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Pike and red swamp crayfish: a new case on predator–prey relationship between aliens in central Spain

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Pike in the Ruidera Lakes (central Spain) chiefly ate the recently introduced crayfish *Procambarus clarkii*. It was the dominant prey in occurrence, number and biomass for every size class and season. Likewise, number (up to 27) and total weight of ingested crayfish were directly related with pike size. The principal prey fish were all introduced species (except the endangered *Blennius fluviatilis*), most native species having disappeared since pike were introduced in 1953.

Key words: pike; *Esox lucius*; *Procambarus clarkii*; predation; feeding; Spain.

INTRODUCTION

The pike *Esox lucius* L., as well as other true predaceous fish (*sensu* Popova, 1967, 1978), was originally absent from the Iberian Peninsula, where it was first stocked for angling purposes in 1949 (Gutiérrez-Calderón, 1955; Pena, 1986; Elvira, 1995*a*). Its present distribution in Spain includes most of the large river basins (Doadrio *et al.*, 1991; Elvira, 1995*b*).

Biological invasions cause a great number of disruptions in original ecosystems all over the world (Drake *et al.*, 1989). In fact, introduction of fish has usually been accompanied by decline or extinction of many native species (Brown, 1989).

The pike becomes increasingly piscivorous as it grows, reaching the top of the aquatic food chain in most communities throughout its circumpolar distribution in the northern hemisphere (Raat, 1988; Maitland & Campbell, 1992). It is considered to be a serious threat to native Spanish fishes (Elvira, 1990, 1995*a–c*, 1996; Elvira & Barrachina, 1996). However, accurate studies on pike diet in Spain are scarce (Pena *et al.*, 1987; Sánchez-Isarria *et al.*, 1989; Santamaría, 1993, 1995). Sostoa & Lobón-Cerviá (1989) described its feeding pattern and Rincón *et al.* (1990) examined its impact on native fish assemblages in small streams.

The fish community of the Natural Park of the Ruidera Lakes consists of nine native species (eight of them Iberian endemics), and six well-acclimatized, introduced species (Almodóvar & Elvira, 1994). Pike were introduced in Ruidera in 1953 (Elvira & García-Utrilla, 1991) and presently are widespread and common (Almodóvar & Elvira, 1994).

Our first aim was to study the predator–prey interactions of pike with native fishes. However, native fishes are restricted now mostly to the middle and upper

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lakes and streams, where pike are rare or absent (Almodóvar & Elvira, 1994). Instead it was found that another alien species, the red swamp crayfish *Procambarus clarkii* (Girard), stocked in Spain from 1973 (Habsburgo-Lorena, 1978), was the most common prey for pike. This paper describes the relative importance of crayfish in pike diet and discusses the eventual persistence in time of this artificial predator–prey relationship.

MATERIALS AND METHODS

STUDY SITE AND FISH FAUNA

The Natural Park of the Ruidera Lakes is a protected territory comprising 14 lakes and a reservoir joined by short streams. It forms part of the upper Guadiana river basin (central Spain). Altitude ranges from 720 to 960 m. Water, supplied by aquifers, runs across the lakes along 28 km of a limestone valley (see a map of the area in Elvira & García-Utrilla, 1991). Physico-chemical features of the waters are described by Almodóvar & Elvira (1994).

The principal aquatic macrophytes are *Potamogeton pectinatus* L., *Myriophyllum verticillatum* L. and *Polygonum amphibium* L. Also, dense stands of *Typha latifolia* L., *Typha domingensis* (Pers.), *Scirpus litoralis* Schrader, *Phragmites australis* (Cav.) and *Cladium mariscus* (L.) are present in the littoral zone of the lakes (Cirujano, 1990). Nevertheless, human uses (chiefly building construction on margins) have disturbed this pristine vegetation deeply, and much of it has been lost.

The fish assemblage consists of 17 species, nine of which are native: *Barbus bocagei* Steindachner, *Barbus comiza* Steindachner, *Barbus microcephalus* Almaça, *Chondrostoma polylepis willkommii* Steindachner, *Leuciscus pyrenaicus* Günther, *Rutilus lemmingii* (Steindachner), *Tropidophoxinellus alburnoides* (Steindachner), *Cobitis paludica* (De Buen) and *Blennius fluviatilis* Asso. The other eight species were introduced by man this century (Elvira & García-Utrilla, 1991; Almodóvar & Elvira, 1994): *Anguilla anguilla* (L.) (native of Spain, but originally absent in Ruidera), *Oncorhynchus mykiss* (Walbaum), *Esox lucius* L., *Cyprinus carpio* L., *Gobio gobio* (L.), *Gambusia holbrooki* (Girard), *Lepomis gibbosus* (L.) and *Micropterus salmoides* (Lacépède). Except *A. anguilla* and *O. mykiss*, which are present only as solitary specimens, the rest of the aliens have been acclimatized successfully and are currently widespread.

