

## THE DIET OF THE MOSQUITOFISH *GAMBUSIA AFFINIS* (BAIRD & GIRARD) (POECILIIDAE) IN MEDITERRANEAN FRANCE

Alain J. CRIVELLI and Vincent BOY

*Station Biologique de La Tour du Valat, Le Sambuc, F-13200 Arles*

*Gambusia affinis* (Baird & Girard), the Mosquitofish, originally native to the coastal region of the southeastern United-States, has been widely introduced throughout the warm temperate and tropical regions of the world in mosquito control programs. This species was introduced in the Camargue, southern France, around 1927 (Spillmann, 1961). Since then it has maintained successful populations along Atlantic and Mediterranean French seacoasts (Chimits, 1947 ; Hoffman, 1957).

Hurlbert and Mulla (1981) showed that *Gambusia* can cause decreases in the abundance of its prey species, especially Crustacea. When food requirements are high, during the breeding season, these effects may lead to intense intraspecific competition for food.

Most of the food studies on *Gambusia affinis* have been carried out in its native range, or to assess the effectiveness of this species in mosquito control. These studies have therefore been restricted to a short period of the year, generally the summer (Sokolov & Chvaliova, 1936 ; Self, 1940 ; Barnickol, 1941 ; Rice, 1941 ; Hess & Tarzwell, 1942 ; Walters & Legner, 1980). In addition, individuals of all sizes have been pooled in these diet studies.

The goal of our study is to compare the diet and the size of the prey ingested by *Gambusia affinis* between sex-classes, throughout the year, in two different habitats located in a geographical area where mosquitofish have been introduced. We will also try to assess the potential for intraspecific competition for food between individuals of different sizes and sexes.

### MATERIAL AND METHODS

*Study area and sampling procedures.* — The wetland of the Camargue and their fish assemblages have been described by Britton and Podlejski (1981) and Crivelli (1981a, b). The Camargue climate is Mediterranean semi-arid to sub-humid with warm dry summers and cold winters. The average air temperature for our sampling period was 14.5 °C (range : February 4.8 °C ; July 24.7 °C).

The two study sites belong to a large network of drainage canals scattered throughout the Camargue, an area located in the Rhône delta, southern France. The first sampling site, Fangouse, is one meter deep, two meters wide ;

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it has almost no submerged vegetation, and is bordered by dense reeds, *Phragmites australis*. In contrast, the second sampling site, Egout de Badon, is 40-50 cm deep, 3 meters wide, and has 100 % cover of dense submerged vegetation including *Ranunculus baudotii*, *Chara sp.*, *Zannichellia palustris*, *Potamogeton sp.*, *Myriophyllum spicatum*, and *Ceratophyllum demersum*. There is no emergent vegetation on the edges of this ditch. In both canals the substrate is clay-mud. These sites were sampled at approximately monthly intervals, from April 1982 to February 1983, with a lift net (mesh size : 1 mm). A typical sample consisted of 150 *Gambusia*. Sampling took place between 11 a.m. and 1 p.m. during the most active feeding period (Rice, 1941 ; Walters & Legner, 1980). The samples for January and February 1983 have been pooled owing to the difficulty of catching fish at this time of the year.

All fish caught were put immediately in 5 % formalin. No regurgitation was observed. Fish were measured (total length) to the nearest mm and weighed to the nearest 0.01 g. All fish > 20 mm were sexed macroscopically : male fish were divided into sexually mature (class 1) and immature (class 3) classes on the presence or absence of gonopodial hooks ; mature (class 4) and immature (class 2) females were distinguished by the presence or absence of a gravid spot. The remaining fish were considered as the non-sexed class (0). The complete digestive tract was removed and the contents placed in a drop of water into a cavity formed between two cover slips on a microscope slide. A second slide was placed over the top, and the contents were then compressed to a constant thickness. The volume of each food item was estimated by measuring the number of squares occupied using a microscope equipped with a gridded screen (Dynascope Vision Engineering Ltd., England). The contents of 25 stomachs were analysed for each sex-class. The percentage of empty stomachs in a group reached a maximum 28 %. In all, 668 stomach at Fangouse and 675 at Egout de Badon were examined.

*Analysis.* — The diet was expressed as the mean of percentage by volume for each category as recommended by Wallace (1981). For the purposes of calculating overlap indices, prey was grouped in 26 taxonomic categories (normally family) which have been lumped into broader categories for the presentation of diet composition (Tables I and II). Percentage diet overlap between and within classes was calculated using an index of overlap from Schoener (1970), as recommended by Wallace (1981) and Linton *et al.* (1981).

$$= 1 - 0,5 \left( \sum_{i=1}^n |P_{xi} - P_{yi}| \right) \times 100$$

where alpha is the overlap index,  $P_{xi}$  is the proportion of food (volume) of item i in the sex-class x,  $P_{yi}$  is the dietary proportion of item i in sex-class y and n is

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TABLE I

*Diet composition (mean percentage volume) in La Fangouse according to sex-classes and month.*

N : number of full stomach analysed ; H' : diversity index (Shannon index) ;

*Food items :*

A : Copepoda ; B : Cladocera ; C : surface insects ; D : Diptera larvae ; E : Coleoptera, adults and larvae ; F : other insects ; G : small benthos ; H : Molluscs ; I : vegetation.

The remaining percentage represents unidentified food items. Values during the reproductive period are enclosed within the box.

