

Predation pressure of introduced mosquitofish (*Gambusia holbrooki* Girard), on the native zooplankton community. A case-study from representative habitats in the lower Mondego river Valley (Portugal).

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ABSTRACT

Mosquitofish, *Gambusia holbrooki*, was introduced into the Iberian Peninsula in 1921, becoming widely distributed in fresh-water systems associated to rural and urban areas. However, the impact of its introduction on natural aquatic communities in such areas has never been properly assessed. In this paper, we evaluate the influence of *G. holbrooki* on the zooplankton community of the river Mondego valley (Central Portugal). Spatial and temporal diet shifts were examined in two representative habitats of central Portugal, a typical rice field and a semi-natural protected wetland. Mosquitofish feed mainly on zooplankton (Copepoda, Cladocera, Rotifera and Ostracoda), although surface insects, such as aphids, collembolans, adult (imago) chironomids and other dipterans may constitute additional food. Although *Gambusia*'s ingestion rates are low, high population densities may cause a considerable predation pressure on zooplankton. *Gambusia* was found to exert a stronger predation pressure on zooplankton in the rice field, where zooplankton presented scarcer populations, than in the semi-natural protected wetland. Consumption rates of *Gambusia* changed as a function of body size and reproductive period. *Gambusia holbrooki* exerted significant predation pressure on native zooplankton populations and certainly competed with other coexisting fish species.

Key words: *Gambusia holbrooki*, zooplankton, impact, predation pressure

RESUMEN

La *Gambusia holbrooki*, fue introducida en la Península Ibérica en 1921, estando ampliamente distribuida en las aguas continentales asociadas a áreas rurales y urbanas. No obstante, el impacto de su introducción sobre las comunidades acuáticas naturales de dichas áreas no ha sido adecuadamente determinada. En este trabajo, evaluamos la influencia de *G. holbrooki* sobre las comunidades del zooplancton del valle del río Mondego (Centro de Portugal). Para ello se examinó la evolución espacial y temporal de la dieta en dos hábitats representativos del centro de Portugal, un campo de arroz y una zona húmeda seminatural protegida. *Gambusia* come principalmente zooplancton (Copepoda, Cladocera, Rotifera y Ostracoda), aunque insectos superficiales como áfidos, colémbolos, adultos (imago) de quironómidos y otros dípteros pueden constituir un alimento adicional. Aunque las tasas de ingestión de *Gambusia* son bajas, elevadas densidades poblacionales pueden producir una considerable presión de depredación en el zooplancton. Se ha encontrado que *Gambusia* ejerce una fuerte presión de depredación sobre el zooplancton en el campo de arroz, donde el zooplancton presenta poblaciones poco densas, que en la zona húmeda seminatural protegida. Las tasas de consumo de *Gambusia* cambian en función de la talla y del periodo reproductivo. *Gambusia holbrooki* ejerce una presión de depredación significativa sobre las poblaciones nativas del zooplancton y verdaderamente compiten con otras especies de peces con las que coexiste.

Palabras clave: *Gambusia holbrooki*, zooplancton, impacto, presión de depredación

INTRODUCTION

Mosquitofish, *Gambusia holbrooki* (Girard) (Cyprinodontiformes: Poeciliidae) is native from the Eastern coast of the United States. It was

introduced into temperate and tropical regions through mosquito control programmes (Cech & Linden, 1986; Haynes & Cashner, 1995; Homski *et al.*, 1994; Lydeard & Belk, 1993). In the Iberian Peninsula, mosquitofish were introduced

in 1921 (Albuquerque, 1956). Today, it is commonly found in disturbed systems, close to both rural and urban areas. Mosquitofish is presently one of the most widely distributed freshwater fish species around the world, and is believed to be the most widely disseminated natural predator in the history of biological control (Bosford *et al.*, 1987). *Gambusia holbrooki* has a high level of plasticity and survival capability, and will easily colonize new habitats. It will reproduce under most conditions, even when food is scarce. Mosquitofish is an opportunistic species. It feeds on zooplankton, aquatic and surface insects, snails, other fish species and algae (Cabral *et al.*, 1998; Crivelli & Boy, 1987; Garcia-Berthou, 1999; Hulbert & Mulla, 1981; Colwell & Schaefer, 1983; Daniels & Felley, 1992; Offill & Walton, 1999). The number of prey ingested by mosquitofish usually depends on its size relative to available prey. Diet changes seasonally with prey availability (Cabral *et al.*, 1998).

Gambusia holbrooki is a voracious species, and has been considered a pest following its introduction into new habitats. Rupp (1996), for instance, reported *Gambusia* feeding on the eggs of economically-desirable fishes, preying on rare indigenous species and decreasing small native aquatic vertebrate and invertebrate populations. *Gambusia* has helped eradicate the mosquito-borne malaria and its introduction is still advocated in some places (Hackett, 1937; in Rupp, 1996; Tabibzadel, 1970, Inei *et al.*, 1992 in Legner, 1995; Singaravelu *et al.*, 1997).

Trophic relationships between mosquitofish and zooplankton were investigated in two representative habitats of the river Mondego valley, a rice field and a semi-natural protected wetland. The aim of the present paper is to give estimates of the predation pressure on natural zooplankton populations, resulting from the introduction of *Gambusia holbrooki* in the Mondego river valley.

