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Effects of Greater flamingo *Phoenicopterus ruber* on macrophytes, chironomids and turbidity in natural marshes in Doñana, SW Spain

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With 4 figures and 3 tables

Abstract: Top predators and nutrient inputs are important factors determining the structure of freshwater aquatic systems. Greater flamingos (*Phoenicopterus ruber*) have been shown to destroy submerged macrophytes and may promote a switch from clear water to turbid water in the temporary marshes of Doñana National Park. We excluded flamingos from twenty 4×4 m plots distributed between two lucios (shallow seasonal lakes) within the marshes from February to July 2004. In July, we measured total suspended solids (TSS), macrophyte biomass and abundance and size of chironomid larvae in the twenty exclosures and twenty adjacent control plots. TSS was lower and macrophyte biomass was higher in exclosures, but not significantly so. Flamingos were found to cause a significant reduction in chironomid abundance and an increase in the proportion of larger larvae. The effect of exclusion was greater where the density of flamingos was highest. Comparison with the results of previous studies suggests that the impact of flamingos is context dependent and largely determined by bird density and/or factors related to macrophyte productivity. Water levels were especially high in 2004 owing to heavy rains, and flamingos may have stronger effects in years of lower rainfall.

Key words: Flamingos, macrophytes, turbidity, nutrients, chironomids, sediment resuspension.

Introduction

Submerged vegetation has a major functional role in shallow wetlands, providing a refuge for invertebrates, changing the nutrient dynamics of the system, and preventing resuspension of the sediments (Jeppesen et al. 1998, Scheffer 1998). It is therefore important to identify the factors that affect the presence and abundance of submerged vegetation. The role of herbivorous waterbirds such as swans, geese and coots has been studied extensively, and is an important factor in the restoration of shallow lakes (Van Donk et al. 1994, Van Donk & Otte 1996, Sondergaard et al. 1996). It is widely accepted that the disturbance of sediments by benthivorous fishes can inhibit the colonization of submerged plants and enhance sediment resuspension (Scheffer et al. 1993, Scheffer 1998). However, the potential effects of benthivorous birds on submerged plants have largely been ignored.

The Phoenicopteridae family (flamingos) includes five species, two of the genus *Phoenicopterus* (*P. ruber* and *P. chilensis*), two of the genus *Phoenicoparrus* (*P. andinus* and *P. jamesi*), and one of the genus *Phoeniconaias* (*P. minor*). The three latter species have very fine structures (lamellae) in the beak, which have evolved for specialised diets based on algae (Jenkin 1957, Vareschi 1978, Hurlbert & Chang 1983), whereas the *Phoenicopterus* species have a broader diet and less fine lamella for filtration (Jenkin 1957). All species are colonial birds, and can reach high densities in the wetlands where they occur. Due to their gregarious behaviour, their feeding habits and their large size,

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their presence may have important ecological effects in the wetlands where they occur. The Greater Flamingo (*Phoenicopterus ruber*) is distributed within Old World tropical and Mediterranean areas. It inhabits mainly shallow saline or alkaline water bodies, frequently in coastal and estuarine zones, forming flocks of tens to thousands of individuals. They are mainly bottom feeders and exhibit several feeding behaviours (including wading, trampling the sediments, movements with the beak on the mud surface, etc.) to catch small invertebrates (insects, crustaceans, molluscs and annelids), algae and plant material (seeds and plant fragments) (Cramp & Simmons 1982, Johnson 1997a).

It has previously been suggested that Greater flamingos (*Phoenicopterus ruber*) have negative effects on submerged plants and on herbivorous birds in the marshes of Doñana National Park in Spain (Duarte et al. 1990, Grillas et al. 1993, Montes & Bernués 1991) and in the Camargue in France (Gallet 1950). Montes & Bernués (1991) compared areas in the Doñana marshes with and without concentrations of flamingos, and found their presence to be associated with a decrease in macrophyte biomass and an increase in turbidity and in phytoplankton abundance (as measured by chlorophyll-*a*). Greater flamingos produce craters of ca. 1 m diameter during their trampling feeding behaviour, and are one of the most abundant waterbirds in Mediterranean wetlands, with population sizes increasing (Wetlands International 2006, Rodríguez-Pérez & Green 2006). They cause damage to rice crops in France and Spain (Tourenq et al. 2001) and have been shown to change sediment properties and to decrease the abundance of benthic invertebrates in Namibia (Glassom & Branch 1997a, 1997b). Their footsteps have been shown to mobilize sediments and nutrients (Comín et al. 1997). However, many factors are likely to affect both the presence of macrophytes and flamingos, and no experimental study has been done in natural marshes (as opposed to artificial, created marshes) before.

