Dramatic impact of alien carp *Cyprinus carpio* on globally threatened diving ducks and other waterbirds in Mediterranean shallow lakes

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ABSTRACT

Mediterranean shallow lakes support high biodiversity but suffer many anthropogenic threats, including introductions of alien fish. We studied the impact of introduction of common carp (*Cyprinus carpio*) to Medina and Zoñar lakes in SW Spain. Both lakes were protected as Ramsar sites because of their importance for waterbirds, particularly the globally threatened white-headed duck (*Oxyura leucocephala* IUCN Endangered) and common pochard (*Aythya ferina* IUCN Vulnerable). Two carp introduction events in Medina lake, with total eradication of carp inbetween, provided a unique opportunity to study the impacts of carp on the waterbird community (counted monthly from 2001 to 2013, with up to 69 species) and submerged macrophyte cover (quantified with satellite images). A comparison of waterbird abundance before and after carp eradication in the smaller Zoñar lake supported the results from Medina lake. Carp consistently led to the destruction of macrophyte beds and a radical change in the waterbird community. After controlling for the influence of depth fluctuations, the numbers and species richness of diving ducks were significantly reduced by carp, whilst the opposite effect was observed for piscivores such as herons. Negative impacts on *O. leucocephala*, *A. ferina*, red-crested pochard (*Netta rufina*) and herbivorous coots (*Fulica* spp.) were particularly pronounced. A significant negative impact of carp was also recorded on greater flamingos (*Phoenicopterus ruber*), black-necked grebes (*Podiceps nigricollis*), little grebes (*Tachybaptus ruficollis*) and gadwall (*Anas strepera*). In contrast, carp presence had a positive impact on grey herons (*Ardea cinerea*). The ongoing expansion of alien cyprinids in the Mediterranean region constitutes a major threat for waterbirds and particularly for sedentary, threatened taxa such as the white-headed duck and red-knobbed coot (*F. cristata*). Of 22 key sites for the isolated Iberian population of white-headed duck identified in a European action plan in 1996, at least 14 have since suffered carp invasions. Further development of successful control methods for carp populations is urgently required to support the conservation of waterbirds in the Mediterranean region.

Keywords: exotic fish · multi-trophic impacts · threatened waterbirds · whole-lake experiment · Mediterranean wetlands · eradication methods

Running title: Carp impacts on waterbirds in a shallow lake

1. Introduction

Aquatic ecosystems have often been protected because of their importance for waterbirds, which can act as flagship species for conservation, and also provide important ecosystem services for humans (Green and Elmberg, 2014). The Ramsar Convention has been highly influential in Europe and elsewhere in the protection of wetlands, especially those holding important concentrations of waterbirds (Tomankova et al., 2013, Guareschi et al., 2015). Although it is generally assumed that waterbirds act as bioindicators of aquatic fauna and flora in general, their value as bioindicators can be limited for several reasons (Amat and Green, 2010, Tomankova et al., 2013, Guareschi et al., 2015). For example, because they breathe air and are highly mobile, they can resist deterioration in water quality better than many invertebrates or plants. On the other hand, their numbers at a given locality may vary because of changes elsewhere along their migration routes. Hence it may not always be possible to relate bird abundance in a lake to changes within the lake's food web, such as those caused by biological invasions.

Some of the world's worst invasive organisms are aquatic taxa, including crayfish, mussel and fish species such as the common carp (*Cyprinus carpio*) (Lowe et al., 2000). These invasive species act as ecosystem engineers and cause profound trophic and non-trophic alterations in ecosystems (Crooks, 2002; Gherardi, 2007; Sousa et al., 2009). Many studies have related an invasion by these taxa to dramatic alterations in the underwater community and the aquatic environment (Parkos et al., 2003; Maceda-Veiga et al., 2013; Mathers et al., 2016). However, their cascading impacts on iconic vertebrate taxa (birds and mammals) are less well understood, although they can be expected to be generally positive for carnivores and negative for herbivores (Prigioni et al., 2006; Tablado et al., 2010; Laguna et al., 2016). Research into the impacts of invasive species typically shows a single snapshot of time (e.g. Parkos et al., 2003; Ilarri et al., 2014; Monroy et al., 2014; Maceda-Veiga et al., 2016), and time-lagged responses in invaded areas may be overlooked (Parker et al., 1999; Strayer et al., 2006). Therefore, there is a need for long-term studies examining the effects of non-native aquatic species on waterbird communities.

Shallow lakes and other Mediterranean wetlands provide habitat and food to many resident and migratory waterbirds, including herbivores, omnivores and piscivores (Rendon et al., 2008; Galewski et al., 2011). Different bird guilds are expected to be affected in different ways by the introduction of invasive fish such as the common carp (*Cyprinus carpio*), which has become widespread in the Mediterranean region in recent decades

(Vilizzi, 2012). Waterbirds that are highly dependent on submerged macrophytes such as the Eurasian coot (*Fulica atra*) and the red-knobbed coot (*Fulica cristata*) (Varo et al., 2008) are likely to be negatively affected, since carp destroy macrophyte beds (Crivelli, 1983; Zambrano and Hinojosa, 1999; Shin-ichiro et al., 2009). *F. cristata* is IUCN Endangered at the European level (BirdLife International 2015). Carp also reduce the density of benthic invertebrates and may impact diving ducks that feed on such invertebrates, including the globally threatened white-headed duck (*Oxyura leucocephala* IUCN Endangered) and common pochard (*Aythya ferina* IUCN Vulnerable) (Winfield et al., 1994; Sánchez et al., 2000). In semi-arid regions such as southern Spain where wetlands are scarce, fish introductions might be particularly harmful for relatively sedentary birds such as *O. leucocephala* and *F. cristata* with specialised habitat requirements (Green et al., 2002; Sebastián-González et al., 2013). On the other hand, the effects might be reduced for omnivorous dabbling ducks (*Anas* spp.) which have large migratory populations, and can obtain food from the shoreline and from terrestrial habitats including croplands (Dessborn et al., 2011, Soons et al., 2016). Finally, piscivorous birds such as herons, grebes or cormorants might benefit from fish introductions (Laguna et al., 2016, but see Kloskowski, 2012).