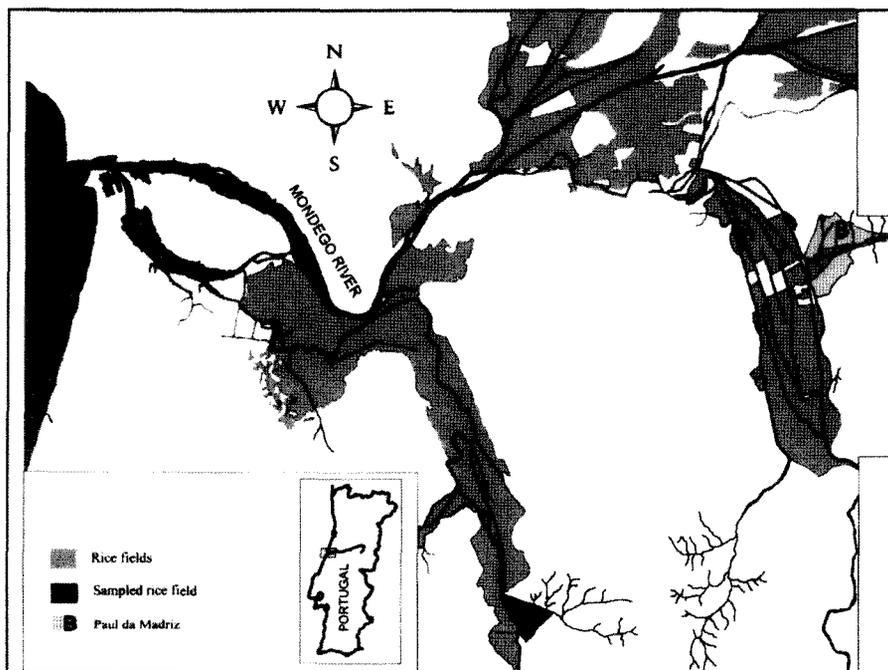


Figure 1. Location of sampling areas in the lower Mondego river valley. *Situación de las áreas de muestreo en el bajo valle del río Mondego.*

Table 1. Relative abundance (%) of main prey in mosquitofish gut contents and calculated Ivlev electivity index values, in the rice field and in the semi-natural protected wetland in the lower Mondego river valley (Portugal). *Abundancia relativa (%) de las principales presas de gambusia en el contenido intestinal y valores del índice de preferencia de Ivlev en el arrozal y en la zona húmeda seminatural protegida en el tramo inferior del valle del río Mondego (Portugal).*

Preys	Average of preys in the gut (%)		Ivlev Electivity Index	
	Rice field	Semi-natural wetland	Rice field	Semi-natural wetland
Copepoda	59.1	46.84	0.18	-0.14
Cladocera	19.45	16.56	-0.2	0.037
Rotifera	11.7	8.39	-0.06	1
Ostracoda	0.5	2.06	1	-0.49
Collembola	2.27	2.73	-0.37	-0.16
Aphidae	4.65	7.45	-0.32	1
Formicidae	0.78	0.43	-0.76	-0.92
Hymenoptera	0.07	0.41	-0.92	-0.67
Dytiscidae	0.01	0.93	-0.96	-0.63
Chrysomelidae	0	0.32	0	-0.79
Hydraenidae	0.08	0	-0.71	0
Hydrophilidae	0.06	0	-0.95	0
Gastropoda	0	0.03	0	-0.86
Coleoptera T	0.008	0	-0.78	0
Chironomidae AD	0.61	0.25		-0.84
Chironomidae LV	0.3	0	-0.85	0
Annelidae	0	0.06	0	-0.92
Diptera AD	0.01	3.88	-0.45	1
Arachnida	0.01	0.36	-0.91	-0.19
Acariformes	0	0.36	0	-0.44
Notonectidae	0	0.01	0	-0.97

T- terrestrial, AD- adult and LV- larvae

The numbers in bold are concerned to preferential Ivlev values

MATERIALS AND METHODS

Study site

The Mondego river valley is located in central Portugal (40°10'N, 08°41'W) (Fig. 1). The valley is about 15,000 ha. The main agricultural crop is rice (Anastacio & Marques, 1995). Winter is mild and summer hot and dry. Study sites were a typical of the area, rice field and a semi-natural protected wetland (Paul da Madriz), both located on the left margin of the river Mondego. Sampling took place in the main irrigation channel of the rice field, and in a heavily vegetated cannal in the wetland area.

Field and laboratory procedures

The sampling programme was carried out between April 1996 and May 1997. Samples were taken fortnightly during the main reproductive season (Cabral & Marques, 1999), and monthly during the rest of the year.

Gambusia holbrooki was collected by electrofishing, at three sites chosen randomly. We used a semi-portable generator to supply a rectified DC current (350-600 V). Discharges lasted approximately 30 minutes, considered enough time to catch almost all fish in the sampling area (i.e. ranging between 3 and 16m²). Sampling was from 10 to 13 h, which is the most intense feed-

ing period. Mosquitofish were immediately preserved in 4% neutralized formaldehyde. Within 48 hrs of fixation, specimens collected were washed with water and preserved in 70% ethanol. Individuals were then counted and grouped according to eight size-classes, i.e. 1 (smaller than 10 mm in length); 2 (11-15 mm), 3 (16-20 mm), 4 (21-25 mm), 5 (26-30 mm), 6 (31-35 mm), 7 (36-40 mm) and 8 (larger than 41 mm in length). Gut contents were examined in five specimens of each size-class sampled at each site. In size-classes 3, 4, and 5, some females and males exhibited identical size and five individuals of each sex were then examined. For gut content analysis, an excision was made from the esophagus up to the ventral region and preys and/or vestiges identified and counted.

Zooplankton samples were obtained by horizontal trawls of a 200 mm mesh plankton net. A digital flow meter was used to determine the volume of water passing through the net. Samples were immediately preserved in 4% neutralized formaldehyde and organisms sorted by size and identified in the laboratory. Many rotifers, nauplii, copepodites of initial stages and cladoceran juveniles were smaller than 200 μ m, thus passing through the mesh size used. Therefore, only gross seasonal trends in zooplankton distribution were examined.

Surface and terrestrial insects were also collected, as described in Cabral *et al.* (1998), in order to estimate if *Gambusia* may change its diet preferences as a function of the availability of these prey.

