

Spatial and temporal fluctuations in presence and use of chironomid prey by shorebirds in the Odiel saltpans, south-west Spain

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Abstract

We studied the seasonal variation in abundance and distribution of shorebirds and chironomid *Chironomus salinarius* larvae in both traditional and industrial salines in the Odiel marshes, south-west Spain, in 2001. We selected 12 ponds that were representative of the different phases of the salt production process. The benthic chironomids were sampled in each pond every 2 months, and the birds were counted weekly. Chironomid larvae were most abundant in spring and autumn, and in the ponds of lower salinity. The density of larvae averaged $7023 \pm 392 \text{ m}^{-2}$ (\pm SE) over the six sampling events. Shorebirds were always more abundant at high tide than at low tide, and were especially abundant during the spring and autumn migration periods when up to 20,775 birds were counted. A total of 24 species were recorded, six of which were present in internationally important numbers. The salines were especially important as foraging and roosting habitat during migration. The percentage of birds that were feeding in the ponds was positively correlated with the abundance of chironomid larvae at accessible depths. The number of feeding birds was also higher in ponds with more chironomid larvae available. Despite more intensive management, industrial salines held higher densities of birds and a similar abundance of chironomids when compared with traditional salines.

Introduction

Many shorebirds or waders (Charadrii) are long distance migrants which migrate thousands of kilometres between breeding and wintering sites and are heavily dependent on passage sites along the flyways, where they can rest and refuel (Alexander et al., 1996; Iverson et al., 1996). Natural and artificial coastal wetlands tend to be highly productive and are a vital habitat for these birds (Velasquez, 1992; Masero et al., 1999), which are very sensitive to habitat change (Alexander et al., 1996). In recent decades, many coastal

wetlands have been destroyed or transformed, resulting in major impacts on shorebird populations (Goss-Custard et al., 1977a, b; Goss-Custard & Moser, 1988).

Artificial wetlands such as salines can provide important foraging habitats for shorebirds, especially at high tide when intertidal marshes are flooded and inaccessible (Pérez-Hurtado & Hortas, 1991). Salt production via the circulation of sea water through a system of ponds in salines is an ancient activity in the Mediterranean region and other warm coastal areas (Britton & Johnson, 1987). Aquatic invertebrates in saltpans represent

abundant prey for shorebirds (Velasquez, 1992), although there are relatively few invertebrate taxa owing to the extreme salinities. Amongst these taxa, chironomid larvae are particularly important (Velasquez, 1992; Pérez-Hurtado et al., 1997).

The Odiel marshes in south-west of the Iberian peninsula are one of the most diverse and productive coastal marsh systems in southern Europe (Castellanos et al., 1998). They are situated on the East Atlantic flyway (Smit & Piersma, 1989), and their importance for waterbirds has led to their protection as a Natural Park, Ramsar site (Bernués, 1998) and Biosphere Reserve. The salines represent 16% of the surface area of the marshes, and are an important feeding and roosting area for shorebirds. During the migration periods and in winter, flocks of over 12,000 birds can regularly be observed. However, there are no previous studies of the shorebird and invertebrate communities in the salines, or of shorebird habitat use.

In this study, we describe the seasonal variation in the abundance and distribution of shorebirds in the Odiel salines, as well as in the abundance and distribution of one of their principle prey species, the chironomid *Chironomus salinarius*. We assess the differences between salt pans of different salinities and between industrial salines (with an intensive salt production process) and traditional salines in their value for shorebirds and their prey. We test whether or not chironomid abundance predicts the abundance of foraging shorebirds in space and time. We consider what changes to current management may increase the shorebird carrying capacity of our study site.

Study area

The Odiel marshes (37°17' N 06°55' W), found in the combined estuaries of the Tinto and Odiel rivers, are tidal marshes with a total surface area of 7,185 ha. The salines occupy 1,185 ha, of which c.1,118 is an industrial saline complex and c.56 ha is a traditional saline (Fig. 1).

In both kinds of salines, sea water is introduced via a tidal canal to a complex of large and deep ponds which act as reservoirs (the primary evaporation ponds PEPs), where the salinity is relatively low and the diversity of invertebrates

relatively high. From there, the water circulates into a system of shallower ponds (the secondary evaporation ponds SEPs) with intermediate salinity and where the invertebrate community is dominated by *C. salinarius* in the benthos and the brine shrimp *Artemia parthenogenetica* in the water column. These two species are the most abundant prey for waterbirds in the salines. *C. salinarius* is actually a species complex requiring further taxonomic study (Armitage et al., 1995). The brine shrimp population is dominated by the diploid form of *A. parthenogenetica* (F. Amat pers. comm., Amat et al., 1995).