Various fish have been shown to have a negative impact on waterbirds. In boreal lakes, pike (*Esox lucius*) predate ducklings whereas perch cause important competition for food (Vaananen et al., 2012). Diving ducks compete with cyprinids and other fish that eat benthic chironomid larvae and molluscs in temperate lakes (Giles et al., 1990; Winfield and Winfield, 1994). Studies in central and northern Europe suggest carp have a negative impact on the breeding success of diving and dabbling ducks (Musil, 2006; Broyer and Calenge, 2010). Such impacts might be expected to be stronger in the Mediterranean region where migratory waterfowl concentrate in winter (Rendón et al. 2008), and high water temperatures all year round increase the activity and food intake of non-native fish such as *C. carpio* (Weber et al., 2015).

In 2003, the cyprinid *C. carpio* was introduced from an adjacent farm pond into Medina lake in SW Spain, a major breeding and wintering area of waterbirds. In order to restore the value of this Ramsar site for birds, the regional government used the piscicide rotenone to eradicate carp in 2007, but a reinvasion occurred when record flooding in the winter of 2010-2011 connected the lake with the nearby River Guadalete. This effectively constitutes a replicated whole lake experiment, and here we examine the effects of *C. carpio* invasion, eradication and re-invasion on the macrophyte cover and waterbird community, including four dominant guilds (herbivorous coots, diving and dabbling ducks, and

piscivores). To confirm that the observed impact of carp invasion on waterbirds is similar in other Mediterranean lakes, we use data from a second lake in SW Spain (Zoñar lake) where carp were eliminated with rotenone in 2006 after an introduction in 1985 (Torres-Esquivias et al., 2009).

Rotenone is highly toxic and can have harmful effects on invertebrates, amphibians and humans (Chandler and Marking, 1982; Rayner and Creese, 2006), but the removal of carp was expected to increase the abundance of submerged macrophytes and of herbivorous and omnivorous waterbirds, as observed with other biomanipulation tools elsewhere (Sondergaard et al., 2008; Vilizzi et al., 2015). To assess the importance of carp invasions at a broader scale, we assess how many of the key sites previously identified for *O. leucocephala* (Green and Hughes, 1996) have been affected by carp invasion.

2. Methods

2.1. Study areas

Located at 30 m above sea level in Cádiz province (36°37'18" N, 6°02'48" W), Medina lake (120 ha) is the third largest natural lake in Andalusia, SW Spain with a catchment area of 1900 ha (Fig. 1). It is a permanent, shallow, closed-basin lake with mean water temperature of 21°C during the annual cycle (Florian et al., 2016). This mesohaline lake has a maximum water depth of 3.5 m due to an artificial overflow, and only dries out in case of extreme droughts, such as in 1990 and 2000 (Rodríguez et al., 2012). Situated 150 km to the north-east in Córdoba province (37°28'59"N, 4°41'23"W), Zoñar lake is a smaller (40 ha), permanent, deeper lake (maximum water depth of 13 m) with a catchment area of 876 ha and a relatively stable water level (± 1 m). Both lakes were declared as hunting refuges by the regional government in 1982. Medina and Zoñar lakes have since been declared as Natural Reserves, wetlands of international importance under the Ramsar convention, and Special Protection Areas and Sites of European Community Importance due to their value for *Fulica* spp. and Anatidae, including *O. leucocephala* and *A. ferina*. Although these species breed there, both lakes are particularly important for waterbirds in the post-breeding and wintering periods (Amat, 1984). The lakes receive birds from nearby temporary or semi-permanent wetlands that dry out in the summer, including the Doñana marshes (Rendon et al., 2008), and Medina lake has often held more than 20,000 ducks and coots. *Cyprinus carpio* invasion extirpated the submerged vegetation of both lakes, which was dominated by *Potamogeton pectinatus*, *Zannichellia* spp. and *Chara* spp.

In the absence of carp, these lakes are mesotrophic (e.g. de Vicente et al., 2012), but carp activity makes them eutrophic with high nutrient and chlorophyll concentrations (Fernández-Delgado 2007; Florian et al. 2016). The piscicide rotenone was applied to Medina lake in September 2007 (PW Rotenone[®], at 4 ml per 10³ litres) and to Zoñar lake in August 2006 (CFT Legumine[®], at 1.2 ml per 10³ litres), killing all carp. Biomass removed was 13416 kg in Medina lake (111.8 kg/ha) (Junta de Andalucía, 2008) and 13000 kg in Zoñar lake (325 kg/ha) (Fernández-Delgado 2007). The regional government (Consejería de Medio Ambiente, Junta de Andalucía) decided to apply this treatment owing to clear evidence of general degradation in biodiversity at these and other lakes after entry of carp (Torres Esquivias et al., 2009).

With the exception of a small number of birds in Morocco, Spain supports the entire biogeographical population of *O. leucocephala* in the Western Mediterranean (<http://wpe.wetlands.org/>). From a European action plan for the species (Green and Hughes, 1996), we identified the 22 wetlands in Spain that were formerly considered Key Sites of particular importance for *O. leucocephala*. We identified which of these sites have since suffered carp invasions by consulting with local managers and scientists in the three autonomous communities affected (Andalusia, Valencia, and Castilla la Mancha).

