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Influence of a carp invasion on the zooplankton community in Laguna Medina, a Mediterranean shallow lake

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ABSTRACT

Influence of a carp invasion on the zooplankton community in Laguna Medina, a Mediterranean shallow lake

The common carp (*Cyprinus carpio*) is a highly invasive species and an ecological engineer. It has been repeatedly shown to increase nutrient concentrations and phytoplankton biomass while destroying submerged macrophytes, although there are few studies from the Mediterranean region. We studied its impact on the zooplankton community in Laguna de Medina lake, a shallow lake in Jerez de la Frontera, south-west Spain. Carp were removed with rotenone in 2007 but returned in 2010-2011. We compared zooplankton sampled monthly from 8 points from May to December in 2008 (without carp) and 2012 (with carp). Extensive macrophyte beds present in 2008 were absent in 2012. As expected, chlorophyll-*a* concentrations, turbidity, total suspended solids and total phosphorus were much higher in 2012. Zooplankton richness decreased from 21 taxa in 2008 to 8 taxa in 2012, accompanied by a decrease in Shannon-Wiener diversity, an increase in Evenness and a change in size distribution with loss of larger taxa. In 2008, the crustaceans were dominated by the macrocladocerans *Daphnia magna* and *Moina brachiata* and the large calanoid copepod *Arctodiaptomus salinus*. In 2012, these three taxa were completely absent and the zooplankton was dominated by the alien cyclopoid *Acanthocyclops americanus* and the rotifers *Brachionus plicatilis* and *Keratella quadrata*. Our results confirm the disappearance of macrocladocera reported by others in mesocosm experiments with carp, and suggest that alien carp facilitate the spread of the alien copepod *A. americanus*.

Key words: *Acanthocyclops*, biomanipulation, Cladocera, invasive species, Mediterranean shallow lake.

RESUMEN

Influencia de la invasión de carpa en la comunidad de zooplancton en la Laguna Medina, un lago somero Mediterráneo

*La carpa común (*Cyprinus carpio*) es una especie altamente invasora y actúa como un ingeniero ecológico en el ecosistema. Se ha demostrado en repetidas ocasiones que aumenta las concentraciones de nutrientes y biomasa del fitoplancton mientras destruye macrófitas sumergidas, aunque hay pocos estudios de la región mediterránea. En este estudio se investigó el impacto de la carpa sobre la comunidad de zooplancton en Laguna de Medina, un lago somero de Jerez de la Frontera, suroeste de España. Las carpas fueron retiradas con rotenona en 2007, pero regresaron en 2010-2011. Se comparó el zooplancton muestreado mensualmente en 8 puntos de mayo a diciembre de 2008 (sin presencia de carpas) y en 2012 (con carpas). Superficies extensivas de macrófitas presentes en 2008 no fueron observadas en 2012. Como era esperado, la concentración de clorofila, turbiedad, sólidos suspendidos totales y el fósforo total fueron mucho más altos en 2012. La riqueza de zooplancton disminuyó de 21 taxones en 2008 a 8 taxones en 2012, acompañado por una disminución en el índice de diversidad de Shannon-Wiener, un aumento en la uniformidad y un cambio en la distribución de tamaños con la pérdida de los taxones de mayor tamaño. En 2008, los crustáceos estaban dominados por los macrocladoceros* Daphnia magna *y* Moina brachiata *y el gran copépodo calanoide* Arctodiaptomus salinus. *En 2012, estos tres taxones estaban completamente ausentes y la* *comunidad estuvo dominada por los aciclopoides invasores* Acanthocyclops americanus *y los rotíferos* Brachionus plicatilis *y* Keratella quadrata. *Nuestros resultados confirman la desaparición de macrocladoceros reportados por otros autores en experimentos de mesocosmos con carpas, y sugieren que la carpa invasora facilita la propagación del copépodo invasor* A. americanus.

Palabras clave: *Acanthocyclops, biomanipulación, Cladocera, especies invasoras, lagos someros mediterráneos.*

INTRODUCTION

The common carp (*Cyprinus carpio*) is widely distributed as an alien species and is considered one of the world's worst invasive species (www.iucngisd.org) because it has a major impact on aquatic ecosystems. It has strong direct effects on the communities of aquatic invertebrates, fish and waterbirds through predation or competition (Weber & Brown, 2009). In addition, carp are ecosystem engineers causing bioturbation and high turbidity through their feeding behaviour (Bajer *et al*., 2009; Kloskowski, 2011). By increasing turbidity and direct consumption, carp reduce the cover of submerged vegetation and promote a shift from a clear- to turbid-state in shallow lakes and a resulting reduction in biodiversity (Bajer *et al*., 2009). Removal of carp in biomanipulations typically results in a recovery of macrophytes together with a drop in turbidity, nutrient concentrations and phytoplankton biomass (Bajer *et al*., 2015).

Carp are omnivorous, feeding largely on macrophytes and invertebrates, and up to 25% of the biomass ingested consists of zooplankton (Meijer *et al*., 1990; Khan, 2003; Britton *et al*., 2007). Carp can therefore affect the zooplankton community in many ways, by direct predation (Miller & Crowl, 2006), by consuming macroinvertebrates that themselves are zooplankton predators (Khan, 2003), through loss of macrophytes that provide shelter, and by increasing phytoplankton biomass and promoting cyanobacterial blooms (Parkos *et al*., 2003). Furthermore, resuspension of sediment particles can interfere with the filtering apparatus of cladocerans (Kirk & Gilbert, 1990), and bioturbation may also affect the dormant stages in sediments, with negative effects on emergence patterns (Angeler *et al*., 2002).