From the secondary evaporation ponds, the water passes to the pre-crystallization ponds (PCPs), a group of shallow and hypersaline ponds where water is stored until it approaches saturation point. Finally, the water then enters the crystallization ponds (CPs), where the salt precipitates and is harvested (Fig. 1). The abundance of invertebrates in these last two classes of ponds fluctuates according to the salt concentration.

Methods

Invertebrate sampling

Twelve ponds covering the range of salinities were selected and sampled throughout 2001, including nine in the industrial salines and three in the traditional salines (Fig. 1). The ponds included two PEPs, six SEPs, two PCPs and two CPs. The traditional saline is more a labyrinth of canals than a complex of ponds, through which the water flows continuously. We did not sample the traditional PEP, which was too deep for shorebirds.

The benthos was sampled every 2 months, selecting four points at random from each pond within the depth range accessible to shorebirds (0–20 cm, Ntiamoa-Baidu et al., 1998). At each point, three core samples were taken to a depth of 3 cm with a 19.6 cm² corer. The salinity was measured at the same time using a densometer. In the laboratory, the sample was filtered through 0.5 and 0.1 mm sieves. In order to separate chironomids from the sediments retained in the sieves, we floated them in saturated salt solution collected

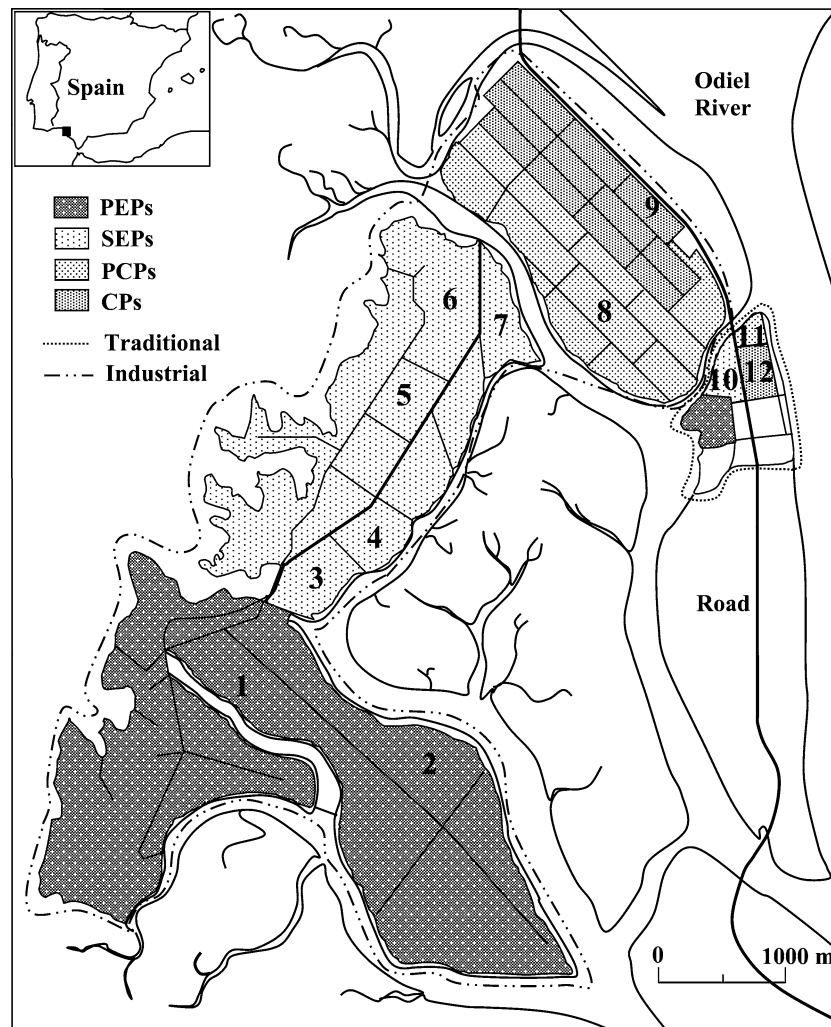


Figure 1. The location of the Odiel salines in SW Spain, and of our study ponds in the traditional and industrial salines.

from a CP. The larvae and pupae were collected from the surface and preserved in 70% ethanol.