2.2. Bird censuses and water depth

For lake Medina, waterbird data were obtained from monthly surveys conducted between 2001 and 2013 with a spotting scope from a series of fixed points around the lake edge, by ornithologists from the Regional Government of Andalusia, as part of their monitoring program for all protected wetlands. For our analyses, the two similar coot species *Fulica* spp. were combined because only small numbers of *F. cristata* were recorded and their identification at a distance is problematic. Amongst other abundant waterbird species, we identified three dominant guilds including diving ducks, dabbling ducks and piscivores. Smaller Podicipidae that feed largely on invertebrates as well as small fish (e.g. Varo et al., 2011) were not included in the piscivore guild, since carp are likely to have negative effects on them through reducing invertebrate abundance, and our objective was to look for positive effects of carp invasion on true piscivores. Water depth was measured at the time of surveys and on other visits by reading a depth gauge placed in the deepest part of lake Medina. To investigate the effect of carp invasion on birds in the deeper lake Zoñar, we extracted bird data from Arenas and Fernández-Delgado (2006) to compare the abundance of coots, A.

ferina and *O. leucocephala* before (2001- 2006) and after (2006-2009) extirpation of carp in Zoñar.

2.3. Macrophyte cover

As Medina is a shallow lake, when carp were absent the submerged vegetation filled the water column during spring and summer and so was visible at the surface. To assess submerged macrophyte vegetation cover at the water surface, we used Landsat L5TM data between 2001 and 2013. Satellite images were taken on approximately a monthly basis by the TM and ETM+ sensors on board the Landsat 5 and Landsat 7 satellites, obtained from the United States Geological Survey. We selected those images free of cloud cover and applied the Normalised Difference Vegetation Index (NDVI, Mather, 1987), which estimates the fraction of active photosynthetic radiation that is intercepted by vegetation based on the reflectance in the red (R) and near infrared (NIR) bands (bands 3 and 4, respectively, for Landsat images, see Alcaraz-Segura et al. 2009 for further details). Using ENVI 4.4 software, one mask was constructed for the total lake surface and a second mask for the cover of terrestrial and aquatic vegetation. These masks were combined to obtain one that contained only aquatic vegetation. The mask area was quantified by the number of pixels (30 m × 30 m each).

2.4. Statistical analyses

Data from Medina and Zoñar lakes were used to independently assess the impact of carp presence on the abundance of coots, *O. leucocephala* and *A. ferina*. Then, we used the replicated whole-lake experiment in Medina to examine the effects of carp invasion in more detail. Using generalised linear models (GLMs with a Quasipoisson error distribution), we analysed the relative contribution of carp invasion and fluctuations in water depth to variation in the total richness and abundance of all waterbird species and of four dominant guilds (herbivorous coots, diving and dabbling ducks, and piscivores). Month was also included as a categorical variable in these models to account for seasonal changes in waterbird abundance. Since the month of carp introduction into Medina lake in 2003 is unknown, we excluded this year from the analyses. Similar analyses were used to explore the impact of *C. carpio* and water depth on the abundance of the most frequently recorded waterbird species (≥ 25 % of occurrence among monthly surveys). Changes in the mean abundance (ratio) of waterbirds in periods with and without carp was calculated as a measure of carp effect size.

To assess the effect of carp on aquatic plants, mean macrophyte cover was compared between periods with and without *C. carpio* in Medina lake using a GLM with Gaussian error distribution. Month and water depth were also included in this model to account for differences in phenology and water depth. Then, we used a series of Quasipoisson GLMs to further explore the relative effect of carp invasion over the full set of potentially confounding factors (changes in macrophyte cover, water depth, and season) on the abundance of coots, *O. leucocephala* and *A. ferina*. Owing to the shortage of suitable Landsat images during some months, the inclusion of macrophyte cover reduced the size of our dataset. To specifically appraise the effects of carp invasion on the reproduction of coots, *A. ferina* and *O. leucocephala*, we compared the number of breeding pairs of these birds before and after carp invasion in Medina lake using a Mann-Whitney test.

The significance of explanatory factors in GLMs was tested using F tests. Log-transformation was applied to waterbird abundance and mean macrophyte cover to improve model fitting. Residual diagnostic plots from the models were used to verify the assumptions of normality and homocedasticity (Zuur et al., 2010). The goodness of fit of models (R^2) was calculated as: (null deviance-residual deviance/null deviance)*100. All statistical analyses were performed in R v.2.15.3 (R Core Team, 2013) using the libraries ‘MASS’ (Venables and Ripley, 2002), and ‘car’ (Fox and Weisberg, 2011). The statistical threshold was $P \leq 0.05$.

3. Results

Up to 32 water bird species were recorded on Medina lake at any one time during the study period (2001-2013), with an overall combined total of 69 species. Numbers peaked in the post-breeding and wintering periods. There were four dominant guilds (herbivorous coots, diving and dabbling ducks, and piscivores), and important concentrations of two globally threatened diving ducks (white headed duck *Oxyura leucocephala* and common pochard *Aythya ferina*) (Table S1). The red-knobbed coot (*Fulica cristata*) was regularly present (Table S1) and up to 7 ferruginous duck *Aythya nyroca* (IUCN near-threatened) were recorded occasionally. Other waterbirds recorded during >25 % of surveys were the greater flamingo (*Phoenicopterus ruber*), the little grebe (*Tachybaptus ruficollis*), the black-necked grebe (*Podiceps nigricollis*), the yellow-legged gull (*Larus michahellis*), the black-necked stilt (*Himantopus himantopus*), the common moorhen (*Gallinula chloropus*) and the purple swamphen (*Porphyrio porphyrio*) (Table S1).