In the Mediterranean region, the effects of carp appear to be stronger than in temperate latitudes because relatively high temperatures all year round increase the levels of fish activity. However, little information is available on how carp affect zooplankton in Mediterranean shallow lakes. Although mesocosm or enclosure experiments have demonstrated a strong impact of carp on zooplankton in semi-arid and temperate lakes (Angeler *et al*., 2002; Williams & Moss, 2003), there is a need for whole lake studies to improve our understanding of their effects at the ecosystem scale.

The objective of the present work was to explore how zooplankton communities were changed by the reintroduction of carp into a Mediterranean shallow lake, and how this was related to changes in physico-chemical variables. Medina lake (120 ha) in southern Spain is a closed basin playa lake protected under the Ramsar Convention because of its importance for waterbirds, including the globally threatened white-headed duck *Oxyura leucocephala*. In 2003, carp entered the lake, leading to a crash in the numbers of waterbirds and a loss of submerged vegetation. In September 2007, carp were eradicated by the regional government using rotenone, with the objective of restoring values for waterbirds. This was initially successful, but carp re-entered the lake in 2010-2011 during extreme winter floods, causing a return to a state with no submerged vegetation and few birds. We studied the consequences for zooplankton and physico-chemical variables by intensive monitoring during two contrasting years: 2008 (without carp) and 2012 (with carp). We consider how the structure of the zooplankton community changed, how the diversity and species richness was affected, and how these changes were related to macrophyte cover, phytoplankton abundance and physico-chemical variables.

MATERIAL AND METHODS

Study site

Lake Medina (Fig. 1) is the third largest inland playa lake in Andalusia (de Vicente *et al*., 2012), located 30 m above sea level (36°37′18″N, 6°02′48″W). The average depth is 1 m and when the maximum depth reaches 3.5 m depth an artificial overflow prevents further filling (Rodríguez-Rodríguez *et al*., 2011). The lake is semi-permanent and mesohaline with basic pH and high alkalinity (de Vicente *et al*., 2012), and was very important for waterbirds when carp were absent, i.e. before 2003 and from 2007 to 2010 (Amat, 1984; Martí & del Moral, 2002; Martínez-Haro *et al*., 2011). The lake is polluted by spent lead shot that accumulated in the sediment prior to protection in 1987 (Mateo *et al*., 2007) and is surrounded by agricultural land that influences hydrology and nutrient loading (Rodríguez-Rodríguez, 2011). Although carp were totally eliminated from the lake in September 2007 (13 416 kg of carp were removed), the alien eastern mosquito fish *Gambusia holbrooki* was not, and was abundant in the littoral zone of the lake during our "without carp" study year.

Sampling Methods

Sampling was carried out at eight different fixed sampling points around the lake (Fig. 1) on a monthly basis (except for the month of June) for the following periods: from January 2008 until December 2008 (without carp) and from May 2012 till December 2012 (with carp). Each point was positioned several metres away from the shoreline, marked with an iron stake, and positioned with a GPS. Sampling was conducted between the hours of 08:00 h and 13:00 h.

The following environmental variables were taken *in situ* with a portable WTW 340I/SET: temperature (°C), pH, conductivity (µS/cm) and dissolved oxygen (mg/l or %). Several water samples were collected for laboratory analyses, as follows. Turbidity was measured with a Hanna instruments HI93703 meter and is expressed as NTU (Nephelometric Turbidity Units). Chloro-

Figure 1. Geographic location of Medina lake (Cádiz. Spain). Circles indicate the eight sampling points. *Localización geográfica de la laguna de Medina (Cádiz. España). Los círculos indican los ocho puntos de muestreo*.

phyll-*a* was extracted with 90% acetone after filtering a known volume of lake water through a GF/F Whatman filter, and measured by spectophotometry using the trichromatic method (Jeffrey & Humphrey, 1975). Total nitrogen concentration (Total N) was measured by digestion with potassium persulfate (Sims *et al*., 1995), and total phosphorus concentration (Total P) by the phosphomolybdate method (APHA, 1995). Total suspended solids (TSS) were determined following APHA (1995) by filtering a well-mixed water sample through a pre-weighed standard glass-fiber filter, then reweighing after drying to a constant weight at 105 °C. Dissolved nutrient concentrations (nitrates, nitrites, ammonium and phosphate) were measured in the filtrate after

Table 1. Summary of environmental variables in Medina lake in 2008 (without carp) and 2012 (with carp). Differences between years (from May to December) were tested with Wilcoxon matched-paired tests. N1: number of valid data, N2: number of matched pairs of data from the same point and same month, *z*: z-score is the normally distributed test value of Wilcoxon's rank test. *Resumen de las variables ambientales en la laguna de Medina entre 2008 (sin carpas) y 2012 (con carpas). Las diferencias entre años (de mayo a diciembre) fueron evaluadas con un test de Wilcoxon para datos emparejados-pareados. N1: número de datos válidos, N2: número de parejas de datos para el mismo punto y el mismo mes,* z*: z es el valor de la prueba de distribución de normalidad en la prueba de rangos de Wilcoxon.*

