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Distribution and Habitat Preferences of the Introduced Mummichog *Fundulus heteroclitus* (Linneaus) in South-western Spain

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The distribution and apparent habitat preference of the common mummichog (*Fundulus heteroclitus*) in south-western Spain were examined during summer–autumn 1996. This introduced species was more or less continuously distributed along the Atlantic coast of Spain, being more abundant in sites near the coastline (usually <10 km inland), mainly in four extensive marshes. The species preferred marsh-related mesohabitats, such as salt lagoons, saltmarsh fish ponds and marsh channels, both natural and man-modified. *Fundulus heteroclitus* was mostly found at salinities >25. It was the most frequently captured fish species, occurring at 81 of the 272 sites sampled; their frequency of occurrence was almost twice that of the second ranked species (*Gambusia holbrooki*). However, in over 80% of cases, *F. heteroclitus* was found alone or with only one sympatric fish species, which usually belonged to a group composed of *Gobius niger,* mugilids, *Anguilla anguilla, Blennius* sp., *Lebias ibera*, *Pomatoschistus* sp. and *Dicentrarchus labrax*. Finally, the origin and dispersal of mummichog in the Iberian peninsula and the potential effects of this species on native fish populations is discussed.

Keywords: introduced species; tidal habitats; marshland; fish assemblages; Spain

Introduction

The mummichog, *Fundulus heteroclitus*, is an exceptionally wide-ranging cyprinodontid fish. It occurs naturally along the east coast of North America from south-western Newfoundland to north-eastern Florida. This species is ubiquitous in North American East Coast salt marshes, being mostly found in sheltered coastal waters. Although occasionally it inhabits freshwater habitats, the species is best known from the tidal salt marsh, a fluctuating physical environment for which mummichogs are well adapted due to considerable flexibility in their ecological requirements (Kneib, 1986).

The first records of *F. heteroclitus* in the Iberian Peninsula are dated between 1973 and 1976 (Hernando, 1975; Coelho *et al.*, 1976). However, the precise date and location of the species' introduction still remains unclear. Although there have been studies describing its life-history pattern (Arias & Drake, 1986; Drake *et al.*, 1987; Fernández-Delgado, 1989) and density (Arias & Drake, 1987, 1989), little is known about the role of *F. heteroclitus* in this new European habitat. The introduction of exotic species can have a negative effect on the functioning of native ecosystems (Dowling & Childs, 1992; Barlow *et al.*, 1987; Richardson & Whoriskey, 1992). It is suspected that mummichogs may have already negatively affected some native endemic species such as the endangered *Lebias ibera*.

This study describes the detailed distribution and abundance of *F. heteroclitus* along the coast of south-western Spain. Also, their habitat preferences, including the composition of the fish assemblages found in those habitats are documented. Finally, the potential causes of the observed pattern of mummichog distribution and the effects of this species on native fish populations are discussed.

Methods

Study area

This study was carried out in an area near the coast in the provinces of Huelva, Sevilla and Cádiz

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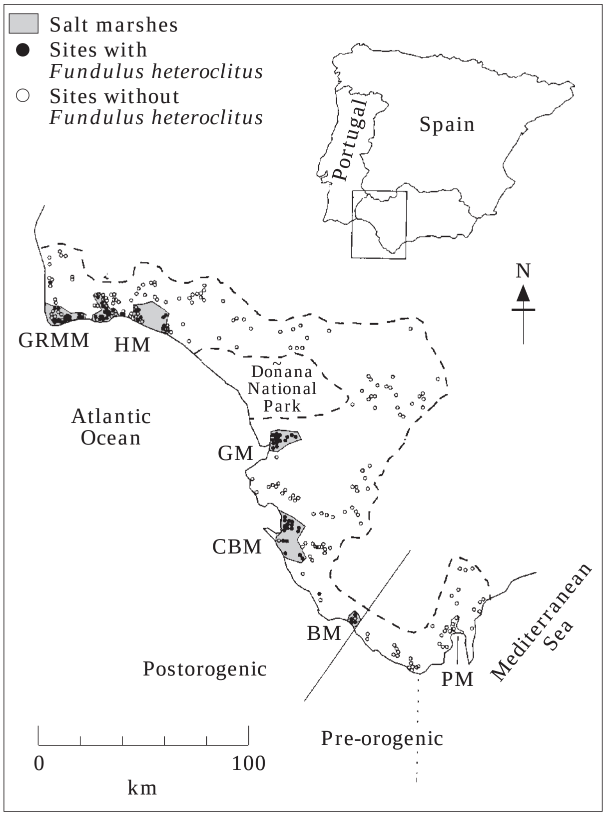