TABLE I

Sex-class	Month	N	H'	Food Items								
				A	B	C	D	E	F	G	H	I
Non-sexed	1	13	0.75	12.5	71.8	7.5	0	0	1.9	0	0	0
	4	24	1.18	7.5	40.7	41.1	7.6	0	0.4	0	0	0
	5	14	1.33	26.9	33.5	8.5	22.7	0	0	0.5	0	0.2
	6	25	1.21	56.7	12.8	6.8	21.9	0	0	0.9	0	0.1
	7	24	0.81	73.4	2.4	3.9	11.9	0	1.8	0.2	0	-
	9	24	1.15	4.0	36.1	3.6	15.8	0	0	0	0	3.8
	10	23	0.95	3.4	56.4	12.7	7.9	0	0	0	0	0.7
Immature male	1	8	0.79	25.4	65.6	6.0	0	0	0	0	0	0
	4	24	1.19	3.6	32.7	32.1	12.9	0	0.9	0.7	0	0.1
	5	12	1.19	35.5	40.6	9.1	3.4	0.7	0	1.4	0	0
	6	0	-	-	-	-	-	-	-	-	-	-
	7	22	1.98	22.3	2.8	5.3	8.4	15.0	3.5	0.3	0	10.9
	9	24	1.65	3.8	23.4	15.7	26.4	1.6	13.3	0	0	4.2
	10	19	1.26	2.9	33.0	37.3	8.7	0	0	0.5	0	0.5
Immature female	1	17	1.05	25.6	60.2	9.5	1.4	0	0	0	0	0
	4	27	1.19	3.4	40.3	39.3	9.7	1.5	5.3	0	0	0.1
	5	22	1.22	24.9	44.9	14.0	7.7	2.5	0.2	0.3	0	0.3
	6	0	-	-	-	-	-	-	-	-	-	-
	7	24	2.07	11.0	2.8	6.8	5.9	8.0	17.8	0.1	0.1	18.8
	9	24	1.38	5.9	18.8	25.1	33.6	0.6	2.5	0	0	2.1
	10	18	1.30	2.7	32.9	26.6	10.2	0	0	0	0	5.3
Mature male	1	17	1.23	25.9	49.8	7.8	16.5	0	0	0	0	0
	4	17	1.19	11.1	36.1	12.9	6.5	0	3.0	0	0	0
	5	15	1.75	24.9	22.2	13.8	6.1	0.6	18.2	0	0	2.3
	6	24	1.53	44.4	9.2	15.5	6.9	6.2	4.9	0.8	0	0.5
	7	23	1.90	10.3	4.6	4.5	16.7	5.5	3.8	0	0	18.4
	9	24	1.23	39.6	22.7	7.4	11.2	0	0	0	0	2.9
	10	20	1.80	3.1	31.2	18.8	4.2	8.0	30.2	0.4	0	1.7
Mature female	1	0	-	-	-	-	-	-	-	-	-	-
	4	0	-	-	-	-	-	-	-	-	-	-
	5	0	-	-	-	-	-	-	-	-	-	-
	6	24	1.60	13.7	0.1	54.6	2.3	4.2	12.4	0.1	0	0.2
	7	25	1.63	0	0	30.4	6.9	39.1	5.3	0	0	0.8
	9	21	1.14	0	0.2	65.5	2.0	6.3	9.3	0	0	4.4
	10	0	-	-	-	-	-	-	-	-	-	

TABLE II

*Diet composition (mean percentage volume) in Egout de Badon according to sex-classes and month. Legend as in table I.*

Sex-class	Month	N	H'	Food items									
				A	B	C	D	E	F	G	H	I	
Non-sexed	1	22	1.17	23.0	52.1	13.6	6.6	0	0	0	0	0	
	4	23	1.37	23.5	36.5	12.3	16.8	0	5.1	0	0	0.3	
	5	12	1.31	14.7	17.1	23.3	40.0	0	0	0.6	0	0	
	6	24	1.19	15.6	52.5	8.6	9.9	0	4.0	1.5	0	0	
	7	19	1.40	23.4	10.0	3.1	5.5	0	8.3	0.1	0	7.4	
	9	24	1.32	2.6	0	30.9	13.9	7.2	0	5.2	0	3.9	
	10	23	0.97	5.2	59.0	4.6	15.5	0	1.8	11.0	0	2.6	
Immature male	1	13	1.49	17.9	36.5	23.1	15.4	0	0	0	1.2	0	
	4	24	1.41	44.5	7.6	14.3	19.1	0	5.1	0	0	0.1	
	5	26	1.46	9.7	24.3	36.4	18.8	0	5.9	0	0	0.3	
	6	-	-	-	-	-	-	-	-	-	-	-	
	7	24	1.83	5.7	5.3	2.4	26.4	4.7	18.7	1.2	4.9	13.6	
	9	26	1.35	0	0	43.8	15.3	15.0	0.9	0.8	1.1	1.5	
	10	18	1.13	2.4	41.6	8.9	8.4	0	2.2	9.7	0	2.1	
Immature female	1	15	1.41	15.7	36.5	29.2	10.9	0	4.4	0	0	0	
	4	25	1.69	30.2	18.2	26.0	10.5	0	9.3	0	0	0.3	
	5	22	1.34	6.1	9.5	43.2	27.5	0	3.6	0.1	0	0	
	6	23	1.62	4.3	21.1	31.4	19.0	1.2	6.9	0	5.7	1.3	
	7	24	2.03	7.6	8.0	5.9	7.9	10.8	22.8	0.3	4.3	12.2	
	9	18	1.63	0	0	38.6	3.4	21.6	10.9	0.1	4.4	0	
	10	22	1.55	3.8	19.6	18.6	14.3	0.6	5.9	7.4	8.3	7.5	
Mature male	1	9	1.21	16.2	39.3	6.1	21.2	0	0	0	2.0	5.1	
	4	11	1.38	40.1	19.2	19.7	9.6	0	3.8	0	0	0	
	5	14	1.52	9.6	18.2	43.4	8.3	0	7.6	0.1	0	3.8	
	6	13	0.93	2.0	0	58.0	18.3	0	2.0	1.7	0	2.0	
	7	22	1.50	17.6	4.2	2.0	14.0	0.6	23.4	1.4	0	20.0	
	9	13	0.97	0	0	50.1	0.4	1.1	0	1.7	1.5	2.8	
	10	22	1.43	2.5	23.9	9.1	17.1	2.4	0	7.4	2.3	7.7	
Mature female	1	0	-	-	-	-	-	-	-	-	-	-	
	4	7	1.04	2.8	25.7	60.7	5.7	0	2.6	0	0	0	
	5	18	1.40	0.3	11.3	48.8	4.1	0	20.1	0.3	0	5.0	
	6	15	1.81	0	0.9	29.9	0	27.3	6.9	0	11.5	4.2	
	7	25	1.94	0	4.3	9.1	4.2	27.9	3.5	0	11.0	25.6	
	9	23	1.65	0	0	45.2	1.9	4.9	13.4	0.9	9.7	2.1	
	10	0	-	-	-	-	-	-	-	-	-	-	