Variable	Unit	Year	N1	Mean	Standard deviation	N2	*z*	*p*
pH		2008	56	8.489	0.57	56	0.477	0.63323
		2012	56	8.489	0.29			
Temperature	°C	2008	56	20.09	6.36	56	3.632	< 0.001
		2012	56	21.36	4.60			
Conductivity	mS/cm	2008	56	10.78	1.35	55	6.451	< 0.0001
		2012	55	6.51	0.78			
Salinity	g/L	2008	56	6.11	0.86	56	6.509	< 0.0001
		2012	56	3.53	0.49			
Dissolved oxygen	mg/L	2008	55	8.19	1.79	47	3.862	< 0.001
		2012	48	9.37	2.80			
Depth	cm	2008	56	62.98	22.72	56	5.477	< 0.0001
		2012	56	85.40	35.12			
Turbidity	NTU	2008	56	22.56	16.43	56	4.478	< 0.0001
		2012	56	35.07	21.86			
Chlorophyll-*a*	µg/L	2008	55	7.86	5.95	55	6.451	< 0.0001
		2012	56	100.97	65.88			
Total N	mg/L	2008	49	3.06	0.68	49	5.005	< 0.0001
		2012	56	2.46	0.65			
Nitrite	mg/L	2008	33	0.09	0.09	33	4.372	< 0.0001
		2012	54	0.02	0.04			
Nitrate	mg/L	2008	32	1.11	1.88	32	4.493	< 0.0001
		2012	56	0.02	0.04			
Ammonium	mg/L	2008	33	0.44	0.38	33	4.985	< 0.0001
		2012	56	0.01	0.02			
Total P	mg/L	2008	53	0.12	0.06	53	4.919	< 0.0001
		2012	56	0.19	0.07			
Phosphate	mg/L	2008	32	0.03	0.06	29	2.043	< 0.05
		2012	56	0.03	0.06			
Total suspended solids	mg/L	2008	56	48.01	27.53	56	3.789	< 0.001
		2012	56	120.31	235.28			

lake water was passed through a standard glass-filter, using a SEAL Analytical AutoAnalyzer 3HR and a SYSTEA Micromac-1000. Usually this filtrate was frozen at −20 °C for some weeks prior to analysis.

Zooplankton were sampled using an acrylic tube sampler as used by Louette & De Meester (2005) with a diameter of 8 cm and a length of 136 cm, which allowed sampling of the entire water column. The tube was inserted vertically to a depth of 70 cm if the depth was sufficient at the fixed sampling point, or less if it was not. Samples were filtered *in situ* through a 64 μm-mesh Nytex screen and preserved in an iodine solution (Lugol).

All zooplankton individuals (including rotifers, copepods, cladocerans and ostracods) were counted and identified to species where possible. For counting, we used an inverted microscope at magnifications 10× and 20×, and for detailed identification we used a light microscope at magnifications from 40x to 100x. Taxa were identified using standard keys, including Dussart (1967, 1969), Flössner (2000), Einsele (1993), Gulyás & Forró (1999, 2001) and Koste (1978). Mean length of each taxon was extracted from the literature. Juvenile stages of cladocerans and copepods could not be identified to species level. Samples with more than 1000 individuals were counted by subsampling. For cladocerans, copepods and ostracods we counted at least the 1/3 of the sample, and for the smaller rotifers we counted at least 1/20th of the sample.

Remote sensing

To assess submerged macrophyte vegetation cover at the water surface, we used Landsat L5TM data between 2008 and 2013. Satellite images were taken by the TM and ETM+ sensors on board the Landsat 5 and Landsat 7 satellites, obtained from the United States Geological Survey. We applied the Normalised Difference Vegetation Index (NDVI, Mather, 1987), which estimates the fraction of active photosynthetic radiation that is intercepted by vegetation (Alcaráz-Segura *et al.*, 2009 and is based on the reflectance in the red (R) and near infrared (NIR) bands (bands 3 and 4, respectively, for Landsat images). Using ENVI 4.4 software, one mask was constructed for the total lake surface and a second mask for the vegetation cover. 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).

Data analysis

Statistical analyses were performed with Past and STATISTICA (version 11; StatSoft, Tulsa, OK) software. Because many variables were not normally distributed, to compare the differences in environmental variables and in the abundance of taxa between the two years, we used non-parametric Wilcoxon matched-paired tests, pairing samples from the same points and months between years (e.g. pairing the sample from point 1 in May 2008 with that from point 1 in May 2012).

We quantified α-diversities for each sample using the Shannon-Wiener index (H'), which takes into account the total number of taxa and their evenness (Magurran, 1988), and is relatively insensitive to the presence of rare species (Anderson, 1978). The Evenness index (J) was used to measure the relative distribution of individual taxa (Krebs, 1989). When calculating the diversity measures, the copepod nauplii were assigned proportionally to the copepod species present in the sample.

For further analysis of relationships between the zooplankton community and environmental variables, we conducted a canonical correspondence analysis (CCA) to examine community composition patterns in the two years, and their relationship with nine environmental variables. The physical parameters (temperature, water depth, turbidity) and chemical data (conductivity, Total P, Total N, dissolved oxygen, chlorophyll-*a* and TSS) formed one data matrix, and the second one included the abundance of zooplankton taxonomic groups. pH was excluded because there was no significant difference in this parameter between the two years (see below). All variables were $\log(x + 1)$ transformed. Permutation tests ($n = 999$) identified the significance of the CCA axes.

RESULTS

Changes in environmental variables

With the exception of pH, all variables differed significantly between 2008 without carp and 2012 with carp (Table 1). The water level in the lake was generally higher in 2012, leading to an increased depth and decreased salinity and conductivity. Temperature, dissolved oxygen, chlorophyll-*a*, Total P, turbidity and total suspended solids (TSS) were all higher in 2012, the increases in chlorophyll-*a* and turbidity being particularly consistent (Table 1, Fig. 2). In contrast, Total N, nitrite, nitrate, phosphate and ammonium concentrations were all significantly lower in 2012 (Table 1). The temperature range recorded for the whole study was from 11.3 °C to 30.1°C.

