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Loss of diversity and degradation of wetlands as a result of introducing exotic crayfish

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Abstract

The introduction of the alocthonous Louisiana red swamp crayfish (*Procambarus clarkii*) in Chozas (a small shallow lake situated in León (North-West Spain)) in 1996 switched the clear water conditions that harboured an abundant and a quite high richness of plants, invertebrates, amphibians and birds to a turbid one followed by strong losses in abundance and richness in the aforementioned groups. Crayfish exclusion experiments done in Chozas previous to this work confirmed the role of crayfish herbivorism on macrophyte destruction that had a trophic cascade effect on the wetland ecosystem. Direct and indirect effects of crayfish introduction on Chozas lake communities have been evaluated and compared with previous conditions before 1996 or with other related lakes in which crayfish were no present. Crayfish had a main role in submerged plant destruction and a potential effect on amphibia and macroinvertebrate population decrease. Plant destruction (99% plant coverage reduction) was directly related to invertebrates (71% losses in macroinvertebrate genera), amphibia (83% reductions in species), and waterfowls (52% reduction). Plant-eating birds were negatively affected (75% losses in ducks species); nevertheless, fish and crayfish eating birds increased their presence since the introduction. Introduction of crayfish in shallow plant-dominated lakes in Spain is a main risk for richness maintenance in these endangered ecosystems.

Introduction

Many studies include the fundamental role of aquatic vegetation in maintaining the ecological integrity of wetlands (e.g. Jeppessen et al. 1990; Moss 1990; Scheffer 1990). Submerged macrophytes participate in a series of feedback mechanisms so that various physical and chemical variables remain within the limits appropriate to their development in the presence of aquatic vegetation. This submerged vegetation also supports a complex trophic chain, completely different from and much more diverse than those present in wetlands without vegetation (Carpenter and Lodge 1986).

Shallow lakes can change abruptly from a situation characterised by abundant submerged vegetation and transparent waters to another characterised by the absence of vegetation and very turbid conditions due to the dominance of phytoplankton. These two extreme situations are considered alternative stable states related to the nutrient load received by the lake (Scheffer 1990). As eutrophication increases, the submerged vegetation is capable of controlling the growth of phytoplankton via diverse mechanisms (allelopathy, zooplankton shelter, nutrient competition, etc. (Jeppesen and Sammalkorpi 2002)) up to rather high nutrient concentrations. Below these concentrations, the disappearance of vegetation due to different causes other than nutrient increase produces a rapid change to high turbidity conditions dominated by phytoplankton.

Amongst the most frequently occurring causes of submerged vegetation destruction, we can cite anthropogenic interferences such as direct mechanical destruction, increased internal load of nutrients due to waste from agricultural farms, alteration of the hydrological cycle due to abusive contributions or extractions (Blindow et al. 1998), the arrival of biocides and other chemical compounds (Vandergaag 1992), excess herbivorism by macroinvertebrates, mammals and birds (Lodge et al. 1998) and the recent introduction of exotic species, especially various decapods (Nyström 1999). Rodríguez et al. (2003) have recently shown that herbivorism by alien crayfish can change eutrophic systems of clear waters previously dominated by vegetation to a turbid state.

For some decades, exotic species of freshwater crayfish has been deliberately introduced. Various hydrographic basins in most parts of Europe have been supplied with alien crayfish from North America (Ackefors 1999), mainly *Procambarus clarkii, Pacifastacus leniusculus and Orconectes limosus*, although other species are being commercially exploited. This worsens the situation of autochthonous decapods even more, as the exotic North American species are vectors of the *Aphanomyces astaci* fungus, though resistant to it (Dieguez-Uribeondo and Soderhall 1993).

Given that many of the freshwater decapod species are generalist omnivores (Cronin 1998; Nyström 1999; Parkyn et al. 2001), the effect of introducing them into aquatic systems is not restricted to displacement of the autochthonous ones but also extends to the rest of the trophic chain levels, favouring species removal and destabilising the self-control mechanisms of submerged vegetation (Axelsson et al. 1997; Gutiérrez-Yurrita et al. 1998; Nyström 1999).