In the absence of alien carp *Cyprinus carpio*, the most abundant waterbirds in Medina lake were coots (*Fulica* spp., up to 12000 individuals in the post-breeding period) and shoveller (*Anas clypeata*) (up to 2164 individuals during winter) (Fig 2 and Table S1). Without carp, the lake showed a higher richness and abundance of diving ducks, with up to 800 *O. leucocephala* and 1136 *A. ferina* outside the breeding period (Tables S1, Figs 3 and 4). A sharp increase in the number of coots ($W=309$; $P<0.001$), *O. leucocephala* ($W=65.5$; $P<0.001$) and *A. ferina* ($W=95$; $P<0.001$) also occurred in Zoñar lake in the absence of carp (Figs 2 and 4). When *C. carpio* were absent, the Medina lake surface was also covered by a large macrophyte bed during summer and autumn, as quantified by satellite images (Fig. 2).

During the two periods of *C. carpio* invasion in Medina lake, mean values of macrophyte cover, and numbers of coots and diving ducks decreased dramatically in a consistent manner (Tables 1, 2, 3 and S1), as seen also in Zoñar lake. The impact was particularly acute for *O. leucocephala*, which almost disappeared in the presence of carp (Fig 4). A strong decrease in number was also observed for *A. ferina*, and the loss of macrophytes was reflected by a similar decline of coot numbers (Fig 2). In fact, variation in macrophyte cover was a major determinant of the monthly variation in coot numbers, as was carp presence (Table 3). Many carp died during the unusually low water levels in summer 2006 (Fig. 5), and the reduction in carp density allowed a recovery of macrophyte cover in 2007 before the rotenone treatment (Fig 2). Changes in abundance of the diving ducks *O. leucocephala*, *A. ferina* and the red-crested pochard *Netta rufina* were mostly related to carp presence, although macrophytes and depth had significant positive effects on *A. ferina* (Tables 2, 3). The numbers of breeding pairs per year of coots ($W=45$; $P=0.003$) and *O. leucocephala* ($W=36$; $P=0.02$) were also markedly reduced after carp invasion in Medina lake, although the reduction was not significant for *A. ferina* ($P > 0.05$).

Although carp presence had no significant effect on the overall abundance and species richness of dabbling ducks, there was a marked decline in gadwall (*A. strepera*) numbers during *C. carpio* invasion (Tables 2 and S1). The presence of carp increased the abundance and richness of piscivorous birds, although the effects were not consistent between species and were only significant at the species level for the small population of grey herons (*Ardea cinerea*) (Tables 1 and 2). A significant negative effect of *C. carpio* on abundance was also observed for the small grebes *T. ruficollis* and *P. nigricollis*, and the greater flamingo (Fig 6). Water depth was influential, and at shallower depths there were increases in abundance of flamingos, herons and stilts as well as decreases in gadwall, grebes and western swamphens (Table 2). However, the partial effect of carp on the abundance of coots, *O. leucocephala*, *A.*

ferina and six other species was highly significant when controlling for variation in water level (Tables 1, 2 and 3).

Of 22 key sites for *O. leucocephala* in the Iberian Peninsula identified in 1996, at least 14 (64 %) have since been affected by *C. carpio* invasion (Table S2).

4. Discussion

We have shown a consistent, drastic impact of invasion by common carp (*Cyprinus carpio*) on waterbirds in two of the many wetlands recently affected by such invasions in Spain and elsewhere in the Mediterranean region. Particularly striking are the impacts on submerged macrophytes, coots and diving ducks, which crash after carp invasion, affecting threatened species such as the white-headed duck (*Oxyura leucocephala*), common pochard (*Aythya ferina*) and the crested coot (*Fulica cristata*). Similar impacts occurred over two invasion periods in Medina lake, and one in Zoñar lake, supporting the notion that the effects of carp on ecosystems are predictable (Weber and Brown, 2009; Vilizzi et al., 2015).

Unlike two previous studies of carp impact on waterbirds at the whole lake level (Haas et al., 2007; Bajer et al., 2009), ours involved two whole-lake experiments with an initial carp introduction, an eradication and finally a second introduction in Medina lake, and an eradication in Zoñar lake. The observed effects cannot be explained on the basis of some confounding variable simultaneously influencing the population size of waterbirds, as might be suspected if there was one single ‘before-after’ experiment. Our results are consistent with previous data showing the ecological impact of carp invasion, mostly collected in ponds and experimental enclosures (e.g. Crivelli, 1983; Lammens and Hoogenboezem, 1991; Zambrano et al., 1999; Parkos et al., 2003). Little previous information was available from Mediterranean shallow lakes (Torres-Esquivias et al., 2009; Laguna et al., 2016), where low water depth and high winter temperatures probably intensify the impact of carp (Meerhoff et al., 2007; Weber et al. 2015).

Our results demonstrate that carp invasion has negative effects on a range of waterbirds including flamingos and grebes, although coots and diving ducks are particularly badly affected. Given the widespread and ongoing invasion of carp in Spanish wetlands (Table S2), the decrease in waterbird abundance is of major conservation concern, particularly for the globally threatened *A. ferina* and *O. leucocephala* as well as the regionally threatened *F. cristata*. White-headed ducks almost disappeared during carp invasion in Zoñar and Medina lakes which, when carp are absent, can harbour up to one third (800) of the estimated biogeographical population (1,600-2,500) of this diving duck in Western Europe

(Muñoz-Fuentes et al., 2013). Habitat loss is one of the major threats to this species, in addition to others such as hunting, lead poisoning, and hybridisation with the North American Ruddy duck (*Oxyura jamaicensis*) (Green et al., 1996; Taggart et al., 2009; Muñoz-Fuentes et al., 2013). Thus, the loss of an important habitat for waterbirds through carp invasion can have major ramifications at the population level, especially in semi-arid regions such as southern Spain where many lakes were drained in the 20th century (Perennou et al., 2012). The situation is expected to worsen due to climate change (Moss et al., 2009), and because an increasing number of lakes used by *A. ferina*, *F. cristata* and *O. leucocephala* in Spain are being degraded through eutrophication and fish introductions (Fox et al. 2016, Table S2). The size of the *O. leucocephala* population in Spain now appears to be limited by the availability of suitable habitat (Almaraz et al., 2004; Sebastián-González et al., 2013), so the loss of suitable habitat by carp invasion is likely to cause an important reduction in population size. Indeed, numbers counted in Spain in recent years have been well below the historical maximum count of 4489 made in 2000 (Torres Esquivias 2009). This decline is thought to be partly due to the recent abundance of carp in El Hondo wetlands in Alicante, which formerly held most of the Spanish *O. leucocephala* population (JA. Gómez and M. Ferrández pers. comm. April 2017).