Changes in zooplankton taxonomic composition

In Medina lake we found 21 zooplankton taxa in 2008 (without carp), but only 8 taxa were found in 2012 (with carp, Table 2). When considering

Table 2. Abundance of zooplankton taxa in 2008 (without carp) and 2012 (with carp). Differences between years were tested with Wilcoxon matched-paired tests, with N pairs of data from the same point and same month (May to December). *P* values are given in italics for the only two taxa for which the difference between years was not statistically significant. Two additional Copepoda were recorded in January-April 2008 (*Diacyclops bisetosus* and *Paracyclops fimbriatus*, one individual of each). *Abundancia de los diferentes taxones de zooplancton en 2008 (sin carpas) y 2012 (con carpas). Las diferencias entre años fueron evaluadas con un test de Wilcoxon para datos emparejados-pareados, con N pares de datos para el mismo punto y en el mismo mes (mayo a diciembre). Los valores* P *son presentados en letras cursivas para los dos únicos taxones para los cuales la diferencia entre años no fue estadísticamente significativa. Dos copépodos adicionales fueron registrados en abril-enero de 2008 (*Diacyclops bisetosus *y* Paracyclops fimbriatus, *un individuo de cada uno).*

	2008				2012						
	sum	median	min	max	sum	median	min	max	N	*z*	*p*
CLADOCERA											
Alona rectangula	146	0	0	39	12	0	0	6	51	3.753	< 0.001
Chydorus pizarri	0	0	0	0	1	0	0	1	—	—	—
Daphnia magna	4065	6	0	704	0	0	0	0	51	4.703	< 0.0001
Diaphanosoma brachyura	353	0	0	215	0	0	0	0	51	3.296	< 0.001
Dunhevedia crassa	120	0	0	56	0	0	0	0	51	3.724	< 0.001
Moina brachiata	2020	0	0	513	0	0	0	0	51	2.803	0.0051
Oxyurella tenicaudis	0	0	0	0	58	0	0	44	51	1.826	*0.0679*
COPEPODA											
Acanthocyclops americanus	33	0	0	12	77328	700	18	10260	51	6.215	< 0.0001
Arctodiaptomus salinus	43698	640	4	3542	0	0	0	0	51	6.215	< 0.0001
Cyclops strenuus	5	0	0	2	0	0	0	0	—	—	—
Megacyclops viridis	36	0	0	10	0	0	0	0	51	3.296	< 0.001
nauplii	34106	252	0	4558	20010	351	11	1944	51	*0.455*	*0.6494*
ROTIFERA											
Asplachna quadridentatus	47	0	0	10	0	0	0	0	51	2.934	< 0.05
Brachionus novae-zelandie	4060	0	0	1894	0	0	0	0	51	4.107	< 0.0001
Brachionus plicatilis	23556	1	0	4104	325895	1766	0	93330	51	5.268	< 0.0001
Brachionus quadridentatus	211	0	0	86	0	0	0	0	51	2.934	< 0.005
Encentrum sp.	14	0	0	14	0	0	0	0	—	—	—
Hexarthra fennica	2494	0	0	708	1	0	0	1	51	2.801	0.0051
Keratella quadrata	305	0	0	305	1521155	0	0	304000	51	4.157	< 0.0001
Lecane lamellata	213	0	0	64	0	0	0	0	51	3.516	< 0.001
Testudinella patina	30	0	0	25	0	0	0	0	51	2.201	< 0.05
OSTRACODA	3734	17	0	714	117	0	0	74	51	5.536	< 0.0001

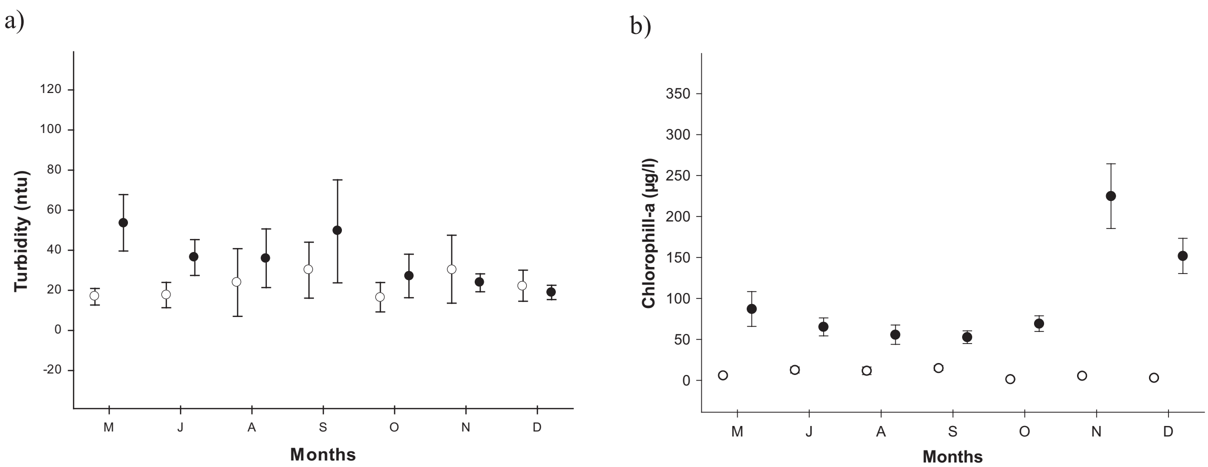

Figure 2. Mean and standard errors of a) turbidity (NTU) and b) chlorophyll-*a* (µg/L) in the months of 2008 and 2012. *Media y error estándar de a) turbidez (NTU) y b) clorofila-*a *(µg/L) en los meses de 2008 y 2012.*