In this study we conducted an exclosure experiment to test the hypothesis that flamingos increase turbidity in the water column and reduce the biomass of submerged macrophytes and the abundance of benthic invertebrates in temporary marshes of Doñana National Park. We carried out the experiment for 6 months during a single hydrological cycle, in two areas within the marshes.

Study site

Our study was carried out in 2004 at two "lucios" (El Lobo and Marilópez) located within the 26,000 ha of natural marshes in Doñana National Park (Fig. 1, Garcia-Novo & Marín 2006). This park is also protected as a Biosphere Reserve, UNESCO

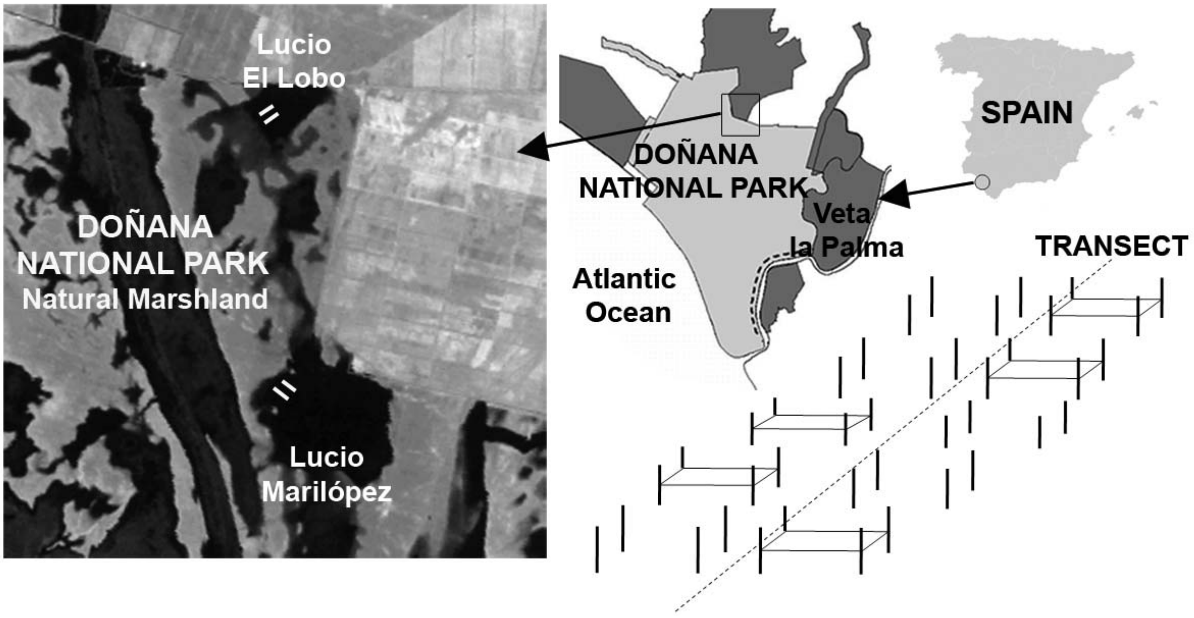

Fig. 1. Map of the study area showing the location within Spain. A schematic drawing shows a close-up of one transect with five pairs of control plots and flamingo exclosures. The large image is a clip of Landsat TM image composed with the band 5, for the area of study at 13th of June 2004, showing flooded areas of the marsh in dark grey. Two straight parallel white lines in each lucio indicate the position of the four transects.

World Heritage site, Ramsar site and an EU Specially Protected Area. “Lucio” is the local name for shallow, seasonal lakes created in depressions within the marsh that remain flooded until the marsh dries up. At the height of the wet season in winter and early spring, lucios are surrounded by and interconnected via shallower areas of marsh that dry out sooner (Espinar et al. 2002). The marsh is fed by freshwater (rainfall and runoff) and isolated from tidal influence of the Guadalquivir estuary. The concentration of salts depends on the frequency and the duration of flooding (Serrano et al. 2006). During the hot and dry summer, the marshland changes from oligohaline to mesohaline (Table 1), with a wide spatial variation depending on distance from freshwater sources, depth, etc. (Garcia-Novo & Marín 2006). The average number of waterbirds wintering in the National Park and its surroundings exceeds 250,000, and more than 20,000 flamingos winter in the area (Aguilera et al. 2006). In very wet years, up to 16,000 pairs breed in the National Park marshes (Martí & del Moral 2002, Johnson & Arengo 2005), although many clutches are lost due to predation and changing water level.