Various types of impact have been documented as regards the introduction of alien crayfish, such as competitive removal of autochthonous crayfish (Soderback 1994; Hill and Lodge 1999) and fish species (Guanz and Wiles 1997; Dorn and Mittelbach 1999), the disappearance of amphibians due to predation (Axelsson et al. 1997; Gerardhi et al. in press), declines in macroinvertebrate fauna (Hanson et al. 1990; Lodge et al. 1998; Nyström and Perez 1998; Nyström et al. 2001; Correia 2002) or the destruction of the aquatic plant cover (Feminella and Resh 1989; Olsen et al. 1991; Nyström 1999; Rodríguez et al. 2003).

The red crayfish of Louisiana (*Procambarus clarkii*) is a generalist crayfish first introduced in Spain in 1974 (Gutiérrez-Yurrita and Montes 1999); since then it has spread throughout Europe. Its impact on wetlands has been described in terms of changes in available food and/or shelter and the breeding success of other species (Gutiérrez-Yurrita and Montes 1999) and other direct effects on the aquatic fauna and flora (Cronin 1996; Nyström and Pérez 1998; Angeler et al. 2001; Rodríguez et al. 2003). However, the extent of these effects on the systems and their canalisation through the trophic chains have not been precisely determined (Nyström 1999).

This paper gives evidence of the effects of predation by an exotic crayfish (*P. clarkii*) on the trophic web of Chozas Lake (León, northwestern Spain) as well as other indirect effects related to the destruction of the aquatic plant habitat. The destabilisation of the trophic chains has produced serious losses in biodiversity and, for the first time, the introduction of an exotic macroinvertebrate can be related to the disappearance not only of aquatic fauna (amphibians and macroinvertebrates) but also various species of birds.

Study area

Chozas Lake is a small, shallow mass of water (9 ha; maximum depth 1.8 m) situated in León (northwestern Spain) surrounded by a small area of meadow wetlands which houses an important nesting colony of lapwings. The lake was traditionally used as an irrigation pool for agriculture, and so water-containing walls were built on the south and west sides in the 1950s to increase its depth. Characteristically, the water level fluctuates greatly, both monthly due to the dry summer (it drops to almost 1 m as regards maximum capacity, and the flooded area decreases to about 3 ha during the summer), and from year to year (serious drought in 1993). The inhabitants of the area have traditionally used the lake for marginal uncontrolled hunting (bird and amphibian hunting, fishing).

The first limnological study was made by Fernández-Aláez (1984) as an example of a wetland with abundant and diverse aquatic vegetation. The lake has been regularly monitored since 1994 onwards.

Materials and methods

This study reviews the existing information on the Chozas Lake communities before the introduction of crayfish and compares it with later studies. The plant biomass samplings and species catalogue done by Fernández-Aláez (1984, 1999) prior to the introduction of crayfish was used as the basis for checking changes in flora. Main nutrients (total phosphorous (TP), soluble reactive phosphorous (SRP), nitrates and ammonium) as well as chorophyll *a* levels and other physical parameters (mainly Secchi disc values that measure light penetration through a water column) following APHA-AWWA-WPCF Standard Methods for the Examination of Water and Wastewater (1989) have been taken from the same sources. The statistical significance of nutrients and Chl. *a* levels were tested by means of Student's *t*-test.

The fauna inventories prior to wetland degradation used as a reference are those by Álvarez and Salvador (1984) for amphibian fauna. The data on over-wintering, breeding and passing birds in Chozas Lake are taken from Alegre et al. (1991), Marcos et al. (1995) and data provided in Purroy (1990). Due to the fact that these studies partially overlap as regards various groups of birds, the inventory with the largest record of species and/or specimens was used to establish the number of species affected and the decrease. The inventory of rare and/or threatened species (according to Blanco and González 1992) present in Chozas was taken from the Purroy (1990) report. Current aquatic bird inventories and populations have been determined since 1999 by fortnightly counting using a 60 magnification × 80 mm Kowa telescope and 8 × 20 Zenit binoculars.