the number of food items. An overlap of 0.30 or less is considered insignificant and any overlap value greater or equal to 0.60 is significant overlap (Zarer & Rand, 1971 ; Keast, 1978). To test whether the diet was adequately characterised by the samples, we have used a reliability method suggested by Wallace and Ramsey (1983). This method calculates a mean and upper 95 % confidence limits for within-class overlap by calculating the overlap between all possible combinations of pairs of fish in a sample taken from one class. When the upper 95 % confidence limit of the mean within-class overlap was smaller than 60 % the sample was considered inadequate, and was not used for between class comparisons.

The width of the mouth aperture of fish was estimated from a linear regression of mouth width on body length (mouth width =  $0.0825 \text{ TL} - 0.080112$ ,  $r = 0.98$ ,  $P < 0.01$ ,  $n = 63$ ). For a given length there was no significant difference between the sexes in the width of the mouth.

The relationship between the size of a prey item ingested by a sex-class and the size of the mouth was calculated as follows : the effect of the month and the sex-class on the size of the fish mouth, and the size of a specific prey item, were tested separately with a two way ANOVA without replication. The same relationship involving simultaneously the month and the sex-class was tested with a multiway analysis of variance (MANOVA, Chatfield & Collins, 1980), and an analysis of covariance (ANCOVA) tested the relationship between the size of the prey and the size of the fish mouth. In contrast of males, mature females are only present during the reproductive period (June to September), and therefore it was not possible to include them in all analyses. A correlation, however, between the size of the prey and the size of the fish mouth for a specific food item in a specific site was calculated for all fish classes, including the mature female class for all the months combined. A one-way ANOVA has also been calculated to detect differences in size of the prey according to sex-class within a time period.

When differences are significant, individual differences are tested with a Newman and Keuls sequential procedure (Sokal & Rolf, 1981).

## RESULTS

The diet of each sex-class of *Gambusia affinis* in both study sites is presented by month in tables I and II. Food items are pooled into nine food categories. Organisms within a category possess similar size and behavioural characteristics. Several differences in diet occur between months, between study sites and between classes. With the exception the non-sexed-class, however, fish of all sex-classes in both study sites show the same seasonal trend in diet composition. Crustacea (free-living cyclopid Copepoda and Cladocera : Chydoridae and Daphniidae) predominate, up to 85 % during the non-reproductive period (October to May), and there is a general switch from Crustacea to Insecta (up to 80 %) during the reproductive season, i.e. from the beginning of June to the end of September (Crivelli, *in prep.*).

Throughout the year, the food eaten by mosquitofish includes both insects taken at the water surface and Diptera larvae (Chironomidae and Empididae). Among the surface insects are aquatic groups (Diptera adults and pupae,

Collembola and Trichoptera) and terrestrial insects (particularly Hymenoptera including Formicoidae). In addition, during the reproductive period a large proportion of the insects consumed are aquatic (Coleoptera, adults and larvae, Hemiptera, Odonata and Ephemeroptera). Small benthos (mainly Hydracarina and Rotifera, up to 11 %), molluscs (mainly *Physa acuta*, up to 11.5 %) and vegetation (algae, pieces of macrophytes and seeds, up to 25 %) are the secondary food items consumed by mosquitofish in the Camargue.

The values of dietary diversity index are presented in tables I and II. The highest value occurs on both sites for all sex-classes in July. Values are generally higher, however, at Egout de Badon than at Fangouse. These are only significantly different in two classes : the mature and immature males (Mann-Whitney test,  $P < 0.05$ ).

Diet overlap values between the two study sites for each sex-class and each month show that fish from both sites have similar diets in autumn and winter (% overlap : 61 to 82 %), but dissimilar diets in July (% overlap : 30 to 59 %). Low overlap in July coincides with high dietary diversity in both sites. Food categories such as freshwater beetles, other aquatic insects and molluscs were the main source of difference in diets between the two study sites. All these food items were consumed in greater frequency by *Gambusia* at the Egout de Badon than in La Fangouse, a possible consequence of the high amount of cover at Egout de Badon, changing the prey availability.

Diet overlap for the sex-classes are presented in figures 1 and 2. In addition the upper 95 % confidence limits of within class overlap are shown for each month and for both sex-classes involved in the calculation of the overlap. At Fangouse, mature females show consistently low values (19.4 to 61.1 %) of overlap against all the other sex-classes. At Egout du Badon mature females have high overlap with other classes during the non-reproductive period (mid-April and mid-May ; 42.8 to 72.5 %), and lower values during the reproductive season (24.3 to 66.6 %). All the other sex-classes show high values (> 60 %) of diet overlap between each other. However, in July and/or June, the diet of the non-sexed class overlaps very little with the other classes in both study sites.

The upper 95 % confidence limits of intraspecific overlap within a sex-class are consistently higher than 60 % showing a high homogeneity of the diet of fish within a sex-class. However, in April and in June at Egout de Badon the mature females have a value under 60 % showing that their diet at this time is more variable and consequently their diet is poorly characterised by the sample (Wallace and Ramsey, 1983). In both these cases no between-class diet overlap values have been calculated.

Linear relationships between monthly dietary diversity index values and the monthly upper 95 % confidence limits of intraspecific diet overlap within a sex-class are significant (Fangouse :  $n = 29$ ,  $r = 0.61$ ,  $P < 0.01$  and Egout de Badon :  $m = 31$ ,  $r = 0.47$ ,  $P < 0.01$ ).