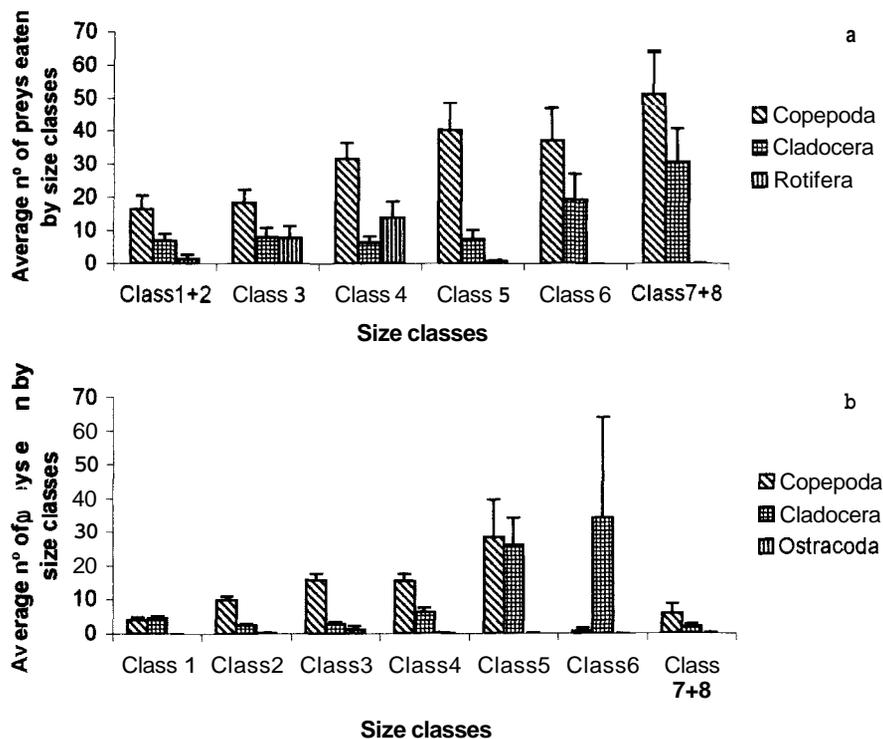


Figure 2. Mean number of prey items (Copepoda, Cladocera and Rotifera) eaten by mosquitofish of each size class (i.e. 1: smaller than 10 mm in length; 2: 11-15 mm, 3: 16-20 mm, 4: 21-25 mm, 5: 26-30 mm, 6: 31-35 mm, 7: 36-40 mm, and 8: larger than 41 mm in length) between April 1996 and May 1997. Bars are of one standard error at either side of the mean. Habitats were, a- rice field, b- semi-natural wetland. *Número medio de presas (Copepoda, Cladocera y Rotifera) comidas por gambusia de cada clase de tamaño (así, 1: menores de 10 mm de longitud; 2: 11-15 mm, 3: 16-20 mm, 4: 21-25 mm, 5: 26-30 mm, 6: 31-35 mm, 7: 36-40 mm, y 8: mayores de 41 mm en longitud) entre Abril de 1996 y Mayo de 1997. Las barras indican el error estándar a cada lado de la media. Los habitats fueron, a- campo de arroz, b- zona húmeda seminatural.*

Data analyses

Prey preferences were evaluated using Ivlev's "Electivity Index" (Ivlev, 1961), defined as $E_i = (r_i - P_i) / (r_i + P_i)$, where r_i is the relative abundance of a prey in a predator's diet and P_i is the prey's relative abundance in the ecosystem. E_i is scaled so that $E_i = -1$ corresponds to total avoidance of prey i , $E_i = 0$ represents non-selective feeding, and $E_i = +1$ shows exclusive feeding on a given prey i . The value -0.5 was the lower limit identifying "preferential" prey. To investigate possible differences in the number of prey ingested by different size-classes and sexual groups (i.e. immatures, males, non-gravid and gravid females, NGF and GF, respectively), a Kruskal-

Wallis rank analysis was used, followed by a non-parametric multiple comparisons test (Zar, 1996). To test whether the diet of *Gambusia* was dependent on seasonal changes in prey availability, the proportion of dominant prey species in stomach contents and habitat were compared. The potential predation pressure caused by mosquitofish on zooplankton was estimated from prey consumption estimates. To do this, we estimated mosquitofish densities (ind m^{-2}) each month, based on the whole set of samples. Densities were then multiplied by the corresponding monthly mean number of prey ingested. To test whether predation pressure (number of prey caught by m^2 , ind m^{-2}) was independent or not from the zooplankton, expressed as a proportion of total prey available in both studied habitats, Pearson correlation analysis were performed on both variables (i.e. mosquitofish density and zooplankton-prey proportion of total prey). Also, correlation analysis validated calculations of predation pressure from prey areal densities.

RESULTS

The most frequent zooplankton groups were Copepoda and Cladocera. According to Ivlev's Electivity Index, the preferential zooplankton prey of mosquitofish in the rice field were copepods, cladocerans and rotifers, while in the semi-natural wetland, preferred prey were copepods, cladocerans and ostracods (Table 1).

Results from the Kruskal-Wallis one-way analysis of variance by ranks, showed that, for the rice field, only cladocerans and rotifers were ingested in significantly different quantities by different mosquitofish size classes (copepoda $\chi^2=9.27$, n.s.; cladocera $\chi^2= 15.76$, $p<0.01$ and rotifera $\chi^2=15.36$, $p<0.01$) (Fig.2a). Males and females ingested copepods and cladocerans in significantly different amounts (copepoda $\chi^2=39.56$, $p<0.001$; cladocera $\chi^2= 41.10$, $p<0.001$ and rotifera $\chi^2=6.52$, n.s.) (Fig. 3a). In the semi-natural wetland, mosquitofish size-classes and sexual groups ingested significantly different amounts of both copepods and cladocerans (size

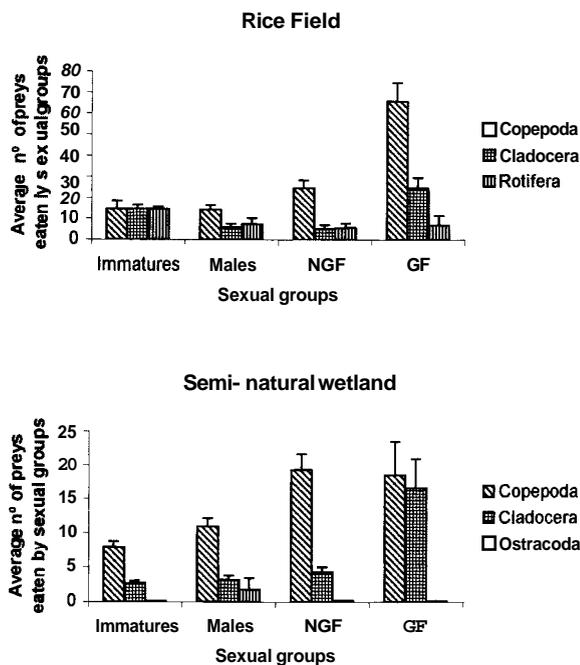


Figure 3. Mean number of prey items eaten by sexual groups of mosquitofish (i.e. immatures, males, non-gravid females: NGF, and gravid females: GF) collected between April 1996 and May 1997 from a- a rice field and, b- a semi-natural wetland. Bars are of one standard error at either side of the mean. *Numero medio de presas comidas por grupos sexuales de gambusia (inmaduros, muchos. hembras no grávidas: NGF, y hembras grávidas: GF) capturados entre Abril de 1996 y Mayo de 1997 de a- el campo de arroz y, b- la zona húmeda seminatural. Las barras indican una unidad del error estandar a cada lado de la media*