FIGURE 1. Map of the study area, with indication of the sites sampled (circles). GRMN, Guadiana river mouth marshes; HM, Huelva marshes; GM, Guadalquivir marshes; CBM, Cádiz bay marshes; BM, Barbate marshes; PM, Palmones marshes.

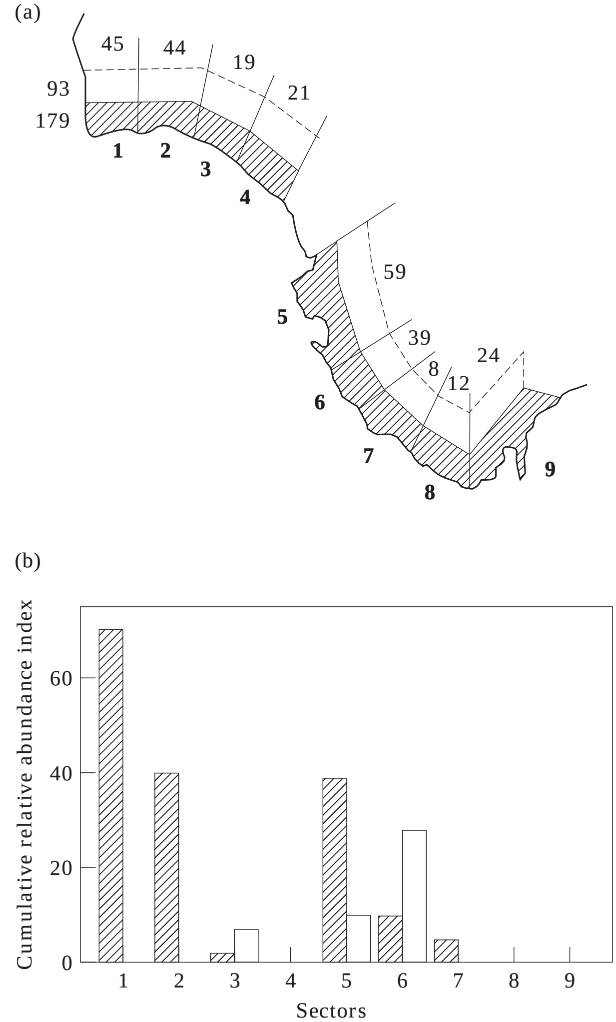

FIGURE 2. Geographical relative abundance index (RAI) distribution of *Fundulus heteroclitus* in the south-western coast of Spain. (a) Sectors in which the study area was divided. The bold numbers indicate the sector and the light ones the number of sites sampled in each sector. (b) Cumulative *F. heteroclitus* relative abundance index per sector. Hatched bars, coastal; open bars, inland.

(south-western Spain) (Figure 1). Doñana National Park has been excluded because it was previously studied by Fernández-Delgado *et al.* (1994).

A complete description of the study area can be found in Fernández-Palacios *et al.* (1988). The area can be divided in two sectors, the post-orogenic one, covering most of the north-western part of the area, and the pre-orogenic surrounding the Gibraltar strait (see the limit between both sectors in Figure 1). The pre-orogenic is very heterogeneous (made of mostly Jurassic limestones and sandstones), and consists of high reliefs, capes and cliffs. The post-orogenic is more homogeneous, composed of Quaternary biogenic chalk and sands, that form flat lands, small bays and long sandy stretches of beach; a morphology that obstructs the drainage of fluvial currents and encourages the formation of marshes and coastal dunes.

