



Shift from clear to turbid phase in Lake Chozas (NW Spain) due to the introduction of American red swamp crayfish (*Procambarus clarkii*)

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Abstract

Lake Chozas (León, NW Spain) until 1997 was a mesotrophic, macrophyte-dominated clear-water lake. The American red swamp crayfish (*Procambarus clarkii* Girard) was introduced in 1995–96. In 1998, it increased its numbers coinciding with reductions in plant density from 97% to less than 10% surface cover. The removal of submerged vegetation was accompanied by a fast switch from clear to turbid, *Microcystis*-dominated conditions in the lake. *In situ* experiments in Lake Chozas using exclosures and enclosures have proved that the red crayfish are efficient predators of macrophytes. This work gives new evidence of the direct relationship between red-crayfish introduction and the shift from clear to turbid conditions in shallow lakes.

Introduction

Submerged and floating macrophytes often have an important role in the maintenance of the clear water state in eutrophic shallow lakes (for a review, see Jeppesen et al., 1997). Macrophyte destruction in these nutrient-rich conditions is generally followed by a switch from a clear to a turbid state dominated by phytoplankton growth. Deep changes occur in both the food-web structure and nutrient levels, as predicted in trophic cascade theories (Carpenter & Kitchell, 1993; Scheffer, 1998). Several mechanisms have been identified as causing the macrophyte loss in shallow lakes, i.e. light shading of the plants by phytoplankton and/or periphyton growth induced by excess nutrient enrichment (Phillips et al., 1978; Balls et al., 1989; Sand-Jensen & Borum, 1991), direct grazing by waterfowl, fish, insects or mammals (see Lodge et al., 1998).

Crayfish have been reported to be one of the most important herbivores in lakes (Lodge et al., 1998). Crayfish predatory activity has been suggested as a potential forward switch from clear to turbid conditions in some lakes (e.g. Harper et al., 1990). However, no clear evidence of this has been presented yet.

Procambarus clarkii Girard is a generalist crayfish introduced in Spain in 1974 (Gutiérrez-Yurrita & Montes, 1999). Their impact on lakes is described in terms of changes in the availability of food resources and/or refuges, on the reproductive success of other species (Gutiérrez-Yurrita & Montes, 1999), and as direct reductions in macrophyte biomass (Cronin, 1996; Nystrom & Pérez, 1998; Angeler et al., 2001). Here we present evidence on the direct effects of crayfish predation on macrophyte biomass in Lake Chozas, as well as other indirect changes in the lake ecosystem driven by their introduction.

Study area

Lake Chozas is a small (9 ha), shallow (max. depth 1.8 m) and fertile lake (200 mg l⁻¹ summer total phosphorus concentration) in León, North-West Spain. The natural morphometry of the lake basin was modified in the sixties by constructing a stone wall, gaining land for crops and increasing water depth to facilitate use for irrigation. The lake was first studied by Fernández-Aláez (1984) and since 1994 to date it has been regularly monitored. Vegetation cover did not change significantly from 1984 to 1997 (Fernández-