Shorebird counts

In each of the study ponds we counted the number of shorebirds of each species that were feeding and resting 1 day each week, using a 20–60 × telescope. On each day, we carried out two counts of 3 h duration, one centred around high tide and the other around low tide. The ponds were always counted at the same time (by choosing to count on the day that high or low tide occurred around

09:00 h) and always following the same route between ponds.

Calculation of the available surface area

In most of the ponds, only shallow areas of 0–20 cm around the edge and around islands are available to foraging shorebirds. The accessible surface area varies with fluctuations in the overall water level, which were monitored by recorded depth at a reference point in each pond at the time of conducting surveys. The depth profile of each pond was established by conducting various

transects, and the surface area accessible for foraging at the time of survey was estimated via image analysis (Sigma Scanpro, version 4.0).

Statistical analysis

The abundance of chironomid larvae and pupae and of shorebirds were analyzed using generalized linear models (GLMs) following GENMOD procedure in SAS (v. 8.2, SAS Institute, 2000). POND and MONTH were included as fixed factors. POND had 12 levels for the shorebird model, but only nine for the chironomid models as three ponds where chironomids were absent in all but one month were removed. MONTH had 12 levels for shorebirds and six for chironomids. For the shorebird model, we also include TIDE as a fixed factor of two levels (low or high). Owing to overdispersion observed in the data for larvae and shorebirds, we used a negative binomial error distribution (Bliss & Fisher, 1953; Kopocinski et al., 1998), log link function and type III tests. Such a model for pupae did not converge owing to the high proportion of zeros, so we conducted a non-parametric analysis using ranks in GENMOD with an identity link (RANK procedure in SAS).

The deviance of each fitted GLM model is analogous to the residual sum of squares in ordinary linear regression. The reduction in deviance compared to the null model is used to assess

the contribution of the model to the explanation of the variance in the data set. The significance of the reduction in deviance can be estimated by comparison with the distribution of the chi-square statistic, with degrees of freedom (df) equal to the change in df compared to the null model. *Post-hoc* differences between two levels of a factor were tested with the Wald chi-square test for differences between least-squares means (SAS Institute Inc., 1997).

Spearman's rank correlations were conducted between the proportion of shorebirds that were feeding and the number of chironomid larvae available, and between salinity and the density of larvae.

Results

Abundance of chironomids

Chironomid larvae were present in the sediments all year round but with a marked pattern in seasonal abundance (Fig. 2) with the first and strongest peak in May (mean of $11,835 \pm 1470$ larvae m^{-2} , mean \pm SE, $n = 804$) and a second peak in November (9933 ± 1063 m^{-2}). The same patterns were observed for large and small larvae collected from the 0.5 and 0.1 mm sieves, although the larger larvae were relatively more abundant when the

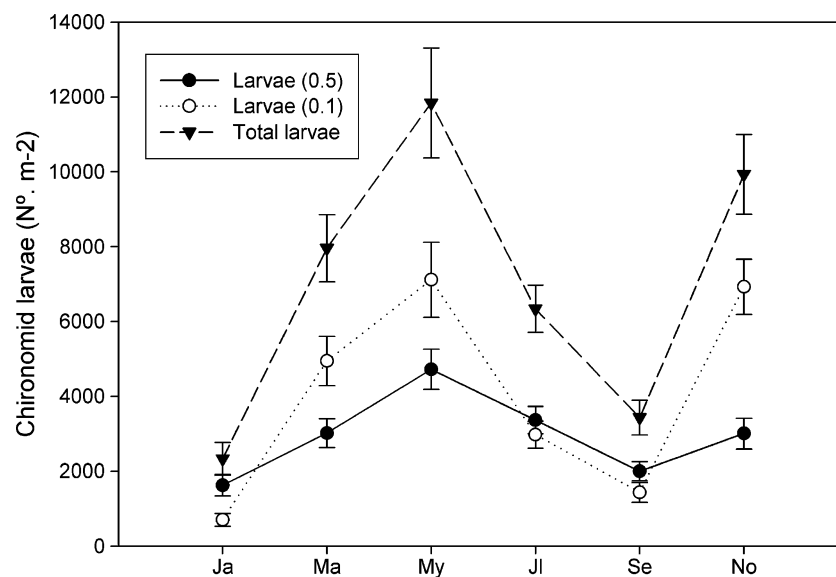


Figure 2. Seasonal variation in the density of chironomid larvae (mean \pm SE, $n = 144$ for each month), in the Odier salt pans in 2001.

