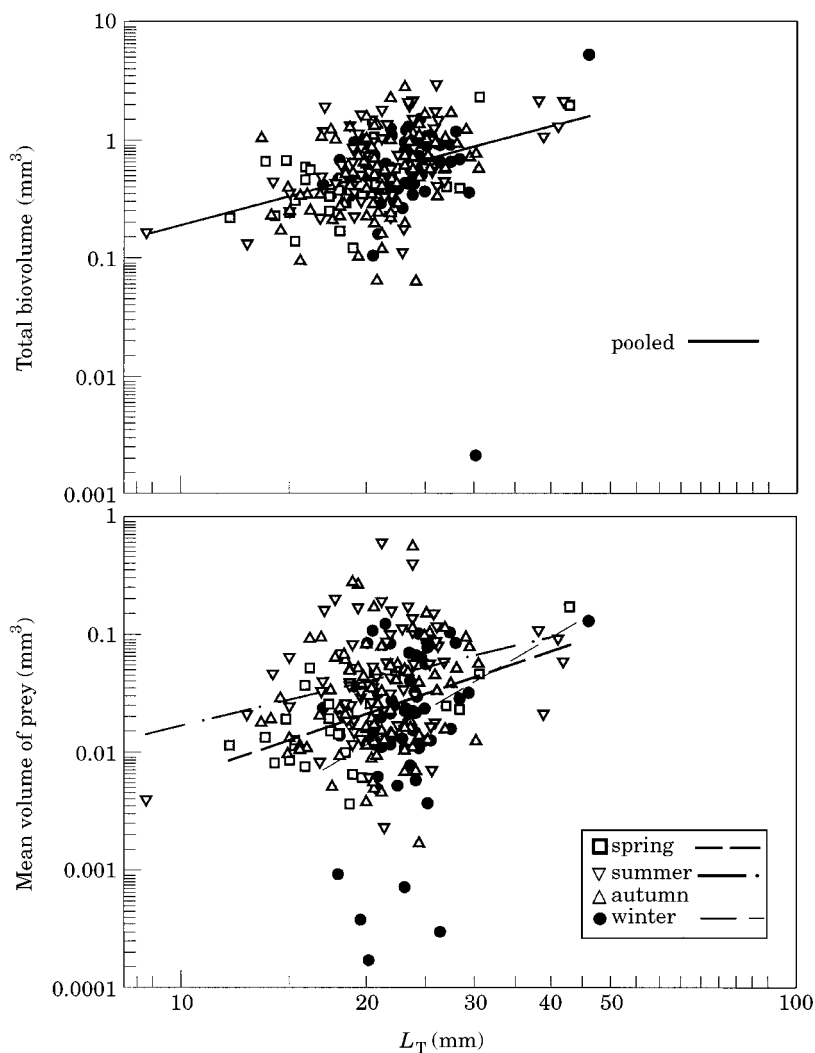


FIG. 4. Ontogenetic and seasonal variation in total biovolume and mean volume of prey of mosquitofish. Regression functions correspond to log-transformation of all variables. Only significant regression functions are shown.

In the Camargue wetlands, crustaceans, particularly cladocerans (chydorids and daphniids), were also the main prey, except in summer, when insects dominated (Crivelli & Boy, 1987). The dominance of insects in summer has also been reported in other populations. In an Australian marsh, mosquito (Culicidae) larvae dominated in summer and crustaceans and terrestrial prey in autumn and winter (Morton *et al.*, 1988). In a Spanish reservoir studied only in summer, the diet was dominated by heteropterans, followed by dipterans and cladocerans (Rodríguez-Jiménez, 1989). This dominance of insects in summer was not found in the present study, in which cladocerans continued to be used. It can be hypothesized that it is less common in deep lakes such as Lake