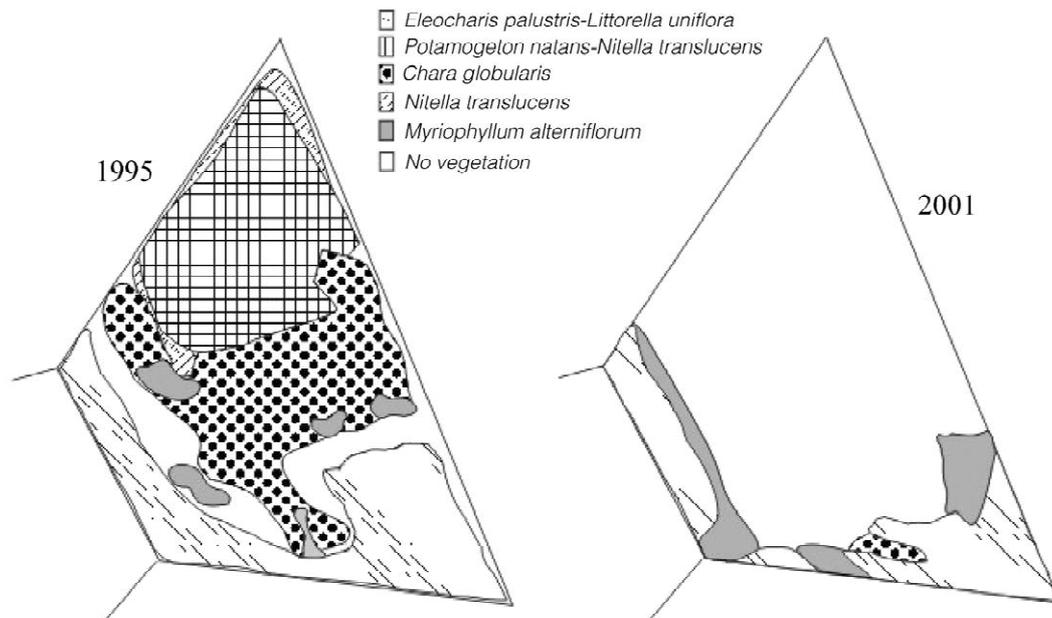


Figure 1. Plant cover in Lake Chozas before (1995) and after (2001) crayfish introduction (1995). The cover of the different plant species (*Eleocharis palustris*-*Littorella uniflora* mixed stands, *Potamogeton natans*-*Nitella translucens* mixed stands, *Chara globularis*, *Nitella translucens*, *Myriophyllum alterniflorum*) on the map of the lake is shown as areas of different hatching.

Aláez, 1984) (Fig. 1a). During this period, the entire bottom of the lake was covered by a diverse macrophyte community. *Chara globularis*, *Nitella translucens*, *Myriophyllum alterniflorum* and *Potamogeton natans* were the dominant species in deeper parts, and *Baldellia ranunculoides*, *Littorella uniflora*, *Glyceria fluitans*, *Juncus heterophyllus*, *Sparganium erectum* and *Eleocharis palustris* covered the shallower parts of the lake.

Several waterfowl used the lake for resting and breeding, including some rare species; for this reason, this lake was included in a list of wetlands of regional interest. Four species of anura amphibians were common in the past and the rare newt (*Pleurodeles waltl*) is also commonly present. Four species of fishes can be found, i.e. tench (*Tinca tinca*), crucian carp (*Carassius auratus*), Spanish rutila (*Chondrostoma arcassi*). The man-introduced mosquito fish (*Gambusia affinis*) has stable populations in this lake, too.

Losses of vegetation were recorded in the early spring of 1997; there was a strong reduction in mean macrophyte density, dropping from almost 800 gDW m⁻² in July 1996, to about 70 gDW m⁻² in August 1997, although levels of plant loss were different depending on species (Fernández-Aláez et al., 2002). Most of the angiosperm stems were found to be cut

along the shores during summer, while the dense mats of Charophytes disappeared from the lake. From 1998 onwards, no submerged vegetation could be found, although during most of the summer, amphibious species such as *Littorella uniflora* and *Ranunculus* sp. remained in dry areas; stems of *M. alterniflorum* were found growing in the wet mud, too.

At the end of 1997, a new species was first detected in Lake Chozas, the omnivorous American red swamp crayfish *Procambarus clarkii*.

Materials and methods

Two types of mesocosms were set up in Lake Chozas between March and August, 2001.

To assess the potential for restoration of the plant communities in this lake, four crayfish exclusion cages were placed in four different locations of the lake with similar percent volume infested (PVI) and plant cover, over areas of relict stands of *Myriophyllum alterniflorum*. A control plot was marked next to each location with the same plant species composition. Each enclosure was 2-m width × 3-m length × 1.8-m height, and sides were covered with rigid-plastic garden net (1 cm. mesh size). The top of each

enclosure was protected with very fine bird-netting. Macrophyte biomass within enclosures was estimated at the beginning of the study, in June 2001 (when crayfish were added to two enclosures at a density of 100 g m^{-2} (i.e. 13 mature individuals per enclosure cage)), and 15 days after crayfish addition.

To isolate direct effects of crayfish on plants from those of fish, 12 control mesocosms (1 m^2 base area), without crayfish, were placed over the naked sediment. All enclosures were made of transparent plastic and fixed to a circular piece of zinc which was pushed into the mud in order to avoid destruction due to crayfish benthic activities. The mesocosms were set in groups of four. Tench, crucian carp or a mixture of both were introduced into separate enclosures of each group, at a known density (ca 200 g m^{-2}), plus a control, fishless enclosure. At the end of the study, in August 2001, enclosures were electrofished and both fish and plants harvested.