The number of crayfish in Chozas was estimated in a previous study (Rodríguez et al. 2003), where a capture–marking–recapture method was used (Krebs 1991), carried out in September 2002. The capture method chosen was that of batteries of small baited traps. The mark used was the same for all the specimens and captures and consisted of a tangential cut in one of the telson parts. The study showed that the number of crayfish in Chozas is around 1 individuals/m^2, with a mean weight of 20 g/specimen. This allows the biomass of red crayfish in Chozas Lake to be calculated as approximately 200 kg/ha. The fish species present along 15 min transects were determined at the same time using an electric fishing technique; then, species present and their numbers as well as the weights and the lengths of individuals were recorded.

Due to the lack of data referring to the macroinvertebrate fauna for Chozas Lake prior to the arrival of *P. clarkii*, the mean values of the number of Genera and Families present in various wetlands around the study area (García-Criado et al. 2004) were used as a reference, differentiating between macroinvertebrates associated with vegetation and benthic ones. The benthic macroinvertebrate samplings in Chozas were carried out using two sampling nets of different pore sizes. Those of macroinvertebrates associated with vegetation were carried out in transects with sampling nets and a Kornijów sampler. For more details on methodology and results, consult (García-Criado et al. 2004).

Results

Changes in physical and chemical variables

From 1984 to 1996, the lake was characterised by the abundant submerged vegetation and great transparency of its waters. Although an increase in the total phosphorus (TP) values from 30 to 60 μg/l was recorded at the beginning of the 1990s, the mean nutrient and chlorophyll values did not vary significantly between 1984 and 1996 (Table 1). After the destruction of the aquatic vegetation in the summer of 1997, the lake switched to the turbid state. The nutrient concentration increased significantly, although some concrete fractions did not change; nevertheless, a significant depletion of nitrates ($P < 0.05$; *t*-test for independent samples) has been noticed. The most important variations correspond to the increase recorded in TP levels. These concentrations rose by 800% (statistically significant; $P < 0.05$) in the first few years after the arrival of the crayfish; in the following years the TP

Table 1. Physical and chemical characterisation of Chozas Lake in periods before and after exotic crayfish introduction, with indication of maximun and minimun values.

	Before 1997	After 1997
Total phosphorous (µg/l)		
Mean	38.8	226.6
Min.	18.801 (SP 94)	23.168 (SP 01)
Max.	69.2 (WI 96)	665.1 (SU 99)
Phosphates (µg/l)		
Mean	8.86	7.9
Min.	0.1 (AU 94)	0.0 (SU)
Max.	37.9 (SP 95)	51.7 (SU 98)
Nitrates (mg/l)		
Mean	0.1	0.0
Min.	0.190 (SP 94)	0:0 (year)
Max.	5.47 (SU 96)	0.11 (AU 99)
Ammonium (mg/l)		
Mean	49.6	13.5
Min.	11.1 (SP 94)	0.0 (SU)
Max.	161.0 (SP 95)	179.2 (AU 99)
Chlorophyll a (mg/l)		
Mean	16.3	68.5
Min.	5.8 (SU 96)	2.5 (SP 01)
Max.	61.6 (WI 96)	161.4 (SU 99)
Secchi (cm light penetration)		
Mean	Bottom	47.6
Min.	No data	19 (SU 99)
Max.	No data	Bottom (SP 01)
Inorg. suspended solids (mg/l)	No data	Max. 22

SP: spring, SU: summer, AU: autumn, WI: winter.

Table 2. Floristic list and species coverage in Chozas Lake in summer. Comparison of three years.