FISH SAMPLING AND DIET ANALYSIS

Pike were captured from September 1991 to January 1994 by electrofishing and occasionally by angling or gillnets. Sample sizes were kept to a minimum to avoid too great an impact on the fish community in this protected Natural Park. As the initial intention was to examine the piscivorous nature of the pike, only large specimens were caught and killed. All fish were measured for fork length (to within 1 mm) and weight (to within 1 g). Fish retained for gut content analysis were injected and placed into a 8% formalin solution.

The stomachs of 71 pike (length range=24·4–98·5 cm, mean=48·93 cm) from all seasons (21 winter, 15 spring, 8 summer and 27 autumn) were dissected. Prey were identified to species (crustaceans and fishes) or order (insects), counted and weighed (wet weight). A comparative collection of bones and scales of local fish species, as well as the key by Elvira (1988) for scales, were used to aid identification. Reconstruction of fish prey lengths was possible in some cases (Mann & Beaumont, 1980). Likewise, lengths of partially digested crayfish were also estimated from the size of the carapace or rostrum, after calculating linear regressions in comparative material.

A *G*-test (Zar, 1984) was used to compare the frequencies of empty stomachs across seasons. Simple linear correlation and linear regression analyses were used to determine the relationships between stomach contents and pike length (Ricker, 1973; Zar, 1984). Analysis of variance was used to test the significance of the regressions (Zar, 1984).

TABLE I. Prey of 71 pike (length = 24·4–98·5 cm) from the Ruidera Lakes (central Spain), their frequencies of occurrence, numbers, wet weights (Wwt) and relative importance index (RI) with percentages indicated for each prey category

Prey category	Frequency (%)	No. (%)	Wwt (g) (%)	RI (%)
Crustacea				
Atyaephyra desmaresti (Millet)	5·88	2·43	0·03	2·56
Procambarus clarkii (Girard)	72·55	82·93	72·43	69·98
Insecta				
Ephemeroptera (nymphs)	1·96	2·84	0·01	1·48
Odonata (nymphs)	1·96	0·41	0·008	0·73
Diptera (Chironomidae larvae)	1·96	0·41	0·001	0·73
Osteichthyes				
Esox lucius L.	5·88	1·22	2·95	3·09
Cyprinus carpio L.	9·80	2·84	8·24	6·41
Gobio gobio (L.)	5·88	1·22	0·31	2·27
Lepomis gibbosus (L.)	7·84	1·63	3·58	4·01
Micropterus salmoides (Lacépède)	9·80	2·84	12·13	7·61
Blennius fluviatilis Asso	1·96	1·22	0·51	1·13

Frequency of occurrence was determined omitting empty stomachs. Numerical frequencies of each prey category were also calculated and together with their weight were expressed as a percentage (Hyslop, 1980). The relative importance index (RI) was used (Hyslop, 1980), as follows:

$$RI = 100\ AI / \sum_{1}^{n} AI$$

where: AI = % occurrence + % total numbers + % total weight.

Dietary data were plotted using the graphical analysis proposed by Tokeshi (1991).

Energy contents of prey were determined by adiabatic bomb calorimetry, water content by drying in an oven at 60° C for 72 h to constant weight, and ash content by burning in a muffle furnace at 600° C for 24 h.

RESULTS

Seasonal variation in the frequency of empty stomachs did not reflect any significant discontinuity in pike feeding activity. The overall frequency of empty stomachs was 28·2%. Seasonal variation showed a significant discontinuity ($G = 19{\cdot}939$; $P < 0{\cdot}001$) in pike feeding activity. Winter and summer appeared as the less active periods. Following the caution proposed by Treasurer (1988), we found that regurgitation was not significant.