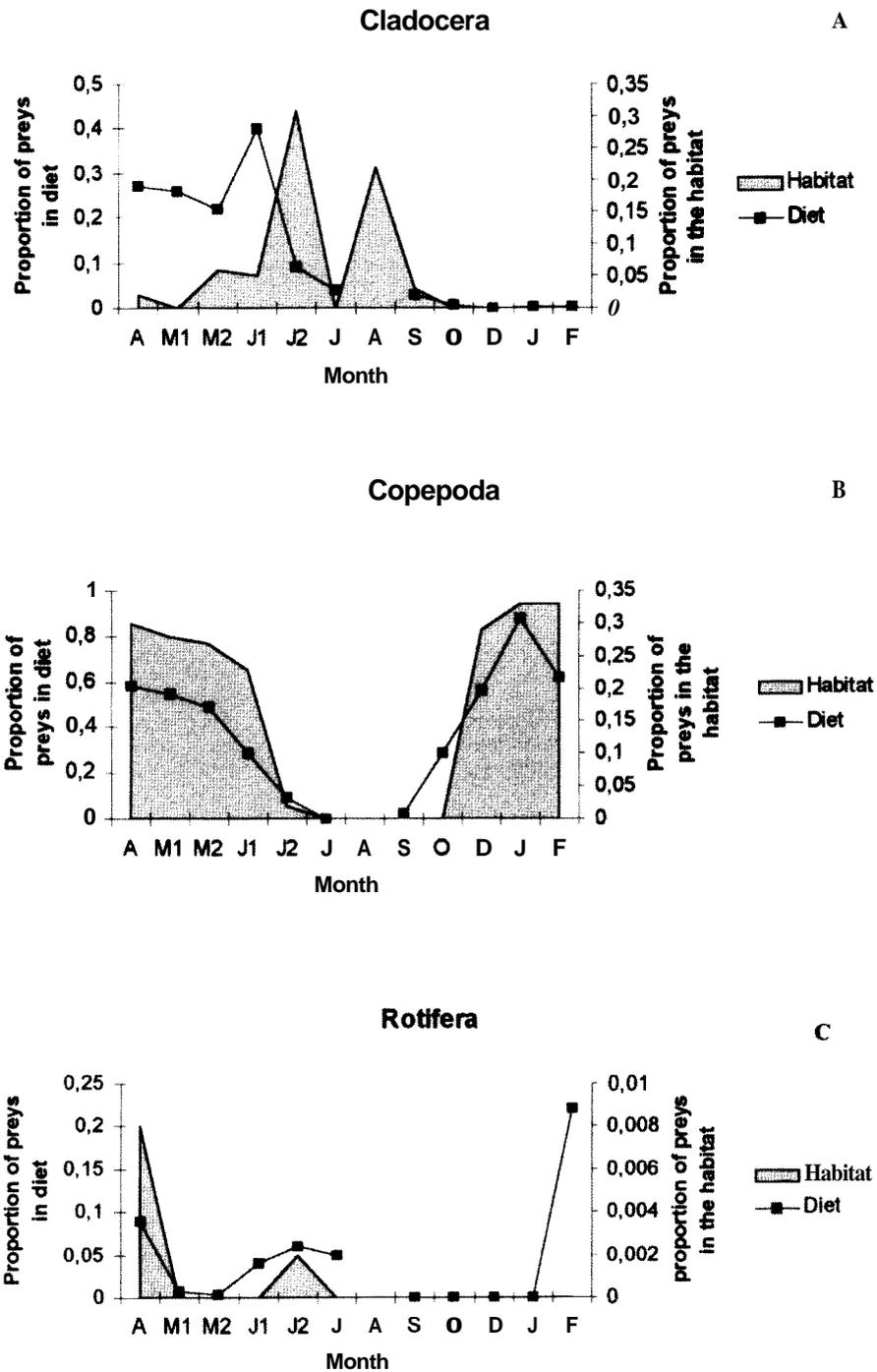


Figure 4. Proportion of mosquitofish main prey (i.e. Cladocera, Copepoda and Rotifera) found in their stomach contents and in the habitat, during the sampling period (April 1996-May 1997) in the rice field. A-Cladocera, B- Copepoda and C- Rotifera. *Proporción de las principales presas de gambusia (Cladocera, Copepoda y Rotifera) halladas en el contenido estomacal y en el hábitat durante el periodo de muestreo (Abril de 1996 a Mayo de 1997) en el campo de arroz. A- Cladocera, B- Copepoda y C- Rotifera.*

classes: copepoda $\chi^2=24.78$, $p<0.001$; cladocera $\chi^2=24.12$, $p<0.001$ and ostracoda $\chi^2=2.27$, n.s.) (Figs. 2b and 3b, respectively). Multiple comparison tests showed that, in the rice field, the largest size-classes (class 7+8) clearly ingested more cladocerans, while medium-small fish apparently preferred rotifers (Fig. 2a). Gravid females ingested more copepods and cladocerans than the other groups (Fig. 3a). In the semi-natural wetland, size-classes 5 and 6 ingested more zooplankton than the other size-classes (Fig. 2b). Gravid females apparently preyed upon cladocerans more than the other sexual groups did (Fig. 3b). On the other hand, non-gravid females ingested more copepods than gravid females, and both female groups ingested more copepods than males and immature fish (Fig. 3b).