Prey size has been examined only for four food items : Copepoda, Cladocera, Diptera adults and pupae, and Diptera larvae. There are many differences in size of the prey ingested by the different sex-classes within a time period (Table III). There is a clear effect of the month on the size of the prey (Table IV), and of the month and the sex on the width of the mouth. These results are confirmed by the MANOVA analysis showing significant effect of the month and the sex on both size of the prey and the width of the mouth

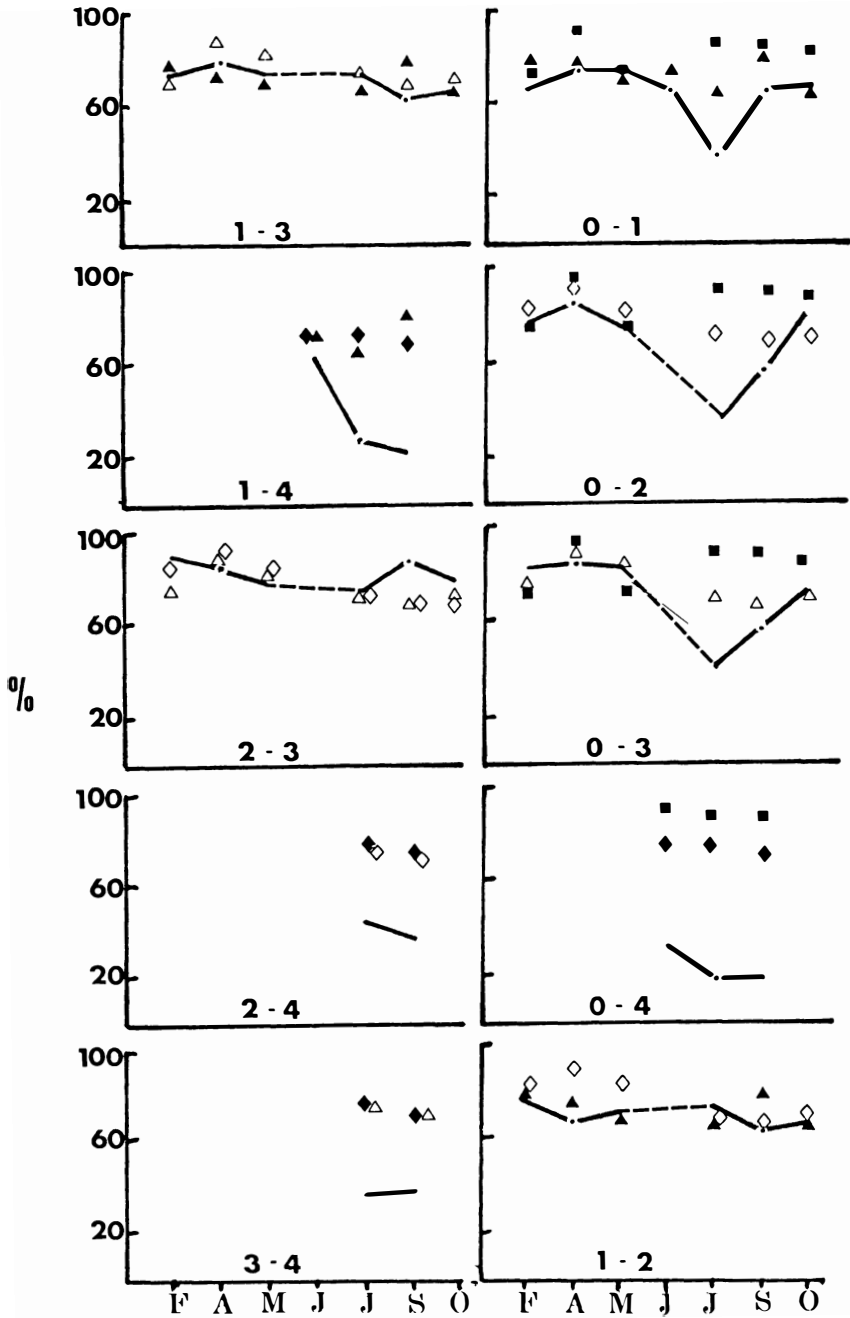


Figure 1. — Diet overlap (line) between the sex-classes. Upper 95 % confidence limits of the mean within class overlap : 0 = non-sexed (■) ; 1 = male mature (▲) ; 3 = male immature (△) ; 4 = female mature (◆) ; 2 = female immature (◇). Dashed line — no data.