The ‘Lucios’ El Lobo and Marilópez are located in the northern part of the Doñana National Park (Fig. 1). They have a surface area of ca. 120 and 300 ha, respectively, and are surrounded by saltmarsh vegetation dominated by perennial *Arthrocnemum macrostachyum*. The maximum depth for both ‘lucios’ is ca. 1 meter, and fluctuates strongly with rainfall and wind direction. The emergent vegetation is dominated by scattered patches of *Scirpus litoralis*. During our study the dominant submerged macrophytes were *Ruppia drepanensis*, *Ranunculus peltatus, Callithriche truncata* and charophytes. Fish species present in both lucios *Cyiprinus carpio*, *Gambusia holbrooki*, *Fundulus heteroclitus*, *Anguilla anguilla* and *Atherina boyeri*. Only the last two species are native to the area.

Material and methods

Experimental plots were established from February 2004, (prior to the emergence of submerged macrophytes stems from the sediment in early spring, Grillas et al. 1993), to July 2004, thus covering most of the flooding cycle (from November 2003 to July in 2004). Two parallel transects of 300–400 m in length were established in each of the lucio del Lobo (Lobo from hereon) and the lucio de Marilópez (Marilópez from hereon, Fig. 1). The minimum distance between the two transects within each Lucio was 90 m. Five pairs of flamingo exclosures and control plots were established along each transect, making a total of 20 exclosures and 20 control plots. Each exclosure and its control were positioned on opposing sides of the transect line, and separated by 20 m. The distance between pairs of plots was 50–80 m (see Fig. 1 for details). The position of each plot was pinpointed via GPS.

Both exclosures and controls were 4×4 m squares delimited by four iron poles pushed vertically into the mud in each corner. Exclosures were created by extending a wire around the poles at a height of ca. 70 cm above the bottom, copying a design used successfully in the nearby Veta la Palma fish ponds (Rodríguez-Pérez & Green 2006). This design takes advantage of the much greater height of flamingos, and the height of the wire was selected after trials confirming that other waterbirds pass comfortably underneath the wire and freely enter the exclosures (Rodríguez-Pérez & Green 2006).

Our plots were visited each month, and physico-chemical measurements were taken. The water depth was measured (always at the same corner of each plot), turbidity was measured with an 8 cm Secchi disk and temperature, conductivity and salinity were measured with a WTW multiprobe 340-i device. During visits, we also took spot measurements of turbidity (using a Hanna HI 93703 probe in Formazine Turbidity Units (FTU) equal to Nephelometric Turbidity Units) from different areas of each lucio that were occupied by flamingo concentrations at that time, and from other points without birds. We counted the flamingos present in each lucio with binoculars and recorded their behaviour (roosting or feeding).

On our final visit on 7–8 July as the flooding cycle was approaching its end, we took samples of macrophytes, chironomids and total suspended solids (TSS) from each plot. TSS was measured with a gravimetric method (American Public Health Association 1998). One litre of water was carefully taken on arrival, being careful to collect it from outside the sediment cloud, caused by our steps, that could influence the measurement. Each sample was later resuspended in the laboratory, then a known volume of sample was filtered through a Whatman GF/C filter which had previously been dried and weighed. Each saturated filter was then dried for 48 h at 70 ºC, kept in a desiccator until the environmental temperature was reached, and then weighed with a precision balance (to the nearest 0.0001 g).

We took four samples of macrophytes per exclosure with a PVC pipe section (0.125 m^2 cross-sectional area) that was pushed into the sediments. All water was extracted with a bowl, and then all macrophyte stems and leaves were cut at the base and removed. To reduce edge effects, the pipe was inserted 1 m in towards the centre of the plot from the middle of each side of the square. In the laboratory, samples were rinsed with tap water to clean them from mud and invertebrates, and dried at 70 ºC for 48 h prior to weighing.

Benthos was sampled by taking four core samples of the upper 5 cm layer of sediments with a 5.5 cm diameter corer from each plot to avoid edge effects. Benthos samples were taken close to macrophyte samples, but from undisturbed areas. In the laboratory, samples were stored in a refrigerator until they could be filtered through a 0.5 mm sieve. Given the dominance of chironomid larvae in benthos samples (in all plots chironomids were > 80 % of invertebrates retained by a 500 microns sieve), only chironomid larvae were retrieved from samples and preserved in formalin. We also restricted the analysis to this group because it is a major food item for flamingos and other waterbirds (Del Hoyo et al. 1992, Johnson 1997a). A subset of chironomid larvae were identified to tribe level. The length of these larvae was later measured under a binocular microscope to the nearest 0.01 microns with the aid of a digital image system. Prior to statistical analysis, the data from the four samples within each plot were pooled, since they were not strictly independent.