Species	% Cover		
	1981	1995	2001
Potamogeton natans	25	20	Absent
Chara globularis	20	25	+
Myriophyllum alterniflorum	15	6	0.5
Littorella uniflora	12	10	1
Nitella translucens	10	12	Absent
Eleocharis palustris	8	12	+
Antinoria agrostidea	4	3	+
Glyceria fluitans	1	2	+
Baldellia ranunculoides	1	1	+
Galium palustre	1	1	+
Juncus heterophyllus	+	2	+
Utricularia australis	+	+	Absent
Ranunculus peltatus	+	+	+
Apium inundatum	+	+	Absent
Scirpus fluitans	+	+	Absent
Mentha pulegium	+	1	+
Total surface covered by macrophytes	97%	95%	<2%

+ = presence.

levels stabilised at around 130 µg/l. The water chlorophyll content has increased 100% ($P < 0.05$; *t*-test for independent samples), with mean concentrations of 69 mg/l in summer at present, so the present trophic status in Chozas can be considered hypertrophic (OECD 1982). This, together with the greatly increased resuspension of the sediment due to wind and waves, as well as to crayfish benthic activities has reduced light penetration of the water to a Secchi disc depth of 28 cm.

Submerged aquatic vegetation

Plant cover did not vary significantly in Chozas Lake from 1984 to 1996 with 95% of the bottom kept covered by a varied community of macrophytes (Fernández-Aláez et al. 1999) (Table 2): *Chara globularis, Nitella translucens*, *Myriophyllum alterniflorum* and *Potamogeton natans* dominated in the deepest areas, *Baldellia ranunculoides*, *Littorella uniflora, Glyceria fluitans, Juncus heterophyllus, Sparganium erectum* and *Eleocharis palustris* covered the shallowest ones.

During the beginning of the summer of 1997, most of the submerged vegetation in the lake was destroyed; the biomass value in summer fell from 800 gDW in 1996 to 70 gDW (a decrease of over 90%), although the different species of macrophytes were affected differently (Fernández-Aláez et al. 2002). Whilst most of the angiosperm stems gradually appeared on the shores over the summer, the dense clumps of Charophytes disappeared completely. Since 1998, no submerged vegetation has appeared in the lake, although there is weak colonisation of the banks at the beginning of spring in areas that dry out in summer, which means that most species are still present but at very low coverage (see Table 2). Currently, the vegetation cover is 2% in early summer, but no macrophyte species can be found within the flooded perimeter as summer advances; in mid-summer, any submerged plant biomass can be recorded.

Macroinvertebrates

Due to the lack of data on macroinvertebrate communities prior to 1997, Table 3 compares the

Table 3. Epiphytic (3a) and benthic (3b) macroinvertebrate groups present in Chozas compared to lakes not colonised by exotic crayfish species (crayfishless). Data from García-Criado et al. (2004).

	Crayfishless	Chozas
Epiphytic macroinvertebrates		
% Hydra	0.3	0
% Oligochaeta	2.1	1
% Hirudinea	0.7	0
% Gastropoda	14	0
% Acari	1.3	0
% Ostracoda	0.8	0.3
% Ephemeroptera	5.4	13.3
% Odonata	55.6	78.6
% Heteroptera	5.4	0
% Lepidoptera	4.8	0
% Trichoptera	3	0
% Diptera	19.5	6.8
% biomass	3.2% biomass in Chozas	
Benthic macroinvertebrates		
% Oligochaeta	8.2	17.6
% Diptera	52.9	82,4
% Others	40.0	0.0
% Biomass	233% higher in Chozas	

The % of biomass corresponds to the ratio: crayfishless lakes biomass/Chozas biomass.

Chozas communities with those of other crayfishless lakes in the area. According to the samplings carried out after crayfish were introduced in Chozas, the current benthic macroinvertebrate fauna (three genera) represents only about 26% of those present in the lakes not invaded by exotic decapods. On the other hand, 72% of frequently appearing genera associated with aquatic vegetation detected in crayfishless lakes could not be detected in Chozas. The number of orders absent from the macroinvertebrate inventory is high (Table 3a) with the complete depletion of all Heteroptera and Trichoptera species as well as the entire Gastropoda and Hyrudinea Classes.