Estimates of the proportion of different zooplankton prey in stomachs and in the habitat allowed to examine mosquitofish diet seasonal changes. In the rice field, copepods were more abundant from October to the beginning of June, while cladocerans were common in May and June, disappeared in July, increased again in August and then declined gradually to their total disappearance in October. The mesh size of sampling nets was too large and, thus, rotifers were not adequately collected. Proportional values plotted are therefore

indicative of real densities but must be regarded with caution. The analysis of these samples indicated a higher proportion of rotifers in April and mid-June. Large numbers during winter were of periphytic species (Fig. 4). Terrestrial prey (e.g. Collembola, aphids, adult chironomids and other adult Diptera) were more frequent from June to September, coinciding with the period when there were proportionally less zooplankton, both in the habitat and in guts analysed (Fig. 5). In the wetland, copepods and cladocerans were frequent throughout the year, except cladocerans in July. Ostracods were relatively abundant in May and September. Copepods were more important in mosquitofish diet than cladocerans and ostracods between April and July. From July, the proportion of copepods in their diet decreased and cladocerans and ostracods became main prey (Fig. 6). The proportion of terrestrial prey (i.e. Collembola, arachnids and acarids) in the habitat was larger from September to December than the rest of the year. In gut contents, terrestrial prey were more abundant in April, October and March (Fig. 7). These data suggest *Gambusia* ingests prey depending on availability in the environment. This trend was particularly clear in the rice field.

During summer, following a decrease in zooplankton, mosquitofish switched prey categories. In the rice field, terrestrial prey were available

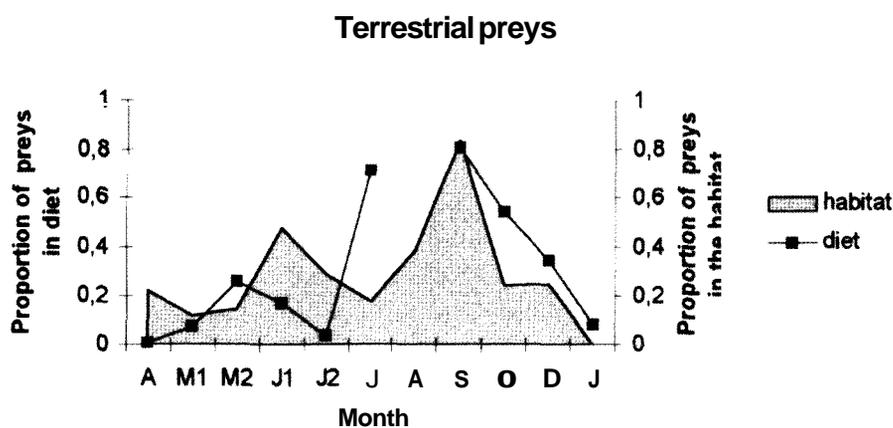


Figure 5. Proportion of mosquitofish main terrestrial prey found in stomach contents and in the habitat, during the sampling period (i.e. April 1996-May 1997) in the rice field. Samples in May and July were taken fortnightly (M1, M2 and J1, J2). *Proporción de las principales presas de gambusias de origen terrestre halladas en el contenido intestinal y en el habitat durante el período de muestreo (Abril de 1996 - Mayo 1997) en el campo de arroz. Las muestras de de Mayo y Julio se tomaron quincenalmente (M1, M2 y J1, J2).*