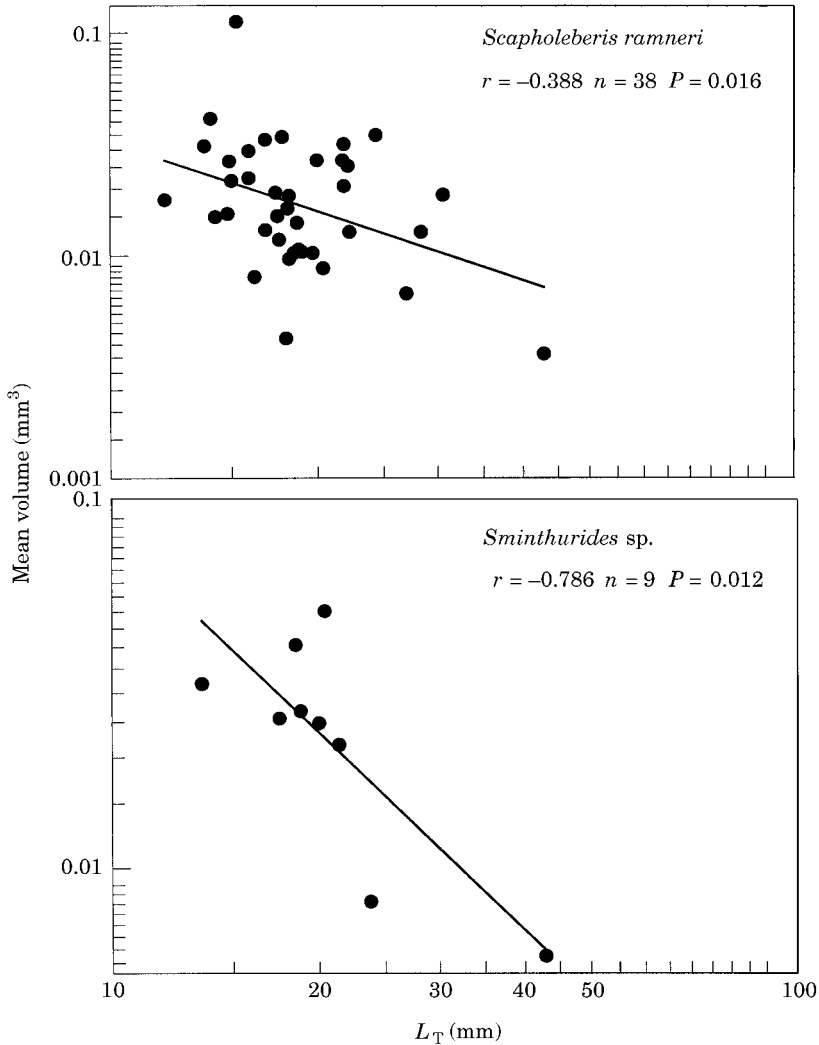


FIG. 5. Ontogenetic variation in mean volume of two prey (*Scapholeberis ramneri* and *Sminthurides* sp.) of mosquitofish.

Banyoles, where culicids are not common and chironomids emerge throughout a long period (c. March–October) (Prat & Rieradevall, 1995).

MICROHABITAT AND ONTOGENETIC DIET SHIFT

The microhabitat and feeding of mosquitofish are closely linked to the water surface (Werner *et al.*, 1978). This microhabitat and feeding type agrees with the enormous variety of mosquitofish prey in Lake Banyoles that were of terrestrial or aquatic neustonic origin. Similar neustonic prey (collembolans and ants) were detected in the Camargue (Crivelli & Boy, 1987). In Australian rivers, ants dominated the diet, followed by heteropterans and dipteran adults (Arthington, 1989). In New Zealand lakes, terrestrial invertebrates, particularly dipterans and

spiders, were important in the diet (Hayes & Rutledge, 1991). Feeding on prey from the neuston or the water column is enhanced by the morphology of mosquitofish, with its flattened head and terminal, upward mouth (Arthington, 1989).

Although mosquitofish are generalist feeders, they demonstrate some selectivity, prey size being particularly important (Miura *et al.*, 1979; Farley, 1980). In Lake Banyoles, mosquitofish diet was diverse but showed an ontogenetic shift to larger prey, from cladocerans (smallest fish also using diatoms and copepod nauplii) to nematoceran adults. This ontogenetic shift, which was present on a single-sample basis, was largely a change in prey categories and not a change in mean size of a certain prey. There was a decrease in mean size of two prey (Fig. 5), despite the general increase of prey size with mosquitofish length. Although larger mosquitofish shifted from cladocerans, particularly *S. ramneri*, to nematoceran adults (larger prey), they consumed smaller individuals of some specific prey (*S. ramneri* and *Sminthurides* sp.). This unusual pattern has been reported rarely. It may have been masked by low taxonomic precision or the procedure of pooling prey species in a few food categories, such as cladocerans.

This negative relationship between mosquitofish length and the size of the two specific prey might be due to size-specific microhabitat use of mosquitofish, linked to spatial heterogeneity. Larger mosquitofish might use a microhabitat where both nematocerans and smaller individuals of *S. ramneri* and *Sminthurides* sp. are more common. Crivelli & Boy (1987) hypothesized that the observed resource partitioning between size classes of mosquitofish could involve differential microhabitat use, small fish preferring shallow water at the margin of a ditch and larger fish preferring the open water at the centre. Miura *et al.* (1979) reported that mosquitofish preferred shallow water and that more young fish selected densely vegetated instead of open water. Alternative explanations for this negative relationship could be related to the deviation of mosquitofish from standard optimal diet theory (Bence & Murdoch, 1986).

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