Vegetation sampling in the lake was done by using a 0.4 m^2 square-box and retrieving all plant matter within it. Plants in the mesocosms were completely cropped, by using a rake. The plants were placed into bags, and gently washed in the laboratory and weighed for fresh weight (FW). Plants were then dried in an oven ($T= 50^\circ\text{C}$, 24 h) and weighed for dry weight (DW).

American red swamp crayfish densities were estimated in September–October 2001 using catch-mark-recatch methods (Krebs, 1999). A slight cut mark made on one of the parts of the telson of caught individuals was used as the mark for later identification upon recapture. This mark was assumed to be lost during ecdysis.

Results

Dynamics of aquatic vegetation and water chemistry in Lake Chozas

The main effects upon *P. clarkii* introduction in Lake Chozas nutrients were: increased TP (i.e. 6–7 times higher than prior to crayfish introduction) (Fig. 2) and total depletion of nitrates within the system while any changes affecting SRP and ammonium levels, as well as pH, conductivity or Alkalinity, were recorded. The illegal disposal of manure has increased over the years; in despite of this, since 2000 summer values of TP dropped to only 2 times higher than pre-crayfish levels.

During the first years after crayfish introduction, Secchi disc visibility was ca 25 cm during summers mostly due to increased chlorophyll *a* concentrations (i.e. 8 times higher) (Fig. 2), and was never more than about 60 cm during the winter. Spring clear-water phases have occurred in 2001, 2002 and 2003, with light reaching the bottom. Despite this, low Secchi disk visibilities remain during the summer, with algal blooms of cyanobacteria which stop cattle from drinking from the lake.

The consistent early spring clear-water phases from 2001 to present have allowed a strong development of submerged vegetation from February (Fig. 1). Plant growth has occurred at two very different parts of the lake, i.e. in dry areas which retain enough humidity during summers, with growth of *M. alterniflorum* and *L. uniflora* germinating from vegetative propagules in the mud; and in permanent water-covered areas with naked sediment, where there has been development of vegetation, too, albeit weak. In the latter, plants have come from seed (e.g. *P. natans*) and from oospores (e.g. Characeae) in late spring, when light and temperature conditions are more suitable. During summer, any kind of submerged vegetation can be found in Lake Chozas, except under crayfish exclusion conditions.

Fauna in Lake Chozas after crayfish introduction

Crayfish introduction has led to dramatic losses in macroinvertebrate and avian (both of wintering and breeding waterfowl) species richness and abundance, indirectly related to the loss of macrophyte cover. Due to direct predation by crayfish on tadpoles (Barbaresi & Gherardi, 2000), all anura amphibians have disappeared from the lake, while the rare newt (*Pleurodeles waltl* Michaelles, 1830) still has small populations. The special conservation status of the lake is now threatened by this loss of biological diversity.

Using a capture-recapture method, we estimated crayfish densities in Lake Chozas to be *circa* 1 ind m^{-2} , although this is likely an underestimate, given the impact of poaching, which occurred on numerous occasions during samplings, on crayfish populations.

Crayfish predation on submerged plants

Crayfish enclosures placed over areas vegetated with *M. alterniflorum* were sampled for macrophyte biomass in mid-June 2001. Enclosures had 95% plant cover, against 35% for the lake, and 70% higher plant biomass (Fig. 3a). Fifteen days after experimental