To estimate waterbird abundance, we used the results of the aerial monthly census of waterbirds carried out in Doñana National Park and its surroundings. We report total numbers counted for the whole census of the park and adjacent areas (including the Veta la Palma fish ponds, see Fig 1.)

Statistical analysis

We used generalized mixed linear models (GLMs, McCullagh & Nelder 1989) to analyse the effect of Treatment (flamingo exclosure and control), Site (Lobo and Marilópez) and water depth. Treatment and Site were included as fixed factors, and Depth as a continuous variable. The Transect (two per site) and Exclosure/Control Pair (nested within Transect) were included as random factors in the analysis, using GLIMMIX procedure (SAS Institute 2005). We initially included Treatment × Site interactions but excluded them from the final model when they were not significant ($p > 0.05$). When *post-hoc* analysis of least-squared means was performed, the significance level (= 0.05) was adjusted with False Discovery Rate (FDR) techniques for repeated-tests (García 2003, 2004).

For TSS and macrophyte biomass, we selected those error distributions and link functions that prevented heteroscedasticity and deviation from model assumptions. TSS was analysed with a lognormal error distribution and an identity link function. Macrophyte biomass was $\log_{10}$ transformed and modelled with an identity link function and normal error distribution. For chironomid counts, we used a negative binomial error distribution and a log link function (Gray 2005).

A model with a binomial error distribution and a logit link function was used to analyze the size distribution of chironomid larvae. The dependent variable was the proportion of chironomid larvae that were smaller or equal to the median size observed (6.475 mm) in control plots. The numerator of the binomially distributed dependent variable was the number of larvae ≤ 6.475 mm, and the denominator was the total number of larvae (see Crawley 1993).

Graphs of TSS, macrophyte biomass and chironomid abundance were produced using geometric means to better represent the skewed data distributions. These were calculated by $\log_{10}$+1 transformation of the raw data, calculation of the arithmetic mean and SE, followed by back-transformation.

Results

During the course of the experiment, a steady increase in evaporation together with a lack of water input produced a gradual decline in depth (Table 1), followed by desiccation by the end of July. Sharp rises in tem-

Table 1. Physical and chemical features of Marilópez and El Lobo lucios in 2004. 'Bottom' indicates that the Secchi disk was visible at the bottom, indicating high visibility.

	Marilópez					
	4th February	10th March	23rd April	11th May	18th June	7th July
Temperature ºC	18	18	26	19	28	30
Salinity %	0.7	0.4	0.7	0.9	2.9	6.6
Conductivity mS cm^{-1}	1.76	1.21	1.67	2.12	5.3	11.38
Depth Min-Max cm	46–51	63–69	52–57	50–53	25–30	8–16
Secchi Min-Max cm	14–19	24–51	22–Bottom	Bottom	5–17	2–Bottom

	El Lobo					
	4th February	10th March	21st April	12th May	18th June	8th July
Temperature ºC	18	18	20	22	27	35
Salinity %	0.7	0.4	0.8	1	3.2	6.8
Conductivity mS cm^{-1}	1.72	1.15	1.89	2.28	5.98	10.93
Depth Min-Max cm	46–51	61–69	47–53	45–50	25–29	12–18
Secchi Min-Max cm	16–21	14–26	30–Bottom	Bottom	12–Bottom	9–Bottom