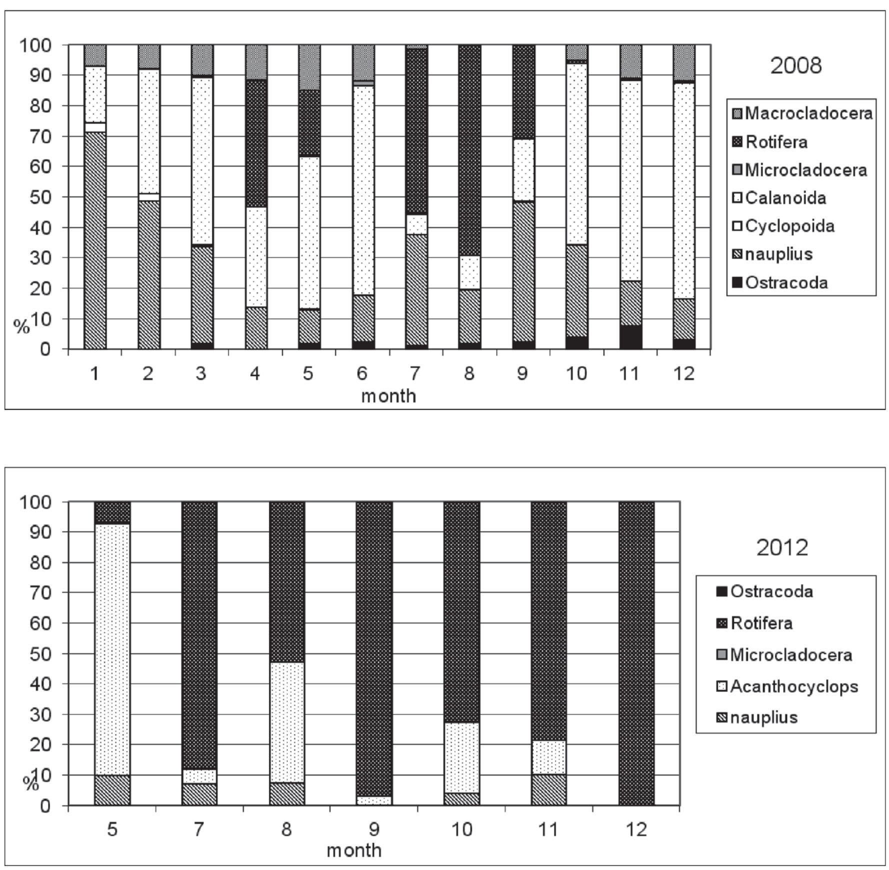

Figure 3. Change of relative abundance of the major zooplankton groups between months in 2008 (without carp) and 2012 (with carp). *Acanthocyclops americanus* was the only copepod recorded in 2012. *Cambio de la abundancia relativa de los principales grupos de zooplancton entre los meses de 2008 (sin carpas) y 2012 (con carpas).* Acanthocyclops americanus *fue el único copépodo registrado en 2012.*

Table 3. Comparison between 2008 (without carp) and 2012 (with carp) in the number of zooplankton taxa, total number of individuals, Shannon-Wiener diversity *H* and Evenness *J*. Differences between years were tested with Wilcoxon matched-paired tests, with paired data from the same point and same month (May to December). *Comparación entre 2008 (sin carpas) y 2012 (con carpas), entre los diferentes taxones de zooplancton, número total de individuos, diversidad de Shannon-Wiener y uniformidad.* H *= diversidad de Shannon-Wiener,* J *= uniformidad. Las diferencias entre años fueron evaluadas con un test de Wilcoxon para datos emparejados-pareados, con pares consistentes en los datos para el mismo punto y en el mismo mes (mayo a diciembre).*

Month	N Taxa 2008	N Taxa 2012	Abundance 2008	Abundance 2012	*H* 2008	*H* 2012	*J* 2008	*J* 2012
5	12	6	16 478	32 606	1.391	0.5854	0.3349	0.2993
7	19	7	18 555	49 535	1.426	0.4564	0.219	0.2255
8	15	5	9 121	26 676	1.346	0.9212	0.256	0.5025
9	12	6	35 542	187 171	1.187	0.1479	0.2731	0.1932
10	10	5	12 092	77 503	1.019	0.7027	0.2771	0.4038
11	14	6	18 716	62 927	1.068	1.194	0.2078	0.5498
12	12	9	8 767	1 548 544	0.909	0.09001	0.2068	0.1216
z	6.058		6.334		3.006		5.582	
p	< 0.0001		< 0.0001		0.002652		< 0.0001	

only months sampled in both years, 19 taxa were still recorded in 2008. Almost all taxa showed significant changes in abundance between years, but three of the remaining species increased markedly in abundance in 2012 (Table 2). In 2008, the crustaceans were dominated in abundance by calanoid copepods (*Arctodiaptomus salinus*) and macrocladocera (*Daphnia magna* and *Moina brachiata*) with a relatively high diversity of rotifers (Table 2, Fig. 3). In 2012, calanoid copepods and macrocladoceran species were absent, and the community was dominated by the cyclopoid copepod *Acanthocylops americanus* and the two rotifer species *Brachionus plicatilis* and *Keratella quadrata* (Table 2). The total abundance of rotifers was much higher in 2012 when carp were present (Table 2). With carp, the largest taxa disappeared and there was a loss of size diversity (Fig. 4).

Measures of diversity of the zooplankton communities differed significantly between the two years. Shannon-Wiener diversity was lower in 2012 in all months except November, whereas differences in Evenness changed between months in an inconsistent manner, being higher in 2012 in four of the seven months (Table 3). Overall, Shannon-Wiener diversity was significantly lower and Evenness was significantly higher in 2012.