It needs to be pointed out that the total macroinvertebrate biomass in Chozas is barely 2% of the mean biomass values in other lakes and that more than 70% of this is exclusively due to Odonata.

Amphibians

The herpetological studies carried out in 1980 by Alvarez and Salvador (1984) record breeding of four species of Anura in Chozas lake: *Hyla arborea*, *Pelobates cultripes*, *Bufo calamita* and *Rana perezi*, and two species of urodeles*, Triturus marmoratus* and *Pleurodeles waltl*, the latter being endemic in the Iberian Peninsula and Morocco.

In the aquatic fauna samplings carried out after the arrival of red crayfish in the lake, no evidence of breeding by any of the Anura species has been confirmed. All the species have become extremely rare (isolated adult specimens of *R. perezi* and *H. arborea* have been detected) or have not been detected (*B. calamita* and *P. cultripes*) nor has it been possible to find evidence of laying, larval stages or adults of *T. marmoratus* there; however, the sharp-ribbed salamander (*P. waltl*) population maintains numerous adults and laying has been observed in the remaining vegetation area.

The data on sharp-ribbed salamander abundance in Chozas, measured as captures per unit of effort (CPUE), show values similar to those of other lagoons in the area not colonised by any crayfish species. CPUE of one individual in Chozas are comparable to those observed in Redos (two individuals) or Sentiz (one individual), both eutrophic lakes dominated by vegetation and without the presence of crayfish, although values of CPUE higher than for 90 individuals have also been recorded in the Villaverde lake, which is similar to the two previously mentioned ones. On the other hand, the CPUE values in the Villadangos lake, which has crayfish and no submerged vegetation, were similar to those of Chozas (one individual).

Water birds

The bibliographical study of the papers on water birds carried out in Chozas prior to 1997 confirms the presence of 50 species in the lake, besides at least another five considered accidental visitors (Table 4). Eleven species used the area for nesting prior to 1997; *Aythia nyroca*, catalogued as SPEC 1 (Tucker and Heath 1994) and considered at risk on a national level (Blanco and González 1992) was censused too. Due to the significance of the lapwing (*Vanellus vanellus*) breeding community, the lake could be considered internationally important (Purroy 1990), according to criteria proposed by Scott (1980). Due to this richness, the lake was included in the Regional Catalogue of Wet Areas of Interest, and a report was written requesting the constitution of an

Table 4. (a) Number of species of birds before and after crayfish introduction in Chozas lake. (b) Anatidae species detected in Chozas before 1997 and their changes in status since crayfish introduction (* decreased populations).

	Before crayfish intro.	After crayfish intro.	% Disappeared
Panel a			
Herbivories and diving ducks	12	7	42
Shorebirds	17	12	25
Ciconiform (stork and allies)	4	4	0
Breeding	11	4	64
Wintering	6	4	34

Panel b	Status in Chozas	After 1997
Anas penelope	Migrant	Not detected
Anas crecca	Breeding	Not detected
Anas platyrhynchos	Breeding	*
Anas acuta	Migrant	Not detected
Anas querquedula	Breeding	Not detected
Anas clypeata	Migrant	*
Aythia ferina	Migrant	Not detected
Aythia nyroca	Migrant	Not detected

ornithological reserve in the lagoon and the adjacent wetland (Purroy 1990).

Although the disappearance of 52% of the species and fall in the population of most bird groups still present have been confirmed, it has to be pointed out that not all the groups have been equally affected (Table 4a). In censuses after 1998 among the shorebirds, environmental change has resulted in the absence of around 32% of the species which frequently appeared in Chozas according to Marcos et al. (1995). Although the numbers have fallen, 50% of them have remained in the lake after the arrival of *P. clarkii*. The chance visitor species or those with large yearly variations have not been included in the calculation of these percentages.

Alegre et al. (1991) report the use of Chozas by 11 species of water birds for nesting. Since the introduction of the red swamp crayfish the absence of breeding in seven species has been noticed; on the other hand, the number of nesting pairs of species dependent on marsh vegetation with floating nests (four species) has decreased, highlighting a 65% fall in the number of coots (*Fulica atra*). The lapwing breeding population is maintained although with a tendency to decrease.