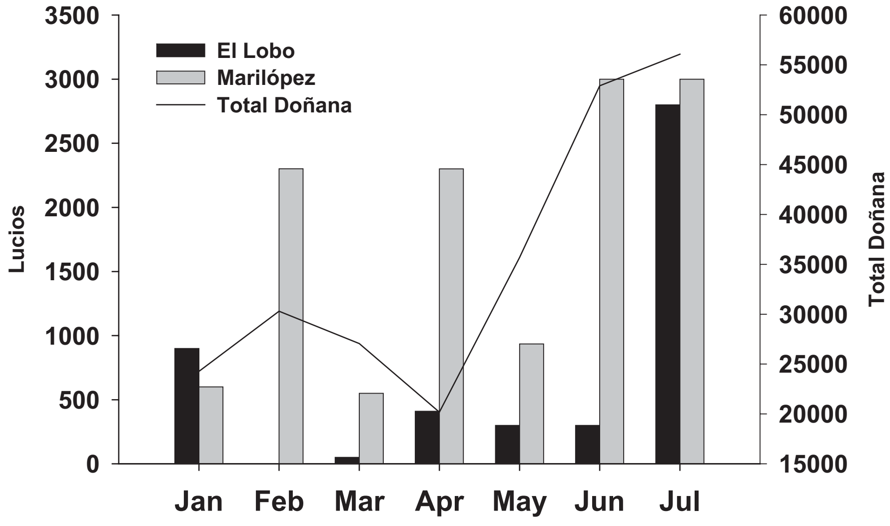

Fig. 2. Monthly aerial counts of flamingos at Marilópez (light grey bars), El Lobo (black bars), and total number of flamingos (straight line) counted for the whole Doñana area during the aerial census for the period from January to July 2004. The left y-axis shows the scale for lucio counts and right y axis for the whole of Doñana. The maximum flooded area was 120 ha for Lobo and 300 ha for Marilópez.

Table 2. Summary of generalized linear models testing the main factors Site (two levels) and Treatment (two levels) on total suspended solids (TSS, g l^{-1}) and macrophyte dry biomass (g m^{-2}, $\log_{10}$ transformed). The interaction was not significant ($p > 0.05$) and was removed from the analysis. Transect and flamingo exclosure/control pair were included as random factors using the GLIMMIX procedure, with identity link function and lognormal error distribution for TSS, and normal error distribution for macrophyte biomass. Marilópez and exclosures were aliased (i.e estimates equal to zero). See methods for details.

	Total suspended solids						Macrophyte biomass					
	Estimate	SE	df_N	df_D	F	p	Estimate	SE	df_N	df_D	F	p
Intercept	4.18	0.21					–1.03	0.07				
Site			1	28	4.20	**0.05**			1	28	35.59	**< 0.0001**
El Lobo	–0.51	0.25					–0.4	0.07				
Treatment			1	28	1.64	0.2			1	28	0.23	0.6
Control	0.32	0.25					–0.04	0.03				

perature, salinity and conductivity occurred over time, and the lucios changed from oligohaline to mesohaline (Table 1).

Marilópez held more flamingos throughout the study than Lobo, and had a higher density of flamingos from February to June inclusive (Fig. 2). The numbers of flamingos using both lucios increased towards the end of the experiment as shallower areas of marsh in Doñana dried out, and as the total numbers of flamingos in Doñana increased (Fig. 2). Throughout the study, flamingos were observed using the areas where our transects were placed. However, until June, most of the flamingos were roosting in flocks (probably feeding at night in the Lucio or in other surrounding areas, e.g. rice fields), whereas from June onwards they spread out more across the lucios and increased feeding activity. Turbidity was visibly increased at the areas where flamingos were feeding. Thus, on 18 June turbidity spot measurements in areas of Lobo not disturbed by flamingos were 20.5 and 36.7 FTU, whereas in areas disturbed by flamingos they were 105 and 172 FTU. Similar measurements for Marilópez were 18.4 and 26.4 for areas without flamingos, and 87 and 121 FTU in areas with active flamingos. The lowest turbidity values (2.2 FTU in Lobo and 2.3 in Marilópez) were recorded in May, when the densest mats of macrophytes occurred.

TSS in July was not significantly different between Treatments (control or exclosures), Sites (lucios) or Depth (Table 2). However, TSS tended to be higher in Marilópez and in flamingo exclosures (Fig. 3A).

At the time of sampling, *Ruppia drepanensis* was the only submerged macrophyte still in flower, the other species (see study site section) having ended their reproductive cycle already. *R. drepanensis* represented the great majority of the biomass of submerged macrophytes sampled. Macrophyte biomass did not differ significantly between Treatments or with Depth (Fig. 3B), but there was a highly significant effect of Site, with more biomass in Marilópez (Table 2).