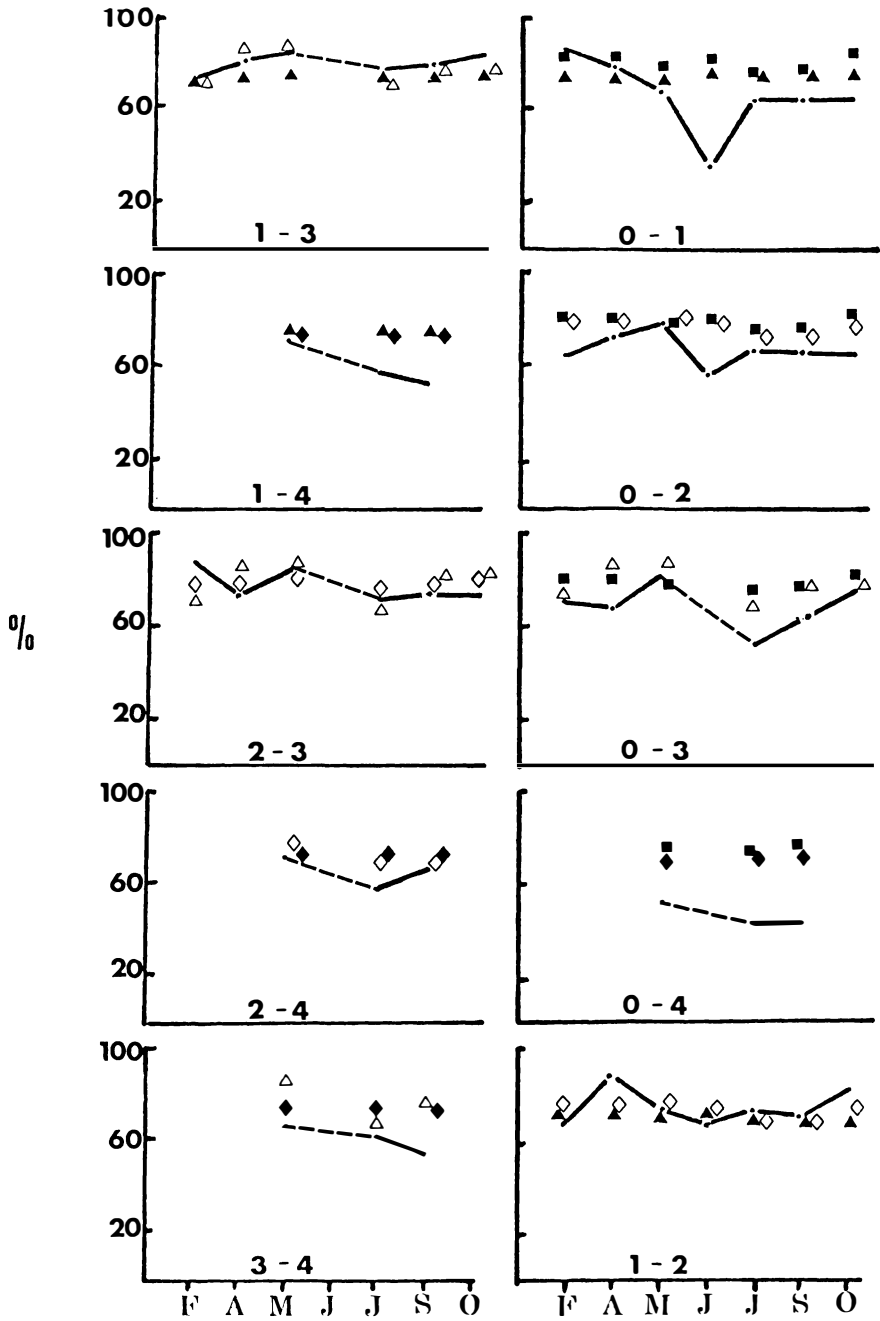


Figure 2. — Diet overlaps (line) at the Egout de Badon between the sex classes. Upper 95 % confidence limits of the mean within class overlap. Symbols as in figure 1.



TABLE III

Analysis of variance for the sizes of the prey within a time period between the sex-classes (\*\* =  $p < 0.01$ ).

	FANGOUSE				EGOUT DE BADON			
	Food item	ANOVA	Newman & Keuls		Food item	ANOVA	Newman & Keuls	
APRIL	CO	n.s.			CO	n.s.		
	CL	**	<u>2</u>	<u>3</u> <u>1</u> 0	CL	n.s.		
	DI	**	<u>2</u>	<u>0</u> <u>3</u> <u>1</u>	DI	**	<u>0</u>	<u>1</u> <u>3</u> 2 4
	DL	n.s.			DL	n.s.		
MAY	CO	n.s.			CO	n.s.		
	CL	**	2	<u>1</u> <u>3</u> 0	CL	n.s.		
	DI	n.s.			DI	n.s.		
	DL	n.s.			DL	**	1	<u>3</u> <u>4</u> <u>2</u> <u>0</u>
JUNE	CO	**	<u>0</u>	<u>1</u> <u>4</u>	CO	n.s.		
	CL	**	0	<u>1</u> <u>4</u>	CL	-		
	DI	**	4	<u>0</u> <u>1</u>	DI	**	0	1 2 4
	DL	n.s.			DL	**	<u>0</u>	<u>1</u> 2
JULY	CO	**	<u>0</u>	<u>1</u> <u>2</u> <u>3</u>	CO	n.s.		
	CL	n.s.			CL	n.s.		
	DI	**	<u>1</u>	<u>3</u> <u>2</u> <u>0</u> 4	DI	n.s.		
	DL	n.s.			DL	**	0	<u>2</u> <u>1</u> <u>4</u> <u>3</u>
SEPTEMBER	CO	n.s.			CO	-		
	CL	**	<u>0</u>	<u>4</u> <u>3</u> <u>1</u> <u>2</u>	CL	-		
	DI	**	<u>4</u>	<u>2</u> <u>0</u> <u>3</u> <u>1</u>	DI	**	<u>0</u>	<u>1</u> <u>2</u> <u>3</u> <u>4</u>
	DL	**	<u>2</u>	<u>3</u> <u>0</u> <u>1</u>	DL	n.s.		
OCTOBER	CO	n.s.			CO	n.s.		
	CL	n.s.			CL	n.s.		
	DI	n.s.			DI	n.s.		
	DL	n.s.			DL	n.s.		
JANUARY - FEBRUARY	CO	n.s.			CO	n.s.		
	CL	n.s.			CL	n.s.		
	DI	n.s.			DI	**	<u>1</u>	<u>3</u> <u>0</u> <u>2</u>
	DL	n.s.			DL	n.s.		

For the Newman and Keuls test, sex-classes underlined are not significantly different ( $P < 0.05$ ). Legend : CO, Copepoda ; CL, Cladocera ; DI, Diptera adults and pupae ; DL, Diptera larvae.

(Table IV). There is no significant relationship between the size of the prey and the width of the mouth for any food item, with the exception of Diptera larvae at Egout de Badon (Table IV). However these analyses have been done considering only the non-sexed, mature and immature males and immature females fish. Mature females, which are not present all the year round were not included. When we calculate linear correlations between the sizes of the different prey categories and the width of the mouth for all sex-classes together, these relationships are highly significant ( $P < 0.01$ ) in both sites for Cladocera ( $r = 0.61$ ,  $n = 26$ ;  $r = 0.51$ ,  $n = 27$ ), Diptera adults ( $r = 0.70$ ,  $n = 29$ ;  $r = 0.79$ ,  $n = 33$ ), and pupae and Diptera larvae ( $r = 0.50$ ,  $n = 29$ ), but not for Copepoda.