The diet of the pike comprised 11 food categories (Table I). No seasonal variation of diet could be detected. Crayfish were the most common prey (72·55% occurrence), followed by carp (9·80%), black bass (9·80%) and pumpkinseed (7·84%). Numerical frequency of crayfish (82·93%) was significantly the highest, with the remaining prey categories representing fewer than 3% numerical frequency. Crayfish were also the most common prey by wet weight (72·23%), followed by black bass (12·13%) and carp (8·24%).

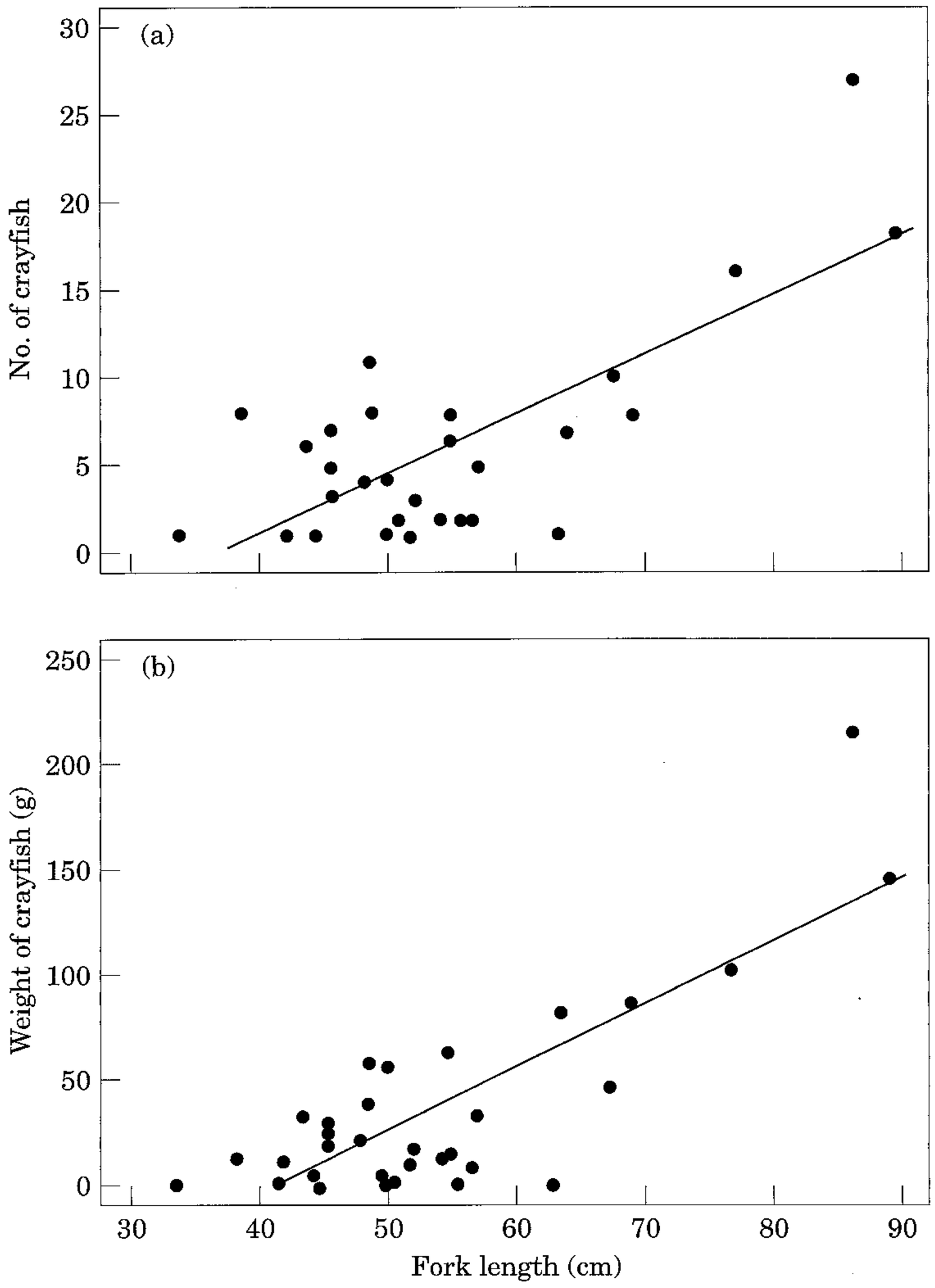

FIG. 1. (a) Number and (b) weight of prey crayfish regressed against pike size. (Number of crayfish)= $-12{\cdot}774+0{\cdot}344$ (length of pike) ($F=37{\cdot}0$, $P<0{\cdot}001$). (Weight of crayfish)= $-129{\cdot}719+3{\cdot}126$ (length of pike) ($F=57{\cdot}9$, $P<0{\cdot}001$).