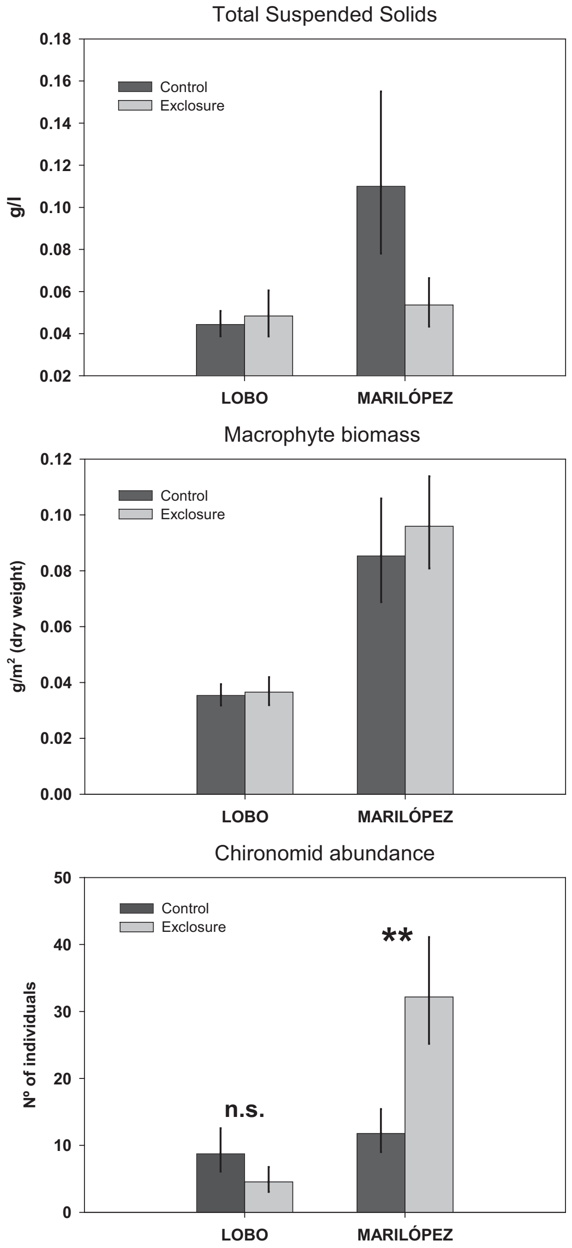

Fig. 3. Geometric mean and back-transformed SE of TSS, macrophyte biomass and chironomid counts for both treatments in the two lucios in July 2004.

Table 3. Summary of generalized linear models testing the main factors Site (two levels) and Treatment (two levels) on chironomid larvae abundance and chironomid size. When the interaction was not significant ($p > 0.05$) it was removed from the analysis. Transect and flamingo exclosure/control pair were included as random factors using the GLIMMIX procedure, with log link function and negative binomial error distribution for chironomid abundance, and logit link and binomial error distribution for chironomid size. Marilópez and exclosures were aliased. See methods for details.

	Chironomid abundance						Chironomids size					
	Estimate	SE	df_N	df_D	F	P	Estimate	SE	df_N	df_D	F	P
Intercept	3.7	0.3					0.39	0.17				
Site			1	27	9.23	**0.005**			1	24	0.02	0.9
El Lobo	–1.68	0.4					0.03	0.2				
Treatment			1	27	0.50	0.5			1	24	4.44	**0.05**
Control	–0.99	0.4					–0.36	0.17				
Site × Treatment			1	27	7.14	**0.01**						n.s.
El Lobo × Control	1.57	0.59										