The functional group most affected by the introduction of crayfish has been waterfowl which use aquatic food resources (surface and diving ducks, coot). Comparing the census of over-wintering species before introduction (Alegre et al. 1991) with the present situation confirms the loss of 50% of species, all of them Anatidae; this Familia seems to be the most affected as the censuses after the introduction of crayfish show that 75% of the eight species recorded by Purroy (1990) are absent (Table 4b).

A series of birds whose presence has increased in this system since the arrival of *Procambarus clarkii* requires a separate mention. Among the Ardeidae, the increase in common herons (*Ardea cinerea*) and the regular presence of cattle egret (*Bulbucus ibis*) is well known, although the total abundance of *Egretta garzetta* seems to have decreased slightly. Likewise, the common stork (*Ciconia ciconia*) populations feeding in Chozas have increased. Adding to this, the presence of a new predator diving species during the winter and beginning of spring, the great cormorant (*Phalacrocorax carbo*) has been recorded.

Discussion

The profound changes occurring in Chozas after the disappearance of aquatic vegetation are in keeping with the theory of alternative stable states in shallow lakes (Scheffer 1990). However, in this case, the mechanism of change from a clear to turbid state has been the mechanical destruction of submerged vegetation as a result of the benthic activity of an invading alien crayfish species, the red swamp crayfish *Procambarus clarkii*. Rodríguez et al. (2003) showed that exclusion of *P. clarkii* from certain areas of the lake using mesocosms allowed plant coverage to reach up to 95%. These experiments showed that the seed bank has the potential to recover vegetation spontaneously in the absence of red crayfish but the predator activity of the crayfish prevents it. Experiments on the inclusion of crayfish densities close to the estimated one in Chozas (see Rodríguez et al. 1993) in areas with 95% vegetation cover demonstrated the destructive capacity of this species, as 60% of the plant biomass was destroyed in 2 weeks.

This and other studies (Anastáçio and Marques 1997; Vila-Escalé et al. 2002) show that even relatively low crayfish densities (lower than 1 ind/m^2) can completely remove submerged vegetation from shallow lakes and streams in the Iberian Peninsula. It is also relevant that other studies within this area point to this species' preference for fresh plant food (Gutiérrez-Yurrita et al. 1998) whilst studies carried out in other places indicate that detritus is the main ingredient of *P. clarkii*'s diet (Bernardo and Ilhéu 1994). There is another reason for specifying the geographical location when determining the disturbing potential of invading decapods and that is the fact that there are no autochthonous predator species in the Spanish lakes which can affect the crayfish populations in any way. Another interesting aspect is that autochthonous white clawed crayfish (*A. pallipes*) do not seem to have the herbivore intensity of the American red crayfish. Studies in lakes with abundant macrophyte vegetation (*Chara* sp.) have been shown to host high densities of autochthonous crayfish (C.F. Rodriguez et al., in preparation).

Various studies (Stein 1977; Rabeni 1992; Dorn and Mittelbach 1999) report that in the areas of origin of most crayfish species (generally America) the populations are subject to predation by different species of fish. Given that some of these fish species have also been introduced into various places in the world, it would be interesting to confirm whether the interaction of these exotic species (see Elvira et al. 1996) into their new systems allows these effects to be reduced.