Crayfish were ingested by pike 33·6–88·5 cm in length. The number of crayfish per stomach was positively correlated with pike length ($r=0{\cdot}74$; $P<0{\cdot}001$), as was mean wet weight of ingested crayfish ($r=0{\cdot}81$; $P<0{\cdot}001$) (Fig. 1).

Fish were the second group of importance in pike diet, in frequency of occurrence (37·2%), numerical frequency (11·0%) and wet weight (27·4%). They were eaten by pike 35·9–98·5 cm in length. Finally, invertebrates (other than crayfish) were ingested by pike 39·2–49·7 cm in length. Thus, pike longer than about 50 cm ate only fish and crayfish.

Overall, the highest relative importance index (RI) (Table I) was for crayfish (69·98%), followed by fish (24·52%) and other invertebrates (5·50%).

Reconstructed lengths of major prey (fish and crayfish) were not significantly correlated with pike size (Fig. 2). This may reflect the almost constant modal size

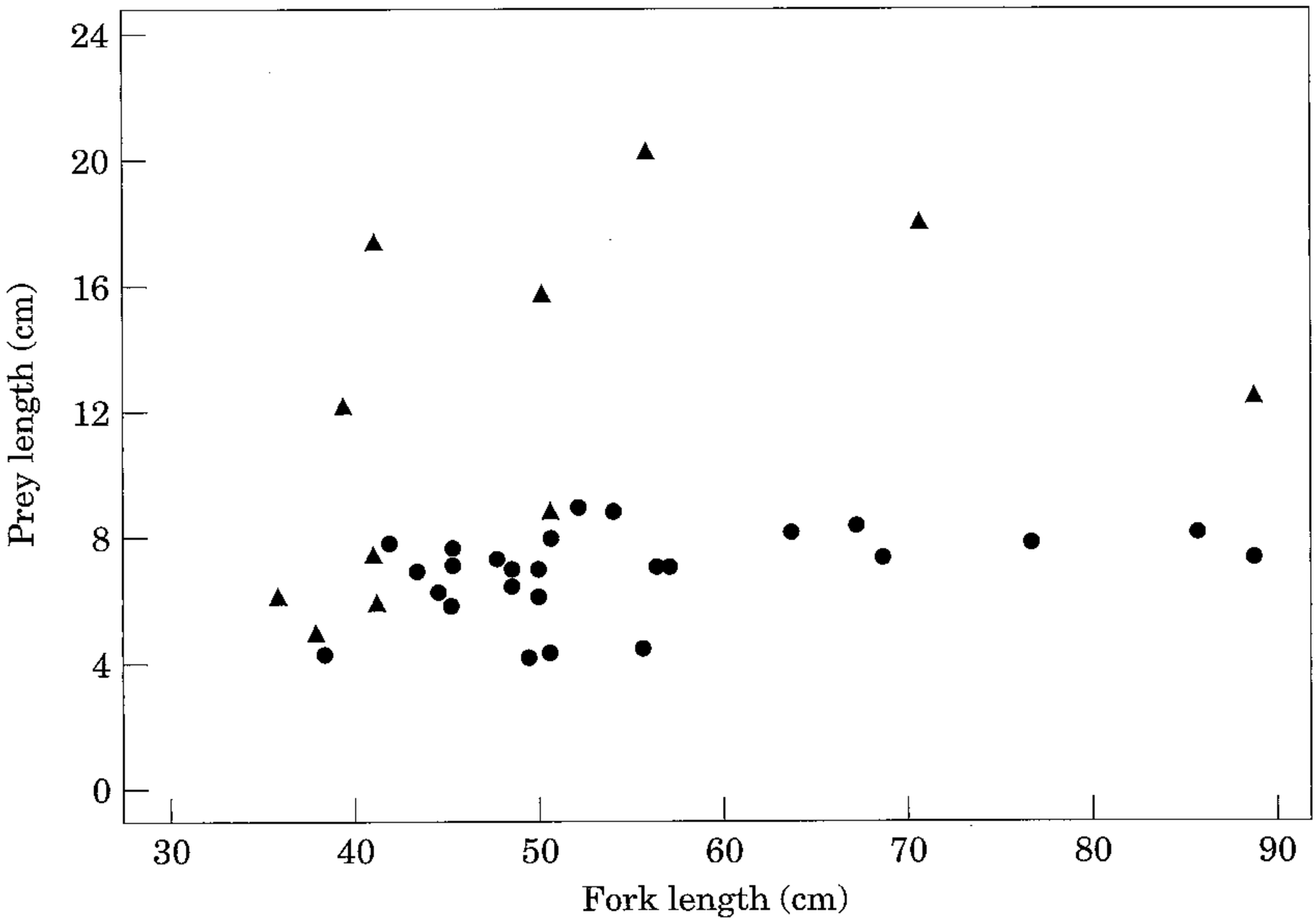

FIG. 2. Reconstructed lengths of main prey (crayfish, ●, and fish, ▲) plotted against fork length of pike.

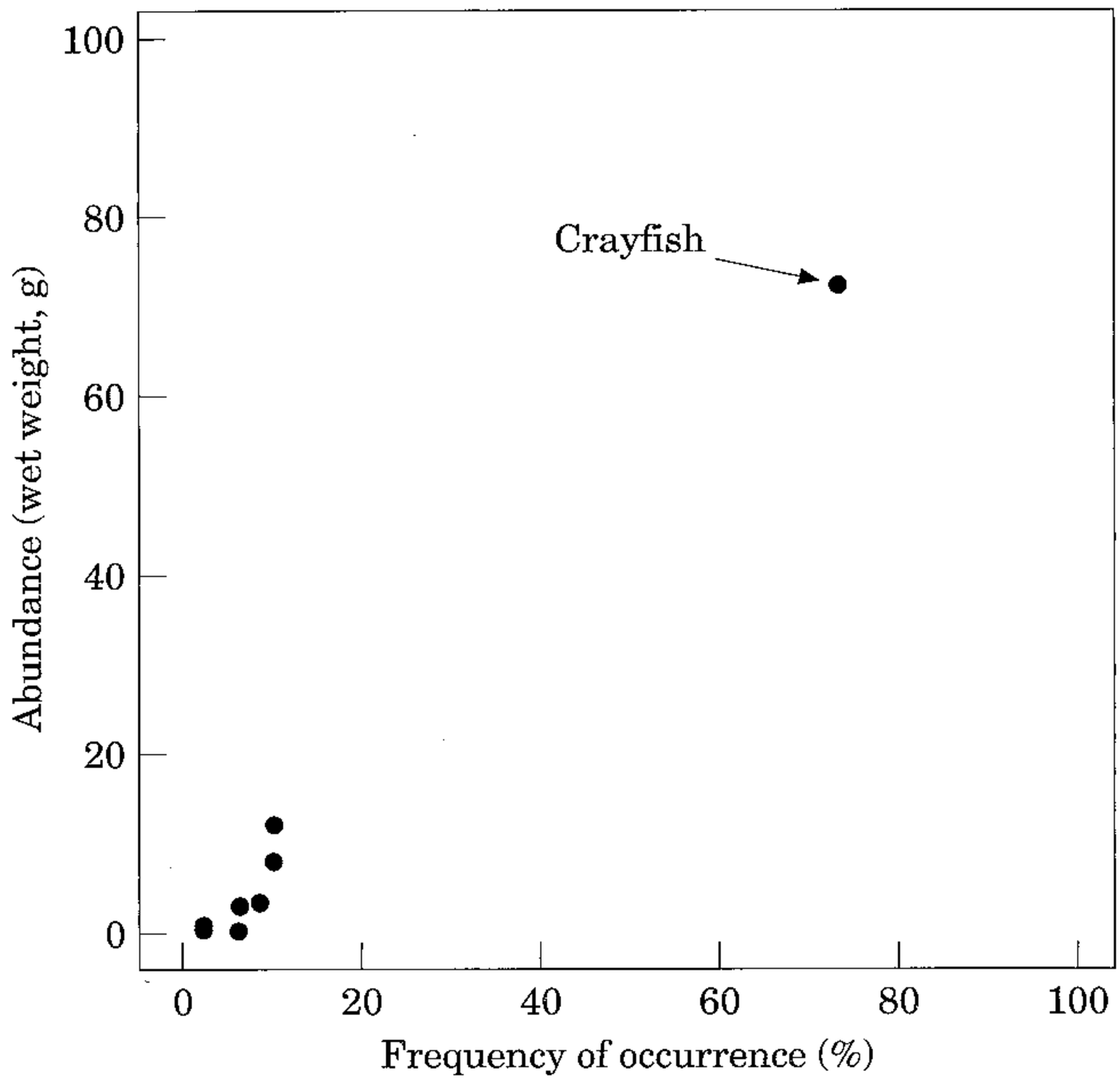

FIG. 3. Graphical analysis of dietary data from Table I.

of available crayfish (around 7–9 cm) and the low number of fish lengths that could be calculated. Nevertheless, the general tendency was that larger pike ate larger prey (Fig. 2).