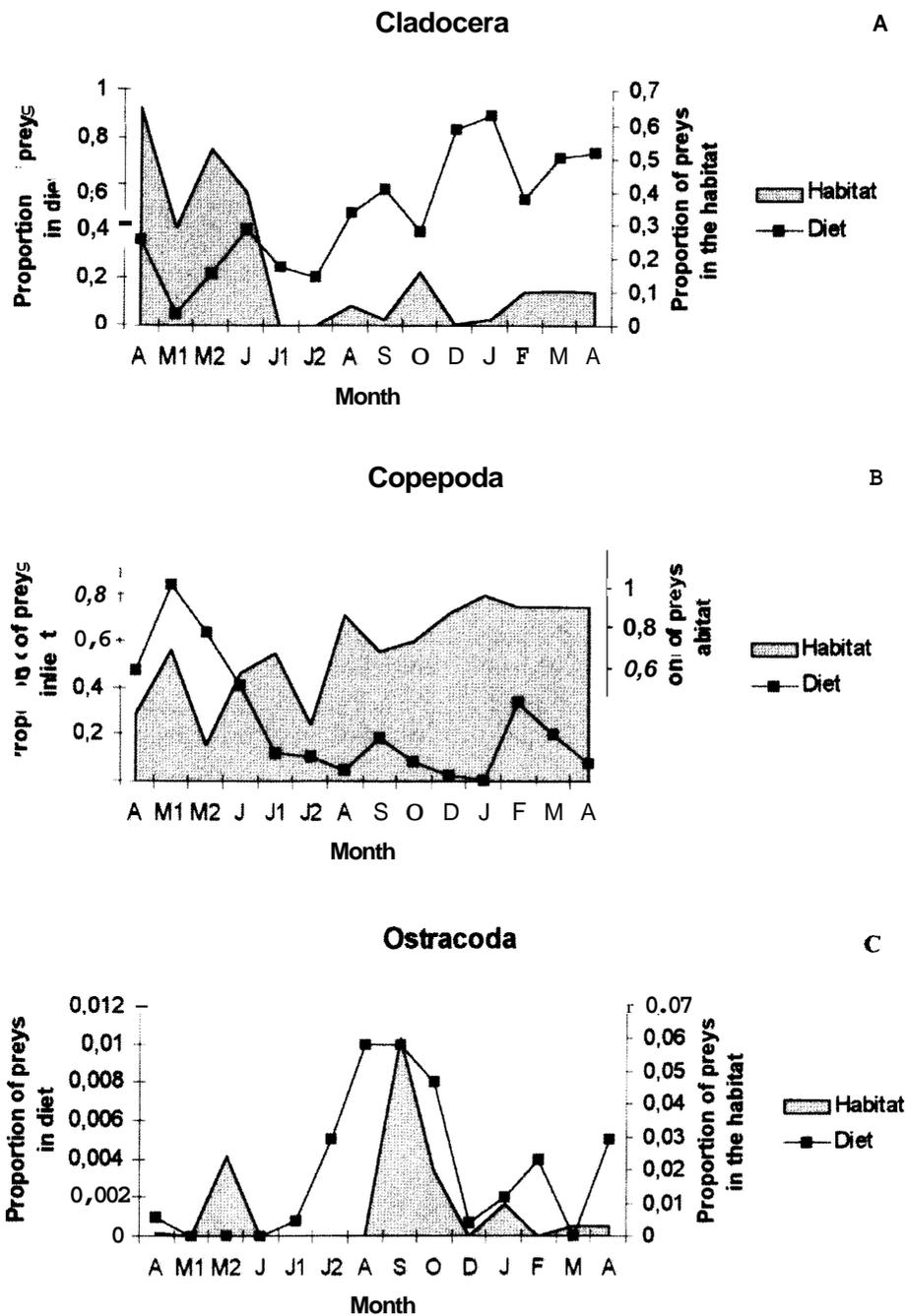


Figure 6. Proportion of mosquitofish main prey (i.e. Cladocera, Copepoda and Rotifera) found in the stomach contents of mosquitofish and in their habitat, during the sampling period (April 1996-May 1997) in the semi-natural wetland. The proportions of these prey in the habitat, refer to mainly adult crustaceans. A-Cladocera, B-Copepoda and C-Ostracoda. Samples in May and July were taken fortnightly (M1, M2 and J1, J2). *Proporción de las principales presas de gambusia (Cladocera, Copepoda y Rotifera) halladas en el contenido estomacal y en su habitat durante el periodo de muestreo (Abril 1996 - Mayo 1997) en la zona húmeda seminatural. Las proporciones de estas presas en el habitat se refieren principalmente a crustaceos adultos. A- Cladocera, B-Copepoda y C-Ostracoda. Las muestras de Mayo y Julio se tomaron quincenalmente (M1, M2 y J1, J2).*

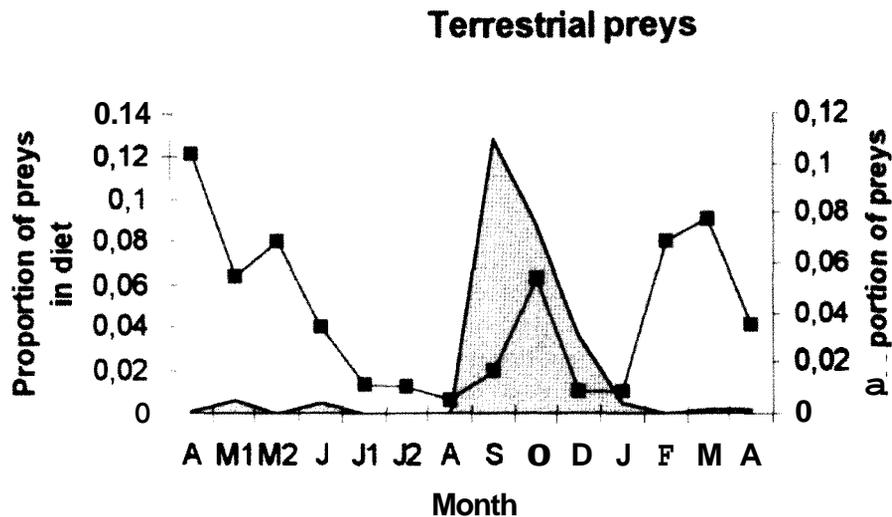


Figure 7. Proportion of mosquitofish terrestrial prey found in stomach contents of mosquitofish and in the habitat, during the sampling period (April 1996-May 1997) in the semi-natural wetland. Samples in May and July were taken fortnightly (M1, M2 and J1, J2). *Proporción de presas terrestres de gambusia halladas en su contenido estomacal y en el habitat durante el periodo de estudio (Abril 1996 - Mayo 1997) en la zona húmeda seminatural. Las muestras de Mayo y Julio se tomaron quincenalmente (M1, M2 y J1, J2).*

throughout the year. However, these prey were more abundant in stomach contents from July to October. In the wetland, terrestrial prey were proportionately less frequent in the diet of mosquitofish. A certain “preference” for terrestrial prey was detected in April and October, coinciding with small peaks in abundance (Figs. 5 and 7). Chironomids and dipterans were ingested more frequently by gravid females than by other groups. In the wetland, arachnids (i.e. spiders and acarids) were alternative prey to zooplankton, and were ingested by all size classes.

Highest predation pressure occurred at peak fish densities, although each individual fish ingested a lower number of prey. Predation on cladocerans was higher in May and in June in the rice field, when fish densities were moderate and individual consumption higher. In August, high predation pressure on cladocerans occurred at high fish density and low individual consumption rates. On copepods, predation pressure was higher in June, at high individual consumption rates. Rotifers were more predated upon in August, when fish densities were high and individual consumption rates lower (Fig. 8).

In the semi-natural wetland, predation pressure on cladocerans was high in July, with large fish densities. Predation pressure on copepods in the wetland was high in August, when individual fish consumption rates were low and fish densities high. On ostracods, predation pressure was high in August, when they were scarce anyway, and fish density and individual fish consumption rates were higher (Fig. 9).

The Pearson correlation analysis showed that predation pressure on copepods in the rice field ($r = 0.36$, n.s.) and in the semi-natural wetland ($r = -0.55$, n.s.) was independent of availability of this prey to mosquitofish in both habitats. The same result was obtained for rotifers ($r = 0.17$, n.s.) and ostracods ($r = 0.52$, n.s.). Mosquitofish predation pressure on cladocerans in the rice field was not significant either ($r = -0.05$, n.s.). In the semi-natural wetland, however, predation pressure on cladocerans was higher when this prey type was scarce ($r = -0.67$, $p < 0.01$). High mosquitofish predation on zooplankton (i.e. ind m^{-2}) does not always result from high availability. This suggests gut content analysis gives good estimates of predation pressure on prey.