CCA relating zooplankton with their environment

According to Canonical Correspondence Analysis (CCA), the two study years are well separated, with abundance values divided along the first and second axes (Fig. 5). The first two axes explain 77.9% of the total variation in the data set. After 1000 permutations, axis 1 accounted for 57.5% (eigenvalue: 0.5313, $p = 0.0001$), and axis 2 20.4% of variation (eigenvalue: 0.1876, $p = 0.001$) (Fig. 5.) Total N and conductivity were positively associated with zooplankton samples from 2008, whereas samples from 2012 were positively associated with dissolved oxygen, chlorophyll-*a*, turbidity, Total P and total suspended solids (Fig. 5).

Changes in vegetation

The loss of submerged vegetation in years with carp was obvious but confirmed by remote sensing using Landsat images (Fig. 6). In 2008, macrophytes (mainly *Potamogeton pectinatus*) filled the water column and were visible at the water surface from May to October inclusive, with a peak cover of 60%. In contrast, no macrophytes were recorded through 2012.

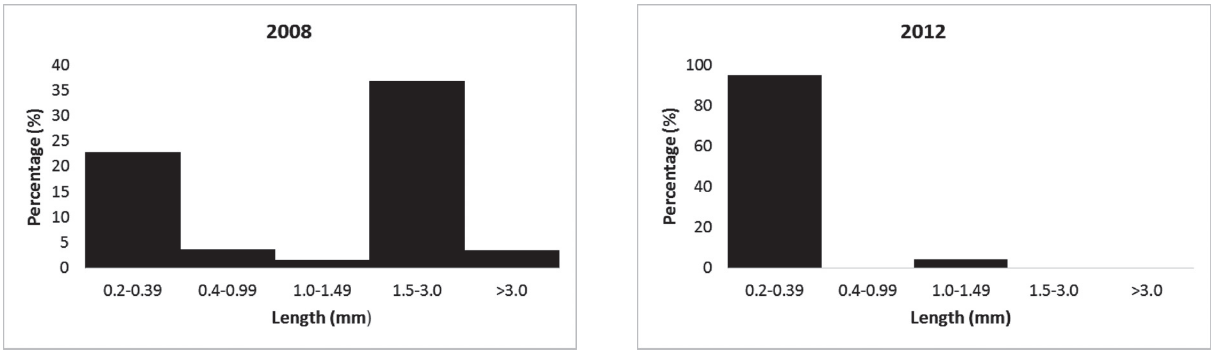

Figure 4. Change in size distribution of the zooplankton between 2008 (without carp) and 2012 (with carp). Based on mean length for each taxon as reported in the literature, and excluding Ostracoda and nauplii larvae. *Cambio en la distribución del tamaño del zooplancton entre 2008 (sin carpas) y 2012 (con carpas). Dependiendo de la longitud media de cada taxón como se informa en la literatura, y excluyendo ostrácodos y larvas nauplio.*