Tidal range in the Atlantic sectors fluctuates between 2·5 and 3 m (see Figure 1), while in the Mediterranean sector (number 9, Figure 1) it is always less than 0·8 m. This difference, along with the intense westernly winds, generates a strong sea current towards the Mediterranean, and also determines the extent of tidal habitat and marsh formation at the river mouths. As a consequence, marshes are much more abundant and extensive along the Atlantic coast than along the Mediterranean, especially in the postorogenic sector (see Figure 1).

The climate in the area is Mediterranean (semi)-humid with mild winters. The average temperature is usually 10–12 °C in winter and about 23–25 °C in summer. The rainfall varies more than temperature. In sector 1 (Figure 1) the annual average rainfall is 500–600 mm, while in sectors 8 and 9 it is greater than 800 mm.

Field sampling

Between August and December of 1996, 272 sites were sampled from potential sites identified on 1:50 000 maps (National Grid of Spain). These included all the water bodies near the coast and/or under tidal influence or placed in low flat lands (usually below 100 m of altitude). At each sampling site, fishes were collected from a 100 m reach.

Each sampling site was classified into one of the following habitat categories: creek (low order streams, usually less than 3rd order); stream (≥3rd order); stream pool (isolated pools in drying streams); man-made channel; pond (small size lakes, usually less than 2 ha); natural marsh; modified marsh (slightly disturbed marshes, with few symptoms of human intervention); altered marsh (moderate to highly disturbed marshes, with clear symptoms of human impacts); saltmarsh fish pond (traditional extensive fish culture); marsh salt mine; fish farm (intensive fish culture); and tidal lagoon.

Different types of sampling gear used in this study included: trawls; fyke nets (prawn traps) 2 mm mesh size (2 m length, 0·1 m entrance diameter); minnow traps (Harrison *et al.*, 1986) (0·5 m length, 0·03 m entrance diameter) and quadrangular (40 × 40 cm) hand nets. The selection of the type and number of fishing gears was decided *in situ* depending on the depth and extension of the water body, the type of aquatic vegetation and the water turbidity. Minnow traps were used in all cases. The active fishing methods (trawls and hand nets) were mainly used to trap species other than mummichog. In this case, the catches were only identified and not counted.

The passive fishing methods (fyke nets and minnow traps) were set for roughly 24 h. Once the sampling was finished, the species caught were identified and the total number of individuals in each of them was counted. The results of this sampling are expressed as catches per unit effort (c.p.u.e.), 1 unit being a passive trap in place for 24 h. To minimize the possible differences in relative abundance due to the different efficiencies of the traps, a relative abundance index (RAI) was used for mummichog following the criteria:

if c.p.u.e. $\leq 4 \Rightarrow \text{RAI}=1$
if c.p.u.e. $4{\cdot}1\text{–}8 \Rightarrow \text{RAI}=2$
if c.p.u.e. $8{\cdot}1\text{–}12 \Rightarrow \text{RAI}=3$
if c.p.u.e. $12{\cdot}1\text{–}16 \Rightarrow \text{RAI}=4$
if c.p.u.e. $>16 \Rightarrow \text{RAI}=5$

Data analysis

To evaluate the relative abundance of the species along its distribution area, the study area was divided into 18 sectors of a similar extent and the cumulative RAI was calculated for each one of them.

To measure habitat and salinity preferences of mummichog and other fish species, the Vanderploeg and Scavia electivity index (E_i^*) was used (Lechowicz, 1982):

$$E_i^* = [W_i - (1/n)]/[W_i + (1/n)]$$

$$W_i = (r_i/p_i)/\left(\sum_i r_i/p_i\right)$$

where r_i = proportion of ‘used’ habitat i or salinity category i; p_i = proportion of ‘available’ habitat i or salinity category i in the environment; n = number of habitat types or salinity categories.

This index (E_i^*) has a value of zero for random use of the variable of interest and a possible range between 1 (maximum preference) and −1 (total rejection).