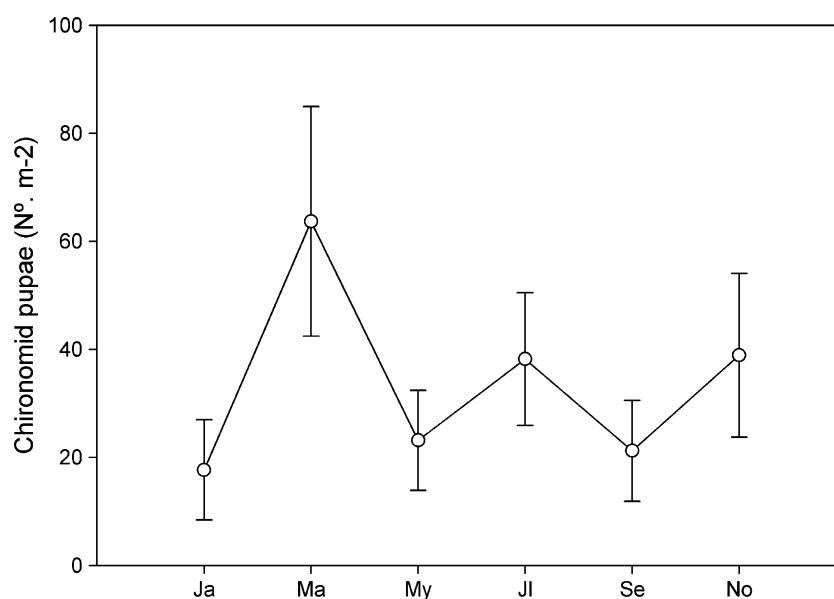


Figure 3. Seasonal variation in the density of chironomid pupae (mean \pm SE, $n = 144$ for each month), in the Odiel salt pans in 2001.

total number of larvae was lower (Fig. 2). Larvae were only recorded in the CPs and the industrial PCP during one month (November for the traditional CP, March for the other two ponds). In the CPs, this was probably owing to the compacted sandy nature of the sediments and the effects of salt crystallization, while in the PCP it was owing to incrustations of gypsum salts on the sediment surface which made it impossible for larvae to enter the sediments and construct their tubes.

The annual average density of chironomid larvae varied between different ponds, with the highest densities recorded in PEPs and SEPs and the lowest in the CPs (Table 1). This suggests a gradual decrease in larval density during the evaporation and crystallization process, as confirmed by a significant negative correlation between average salinity in each pond and the average larval density ($r_s = -0.713$, $p = 0.008$, $n = 12$). There were no consistent differences between industrial and traditional salines in the abundance of larvae for a given salinity type (Table 1).

GLMs revealed highly significant effects of POND, MONTH and the POND*MONTH interaction on the abundance of benthic chironomid larvae (Table 2). Thus, there were strong differences in abundance between different ponds and times of the year, while seasonal differences varied between ponds (as shown by differences between

ponds in the month when abundance peaked, Table 1). Similar results were recorded for GLMs analysing the numbers of large (those retained on a 0.5 mm sieve) and small (those retained on a 0.1 mm sieves) larvae (Table 2). In a GLM for benthic pupae, the POND*MONTH interaction was highly significant (Table 2), indicating that seasonal patterns in chironomid emergence (Fig. 3) were not consistent between ponds.

Abundance of shorebirds

A total of 24 shorebird species were recorded in the study area, the most abundant being dunlins (*Calidris alpina* (L.)), black-tailed godwits (*Limosa limosa* (L.)), and curlew sandpiper (*Calidris ferruginea* (Pontoppidan)) (Table 3). The highest count was of 20,775 birds in April. The total numbers of shorebirds showed a strong seasonal pattern, with peak counts in April and August coinciding with the pre- and post-breeding migration periods (Fig. 4). The post-breeding migration was the stronger and more prolonged, with high counts being recorded from July to September. In contrast, the pre-breeding migration was only marked during April (Fig. 4). The number of birds recorded in the salines was always higher at high than at low tide (Fig. 4). The proportion of birds that remained at low

Table 1. Annual average salinity, size and density of chironomid larvae recorded in individual saltpans in Odiel, 2001