In conclusion, pike in Ruidera is a specialist predator (*sensu* Tokeshi, 1991). Figure 3 shows a graphical analysis of occurrence/abundance, where one datum point is located towards the top right-corner of the graph (the specialized prey

TABLE II. Water, ash, major components and energy content of prey

	P. clarkii	*L. gibbosus*	*M. salmoides*	*L. pyrenaicus*
% Water	78·43 ± 0·227	74·62 ± 0·421	75·73 ± 0·454	72·15 ± 0·314
% Ash	29·40 ± 1·428	23·14 ± 0·891	17·67 ± 2·029	16·52 ± 0·212
% Protein	50·69 ± 0·983	61·12 ± 0·537	67·46 ± 1·464	62·24 ± 0·078
% Lipid	5·40 ± 0·566	10·53 ± 0·658	10·17 ± 0·460	16·15 ± 0·064
% Carbohydrate	14·50 ± 0·120	5·20 ± 0·304	4·68 ± 0·106	5·08 ± 0·071
kcal g^{-1} ash-free dry weight	3·347 ± 0·0013	4·083 ± 0·0187	5·776 ± 0·0016	5·805 ± 0·0057

Values shown are means ± 1 S.D., based on three replicates.

item: crayfish), while the other points are scattered near the frequency axis, within the generalist area (see Tokeshi, 1991).

Water, ash, major components and energy content of some real (*P. clarkii*, *L. gibbosus* and *M. salmoides*) and potential prey (*L. pyrenaicus*) are given in Table II. Further data on biochemical composition and energy content of the red swamp crayfish were reported by Fernandes *et al.* (1994). Crayfish contain little energy, compared with fish, but are eaten in large numbers, are easily digestible, and may contribute substantially to overall energy intake of pike.

DISCUSSION

The percentage of empty pike stomachs found in Ruidera (28·2%) was lower than known from other populations (Mann, 1976; Vøllestad *et al.*, 1986; Pena *et al.*, 1987; Chapman *et al.*, 1989; Santamaría, 1993, 1995). Treasurer (1988) considered that many results have underestimated the importance of regurgitation. Thus, Santamaría (1993) found 70·54% of stomachs to be empty, but all the fishes were caught with gillnets, an unsatisfactory capture method because of the high level of regurgitation (Treasurer, 1988). The high activity pattern of pike in Ruidera may be due to the geographic situation of the study area (39°00′ N, 3°00′ W), the southernmost studied; with a high surface water temperature ranging from 3 to 26° C (monthly average about 14° C) (Almodóvar & Elvira, 1994).

The bulk of the pike diet in Ruidera was formed by crayfish, with fishes second in importance. These results differ from those generally found in native populations both from North America (Diana, 1979, 1980) and Europe (Mann, 1976, 1982; Vøllestad *et al.*, 1986), where it is a fish predator when adult. Also, Sostoa & Lobón-Cerviá (1989) studied fish predators in the river Matarraña, NE Spain, and concluded that pike was a generalist-opportunist species, feeding mainly on fish (92·9% occurrence).

However, in Loch Choin, Scotland, pike were the only fish present. Here, young pike fed on invertebrates, while large pike preyed on smaller pike (Munro, 1957). Mann (1982) found that in the River Frome, U.K., cannibalism on pike aged between 6 months and 2 years accounted for most of their natural mortality. Kipling (1983, 1984) suggested that in the absence of other food, cannibalism was a major factor in the survival of the pike population in

Windermere, U.K. This was not the case in Ruidera, where cannibalism was present but not significant (5·88% in frequency, Table I).

Chapman *et al.* (1989) described pike food from several lakes in Canada, where occurrence of invertebrates was sometimes very high. Unfortunately, they did not provide any parameter of prey abundance, so that their results may overemphasize the importance of small prey items in the diet.