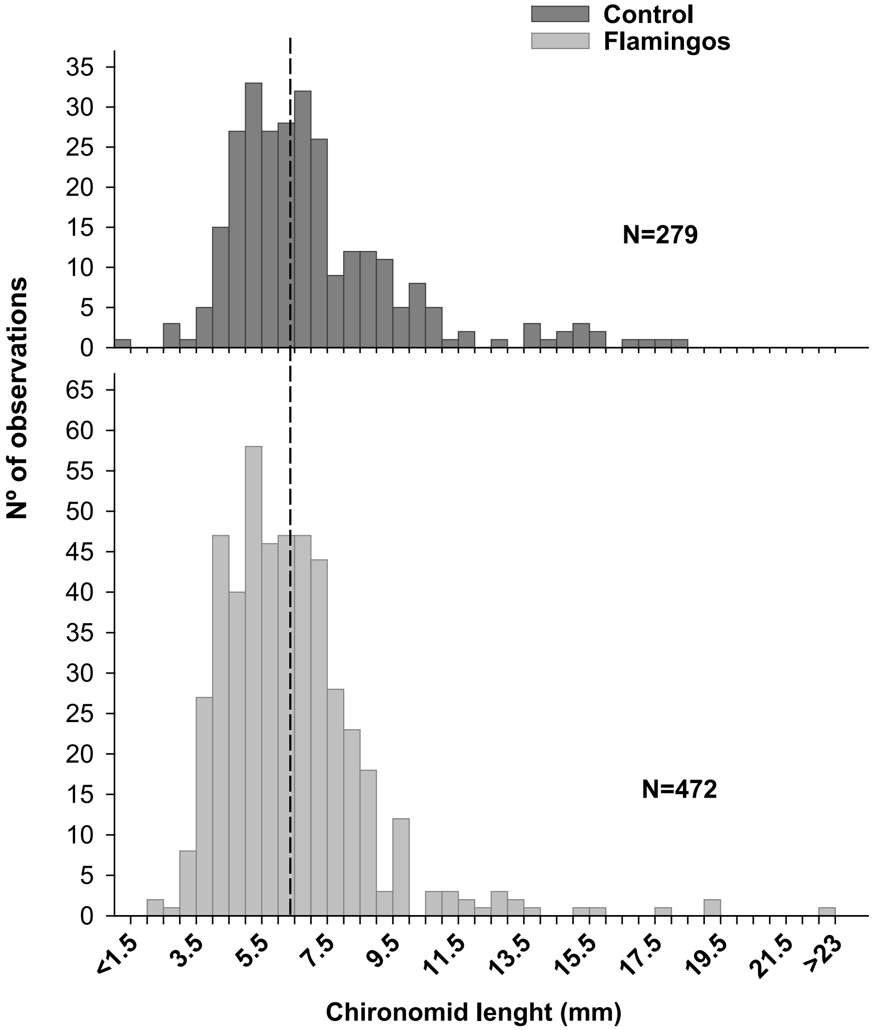

Fig. 4. Size frequency distribution of chironomids sampled from controls and exclosures, combining data for both lucios. The intervals for length in the x-axis are of 0.5 mm. N refers to the total number of chironomids recorded in each treatment. The dashed line shows the median value of 6.475 mm.

Both tribes Chironomini and Tanytarsini were represented amongst chironomid larvae. Density of larvae was higher in Marilópez (Table 3, Fig. 3C). The effect of Treatment varied between lucios, as shown by a highly significant Treatment × Site interaction (Table 3). Post-hoc tests showed larval abundance to be significantly higher in exclosures than controls for Marilópez, with no Treatment effect for Lobo (control vs. exclosure: Marilópez $t_{27} = 2.43$, $p = 0.03$; Lobo $t_{27} = 0.42$, $p = 0.2$; Fig. 3C).

In a GLM of larval size, Treatment had a significant effect in the absence of a site effect (Table 3). The treatment × site interaction was not significant (p = 0.9). A higher proportion of large larvae were found in controls than in exclosures. Whereas 58 % of larvae in exclosures were less than 6475 μm in length, this was true for only 50 % of those in controls (Fig 4). Depth did not have a significant effect in any of the analyses.

Discussion

Our exclosure experiment did not provide support for previous suggestions that greater flamingos reduce biomass of submerged macrophytes and increase turbidity in the natural marshes of Doñana National Park (Montes & Bernués 1991, Duarte et al. 1990, Grillas et al. 1993). These results are surprising, given that direct observation shows that feeding flamingos do damage macrophytes and create clouds of suspended sediments in the precise points where they are standing, as indicated by our spot turbidity measurements. However, our results indicate that these effects were not detectable at a broader scale across a lucio after five months of exclusion, and contrast with results of a previous experiment in a nearby area. A significant effect of flamingos on *Ruppia maritima* was recorded in fish ponds in Veta la Palma, an area adjacent to Doñana National Park (Fig. 1 and Rodríguez-Pérez & Green 2006). Since most of these ponds were created in 1993, the density of flamingos in the National Park has decreased, and Veta la Palma has become the preferred area for flamingos (Aguilera et al. 2006), which are the dominant waterbird species there in terms of biomass (Rodríguez-Pérez & Green 2006). Additionally, fish ponds present a higher salinity and turbidity, which increases the stress on *Ruppia* and may increase its susceptibility to other stressors such as waterbirds.

Our study year (2004) was a very wet year with a particularly high extension and biomass of submerged macrophytes across the temporary marshes of the National Park, and this fact might have influenced the outcome by minimizing the effect of flamingos. Our results show that a stronger effect of flamingos on chironomid abundance was observed at the site (Marilópez) with a higher density of flamingos. Such density effects are also to be expected for macrophyte impacts, and we observed a trend for lower TSS in exclosures in Marilópez (Fig. 3).