Decreased macroinvertebrate populations as a result of the increased densities of autochthonous and exotic freshwater crayfish have been repeatedly documented in studies on the trophic role of these species in streams and lakes (Hanson et al. 1990; Lodge et al. 1994; Nyström and Perez 1998; Nyström et al. 2001; Correia 2002, amongst others). These studies have confirmed under both experimental and natural conditions the incidence of crayfish predation on macroinvertebrate fauna, demonstrating that some decapod species (for example, *P. clarkii*) change their diet from plant food and detritus to an animal diet in relation to the availability of macroinvertebrates (Correia 2002). The disappearance rate for macroinvertebrates associated with vegetation recorded in Chozas was very high (72% of Genera), although these groups are not directly related to crayfish predation. Amphibian diet studies comparing this same lake and others with the same environment (Santos et al. 1986) also showed that, prior to the introduction of exotic crayfish, the macroinvertebrate fauna of Chozas was more widely diversified. Therefore, it can be stated that vegetation destruction has had a greater incidence on the macroinvertebrates of Chozas than the direct effects of crayfish predation and even there is a group, Chironomidae, that despite being more vulnerable to crayfish predation due to its benthic habitat, increased their numbers when compared with other crayfishless lakes. This fact seems to be related with the increased naked sediment area as chironomid densities are similar to those found in non-vegetated lakes.

The vulnerability of egg-laying and young amphibians of different species has been documented in various studies (Gherardi et al. in press; Axelsson et al. 1997; Nyström and Abjörsson 1999) and it is highly likely that the predation of *P. clarkii* significantly affects recruitment of all the amphibian species. During samplings, no adult specimens of the Anura species have been detected, except for some specimens of *H. arborea* and *R. perezi* near the lake. About the newts, absence or presence of *T. marmoratus* (neither larvae nor adults) seems to confirm the disappearance of this species from Chozas.

The persistence of *P. waltl* in Chozas could be sustained by its possessing chemical defences in its epithelium. Various amphibians present this type of defence against predators (Petranka et al.

1988; Bridges and Gutzke 1997), mainly fish and other invertebrates, although Crossland (1998) has documented its lower efficacy against crayfish. In Chozas, the crayfish were observed attacking the uropygium of the sharp-ribbed salamanders trapped in the sampling nets, killing but not devouring them; similar behaviour has been documented by Axelsson et al. (1997) who state that *Pacifastacus leniusculus* preys on larvae of *Bufo* sp., endowed with chemical defences in their epithelium, but does not devour them.

These observations demonstrate direct predation seem to have contributed to rarefaction of all the species of anura and *T. marmoratus* in Chozas lake, as well as the probable decrease in breeding potential. However, indirect mechanisms associated with the destruction of vegetation (for example, *H. arborea* males select areas with floating vegetation and avoids areas without vegetation (García et al. 1987)) and with the collapse of the trophic chains based on the macroinvertebrates (the diet of urodeles is based 60% on macroinvertebrates (Santos et al. 1986)) could be the most likely causes of the decrease in amphibian populations.

Unfortunately, since García et al. studies any amphibian populations research have been done in this geographic area so there is any kind of control of our results and, when explaining the dynamics of any amphibian population, the decreasing tendency recorded in amphibian populations all over the world must be considered (Sarkar 1996; Houlanan et al. 2000). Its causes are barely understood, but it has also been detected in most aquatic systems in our latitudes.

The relationship existing between aquatic plant cover and water birds has been repeatedly documented in various studies (Mitchell and Wass 1996; van Donk and Otte 1996; Sondergaard et al. 1998; Blindow et al. 2000). Although many of them have established their work regimes trying to measure the effect of bird herbivorism on the plant communities (see Mitchell and Perrow 1998), there is a good correlation between the presence of plants and abundance of most water birds. In this sense, the studies based on the analysis of long seasonal series of data (Hargeby et al. 1994; van Donk and Otte 1996; Blindow et al. 2000) have allowed a positive correlation of the establishment of clear water states to years of high bird density.

The data recorded in Chozas throughout the last decade are consistent with the results given in the previously mentioned studies, with the special feature of the change from a transparent to a turbid state not being due to a eutrophication process but to the introduction of alien crayfish. Both herbivores (anatids and coots) and other birds have seen a reduction in the available food due to the direct destruction of vegetation and the indirect disappearance of the communities of plant-associated macroinvertebrates. This effect is shown particularly in the population variations among anatids, a well represented group before 1997 and practically non-existent now.