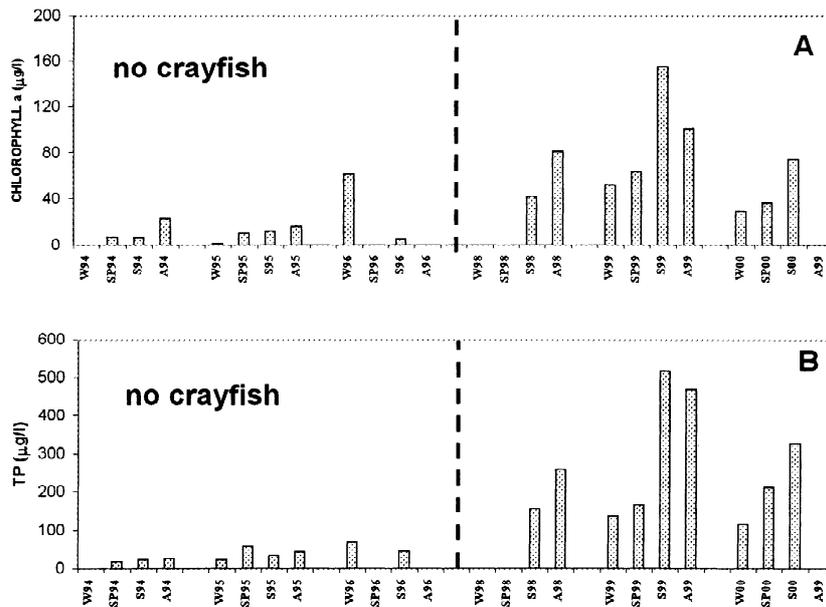


Figure 2. Seasonal dynamics in chlorophyll *a* (A; in mg l^{-1}) and total phosphorus (B; in mg l^{-1}) concentrations in Lake Chozas before and after crayfish introduction.

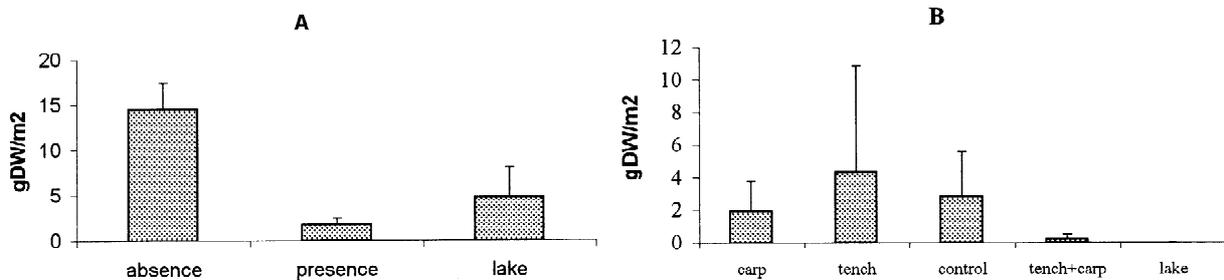


Figure 3. Plant densities (gDW m^{-2}) in experimental mesocosms in Lake Chozas in June 2001. A – *Myriophyllum alterniflorum* densities in enclosures with crayfish (2 ind m^{-2}) ('presence'), without crayfish ('absence'), and in unprotected areas of the lake ('lake'). In July 2001, the lake presented less than 5% plant cover, while percentages were substantially higher in enclosures. B – *Potamogeton natans* growth in mesocosms without crayfish but with 200 g m^{-2} of different fish species (i.e. tench (*Tenca tenca*), crucian carp (*Carassius auratus*), or a mixture of both (tench+carp)) and in the lake (lake). Lake controls had no plant growth (naked sediment).

crayfish introduction into enclosures, there was a near 60% reduction in plant biomass compared to that at the beginning of the experiment. Most of the plant biomass was found floating inside the cages, probably after being cut by the crayfish. Thus, most of the damage to plants by crayfish was non-consumptive. Plant cover (%) inside the crayfishless enclosures remained at near 90% until the end of the experiment in August; then, vegetation cover in control plots was less than 5%.

Macrophyte recovery and fish effects

At the end of the experiment, 10 of the 12 enclosures harboured a very dense mat of *Potamogeton natans*

(i.e. max. 114 g m^{-2}) (Fig. 3b). All the treatments showed the same turbidity conditions as the lake. Although fish activity had no significant effect on plant growth ($p < 0.05$, *t*-test for dependent samples), recovery of biomass was much lower in the mesocosms having a mixture of fish species. None of the lake control plots nor any other area of the lake showed growth of *P. natans*, in spite of the great number of seedlings detected in late spring.

Discussion

Direct predation on macrophytes by American red swamps crayfish *Procambarus clarkii* seems to have

been the mechanism for the disappearance of vegetation in Lake Chozas. The hypothesis of a gradual process of eutrophication favoured by the illegal discharge of manure in nearby areas of the lake can be rejected on the basis of observation that in 1997, when vegetation disappeared, plant growth was normal and it accumulated on the shores after experiencing mechanical damage (i.e. it was cut or torn out).

On the other hand, experiments conducted with medium densities of *P. clarkii* (Feminella & Resh, 1989; Anastácio & Marques, 1997) in areas with relict vegetation, have demonstrated a short-term effect of direct mechanical destruction of the plant growth by the crayfish. Also, the predatory activity of *P. clarkii* involved non-consumptive damage to the aboveground plant biomass because cut stems floated and were driven away from the crayfish by wind-induced surface currents, while affected belowground plant biomass could be totally consumed by the crayfish.