In addition to differences in the density of flamingos, other factors may explain the different results for el Lobo, Marilopez and Veta la Palma (see Rodríguez-Pérez & Green 2006). First, owing to poor visibility we were unable to quantify macrophyte cover in a non-destructive manner during the course of our study, and it is possible that significant effects may have occurred earlier (e.g. biomass may have been faster to reach a peak in exclosures). Second, given the reduced size of exclosures, Flamingos feeding close to our exclosures are likely to have increased turbidity within them, and it is possible we would have had significant results with larger exclosures.

We found flamingos to have a significant effect on benthic chironomid larvae, reducing their density (in Marilópez) and changing their size distribution. Greater flamingos consume chironomid larvae (Johnson 1997a), and we have also found them to reduce the density of benthic chironomids and polychaetes in the Veta la Palma fish ponds (Rodríguez-Pérez 2006). Exclosure experiments have also shown Greater flamingos to have strong effects on a polychaete-dominated benthic community in coastal lagoons in Namibia (Glassom & Branch 1997a, 1997b). These authors showed how the exclusion of flamingos increased the abundance of three polychaete species up to three times inside exclosures compared to control plots, as well as changing the physico-chemical propertiesof sediments. Additionally, exclosure experiments showed Andean flamingos to have major effects on benthic primary producers, and meiofauna and flora (Hurlbert & Chang 1983).

The exclosure effects we observed on chironomids are clearly attributable to flamingos. The only other birds in the area with sufficient height to be excluded were small numbers of Glossy Ibis (*Plegadis flacinelus*), but none were seen near exclosures and this species preys mostly on beetles and Odonata larvae (Macías et al. 2004). Fish could enter inside controls and exclosures without restrictions.

Although we only found chironomid abundance to be higher in exclosures in Marilópez, where flamingo density was higher, this does not necessarily indicate that flamingos were not consuming chironomids in Lobo as well, but instead suggests that the reduced density of birds precluded the detection of significant effects. We also found chironomid larvae to be larger in controls. If flamingos selected large chironomid larvae, we would expect the opposite effect, i.e. larvae to be smaller in controls (see Sánchez et al. 2006 for such a result for waders). As flamingos have fine lamellae capable of filtering plankton, it seems possible our result was due to them selecting small larvae. Another possible explanation for our size effect is that an increase in larval density in exclosures led to a reduced size to inhibition of growth rates by competition (Armitage et al. 1995). However, this could not explain why we recorded an interaction between site and treatment. A third explanation could be a difference between treatments in the relative abundance of different chironomid species of different size (see Fuentes et al. 2005). It is noteworthy that, although controls had a higher proportion of larvae with length > 6.475 mm, the maximum length was recorded in exclosures (Fig. 4).

The exclusion of vertebrate predators often leads to indirect effects on the size distribution of benthic invertebrates, mediated via competition or interactions with invertebrate predators themselves released from predation pressure (Sih et al. 1985, Thrush 1999). Thus, it is also possible that the density of predatory invertebrates, such as beetles or dragonfly larvae, increased in flamingo exclosures leading to a reduction in chironomid size. However, such predatory invertebrates may not be selective predators amongst the size range of chironomid larvae we recorded (Wellborn et al. 1996).

Conservation management has led to a marked increase in the size of the Greater flamingo population in Doñana and across the Mediterranean region since 1970, making this one of the most abundant breeding waterbirds in terms of biomass (Johnson 1997b, Wetlands International 2006, Aguilera et al. 2006). Although there was a decrease in the numbers of flamingos using the natural marshes of Doñana following the creation of nearby fish ponds, numbers there have began to recover in recent years (Aguilera et al. 2006). As the whole Spanish population continues to increase, numbers in the National Park are also likely to continue increasing. Thus, the chance of flamingos reaching sufficient densities to have an important impact on macrophytes and benthos may increase in the future, especially in years of low rainfall when flamingos are more concentrated in available habitat than in 2004.

In conclusion, greater flamingos have a pronounced effect on the benthic invertebrates in temporary marshes, as has previously been observed in more permanent habitats. Although they reduce the cover of submerged vegetation in brackish fish ponds, this has yet to be demonstrated conclusively for natural marshes. Our study suggests that the impact of flamingos on wetland communities is highly context dependent, and that both the density of flamingos and environmental factors related to macrophyte growth (flooding regime, salinity, etc.) are likely to be important. More research is required to understand the nature of the relationship between flamingos and submerged vegetation at different spatial and temporal scales.

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