To analyse the relationship between the mummichog and the rest of the fish species captured E_i^* has been calculated. Here, the ‘used’ variable i was the frequency of coexistence of the species i with *F. heteroclitus*, and the ‘available’ variable i was the absolute frequency of appearance of that species.

To group the different fish species found in the study area according to their habitat preferences, a principal component analysis (PCA) was carried out on a ‘habitat type × fish species’ matrix, where each a_{ij} was the habitat i electivity index (E_i^*) of species j. Thus, species with similar habitat preferences should appear grouped.

To calculate the mummichog preference of coexistence with other fish species, the residuals of the regression line between the absolute frequency and the frequency of coexistence with *F. heteroclitus* of each species has been computed. Thus, those species with higher residual absolute value can be considered as ‘preferred’ or ‘rejected’ by *F. heteroclitus*, independently of their absolute frequency of appearance.

Results

Distribution

Fundulus heteroclitus was found, more or less continuously, along the Atlantic coast of southern Spain, from the mouth of the Guadiana River (Huelva) to the marshes of the Barbate River (Figure 1). *Fundulus heteroclitus* was captured in 81 of 270 sites sampled. The species tended to be found in four main areas (Figure 1) coinciding, in general, with extensive marshes. *Fundulus heteroclitus* was never found in sites

Table 1. Habitat types sampled in south-western Spain and frequency of appearance of *Fundulus heteroclitus* in each of them

Habitat	Available ($n=270$)	Used ($n=81$)	Preference index (E_i^*)
Marsh salt-mines	19	17	0·46
Saltmarsh fish ponds	10	9	0·46
Modified marsh	15	13	0·45
Natural marsh	23	18	0·41
Fish farm	4	3	0·39
Altered marsh	13	8	0·30
Tidal lagoon	4	2	0·20
Stream pool	46	6	− 0·43
Man-made channel	20	2	− 0·54
Pond	15	1	− 0·66
Creek	82	2	− 0·86
Stream	19	0	− 1·00

Table 2. Salinity categories selected by *Fundulus heteroclitus* in south-western Spain

Salinity categories	Available ($n=262$)	Used ($n=76$)	Preference index (E_i^*)
≤1	133	6	− 0·79
1·1–5	22	2	− 0·62
5·1–25	26	8	− 0·11
25·1–50	58	43	0·32
>50	23	17	0·32

far (usually no more than 10 km, maximum 18 km) from the coast line.

Habitat preferences

The species was found in 11 of the 12 habitat categories established (Table 1), and preferred marsh-related habitats, specially salt lagoons, saltmarsh fish ponds, marshes (both natural and man-modified), fish farms and tidal lagoons. Mummichogs were not found in inland water bodies (stream pools, man-made channels, ponds, creeks and streams) (Table 1). Thus, *F. heteroclitus* were restricted to the saline habitats, usually with salinity values higher than 25 (Table 2).

To evaluate the distribution pattern of the relative abundance of *F. heteroclitus* along its distribution, the sum of the RAI values per sector (cumulative RAI) into which the study area was divided is shown in Figure 2(a and b). The RAI values differed significantly between sectors (Kruskal–Wallis statistic = 14·8, $P<0{\cdot}022$). Along a gradient of distance from the coast, significantly more mummichogs were captured in the coastal sector than in the inland one (Mann–Whitney test: $Z=2{\cdot}67$, $P=0{\cdot}0075$) [Figure 2(b)]. Sector 1 contained the extensive marshes of the lower Guadiana River. In contrast, sectors 4, 8 and 9 did not contain any marsh areas, except the small Palmones marshes in sector 9.

Fish species assemblages

A total of 21 fish species was captured (the mugilids were considered as one taxon, although five species were identified) (Table 3). *Fundulus heteroclitus* was the species captured most frequently (81), almost twice as much as the species that ranked second (*Gambusia holbrooki*: 41 times); both are exotic introductions to the Iberian Peninsula. Other species were divided into two groups: those associated with *F. heteroclitus* (positive E_i^* values) and those that did not coexist with it (negative E_i^* values) (Table 3).