The severe impacts of carp invasion on the macrophyte cover and abundance of coots, globally threatened diving ducks and other waterbirds are likely to be explained by several mechanisms that are not mutually exclusive. As a result of its feeding activity, carp reduces macroinvertebrate abundance and macrophyte cover through feeding, uprooting and increasing turbidity (Crivelli, 1983; Kloskowski et al., 2011; Shin-ichiro et al., 2009; Florian et al., 2016). The loss of macrophytes is likely to cause the observed negative effect on coots, which are herbivorous (Brinkhof, 1997, Varo et al., 2008). We found evidence that removal of macrophytes also affects *A. ferina*, which is omnivorous (Kear et al., 2005). However, the major impact on diving ducks is likely to have been through competition for benthic invertebrates (particularly chironomidae larvae) upon which both carp (García-Berthou, 2001) and diving ducks feed (Winfield and Winfield, 1994, Sánchez et al., 2000). Our results agree with Laguna et al. (2016) who reported a concomitant decrease in the abundance of macrophytes and the diving duck *N. rufina* in enclosures with carp in a Mediterranean wetland. Finally, the reductions in waterbird abundance may have been partly caused by the increased turbidity that impedes visual foraging of diving ducks and grebes (Winfield and Winfield, 1994; Carbone et al., 1996).

Among the dabbling ducks, such alterations in the aquatic environment are most likely to affect gadwalls (*A. strepera*) which feed in submerged vegetation close to the water surface (McKnight, 1998; Kear et al., 2005), explaining why we found negative effects of carp and increasing depth on this species. We did not find significant changes in the abundance of mallards (*A. platyrhynchos*) which often exploit terrestrial habitats (Soons et al., 2016), or of the largely zooplanktivorous shoveler (*A. clypeata*) (Guillemain et al., 2000), even though the zooplankton community in Medina lake radically changed after carp invasion (Florian et al., 2016). *A. clypeata* may be able to exploit the smaller copepods that dominate zooplankton in the presence of carp (Matsubara et al., 1994, Florian et al., 2016). The observed decrease in the abundance of other invertivores such as the greater flamingo (*Phoenicopterus ruber*) and the black-necked grebe (*Podiceps nigricollis*) is not surprising because they are dependent on larger invertebrates such as chironomid larvae and other insects (Varo et al., 2011, Rodríguez-Pérez and Green, 2012). The negative impact of carp on macroinvertebrates has been demonstrated in Zoñar lake (Ferrerías-Romero et al., 2016).

Although breeding numbers of waterbirds were reduced by carp, as reported elsewhere in Europe (Musil, 2006), our study particularly shows the impacts of carp in the post-breeding and wintering periods when bird numbers are highest and when carp remain active because of the high temperatures in southern Spain. Some comparisons of impacts on birds can be made with previous studies, but are hindered by the lack of data elsewhere on diving ducks. The reduction in total abundance of diving and dabbling ducks combined was only slightly higher in Medina lake (2.25 fold) than values (1.84-2.10) reported in a USA temperate lake at similar carp densities to Medina lake (112 vs 110 kg/ha) from September to December by Bajer et al. (2009). The decrease in the total combined abundance of particular species common to our study and a previous one (*Fulica atra*, *Anas clypeata*, *A. querquedula*, *A. crecca*, and *Gallinula chloropus* summed together) was lower in ours (4.47) than the range (5-15) reported in temperate experimental lakes in Germany at 100-120 carp/ha from May to September (see the omnivory guild in Haas et al., 2007). However, our results suggest that of this group of 5 species only coots seem particularly sensitive to carp. Furthermore, the impacts of carp we observed on ducks in the winter period have not been reported from temperate regions, where carp would be much less active. In addition, our figures include periods relatively soon after carp invasion when the abundance of larger carp having most impact (Kloskowski, 2011) was probably still low. The census data suggest that more than two years after carp enter the lake, the reduction in waterbird numbers at Medina Lake is considerably stronger than our analyses suggest. Unfortunately, our study is not sufficient to

provide a safety threshold of carp abundance. The rotenone treatment allowed us to demonstrate ecological impact with a carp biomass of 112 and 325 kg/ha, a range consistent with Bajer et al. (2009) who suggested that 100 kg carp/ha may already cause a dramatic decline in macrophyte and waterbird abundance. Nonetheless, regional differences in water temperature and other traits such as the size structure of carp populations also influence their ecological impact (Goolish and Adelman, 1984; Kloskowski, 2011; Weber et al., 2015).

Rotenone application reversed the severe impacts of carp on macrophytes and waterbirds in Medina and Zoñar lakes. Despite its efficacy, rotenone is now banned in Spain due to its strong side effects on other taxa (Chandler and Marking, 1982; Rayner and Creese, 2006). Repeated seining and physical barriers can be alternative, more environmentally safe methods for carp control (Stuart et al., 2006; Bajer et al., 2011), and further research is required to develop effective methods that can be applied to Mediterranean lakes. Our study demonstrates the negative effects of carp on globally threatened bird species, and it is very important to take measures preventing the spread of carp into those natural and artificial wetlands that currently remain free of this invasive species. The ongoing expansion of alien cyprinids in the Mediterranean region, including *C. carpio* (Vilizzi, 2012; Maceda-Veiga et al., 2017) and the *Carassius* species complex (Wouters et al., 2012; Ribeiro et al., 2015), can be expected to have a major negative impact on the conservation of waterbirds and other aquatic fauna. Owing to interests for sport fishing and human consumption in some parts of Europe, there are attempts to exclude *C. carpio* from regional lists of invasive species in Europe (e.g. it is excluded from the Spanish decree RD 630/2013 implementing measures against invasive species). Studies like ours are necessary to improve our ability to predict and manage impacts caused by alien fish stocks.