## DISCUSSION

*The diet of Gambusia affinis.* — The results obtained in the Camargue are very similar to those described in the literature (Rees, 1934; Barnickol, 1941; Rice, 1941; Hess & Tarzwell, 1942; Maglio & Rosen, 1969; Walters & Legner, 1980; Schoenherr, 1974). However, Crustacea never formed as important a component of the diet of mosquitofish in these studies as was found in Camargue. This may be due to the fact that most of the studies were carried out only during the reproductive season, when aquatic and terrestrial insects are the most important food items.

Among the Crustacea, Cladocera (Chydoridae and Daphniidae) are the most important group. Copepoda are less important, and Ostracoda are completely absent. Walters and Legner (1980) also mentioned the total absence of Ostracoda in the diet of *Gambusia*, and they attribute it to the fact that most of the species of this group have a benthic existence, unlike the other group of Crustacea which are mainly planktonic. Chydoridae and Daphniidae, which decrease in the diet from January to September, increase again in importance in late autumn-early winter when fish become less active and predation pressure is reduced. Hulbert and Mulla (1981) mentioned that *Gambusia affinis* causes a major reduction in all populations of Cladocerans in spring and summer (see also Walters & Legner, 1980), but Williams (1983) suggests that invertebrate predation on Chydoridae could be more significant than fish predation. Hulbert and Mulla (1981) also indicate that Copepoda are much less affected than Cladocera by the predation of mosquitofish.

During the reproductive season (June to September) terrestrial insects are an important additional food source. This was described for *Gambusia affinis* elsewhere (Washino & Hokama, 1967; Harrington & Harrington, 1961; Stearns, 1983), and for other Cyprinodontidae (Brosset, 1982). It is striking that no mosquito larvae (Culicidae) have been detected in the diet of mosquitofish, though they are very abundant in the Camargue (Rioux, 1958). This is in accordance with the disappointing reports in some countries using *Gambusia affinis* for mosquito control (Haas & Pal, 1984). As only one individual of young *Gambusia* was ever found in 1343 stomach contents; cannibalism is very infrequent in the Camargue, though it occurs elsewhere (Dionne, 1985).

In contrast to La Fangouse, molluscs (*Physa acuta*) seem to be an important additional food source at the Egout de Badon for all fish except the smallest. This difference between the two study sites may be explained by the pre-

TABLE IV  
*Analysis of variance of prey size against various variables.*

	FANCOUSE				ECOUT DE BADON			
	SIZE OF		PREY		SIZE OF		PREY	
	CO	CL	DI	DL	CO	CL	DI	DL
<u>Two way ANOVA</u>								
between month	***	**	N.S.	*	**	***	N.S.	**
between sex-classes	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
<u>MANOVA</u>								
between month	**	**	N.S.	**	*	**	N.S.	*
between sex-classes	**	**	**	**	**	**	**	**
<u>ANCOVA</u>								
with width of the mouth	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	*

Legend : CO, Copepoda ; CL, Cladocera ; DI, Diptera adults and pupae ; DL, Diptera larvae  
 \*\*\* = P < 0.001 ; \*\* = P < 0.05 ; NS = P > 0.05.

sence of abundant submerged vegetation at Egout de Badon. Watson and Rose (1985) show that gastropod molluscs (*Physa*) are much more abundant in aquatic macrophytes than adjacent unvegetated areas. Molluscs are eaten only in summer month when food requirements of fish are maximum and other more favoured organisms may be in short supply. Finally, the diet of *Gambusia affinis* in the Camargue is relatively similar in both study sites. However, at any one time, different sex-classes show important differences in diet (overlap < 60 %). This demonstrates that all sex and age-classes must be sampled in order to adequately characterise the diet of a population.

*Resource partitioning among sex-classes.* — High food overlap indices (> 60 %) during the non-reproductive season (October to May) indicate a very similar diet for individuals of all sex-classes of *Gambusia*. This may lead to a strong intraspecific competition if food is short. During the reproductive season the picture is different, as mature females have a totally different diet from all other classes of *Gambusia*. In this way, during this period of high reproductive investment, females have a feeding niche which is different from that of other *Gambusia*. If intraspecific food competition occurs, this partitioning food resource may allow individual female *Gambusia* to achieve high reproductive output. The non-sexed fish represented mainly by new born fish difficult to sex macroscopically, also generally have a different diet (more Crustacea rather than insects) from all other *Gambusia* in June and July, which may help them to grow more quickly in their first days of life. Such a difference in diet may be due to micro-habitat selection : small fish prefer shallow water at the margin of the ditch to the open water at the centre favoured by larger fish (e.g. mature females). All the other fish have a similar diet during this period and could compete for food to a certain extent.

Similar results are found in the analysis of the size of the prey ingested by the different sex-classes and its relationship with the width of the mouth of the fish. Mature females (2.44-3.44 mm mouth width) eat larger prey than the other *Gambusia*, except in the case of Copepoda. However, the Copepoda are so small that they can be ingested by all sex-classes of fish. Within the other sex-classes there is no relationship between the size of the prey and the width of the mouth except in one case (Table IV). This may be explained by the overlap in total length, and thus in width of the mouth, of these sex-classes : non-sexed (0.89-1.41 mm mouth width) ; mature male (1.68-2.13 mm MW) ; immature male (1.65-2.02 mm MW) ; immature female (1.69-2.38 mm MW). The energy content of Crustacea and insects does not seem to be very different, nor the handling time of the prey. The consumption of large prey is thus very profitable for the mature females.