Fundulus heteroclitus appeared alone or with only one other species of fish in over 80% of cases. Mummichogs were never caught with four or more species. However, in some saltmarsh fish ponds the mummichog coexisted with 10 fish species (Arias & Drake, 1987).

According to their habitat preferences, five groups of species were obtained following the PCA of the ‘ species × E_i^* index ’ matrix, based on their correlations with both PC1 and PC2 [Figure 3(a)]. Each group of species could be assigned to a particular habitat [Figure 3(b)]. *Fundulus heteroclitus* was clearly isolated from the remaining groups. As expected, *F. heteroclitus* preferred saltmarsh-related habitats. The group, composed of *Gobius niger* (GN), mugilids

TABLE 3. Frequency of occurrence of the fish species captured during the *Fundulus heteroclitus* field survey and frequency of coexistence with this cyprinodontid in south-western Spain

Species	Frequency	Frequency of coexistence with *F. heteroclitus*	E_i^*
Fundulus heteroclitus (FH)	81	81	
***Gobius niger* (GN)**	12	10	0·64
***Mugilids* (MM)**	33	18	0·50
***Anguilla anguilla* (AA)**	28	14	0·47
***Lebias ibera* (LI)**	8	5	0·47
***Pomatochistus* sp. (PS)**	30	11	0·34
Atherina boyeri (AB)	15	5	0·27
Sygnathus acus (SA)	4	1	0·16
Cyprinus carpio (CC)	6	2	0·10
Gambusia holbrooki (GH)	42	8	− 0·06
Cobitis paludica (CB)	10	1	− 0·29
Barbus sclateri (BS)	27	0	− 1·00
Leuciscus pyrenaicus (LP)	9	0	− 1·00
Chondrostoma polylepis (CP)	7	0	− 1·00
Micropterus salmoides (MS)	5	0	− 1·00
Lepomis gibbosa (LG)	4	0	− 1·00
Dicentrarchus labrax (DL)	2	0	− 1·00
Cichlasoma facetum (CF)	2	0	− 1·00
***Blennius* sp. (BL)**	2	0	− 1·00
Tinca tinca (TT)	1	0	− 1·00
Tropidophoxinelus alburnoides (TA)	1	0	− 1·00

n=270.
[a]The mugilids include *Liza ramada*, *Liza saliens*, *Liza aurata*, *Chelon labrosus* and *Mugil cephalus*.
The E_i^* index reflects the probability of finding each species coexisting with *Fundulus heteroclitus*.
Bold type indicates species found in the same habitat as mummichogs.

(MM), *Anguilla anguilla* (AA), *Blennius* sp. (BL), *Lebias ibera* (LI), *Pomastoschistus* sp. (PS) and *Dicentrarchus labrax* (DL), was not significantly correlated with any PC axis. This group was not directly related with any of the habitat types observed in the PCA and can coexist with *F. heteroclitus*.

The distribution of the residuals in relation to the absolute frequency of occurrence of each species (Figure 4, see Methods), points out positive associations between mummichogs and mugilids, *G. niger* and *A. anguilla*. The remaining species potentially coexisting with *F. heteroclitus* (*Pomatoschistus* sp., *L. ibera* and *Blennius* sp.), did not display either a positive or negative association with this species (Figure 4).

Discussion

On the origin and dispersal of F. heteroclitus *in the Iberian Peninsula*

The taxonomic status and origin of *F. heteroclitus* in the Iberian Peninsula has been a long debated and controversial subject since the first record of the species in 1973 (Hernando, 1975; Coelho *et al.*, 1976; Gómez-Caruana *et al.*, 1984, 1987; Fernández-Delgado *et al.*, 1986; Bernardi *et al.*, 1995). It seems that the species was originally introduced in the marshes of the province of Huelva in the early 1970s, with individuals coming from the northern population (Nova Scotia) of its natural distribution area (Bernardi *et al.*, 1995). This is the only known mummichog population outside of its natural habitat. However, the way in which this introduction was accomplished remains unknown. It is not possible that the mummichog could have arrived in Spain accidentally with the first red swamp crayfish (*Procambarus clarkii*) introductions as has been hypothesized, because this crustacean was delivered in June 1973 in the Badajoz province (150 km from the nearest point of its actual distribution). It was not until 1974 when the red swamp crayfish was introduced in the Guadalquivir marshes (Delibes & Adrián, 1987). Even before those introductions Hernando (1975) captured adult mummichogs, both in the Guadalquivir (March, 1973) and Guadiana marshes (April, 1974).