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Figure 1

Figure 2

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Figure 6

Table 1 Results of GLM models on the effects of the alien carp *Cyprinus carpio*, month and water depth on the abundance and richness of all waterbird species and four dominant guilds (herbivorous coots, diving and dabbling ducks, and piscivores) in Medina lake. Explained deviance is shown as a measure of goodness of fit (R^2) of the models. Regression estimates for carp and depth effects indicate the magnitude and direction of the partial effects of *C. carpio* and water depth fluctuations on bird values in models including month as a predictor. Bold values indicate significance at $P \leq 0.05$.

	<i>C. carpio</i>		Estimates $\pm$ S.E. for carp effect	Month		Water depth		Estimates $\pm$ S.E. for depth effect	R^2
	Test, df	P value		Test, df	P value	Test, df	P value		
All bird species									
Abundance	$F_{1,91}=15.33$	<0.001	-0.24 ± 0.06	$F_{11,91}=0.58$	0.84	$F_{1,91}=0.01$	0.92	-0.01 ± 0.09	11.95%
Richness	$F_{1,91}=1.76$	0.19	-0.08 ± 0.06	$F_{11,91}=0.59$	0.84	$F_{1,91}=0.28$	0.59	-0.05 ± 0.09	4.89%
Herbivorous coots	$F_{1,91}=38.70$	<0.001	-0.56 ± 0.09	$F_{11,91}=0.91$	0.53	$F_{1,91}=1.75$	0.19	0.20 ± 0.15	22.74%
Diving ducks									
Abundance	$F_{1,91}=55.17$	<0.001	-0.73 ± 0.09	$F_{11,91}=1.02$	0.44	$F_{1,91}=0.08$	0.78	0.05 ± 0.16	33.26%
Richness	$F_{1,91}=25.48$	<0.001	-0.48 ± 0.09	$F_{11,91}=0.79$	0.64	$F_{1,91}=0.35$	0.56	0.09 ± 0.16	22.32%
Dabbling ducks									
Abundance	$F_{1,91}=0.08$	0.78	-0.02 ± 0.08	$F_{11,91}=1.35$	0.21	$F_{1,91}=0.07$	0.79	-0.03 ± 0.12	10.93%
Richness	$F_{1,91}=0.49$	0.78	-0.05 ± 0.07	$F_{11,91}=3.43$	<0.001	$F_{1,91}=2.14$	0.14	0.16 ± 0.11	21.21%
Piscivores									
Abundance	$F_{1,91}=20.79$	<0.001	0.13 ± 0.09	$F_{11,91}=12.23$	<0.001	$F_{1,91}=0.35$	0.56	0.26 ± 0.14	68.37%
Richness	$F_{1,91}=0.18$	0.67	0.06 ± 0.15	$F_{11,91}=3.72$	<0.001	$F_{1,91}=0.31$	0.58	-0.13 ± 0.23	25.33%

Table 2 Results of GLM models on the effects of the alien carp *Cyprinus carpio*, depth and month on the abundance of the most frequently recorded waterbird species in Medina lake (2001-2013). Explained deviance is shown as a measure of goodness of fit (R^2) of the models. Regression estimates for carp and depth effects indicate the magnitude and direction of the partial effect of *C. carpio* and water depth fluctuations on bird numbers in models including month as predictor. Bold values indicate significance at $P \leq 0.05$.