Therefore, the absence of dietary overlap and intraspecific food competition between mature females and other fish is largely explained by their larger size and their capacity to take larger prey. Morphological characters (e.g. position of the mouth, mouth width) are known to be important in prey selection (Nilsson, 1978 ; Paine *et al.*, 1982 ; Greenfield *et al.*, 1983 ; Magnan & Fitzgerald, 1984). In contrast, Werner (1977) claims that habitat dimension also plays an important role in segregating fish species. Habitat selection also segregates age-classes of the same species, and consequently their diet (Keast, 1978 ; Persson, 1983) ; it has been demonstrated in *Gambusia* by Maglio and Rosen (1969). Due to the limited size of the marshes in which *Gambusia* live, habitat segregation is difficult to establish. However, such a segregation may explain

partially the partitioning of food found in this study between mature females and other sex-classes. Walsh and Fitzgerald (1984) showed that the different roles played by reproductive males and females of three species of sticklebacks may explain their differences in diet (prey type and size) during the breeding season, the diets being similar during the post-breeding season.

Large size in fish has an obvious reproductive advantage, in that fecundity and life-time reproductive output are exponentially related to size at maturation (Bagenal & Braum, 1968). This is also true in *Gambusia* (Crivelli, *in prep.*). In addition, sexual dimorphism in *Gambusia* enables the exploitation of different food resources during the breeding season by females, males and immature fish, and thus prevents food competition. Large size may also enable females to eat certain food resources (e.g. surface insects by aggressive dominance (Itzkowitz, 1971 ; Schoenherr, 1974 ; Martin, 1975).

## SUMMARY

The diet of *Gambusia affinis*, an exotic fish species, in the Camargue, southern France was dominated by Crustacea during the non-reproductive period. During the breeding season, however the fish consumed a variety of aquatic insects in their diet.

The diets of males and immature fish overlapped considerably (61.9-95.6 %). Mature females, which were present only from June to September, took more terrestrial insects at the water surface and freshwater beetles than the other classes, and their diet overlapped much less. The same pattern of differential utilization between mature females and other sex-classes was observed when diets were classified according to the size of prey items.

The large size of mature females allowed them to exploit large food which could not be eaten by the other sex-classes. Where fish predation causes a decline in the abundance of the smaller prey items leading to intraspecific competition for food, then this differential utilization could allow breeding females which have high food requirements to achieve higher reproductive output.

## RÉSUMÉ

Le régime alimentaire de *Gambusia affinis*, espèce introduite en Camargue, est essentiellement constitué par des crustacés d'octobre à mai. Pendant la période de reproduction, de juin à septembre, les poissons mangent surtout des insectes aquatiques. Le régime alimentaire des mâles matures et celui des immatures se chevauche considérablement (61.9-95.6 %). Les femelles matures, présentes seulement de juin à septembre, mangent plus d'insectes terrestres à la surface de l'eau et d'insectes aquatiques que les autres classes de poissons. Par conséquent, leur régime alimentaire se distingue bien de celui des autres poissons. La même chose est observée si l'on considère la taille des proies ingérées.

La grande taille des femelles matures leur permet d'exploiter une source de nourriture qui n'est pas disponible pour les autres classes de poissons. Lorsque la prédation par les poissons réduit l'abondance des proies les plus petites, il se crée une situation potentielle de compétition intraspécifique pour la nourriture. Les femelles matures, cependant, peuvent pleinement satisfaire leurs besoins alimentaires, intenses en période de reproduction, en exploitant des ressources différentes des autres classes de poissons, et elles peuvent ainsi maximiser leur succès de reproduction.

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## REFERENCES

- BAGENAL, T.B. and BRAUM, E. (1968). — Eggs and early life history. In *Fish Production in Fresh Waters*. W.E. Ricker (Editor). Blackwell, Oxford.
- BARNICKOL, P.E. (1941). — Food habits of *Gambusia affinis* from Reelfoot Lake, Tennessee, with special reference on malaria control. *J. Tennessee Acad. Sci.*, 16 : 5-13.
- BRITTON, R.H. and PODLEKSKI, V.D. (1981). — Inventory and classification of the wetlands of the Camargue (France). *Aquat. Bot.*, 10 : 195-224.
- BROSSET, A. (1982). — Le peuplement de Cyprinodontes du bassin de l'Ivindo, Gabon. *Rev. Ecol. (Terre Vie)*, 36 : 233-292.
- CHATFIELD, C. and COLLINS, A.J. (1980). — *Introduction to multivariate analysis*. Chapman & Hall, New York.
- CHIMITS, P. (1947). — Note sur l'acclimatation du *Gambusia holbrooki* dans les étangs des Landes. *Bull. Franc. Pisc.*, 147 : 79-82.
- CRIVELLI, A.J. (1981a). — The biology of the Common Carp, *Cyprinus carpio* L. in the Camargue, Southern France. *J. Fish. Biol.*, 18 : 271-290.
- CRIVELLI, A.J. (1981b). — Les peuplements de poissons de la Camargue. *Rev. Ecol. (Terre Vie)*, 35 : 617-671.
- DIONNE, M. (1985). — Cannibalism, food availability, and reproduction in the Mosquito fish (*Gambusia affinis*) : a laboratory experiment. *Amer. Nat.*, 126 : 16-23.
- GREENFIELD, D.W., GREENFIELD, T.A. and BRINTON, S.L. (1983). — Spatial and trophic interactions between *Gambusia sexradiata* and *Gambusia puncticulata yucatanana* (Pisces : Poeciliidae) in Belize, Central America. *Copeia*, 1983 : 598-607.
- HAAS, R. and PAL, R. (1984). — Mosquito larvivorous fishes. *Bull. Ent. Soc. Amer.*, 30 : 17-25.
- HARRINGTON, R.W. and HARRINGTON, E.S. (1961). — Food selection among fishes invading a high subtropical saltmarsh : from onset of flooding through the progress of a mosquito brood. *Ecology*, 42 : 646-666.
- HESS, A.D. and TARZWELL, C.M. (1942). — The feeding habits of *Gambusia affinis affinis*, with special reference to the malaria mosquito *Anopheles quadrimaculatus*. *Amer. J. Hyg.*, 35 : 142-151.
- HOFFMANN, L. (1957). — Les effets de la vague de froid de février 1956 sur la faune des vertébrés de Camargue. *Terre Vie*, 11 : 186-197.
- HURLBERT, S.H. and MULLA, M.S. (1981). — Impacts of Mosquitofish (*Gambusia affinis*) predation on plankton communities. *Hydrobiologia*, 83 : 125-152.
- ITZKOWITZ, M. (1971). — Preliminary study of the social behavior of male *Gambusia affinis* (Baird & Girard) (Pisces : Poeciliidae) in aquaria. *Chesapeake Science*, 12 : 219-224.