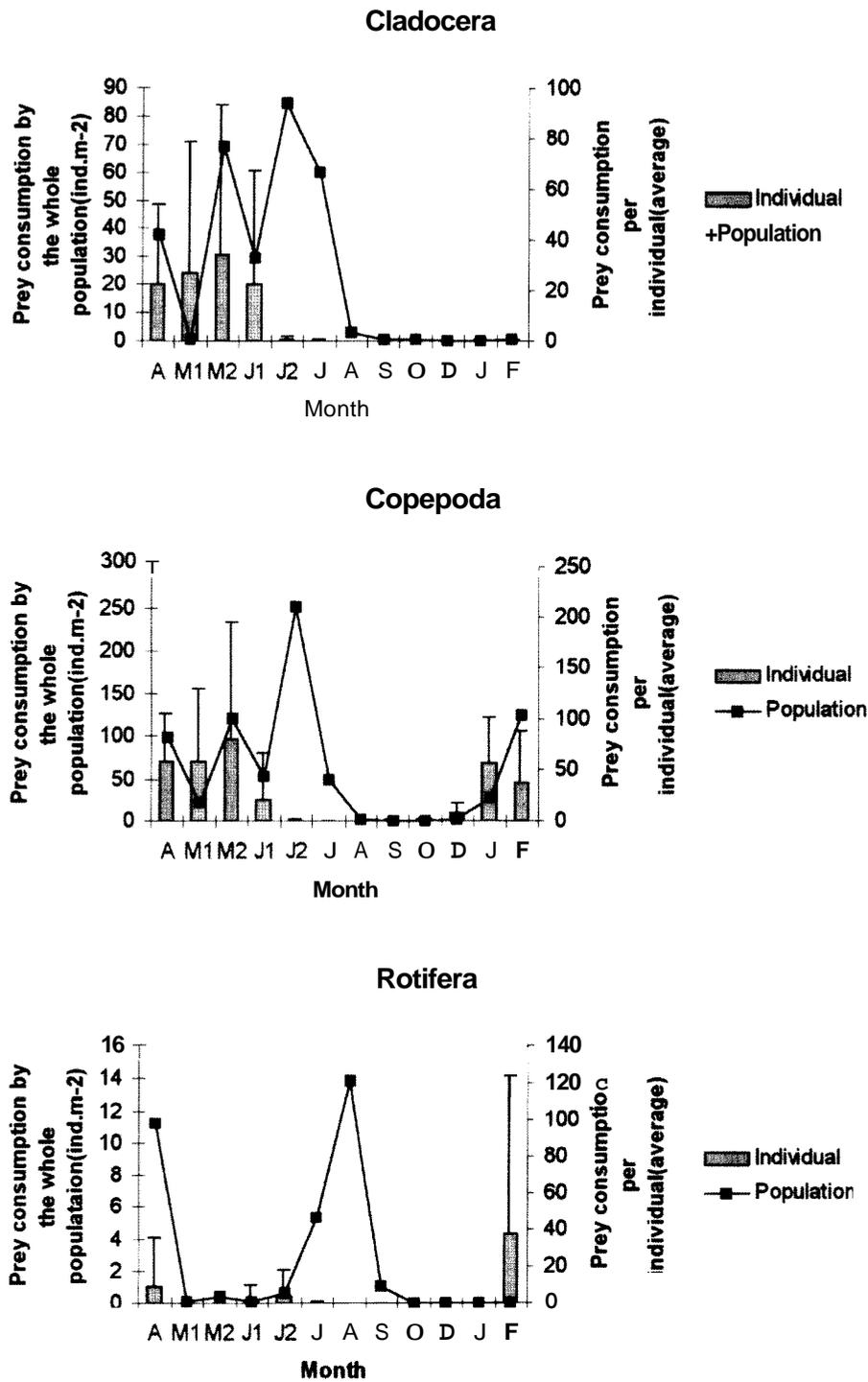


Figure 8. Prey consumption (ind m⁻²) by the whole mosquitofish population in the rice field. A- Cladocera, B-Copepoda and C- Rotifera. Samples in May and July were taken fortnightly (M1, M2 and J1, J2). *Consumo de presas (ind m⁻²) para toda la población de gambusias en arrozal. A- Cladocera. B- Copepoda y C- Rotifera. Las muestras de Mayo y Julio se tomaron quincenalmente (M1, M2 y J1, J2).*