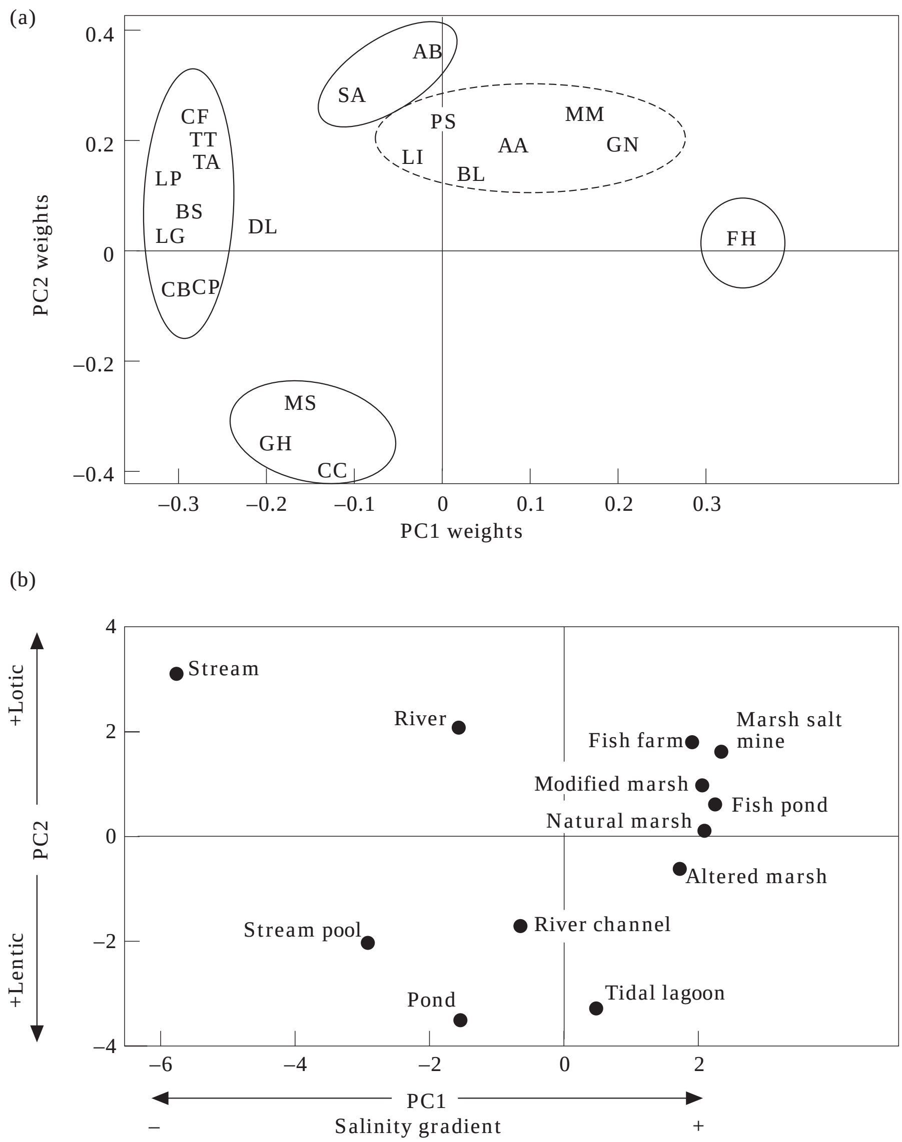

FIGURE 3. (a) Fish species grouping after a principal component analysis (PCA) of their habitat preference index (E_i^*) matrix. Circled species displayed a significant (P<0·05) correlation with a PC axis. (b) habitat grouping after the aforementioned PCA. The key for the species initials can be found in Table 2. PC1 and PC2 account for 31·8 and 22·3% of variance, respectively.