In addition, the effects on the nesting bird communities, apart from the already mentioned reduction in available food sources, can be related synergically to the red crayfish reducing the marshy areas where floating nests are built and only the existence of a marginal lakeside wood has allowed certain nesting to persist in the area (F.J. Purroy, pers. comm.).

It is of interest too, due to its importance for the implementing of environmental policies, that the three species detected before 1997 and classed as being in danger, *Ardeola ralloides, Plegadis falcinellus* and the already mentioned *Athya nyroca,* have not been included in any census after that year. Likewise, the inventory of vulnerable or rare species (Blanco and González 1992) in Chozas before *P. clarkii* was detected to be 10 species (Purroy 1990), of which 70% have not been inventoried again.

The incidence of the shorebird group has been quantitatively lower, perhaps due to the fact that they exploit resources related to the lake shore area, less affected by the presence of crayfish. In another respect, an increase in the Ardeidae and Ciconiidae populations has been observed, which has been recorded in other studies (Barbaressi and Gerardhi 2000; see Gherardi and Holdich 1999). It could be related to the abundance of crayfish populations, as they are a preferential prey of these birds. Similarly, the winter presence of great cormorants (*P. carbo*) in the last few years also benefits from the abundance of exotic crayfish in the aquatic systems (Barbaressi and Gherardi 2000). However, the generalised spread of this species in continental waters of the Iberian Peninsula is being studied and could be due to various causes (De Nie 1995).

Table 5. Summary of main changes in flora and fauna losses in Chozas before and after crayfish introduction (gen: number of genus, sp.: number of species).

	Before crayfish intro.	After crayfish intro.	% Disappeared
Vegetation coverage	95%	<3%	99
Macroinvertebrates (Gen)	31	9	71
Waterfowl (sp.)	50	26	52
Amphibians (sp.)	6	1	83

Reviewing all the taxonomic groups affected by the introduction of red crayfish shows the spread throughout the trophic chain (Table 5), and the direct and indirect effects of crayfish on the lake communities must be differentiated (Figure 1). The crayfish main negative direct effect on ecosystem is the elimination of submerged vegetation and the reduction of macroinvertebrate populations; both effects in fact mean a dramatic depletion of food resources, shelter and laying sites affecting the whole trophic web. Moreover, the change to a turbid state caused by the disappearance of vegetation has a feedback effect reducing light conditions for vegetation development and affecting macrophyte recolonisation even at low crayfish densities. This turbid state seems to be accompanied by an increase in the densities of benthivore fish (Jeppesen and Sammalkorpi 2002), which favours an increase in piscivorous birds such as herons, egrets, storks, grebes and cormorants. In another respect, there seems to be a positive direct effect on its predators (ardeidae and ciconiiformes), which tend to increase in density.

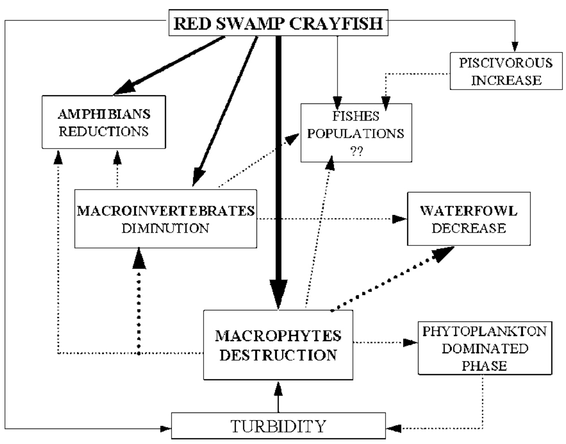

Figure 1. Direct and indirect effects of the exotic red swamp crayfish (*Procambarus clarkii*) on Chozas ecosystem. (continuous arrow: direct effects, dotted arrows: indirect effect).

This study shows that the introduction of the red swamp crayfish *Procambarus clarkii* to the Iberian aquatic systems has dramatic effects on whole ecosystem processes, with direct and indirect repercussions on both flora and fauna communities, mainly as a result of the great predatory effect on submerged vegetation.

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