	<i>C. carpio</i>		Estimates $\pm$ S.E. for carp effect	Month		Water depth		Estimates $\pm$ S.E. for depth effect	R^2
	Test, df	P value		Test, df	P value	Test, df	P value		
Herbivorous coots									
<i>Fulica</i> spp.	F _{1,91} =38.70	<0.001	-0.56 $\pm$ 0.09	F _{11,91} =0.91	0.53	F _{1,91} =1.75	0.19	0.20 $\pm$ 0.15	22.74%
Diving ducks									
<i>O. leucocephala</i>	F _{1,91} =77.64	<0.001	-1.59 $\pm$ 0.19	F _{11,91} =0.68	0.75	F _{1,91} =0.73	0.39	-0.25 $\pm$ 0.29	48.81%
<i>N. rufina</i>	F _{1,91} =31.99	<0.001	-0.99 $\pm$ 0.17	F _{11,91} =0.72	0.72	F _{1,91} =1.72	0.19	0.41 $\pm$ 0.32	28.60%
<i>A. ferina</i>	F _{1,91} =43.25	<0.001	-0.86 $\pm$ 0.13	F _{11,91} =1.22	0.29	F _{1,91} =3.14	0.08	0.39 $\pm$ 0.22	30.85%
Dabbling ducks									
<i>A. strepera</i>	F _{1,91} =22.57	<0.001	-0.66 $\pm$ 0.13	F _{11,91} =0.64	0.79	F _{1,91} =9.37	0.003	0.74 $\pm$ 0.25	21.34%
<i>A. platyrhynchos</i>	F _{1,91} =0.05	0.83	0.02 $\pm$ 0.09	F _{11,91} =1.29	0.24	F _{1,91} =1.50	0.22	-0.16 $\pm$ 0.13	12.44%
<i>A. clypeata</i>	F _{1,91} =2.74	0.10	-0.24 $\pm$ 0.14	F _{11,91} =13.47	<0.001	F _{1,91} =1.34	0.25	0.25 $\pm$ 0.22	60.76%
Piscivores									
<i>P. cristatus</i>	F _{1,91} =1.96	0.164	0.14 $\pm$ 0.10	F _{11,91} =3.91	<0.001	F _{1,91} =13.98	<0.001	0.58 $\pm$ 0.16	32.77%
<i>A. cinerea</i>	F _{1,91} =17.65	<0.001	20.83 $\pm$ 5356.01	F _{11,91} =3.72	<0.001	F _{1,91} =68.38	<0.001	-0.64 $\pm$ 0.10	86.10%
<i>E. garzetta</i>	F _{1,91} =3.26	0.07	0.38 $\pm$ 0.23	F _{11,91} =3.73	<0.001	F _{1,91} =6.68	0.011	0.71 $\pm$ 0.31	29.47%
Other abundant birds									
<i>P. ruber</i>	F _{1,91} =26.12	<0.001	-1.47 $\pm$ 0.30	F _{11,91} =2.39	0.01	F _{1,91} =20.94	<0.001	-1.82 $\pm$ 0.40	52.49%
<i>L. michahellis</i>	F _{1,91} =1.69	0.18	0.25 $\pm$ 0.20	F _{11,91} =3.12	0.001	F _{1,91} =0.28	0.60	-0.15 $\pm$ 0.28	24.88%
<i>T. ruficollis</i>	F _{1,91} =53.94	<0.001	-1.06 $\pm$ 0.15	F _{11,91} =2.05	0.03	F _{1,91} =13.48	<0.001	0.93 $\pm$ 0.26	37.53%
<i>G. chloropus</i>	F _{1,91} =0.67	0.42	0.13 $\pm$ 0.16	F _{11,91} =1.41	0.18	F _{1,91} =2.87	0.09	3.03 $\pm$ 0.83	18.50%
<i>P. nigricollis</i>	F _{1,91} =41.19	<0.001	-0.93 $\pm$ 0.14	F _{11,91} =0.70	0.72	F _{1,91} =5.88	0.02	0.63 $\pm$ 0.26	30.17%
<i>P. porphyrio</i>	F _{1,91} =0.95	0.33	-0.34 $\pm$ 0.34	F _{11,91} =1.53	0.14	F _{1,91} =18.45	<0.001	3.03 $\pm$ 0.83	29.30%
<i>H. himantopus</i>	F _{1,91} =0.12	0.73	-0.09 $\pm$ 0.26	F _{11,91} =1.15	0.34	F _{1,91} =28.46	<0.001	-1.95 $\pm$ 0.37	30.29%

Table 3 Results of GLM models on the effects of the alien carp *Cyprinus carpio*, month and water depth on mean macrophyte cover, and for the effects of these four predictors on the abundance of coots (*Fulica* spp.) and the two threatened diving ducks (*Oxyura leucocephala* and *Aythya ferina*). Explained deviance is shown as a measure of goodness of fit (R^2) of the models. Regression estimates for the carp effect indicate the magnitude and direction of the partial effect of *C. carpio* on macrophytes and bird numbers in models including all the predictors stated in the table. Bold values indicate significance at $P \leq 0.05$.

Dependent variable	Predictors	test, df	P value	Estimates $\pm$ S.E. for the carp effect	R^2
Macrophyte cover	<i>C. carpio</i>	$F_{1,66}=15.68$	<0.001	-1.35 ± 0.34	37.90%
	Month	$F_{11,66}=2.51$	0.011		
	Water depth	$F_{1,66}=1.01$	0.32		
<i>Fulica</i> spp.	<i>C. carpio</i>	$F_{1,65}=18.96$	<0.001	-0.49 ± 0.11	39.13%
	Macrophyte cover	$F_{1,65}=8.19$	0.005		
	Month	$F_{11,65}=0.54$	0.87		
	Water depth	$F_{1,65}=1.92$	0.17		
<i>O. leucocephala</i>	<i>C. carpio</i>	$F_{1,65}=42.03$	<0.001	-0.49 ± 0.11	51.72%
	Macrophyte cover	$F_{1,65}=0.05$	0.81		
	Month	$F_{11,65}=0.88$	0.56		
	Water depth	$F_{1,65}=0.49$	0.48		
<i>A. ferina</i>	<i>C. carpio</i>	$F_{1,65}=26.35$	<0.001	-0.89 ± 0.17	43.99%
	Macrophyte cover	$F_{1,65}=5.36$	0.02		
	Month	$F_{11,65}=1.46$	0.17		
	Water depth	$F_{1,65}=5.78$	0.02		

Fig 1 Geographic location of Medina (Cadiz) and Zoñar (Córdoba) lakes (SW Spain)

Fig 2 Simultaneous variation in coot abundance (*Fulica* spp.) and submerged macrophyte cover, as quantified by satellite images, in Medina lake showing the effects of two periods (2004-2007 and 2011-2013) of common carp (*Cyprinus carpio*) invasion. 2003 is excluded because carp was introduced this year but the month of entry is unknown. The boxplot shows changes in coot abundance (*Fulica atra*) before (2001-2006) and after (2006-2009) carp eradication in Zoñar lake.

Fig 3 Monthly variation (mean $\pm$ S.E.) in the abundance of coots (*Fulica* spp.), the globally threatened white-headed duck (*Oxyura leucocephala*) and common pochard (*Aythya ferina*) in Medina lake during the study period (2001-2013).

Fig 4 Fluctuations in the abundance of the globally threatened white-headed duck (*Oxyura leucocephala*) and common pochard (*Aythya ferina*) in Medina lake showing the effects of two periods (2004-2007 and 2011-2013) of common carp (*Cyprinus carpio*) invasion. 2003 is excluded because carp was introduced this year but the month of entry is unknown. Boxplots show changes in the number of these two species before (2001-2006) and after (2006-2009) carp eradication in Zoñar lake.