- KEAST, A. (1978). — Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. *Env. Biol. Fish.*, 3 : 7-31.
- LINTON, L.R., DAVIES, R.W. and WRONA, F.J. (1981). — Resource utilization indices : an assessment. *J. Anim. Ecol.*, 50 : 283-292.
- MAGLIO, V.J. and ROSEN, D.E. (1969). — Changing preference for substrate color by reproductively active Mosquitofish, *Gambusia affinis*. *Amer. Mus. Novitates*, 2397 : 1-37.
- MAGNAN, P. and FITZGERALD, G.J. (1984). — Mechanisms responsible for the niche shift of Brook charr, *Salvelinus fontinalis* Mitchill, when living sympatrically with Creek chub, *Semotilus atromaculatus* Mitchill. *Can. J. Zool.*, 62 : 1548-1555.
- MARTIN, R.G. (1975). — Sexual and aggressive behavior, density and social structure in a natural population of Mosquitofish, *Gambusia affinis holbrooki*. *Copeia*, 1975 : 445-454.
- NILSSON, N.A. (1978). — The role of size-biased predation in competition and interactive segregation in fish. In : *Ecology of freshwater fish production*. S.D. Gerkury (Editor), Blackwell Scientific Publishers, Oxford, pp. 303-325.
- PAINE, M.D., DODSON, J.J. and POWDER, G. (1982). — Habitat and food resource partitioning among four species of darters (Percidae : *Etheostoma*) in a southern Ontario stream. *Can. J. Zool.*, 60 : 1635-1641.
- PERSSON, L. (1983). — Food consumption and competition between age classes in a Perch *Perca fluviatilis* population in a shallow eutrophic lake. *Oikos*, 40 : 197-207.
- REES, D.M. (1934). — Notes on the Mosquitofish, *Gambusia affinis*, in Utah. *Copeia*, 1934 : 157-159.
- RICE, L.A. (1941). — *Gambusia affinis* in relation to food habits from Reelfoot Lake, with special emphasis on malaria control. *J. Tennessee Acad. Sci.*, 16 : 77-87.
- RIOUX, J.A. (1958). — *Les culicidés du « Midi » méditerranéen*. Paul Lechevalier, Paris, 301 pp.
- SCHOENER, T. (1970). — Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology*, 51 : 408-418.
- SCHOENHERR, A.A. (1974). — *Life history of the Topminnow, Poeciliopsis occidentalis (Baird & Girard) in Arizona and an analysis of its interaction with the Mosquitofish Gambusia affinis (Baird & Girard)*. PhD Thesis, Arizona State University, Tempe.
- SELF, J.T. (1940). — Notes on the sex cycle of *Gambusia affinis affinis* and on its habits and relation to mosquito control. *Amer. Midl. Nat.*, 23 : 393-398.
- SOKAL, R.R. and ROHLF, F.J. (1981). — *Biometry*, 2nd Edition. Freeman & Company, New York.
- SOKOLOV, N.P. and CHVALIOVA, M.A. (1936). — Nutrition of *Gambusia affinis* on the rice fields of Turkestan. *J. Anim. Ecol.*, 5 : 390-395.
- SPILLMANN, C.J. (1961). — *Poissons d'eau douce*. Paul Lechevalier, Paris, *Faune de France*, 65.
- STEARNS, S.C. (1983). — A natural experiment in life-history evolution : field data on the introduction of Mosquitofish (*Gambusia affinis*) to Hawaii. *Evolution*, 37 : 601-617.
- WALLACE, R.K. (1981). — An assessment of diet-overlap indexes. *Trans. Amer. Fish. Soc.*, 110 : 72-76.
- WALLACE, R.K. and RAMSEY, J.S. (1983). — Reliability in measuring diet overlap. *Can. J. Fish. Aquat. Sci.*, 40 : 347-351.
- WALSH, G. and FITZGERALD, G.J. (1984). — Resource utilization and coexistence of three species of sticklebacks (Gasterosteidae) in tidal salt marsh pools. *J. Fish Biol.*, 25 : 405-420.
- WALTERS, L.L. and LEGNER, E.F. (1980). — Impact of the Desert Pupfish, *Cyprinodon macularius*, and *Gambusia affinis affinis* on fauna in pond ecosystems. *Hilgardia*, 48 : 1-18.
- WASHINO, R.K. and HOKAMA, Y. (1967). — Preliminary report on the feeding pattern of two species of fish in a ricefield habitat. *Proc. Calif. Mosq. Control Assoc.*, 35 : 84-87.
- WASTON, W.G. and ROSE, F.L. (1985). — Influences of aquatic macrophytes on invertebrate community structure, guild structure and microdistribution in streams. *Hydrobiologia*, 128 : 45-56.
- WERNER, E.E. (1977). — Species packing and niche complementary in three sunfishes. *Amer. nat.*, 111 : 553-578.
- WILLIAMS, J.B. (1983). — A study of summer mortality factors for natural populations of Chydoridae (Cladocera). *Hydrobiologia*, 107 : 131-139.
- ZARET, T. and RAND, A.S. (1971). — Competition in tropical stream fishes : support for competitive exclusion principle. *Ecology*, 52 : 336-342.