Fundulus heteroclitus was recorded in March 1976 on the Portuguese side of the Guadiana marshes (Coelho *et al.*, 1976), in the Cádiz marshland in the summer of 1983 (Arias & Drake, 1986) and in the Barbate marshes in November 1996 (this study), where the species is known approximately from 1993 (local fishermen, pers. comm.). It seems that mummichogs quickly colonized the Guadalquivir and Guadiana marshes (i.e. in the north-westerly direction). However, the south-eastern dispersion of this species was much slower and apparently this process has stopped at the Barbate marshes.

Locally, Arias and Drake (1989) observed that the mummichog quickly colonized the coastal fringe of the Cádiz bay salt marshes. However, the inland dispersion of the species in these marshes seemed to be much slower. Six years after the first record of its appearance in this area, the mummichogs still have not colonized many habitats.

Where it is endemic, *F. heteroclitus* seems to display a very small home range and usually inhabits the same habitat patch for extensive time periods (Lotrich, 1975). Thus, the trigger to leave a site and the way certain individuals arrive at a new location—the

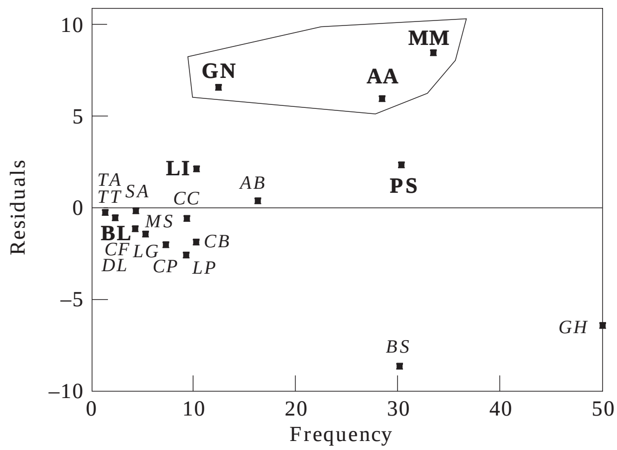

FIGURE 4. Preference of coexistence of the different fish species with *Fundulus heteroclitus* (see methods). The positive departure of the residuals indicates affinity. Those in bold face represent species occupying a similar habitat to *F. heteroclitus* and that can be truly compared.

precise dispersal mechanism of this species—is unknown. It is possible that this colonization process could be facilitated by man, through direct transport of individuals from one site to another. Also, under natural circumstances, the dispersal velocity could be related to some coastal characteristics, as will be discussed later.

Habitat preferences and actual distribution

Doadrio *et al*. (1991) fix the distribution of *F. heteroclitus* at the marshes of the Cádiz Bay. With this work the distribution area of *F. heteroclitus* in the Iberian Peninsula is extended to the Barbate marshes. The species has not been found in any of the sites sampled in the Mediterranean coast, including 76 sites sampled in the Granada and Almeria provinces (Fernández-Gelgado *et al*., 1997), the River Ebro delta marshes and the rest of the Catalonian coast (García-Berthou & Moreno-Amich, 1991), nor in the most south-westerly portion of the Portuguese coast (Beja, 1991). The reasons for such a distribution can be related to the habitat preferences displayed by mummichogs, i.e saltmarsh areas with some human influence. *Fundulus heteroclitus* exhibits a life history closely linked to the intertidal salt marsh (Kneib, 1984), but with very few microhabitat preferences (Weisberg, 1986). Typical marsh areas, such as those previously mentioned, are almost lacking from the Mediterranean coast of southern Spain and from most of south-western Portugal.