Other introduced pike in Spain were almost exclusively piscivorous from about 30 cm in length (Pena *et al.*, 1987; Sánchez-Isarria *et al.*, 1989; Santamaría, 1993, 1995). In these populations, the cannibalism ratio in number varied from 2·15 to 15·19%.

The red swamp crayfish which is native in southern U.S.A. and northern Mexico, was stocked first in Spain from 1973. It has spread rapidly into southern and central Spain (Habsburgo-Lorena, 1978), Portugal (Adao & Marques, 1993), France (Vigneux *et al.*, 1993) and NW Italy (Millot & Millot, 1991). At the same time, the native crayfish *Austropotamobius pallipes lusitanicus* (Mateus) was attacked by the fungus (Aphanomycosis) and its population numbers fell dramatically (Cuéllar & Coll, 1983). Nowadays, the native crayfish is extinct in Ruidera, whereas the red swamp crayfish is very common in every lake and stream. There are no demographic data about exotic crayfish in the area, but it certainly represents an easily available prey for pike.

Crayfish are a rare prey for pike. Mann (1976) reported the occasional occurrence of *A. pallipes pallipes* (Lereboullet) in pike diet from the River Stour. Exotic populations of pike formerly studied in Spain did not include any species of crayfish in their diets (Pena *et al.*, 1987; Sánchez-Isarria *et al.*, 1989; Sostoa & Lobón-Cerviá, 1989; Rincón *et al.*, 1990; Santamaría, 1993, 1995), even though the red swamp crayfish was present in some areas.

A similar case of predator–prey relation between aliens has been described by Hickley *et al.* (1994) with the largemouth black bass and red swamp crayfish both acclimatized in Lake Naivasha, Kenya. There, crayfish was the principal food for bass over 26 cm (52% occurrence, 63% abundance) (Hickley *et al.*, 1994). The fish community of that lake was also highly disturbed, since the five species present were introduced, whereas the single native fish species was last recorded in 1962. Black bass were stocked from 1929 to 1951 (Hickley *et al.*, 1994) and the crayfish in the early 1970s (Huner & Avault, 1978). This predator–prey interaction was also recent and its persistence over time may be doubtful.

In fact, the demographic status of pike in Ruidera is far from being in equilibrium. On the contrary, the pike population persists through a feeding strategy based on crayfish. The area was formerly occupied by native fishes which are now extinct or nearly so. We may infer that the introduced pike fed initially on native fish, but when the native populations fell, the pike switched to a diet based on crayfish and other fish aliens (only native *B. fluviatilis* is ingested occasionally, Table I).

Elvira (1995*a*) and Elvira & Barrachina (1996) have suggested a similar but more catastrophic succession in the neighbouring Daimiel National Park. In that wetland, pike eliminated nearly all the fish community and then, despite the presence of red swamp crayfish as an available prey, pike became extinct in 1986. The present fish population consists only of *C. carpio* and *G. holbrooki* (Elvira & Barrachina, 1996).

Spanish national and regional administrations reduced the stocking of pike during the 1970s (Lobón-Cerviá *et al.*, 1989), with only 150 000 fish stocked in 1979. The only public fish farm rearing pike in Spain was closed in the following decade. There are no data for pike population parameters at a national level, but some anglers would like further stocking in rivers and reservoirs. In fact, pike seems to be disappearing in several Spanish localities. According to Lelek (1987), many native pike populations in European waters are maintained only through stocking because of high fishing pressure.

The versatility of pike foraging behaviour may be an important adaptive feature, which may facilitate its persistence in Spanish waters. Mann (1982) discussed predator–prey relationship and reached the conclusion that pike were opportunist piscivores that preyed chiefly upon the more abundant and vulnerable species and had an ability to switch from one food source to another. Nevertheless, eventual success of a shift to cannibalism, as described by Munro (1957), is unpredictable. Likewise, a diet based on crayfish could also be untenable owing to the low energy content (Table II).

Accurate studies of demographic features of pike are necessary to understand the evolution of its allochthonous populations in Spain. Likewise, it would be necessary to extend this kind of research to other introduced fish predators in Spanish waters, such as *M. salmoides* (stocked from 1955), *Silurus glanis* L. (in 1974), *Perca fluviatilis* L. and *Stizostedion lucioperca* (L.) (in the early 1970s), in order to determine their eventual impact on native species.

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