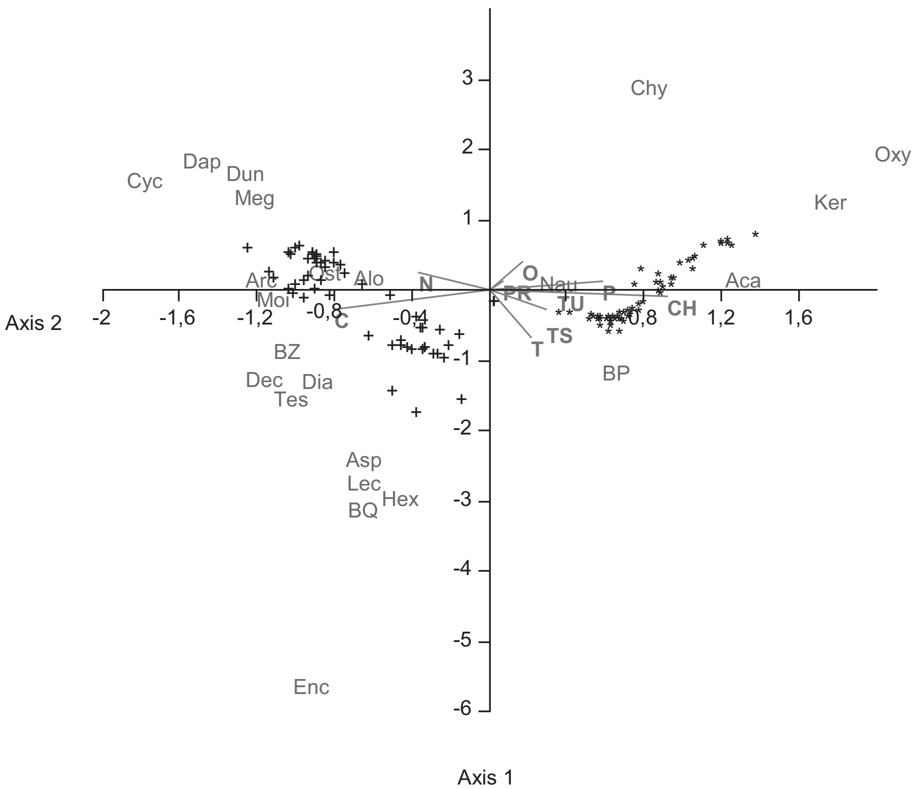

Figure 5. Canonical Correspondence Analysis (CCA) of zooplankton taxa and how they relate to the following environmental variables: T = temperature. C = Conductivity. O = dissolved oxygen. PR = Depth. TU = turbidity. TS = total suspended solids. CH = chlorophyll-*a*. N = total nitrogen. P = total phosphorus. * indicates samples from 2012 (carp) and + from 2008 (without carp). *Análisis de Correspondencia Canónica (CCA) de los taxones de zooplancton y cómo se relacionan con las siguientes variables de entorno: T = temperatura. Con = Conductividad. O = oxígeno disuelto. Prof. = profundidad. Tur = turbidez. TSS = sólidos suspendidos totales. Chlo = clorofila* a. *N = nitrógeno total. P = fósforo total. * Indica muestras de 2012 (con carpas) y + de 2008 (sin carpas). Taxa are as follows (Los taxones son los siguientes): Aca = Acanthocyclops americanus. Alo = Alona rectangula. Arc = Arctodiaptomus salinus. Asp = Asplachna quadridentatus. BP = Brachionus plicatilis. BQ = B. quadridentatus. BZ = B. novae-zelandie. Chy = Chydorus pizarri. Dap = Daphnia magna. Dec = Decapoda larvae. Dia = Diaphanosoma brachyura. Dun = Dunhevedia crassa. Enc = Encentrum sp. Hex = Hexarthra fennica. Ker = Keratella quadrata. Lec = Lecane lamellata. Meg = Megacyclops viridis. Moi = Moina brachiata. Nau = nauplius. Ost = Ostracoda. Oxy = Oxyurella tenicaudis. Tes = Testudinella patina.*

DISCUSSION

Ecological change to a shallow lake after introduction of carp

The presence of carp in Medina shallow lake has caused a marked increase in phytoplankton biomass (as measured by chlorophyll-*a* concentration), turbidity and Total P concentration, as well as the loss of submerged macrophytes. These changes represent a marked increase in trophic status (see also de Vicente *et al.*, 2012), and are consistent with repeated observations of the effects of introduced carp elsewhere in Spain (Angeler *et al.*, 2002; Rodrigo *et al.*, 2013) and across several continents (Weber & Brown, 2009; Kloskowski, 2011; Kulhanek *et al.*, 2011; Fischer *et al.*, 2013; Bajer *et al.*, 2015). Remote sensing has confirmed that these impacts in Medina Lake are consistent over two cycles, with the loss of submerged macrophytes and increase in turbidity in 2004-2007 (first period with carp) and from 2012 until now (second period with carp) (Fig. 6, see also Green *et al.*, 2014). Although these effects of carp are known to depend on their body size and abundance (Nieoczym & Kloskowski, 2014), unfortunately we have no quantitative data on the age structure and density of carp from Medina.

The increase in Total P we recorded is consistent with the resuspension of sediments in the water column which also contributed to the increased turbidity and TSS (Matsuzaki *et al.*, 2007; Fischer *et al.*, 2013). Phosphorous is bound to the resuspended material (Lougheed *et al.*, 1998; de Vicente *et al.*, 2012). Earlier studies report increased concentration of Total N after the introduction of carp (Angeler *et al.*, 2002; Fischer *et al.*, 2013). We found a reduction in Total N in 2012 with carp, but this is likely to be a direct consequence of the higher water level that year (i.e. a dilution effect caused by the higher levels of precipitation).

Following carp reintroduction, the macrophyte cover of the Lake Medina decreased dramatically (Fig. 6). Loss of macrophytes further enhances the resuspension of sediments owing to wind action, which is important in Medina

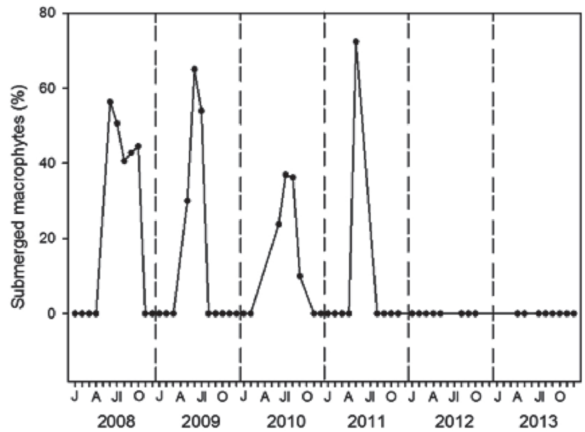

Figure 6. Changes in surface cover of submerged macrophytes between 2008-2010 (without carp) and 2012-2013 (with carp) as detected by remote sensing based on NDVI from Landsat images. Carp entered in the winter of 2010-2011 and were present at low density during 2011. *Cambios en la superficie de cobertura de los macrófitos sumergidos en el periodo 2008-2010 (sin carpas) y 2012-2013 (con carpas) detectadas por teledetección basada en NDVI a partir de imágenes Landsat. Las carpas entraron en el invierno de 2010-2011 y estuvieron presentes en baja densidad durante el año 2011.*

lake (de Vicente *et al.*, 2012). The marked increase in chlorophyll-*a* concentration we recorded is likely due to a combination of the loss of macrophytes, the increase in phosphorus availability and the loss of the large cladocera which are particularly effective filter feeders of phytoplankton (Carpenter 1988; Arnott & Vanni, 1993).

Impact of carp on zooplankton

Salinity is a major factor determining community composition in Mediterranean waterbodies, and species richness in zooplankton generally decreases with increasing conductivity (Frisch *et al.*, 2006; Boix *et al*, 2008; Waterkeyn *et al.*, 2008). Cladocera are particularly sensitive to high salinities (Green *et al.*, 2005; Badosa *et al.*, 2010). In our case, we found higher species richness when salinity was higher, because the negative impact of carp on zooplankton richness overrode the influence of reduced salinity in 2012. The three species that were dominant in 2012 (*Acanthocyclops americanus, Brachionus plicatilis* and *Keratella quadrata*) are all tolerant of a broad range of salinities (Antón-Pardo & Armengol, 2012) and would be likely to be abundant at the lower salinities recorded in 2008 if carp had been present.