The strong increase in nutrient concentrations in the lake after macrophyte destruction in Lake Chozas could have been due to various factors, i.e. (deposition) of manure detected prior to 1997 elevated total phosphorus (TP) to max. 0.06 mg l^{-1} , and this practice has been continued. On the other hand, increases in TP coincident with macrophyte loss have been estimated in $0.03\text{--}0.5 \text{ mg l}^{-1}$ (Jupp & Spence, 1977; Balls et al., 1989; van der Berg et al., 1999); these increases may be even higher in small lakes (e.g. 0.65 mg l^{-1} in lakes smaller than 3 ha, according to Jeppesen et al., 1990) and reach 0.9 mg l^{-1} in lakes in the Mediterranean region (Bécares et al., 2002).

On the other hand, because of the activity of benthivorous crayfish such as *P. clarkii*, nutrient translocation derived from the consumption and processing of organic matter compartments (Hessen et al., 1993; Gutiérrez-Yurrita & Montes, 1999; Angeler et al., 2001) co-occurs in Lake Chozas with the abovementioned processes.

Following the population explosion of *P. clarkii* in Lake Chozas, two areas can be clearly delimited in the lake (see Fig. 1). Shallow areas, which desiccate over the summer but can retain sufficient pore water to allow the survival of vegetative propagules (mainly *M. alterniflorum* and *L. uniflora*, but also of *Characeae*), and areas of the lake with permanent waters, absence of vegetation and even asexual propagules, which are predated upon by the benthivorous crayfish *P. clarkii*. However, a bank of seeds and oospores must still remain, as plants can germinate in late spring, as noted

from diving observations in this lake.

A number of studies have established that the shallow distribution of submerged vegetation in shallow lakes, such as in Lake Chozas, is directly related to decreasing light levels caused by progressive eutrophication (Balls et al., 1989; Moss, 1990; Sand Jensen & Borum, 1991, among others). However, a phenological analysis of *P. clarkii* in Lake Chozas allows to attribute the distribution of plant density in areas of the lake to the predatory activity of this crayfish species on the plants.

P. clarkii sampled using seeded traps showed that this species slows down its activity during long periods of the winter, probably because of the low water temperatures. By the end of spring, with mean water temperatures in excess of 10°C , cut plant stems were observed on the shores of the lake, suggesting that the crayfish come out of their winter lethargy then, and predate on the plants. The predatory winter slowdown allows for a strong and rapid development of submerged vegetation from vegetative propagules in shallow parts of the lake by the end of winter.

At the end of spring three concurrent processes may take place in Lake Chozas, i.e. seed germination of *P. natans* and of *Characeae* oospores; the end of the winter lethargic period of the red crayfish, and the initiation of a rapid process of lake desiccation due to the increased evaporation rates in spring and summer. Within one month, 20% of the lake will dry out, exposing the sediment to the air, and allowing turions and tubers developing in these areas to escape the predatory activity of the crayfish and survive in the wet mud until the next growing season.

The permanently submerged areas suffered extremely intense predation by the crayfish during 6–7 months, both acting on plant species known to be preferred by crayfish, such as *Characeae* species (Cronin, 1996; Nystrom et al., 1996) and on most other macrophyte species present, causing in all cases their total extermination.

Crayfish exclosures in Lake Chozas demonstrated a clear recovery of *P. natans* (see also Feminella & Resh, 1989), with no substantially negative effects of fish. However, *Characeae* did not recover within exclosures, suggesting high turbidity favours the growth of floating-leaved plants (e.g. *Potamogeton* sp.) over totally submerged plants (e.g. *Chara* sp.) (Moss, 1990).

The excessive nutrient load, intense sediment bioturbation due to crayfish benthivory, and strong wind-induced solids resuspension (i.e. decreases in Secchi

disc visibilities of in excess of 20 cm following storm events, and later increases with settling out), drive the ecosystem to a turbid phase dominated by phytoplankton growth. With the next rainy season, the filling of the lake basin with rainwater will re-initiate the cycle.

Experiments and observations in Lake Chozas lead us to think that eliminating *P. clarkii*, and the natural recovery of submerged macrophytes would mean larger nutrient uptake and the attenuation of wind and wave effects, leading to the complete restoration of the original fauna and macrophyte community existing in the lake prior to 1997.

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