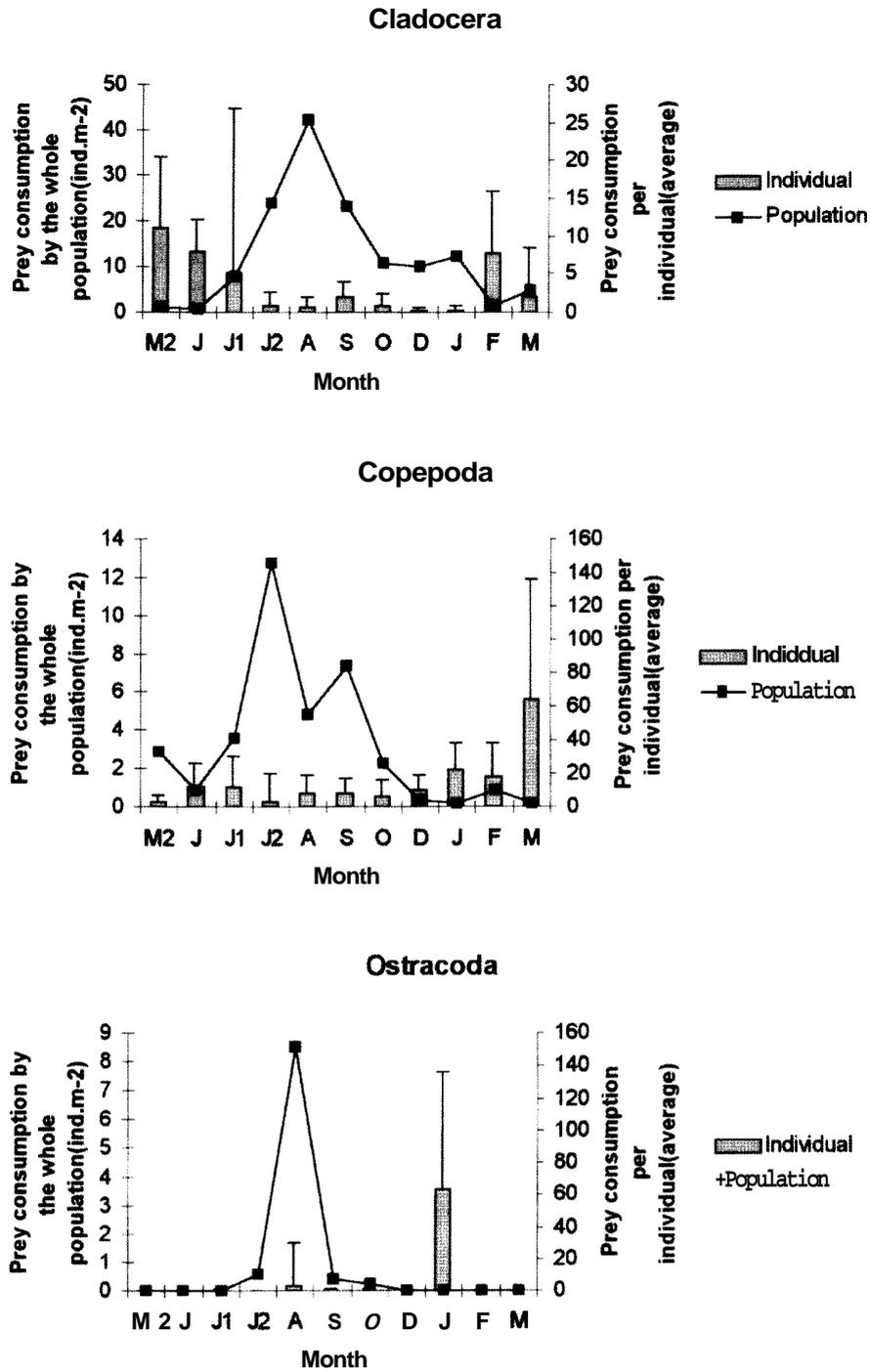


Figure 9. Prey consumption (ind m-2) by the whole mosquitofish population on prey in the semi-natural wetland. A- Cladocera, B-Copepoda and C- Ostracoda. Samples in May and July were taken fortnightly (M1, M2 and J1, J2). *Consumo de presas (ind m-2) para toda la población de gambusias en la zona húmeda seminatural. A- Cladocera, B- Copepoday C- Ostracoda. Las muestras de Mayo y Julio se tomaron quincenalmente (M1, M2 y J1, J2).*

DISCUSSION

Mosquitofish are morphologically adapted to feed near the water surface, having a flattened head and a terminal upward-directed mouth. Also, the position of the head during feeding is flexible, so the mouth can change from a dorso-terminal to a ventral position. This flexibility allows mosquitofish to feed at the surface, on the benthos and in the water column (Arthington & Marshall, 1999). The analysis of stomach contents revealed, in agreement with other studies (Colwell & Shaefer, 1983; Crivelli & Boy, 1987; Daniels & Felley, 1992; Hulbert & Mulla, 1981; Mansfield & Mcardle, 1998; Cabral *et al.*, 1998), that mosquitofish fed primarily near the surface on copepods and cladocerans, both in the rice field and in the semi-natural wetland. Hulbert & Mulla (1981) concluded that cladocerans were more vulnerable to mosquitofish predation than copepods. In our study area, however, we observed the opposite, copepods being the most ingested prey group (59.1% in the rice field and 46.8% in the wetland). However, gut content ratios (Cladocera vs. Copepoda) could be explained by respective availability, as copepods were generally much more abundant than cladocerans (rice field: 62.8% the copepods vs. 16.1% the cladocerans; wetland: 61.7% the copepods vs. 16.7% the cladocerans; Cabral *et al.*, 1998). Fish pigmentation, feeding behaviour and body shape can also influence predators' choice (O'Keefe *et al.*, 1998; Atsui & Hiroaki, 1998; Viitasalo *et al.* 1998).

Garman (1991) explained the ingestion of terrestrial prey by a cyprinid species as a general response of predator fish to seasonal decreases in availability of aquatic prey. In our study, although terrestrial prey were present all year, their consumption increased during summer, suggesting the switch to terrestrial prey was a response to zooplankton scarcity (Figs.4, 5, 6 and 7).

The increase in mosquitofish predation (i.e. ind ingested m⁻²) was independent of prey availability, representing a real measure of trophic pressure. Before the reproduction period of mosquitofish, calculated predation pressure was not

intense because prey were abundant, but fish densities low. During spring and the beginning of summer (i.e. the reproduction period), mosquitofish density increased and intense feeding on zooplankton was registered. Densities of immature fish were high during this period and they are known to feed almost exclusively on zooplankton. Wurstsbaugh *et al.* (1980) explained that the immature mosquitofish could cause a higher impact on prey populations than adult fish, because they are able to consume over 100% of their own weight daily. As immature individuals grow in size, they are able to feed on a wider range of zooplankton. Large-bodied zooplankton will replace smaller species under intense predation regimes (Brooks & Dodson 1965; Wetzel, 1993). Intense predation pressure was exerted at high fish density, although, occasionally, predation pressure was due to large individual consumption.

Zooplankton populations often decline by mid-summer. Strong predation by mosquitofish can enhance this decline and cause a more durable "perturbation" on zooplankton. Actual lower Mondego river valley zooplankton will decrease and small zooplankton will replace them.

Like other *Gambusia* species, the ability of *Gambusia holbrooki* to adapt to different, often harsh, habitats by modifying its life history (Haynes & Cashner, 1995), may explain differences between the two populations studied in the lower river Mondego valley. In the present study, we examined predation pressure of *Gambusia holbrooki* on its main prey, zooplankton. Mosquitofish might have strong effects on copepod and cladoceran populations. Direct and indirect impacts of mosquitofish on vulnerable indigenous fish species could be important. This is an issue in bad need of further research.

The introduction and establishment of exotic species is apparently more difficult in undisturbed, natural or semi-natural ecosystems. Habitat protection is thus needed, particularly when fish species are deliberately displaced and, for instance, aquarium fishes introduced into natural freshwater systems.

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