As in previous studies (Lougheed *et al*., 1998; Miller & Crowl, 2006), in Lake Medina zooplankton taxonomic and size diversity was reduced after carp invasion. The loss of large bodied species such as macrocladocera and *Arctodiaptomus* and the switch to domination by smaller cyclopoids and rotifers in the presence of carp has been recorded before (Angeler *et al*., 2002; Matsuzaki *et al*., 2009). Dominance by *Brachionus* and *Keratella* rotifers in the presence of carp was also observed by Fischer *et al*. (2013). *Keratella quadrata* is favoured by eutrophic conditions (Xue *et al*., 2014). Our results are consistent with limited data on zooplankton collected by others at our study site prior to the original carp introduction, which showed that the macrocladocera *Moina salina*, *Daphnia magna* and *Chydorus pizarri* were abundant in 2002-2003 (Junta de Andalucía, 2005). Large zooplankton species are suppressed by planktivorous fish in general (Brooks & Dodson, 1965; Jeppesen *et al*., 1999). The removal of large cladocera which are so effective as filter-feeders promotes the abundance of smaller zooplankton, especially cyclopoid copepods (Arnér *et al*., 1998) and rotifers (Gilbert, 1988). Cyclopoids have higher fecundity and shorter development time than macrocladocera (Castilho Noll & Acrifa, 2007), and so can compensate more easily for predation pressure. They also have more effective escape behaviour (Lampert & Sommer, 1997).

Although carp eat zooplankton (Britton *et al*., 2007), it is unlikely that predation effects alone explain these changes, and there is experimental evidence that carp prefer copepods to *Daphnia* (Meijer *et al*., 1990). We found large copepods such as *Megacyclops viridis* only without carp. Carp are ecosystem engineers that also affect zooplankton indirectly by creating a hostile environment without submerged macrophytes, and with high concentrations of suspended particles and cyanobacteria. Resuspended particles suppress the growth of large cladocera (Meijer *et al*., 1990), and turbid-waters are often dominated by rotifers and copepods (Cottenie *et al*., 2001; Lind, 2003). Macrophytes provide refugia and food for zooplankton and promote species richness for microcrustaceans and rotifers (Lougheed & Chow-Fraser, 2001; Bagella *et al*., 2010; Xue *et al*., 2014). The loss of macrophyte cover is typically followed by a shift towards rotifers and small-bodied zooplankton (Hansen & Jeppesen, 1992; Hanson & Butler, 1994) and the release of phytoplankton from top-down control (Schriver *et al*., 1995).

Cyanobacteria can have a negative effect on macrocladocera (Ferrao-Filho & Kozlowsky-Suzuki, 2011), and may have contributed to their decline in Medina. Occasional monitoring of phytoplankton by the regional environmental agency suggests a large increase in abundance of cyanobacteria of the orders Chroococcales and Nostocales after the carp invasion. They found that abundance of Chroococcaceae (mainly *Chroococcus* sp.) increased by roughly three orders of magnitude from 0.72-7.39 ml^{-1} in 2002-2003 (without carp) to 5142 ml^{-1} in 2005 (with carp).

Gambusia holbrooki was present in Medina throughout the study, and also feeds extensively on copepods, cladocerans and rotifers (Cabral *et al*., 1998). Our results indicate that carp have a much greater impact on the zooplankton community than *Gambusia*, which are largely confined to the shallow lake edge and are not seen at the depths where we sampled (personal observation). Enclosure experiments have suggested that *Gambusia* can eliminate cladocerans on their own (Angeler *et al*., 2002), but our results suggest this is not the case in large, shallow lakes.

Alien copepod with an alien fish

The only abundant crustacean species in the presence of carp was the pelagic *Acanthocylops americanus,* which is also associated with eutrophic waterbodies (Miracle *et al*., 2013). It was introduced from North America to Europe where it was first recorded in the early 20^{th} century, and still appears to be spreading (Alekseev, 1998; Alekseev *et al*., 2002; Miracle *et al*., 2013). It is abundant in many lakes and rivers across Europe including Spain, and has been reported from Doñana to the west of Medina lake (Fahd *et al*., 2009). The dominance of this invasive cyclopoid in the presence of alien carp is particularly striking given the near absence of cyclopoids when carp were absent. This apparent association between an alien fish and alien zooplankter may represent a case of facilitation between invasive species, and warrants more investigation. High densities of *A. americanus* have been reported to be associated with high availability of rotifers (Enríquez *et al*., 2010). The similar *A. robustus* feeds on rotifers (including *Keratella*) and even cladocerans, whilst the nauplii feed on phytoplankton (Gliwicz & Umana, 2004; Enríquez García *et al*., 2010). Given its dominance, if *A. americanus* had not been introduced to Europe, it is likely that some other native copepod would have been more abundant in the zooplankton community in Medina in 2012. Future research should focus on competitive interactions between this alien copepod and native species.

CONCLUSION

The monitoring of zooplankton provided a clear measure of the ecological impact of carp in Medina shallow lake. The presence of carp was associated with a radical change in the composition of the zooplankton community and a major reduction in species richness. Given that *Gambusia* were still present when carp were absent, these changes were greater than those that would be expected on the basis of mesocosm experiments elsewhere. This is probably because of the major transformation from a clear water lake rich in macrophytes, to a turbid lake with abundant phytoplankton caused by carp activity. These bioturbation effects are likely to be particularly acute in Medina lake, owing to the warm Mediterranean temperatures that promote carp activity throughout the annual cycle, as well as the absence of piscivorous fish that can exert top-down control on carp abundance (Bajer *et al*., 2012).

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