The maximum *F. heteroclitus* relative abundance (up to 63 individuals trap^{-1} h^{-1}) was found in the largest area of salt marsh (Huelva and Cádiz marshes). Also, *F. heteroclitus* was the species that inhabited more types of habitats (11 of 12), lacking or being very scarce only from those with unidirectional flow such as streams and man-made channels. These freshwater habitats tend to be inland, which may help to explain the low density value obtained for those sites far from the coastline. The lowest abundance values found for *F. heteroclitus* could be because this species had recently colonized the area, and/or that a suitable habitat did not exist for it.

On the Atlantic coast of the Iberian Peninsula, *F. heteroclitus* inhabited a wide range of salinities, but preferred the most saline sites, usually above 25. However, according to Weisberg (1986), *F. heteroclitus* is unaffected by salinity and has been reported in freshwater habitats (Rozas & Odum, 1987). Thus, *F. heteroclitus* may be absent from many freshwater water bodies not because of the water/salt content, but due to other factors, such as the lack of tidal fluctuations and the presence of natural or man-made barriers.

Potential effects of mummichog on native fish populations

Fundulus heteroclitus was the most widespread species and probably the most abundant of all the fish captured. This illustrates the great success of the species in this new habitat. This could be due to a number of factors, such as the capacity to survive in water where the salinity range is large (0–128) (Feldmeth & Waggoner, 1972) and the high productivity of these tidal habitats (29·8% of the habitats sampled were tidal marshes) (Valiela *et al*., 1977; Meredith & Lotrich, 1979; Arias & Drake, 1989). These characteristics allow *F. heteroclitus* to colonize a range of habitats, including those that are very marginal and used by few other species. In 19·7% of the sites sampled where mummichog was found, only two or more other species were found, suggesting that the mummichog is occupying an extreme habitat (an empty niche), not previously occupied by any of the native species. On the other hand, if *F. heteroclitus* were not filling an otherwise empty niche, it seems obvious that a species with such an expansion capacity, along with its productivity, must have a great influence on the local fish populations. *Fundulus heteroclitus* is clearly the dominant species in these marsh habitats under tidal influence, at least for fish within its size range (Arias & Drake, 1987). At present, it is not known which species, if any, have been outcompeted by *F. heteroclitus*.

Arias & Drake (1987) observed high densities of *F. heteroclitus* in the salt marshes of Cádiz Bay, where the maximum biomass was 2049 kg ha^{-1}. In spite of this, it seemed that the species did not affect the productivity of commercial fish species cultivated in those marshes. However, Arias & Drake (1987, 1989) proposed that this extremely high productivity may be affecting the energy fluxes in these ecosystems, at least removing part of the trophic resources that might be consumed by other fish species.

If mummichog were outcompeting other species, the mechanisms of this potential exclusion have not been directly evaluated and remain unknown. However, direct predation does not seem to be a factor because *F. heteroclitus* consumes only invertebrates and plants in the study area (Hernando, 1975; Arias & Drake, 1986). Also, the competition for food does not seem to be a decisive factor due to the enormous productivity of the areas where it is found. Therefore, perhaps, the competition for space could be the best explanation for this apparent segregation observed for mummichog and other fish species in the study area.

It is difficult to evaluate the precise ecological consequences of the mummichog introduction in southern Iberia, especially due to the fact that the original environmental conditions existing in the area where it was introduced are unknown. However, it is probable that some effects may have been negative. Some local fish species may have been displaced, and there have been probable economic losses in traditional prawn fishery yields which are known to be heavily consumed by mummichog (Arias & Drake, 1986). On the other hand *F. heteroclitus* is consumed in large quantities by very important commercial fish species, such as large *Sparus aurata* and *Dicentrarchus labrax* (Arias, pers. comm.). Also, mummichog seems to have a positive effect on some endangered birds, like spoonbills (*Platalea leucorodia*), storks (*Ciconia ciconia*) and several ardeids (*Ardea* sp. *Egretta garzetta*, etc.) (Delecourt, pers. comm.). Clearly, the potential impacts of *F. heteroclitus* in the environmentally rich tidal wetlands of south-western Spain should be further investigated.

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