Fig 5 Changes in water depth in Medina lake during the study period (2001-2013)

Fig 6 Variation in the abundance (mean $\pm$ S.E.) of *Netta rufina*, *Anas strepera*, *Tachybaptus ruficollis*, *Phoenicopterus ruber* and *Podiceps nigricollis* (from top left to bottom right) showing the effects of two periods (2004-2007 and 2011-2013) of common carp (*Cyprinus carpio*) invasion in Medina lake. 2003 is excluded because carp was introduced this year but the month of entry is unknown.

Table S1 Mean, minimum and maximum richness and abundance of total number of waterbirds, plus the abundance of frequently recorded species (≥ 25 % among monthly surveys) in Medina lake in the presence and absence of the alien carp *Cyprinus carpio* (data for 2001-2013, N = ? surveys). Effect size indicates the magnitude of change in waterbird numbers with and without carp (the higher mean bird abundance in each row divided by the lower mean abundance).

	Without <i>C. carpio</i>		With <i>C. carpio</i>		Effect size
	Mean	Range	Mean	Range	
All waterbirds					
Abundance	3296	0-19500	897	0-10255	-3.67
Richness	12	0-26	13	0-32	1.00
Coots					
<i>Fulica atra</i>	2468	0-12000	430	0-9400	-5.74
<i>F. cristata</i>	3	0-32	1	0-44	-3.00
Diving ducks					
Abundance	285	0-1703	36	0-589	-7.92
Richness	3	0-7	2	0-5	-1.50
<i>Aythya ferina</i>	114	0-1136	16	0-174	-7.13
<i>Oxyura leucocephala</i>	125	0-780	11	0-463	-11.36
<i>Netta rufina</i>	49	0-490	9	0-77	-5.44
Dabbling ducks					
Abundance	313	0-2961	230	0-1822	-1.36
Richness	2	0-7	2	0-6	1.00
<i>Anas clypeata</i>	199	0-2164	54	0-642	-3.69
<i>A. platyrhynchos</i>	131	0-958	149	0-1822	1.13
<i>A. strepera</i>	61	0-454	13	0-180	-4.69
Piscivores					
Abundance	28	0-313	65	0-718	2.32
Richness	1	0-5	2	0-6	2.00
<i>Podiceps cristatus</i>	20	0-130	37	0-206	1.85
<i>Ardea cinerea</i>	6	0-102	2	0-25	-3.00
<i>Egretta garzetta</i>	0	0-2	0	0-6	1.00
Other abundant birds					
<i>Phoenicopterus ruber</i>	63	0-961	3	0-99	-21.00
<i>Larus michahellis</i>	8	0-167	13	0-195	1.6
<i>Tachybaptus ruficollis</i>	103	0-690	7	0-75	-14.71
<i>Gallinula chloropus</i>	3	0-16	7	0-74	2.33
<i>Podiceps nigricollis</i>	56	0-268	10	0-121	-5.6
<i>Porphyrio porphyrio</i>	0	0-6	1	0-14	1.00
<i>Himantopus himantopus</i>	5	0-68	4	0-31	-1.25

Table S2. Key sites for *Oxyura leucocephala* identified in a European action plan for this globally threatened species (Green & Hughes, 1996), and details of carp invasion since their identification. Carp removal occurred through rotenone application (R) or through desiccation of the semi-permanent lagoon (D) in 2016 (a dry year). Sources are: AC, Antonio Camacho pers. comm., April 2017; CMAOT, Consejería de Medio Ambiente y Ordenación del Territorio, Junta de Andalucía; CAMCD, Conselleria de Agricultura, Medio Ambiente, Cambio Climático y Desarrollo Rural, Generalitat Valenciana; CFD, Carlos Fernández-Delgado pers. comm., April 2017.

Key Site	Province	Carp entered since 1996	Date of carp entry	Date of carp removal	Source
Embalse de El Hondo	Alicante	Yes			CAMCD
Albufera de Adra	Almería	Yes	2011		CMAOT
Cañada de la Norias	Almería	Yes	c.1996		CMAOT
Salinas de Cerrillos	Almería	No			CMAOT
Laguna de Medina	Cádiz	Yes	2011		CMAOT
Lagunas de Espera	Cádiz	No			CMAOT
Lagunas del Puerto de Santa María	Cádiz	Yes	Unknown		CMAOT
Laguna del Tarelo (Parque Natural de Doñana)	Cádiz (Doñana)	No			CMAOT
Laguna de Pedro Muñoz	Ciudad Real	No			AC
Embalse de Malpasillo	Córdoba	Yes	Unknown		CFD
Laguna Amarga	Córdoba	No			CMAOT
Laguna de Zoñar	Córdoba	Yes	1985	2006 R	CMAOT
Laguna del Rincón	Córdoba	No			CMAOT
Laguna del Acebuche (Parque Natural de Doñana)	Huelva (Doñana)	Possibly			CFD
Laguna Honda	Jaén	No			CMAOT
Veta la Palma	Sevilla (Doñana)	Yes	Unknown		Walton et al. 2015
Lebrija-Las Cabezas: Laguna del Taraje	Sevilla	Yes	Before 2006	2016 D	CMAOT
Lebrija-Las Cabezas: Cigarrera	Sevilla	Yes	Unknown	2016 D	CMAOT
Embalse de la Coronela	Sevilla	Yes	Unknown		CMAOT
Laguna de Arjona	Sevilla	Yes	Unknown		CMAOT
Laguna del Gosque	Sevilla	Yes	Unknown	2016 D	CMAOT
Dehesa de Monreal	Toledo	Yes	Unknown		AC