Pond	Pond type	Management	Salinity (g/l)	Total surface area (m ²)	Available surface (m ²)	Chironomid density (m ⁻² , mean ± SE)	Peak density (month)
1	PEP	I	30	842,200	550 ± 400	3984 ± 1267	8068 (Nov)
2	PEP	I	40	790,700	5787 ± 1229	20,396 ± 5688	44,671(May)
3	SEP	I	90	196,100	48,039 ± 5948	2505 ± 951	5817(Mar)
4	SEP	I	90	171,900	37,165 ± 14641	5846 ± 1814	13,461 (Mar)
5	SEP	I	70	176,300	34,215 ± 2168	9193 ± 2806	19,873 (Nov)
6	SEP	I	70	512,200	43,552 ± 3170	13,234 ± 3144	25,223 (Nov)
7	SEP	I	70	179,100	13,434 ± 951	10,389 ± 3564	23,524(Nov)
8	PCP	I	100	164,500	77,109 ± 969	106 ± 106	637(Mar)
9	CP	I	160	90,253	51,828 ± 40623	64 ± 44	255(Mar)
10	SEP	T	40	41,938	8943 ± 0	6723 ± 3563	24,331(Nov)
11	PCP	T	80	28,092	6154 ± 0	5761 ± 2619	17,028(May)
12	CP	T	90	37,579	11,428 ± 0	226 ± 226	1359 (Nov)

See methods for details of pond type and how available surface area was calculated. I = industrial, T = traditional.

tide varied between seasons, and was higher during spring migration than autumn migration (Fig. 4).

In a GLM, there were highly significant main effects of POND, MONTH and TIDE on the number of shorebirds (Table 2). All two way

Table 2. Summary of GLM models testing the effects of POND, MONTH and TIDE on the abundance of Chironomidae larvae and pupae and shorebirds in the Odiel salines

	Effect	df	Chi-Square	<i>p</i>
Total larvae	Pond	8	71.84	< 0.0001
<i>n</i> = 216	Month	5	67.56	< 0.0001
D = 4.92%	Pond*Month	40	99.65	< 0.0001
0.5 Larvae	Pond	8	44.6	< 0.0001
<i>n</i> = 216	Month	5	27.25	< 0.0001
D = 4.32%	Pond*Month	40	97.25	< 0.0001
0.1 Larvae	Pond	8	85.6	< 0.0001
<i>n</i> = 216	Month	5	101.03	< 0.0001
D = 8.30%	Pond*Month	40	129.48	< 0.0001
Pupae	Pond	8	10.25	0.2477
<i>n</i> = 216	Month	5	6.25	0.2823
D = 35.03%	Pond*Month	40	76.94	0.0004
Shorebirds	Pond	11	671.93	< 0.0001
<i>n</i> = 467	Month	11	213.73	< 0.0001
D = 14.99%	Tide	1	84.24	< 0.0001
	Pond*Month	121	758.19	< 0.0001
	Pond*Tide	11	71.4	< 0.0001
	Month*Tide	11	44.65	< 0.0001

For larvae, totals are modelled as well as the number of larvae retained on 0.5 mm and 0.1 mm sieves. Main effects shown are those observed when interactions are not included in the model. D = percentage of additional deviance explained by the final model in comparison to null models. See methods for more details.

Table 3. Shorebird species recorded in our study site and their abundance

Common name	Latin name	Mean count ±SE	Range of counts	Mean number of feeding birds ±SE	Range of feeding birds	% feeding in traditional salines
Dunlin*	<i>Calidris alpina</i>	1750 ± 453	17–15,689	803 ± 262	7–1068	0.3
Black-tailed godwit*	<i>Limosa limosa</i>	1209 ± 254	0–6684	232 ± 56	0–1309	9.5
Curlew sandpiper	<i>Calidris ferruginea</i>	925 ± 220	0–5567	459 ± 122	0–3214	0.0
Redshank	<i>Tringa totanus</i>	693 ± 91	5–2170	366 ± 50	2–1310	5.3
Ringed plover*	<i>Charadrius hiaticula</i>	332 ± 67	0–1780	97 ± 32	0–1182	0.2
Avocet*	<i>Recurvirostra avosetta</i>	309 ± 43	2–1155	42 ± 9	0–227	1.4
Grey plover	<i>Pluvialis squatarola</i>	253 ± 56	0–1313	30 ± 14	0–480	0.2
Kentish plover*	<i>Charadrius alexandrinus</i>	179 ± 50	0–1561	72 ± 30	0–1180	0.0
Little stint	<i>Calidris minuta</i>	166 ± 36	0–888	143 ± 29	0–885	1.0
Black-winged stilt*	<i>Himantopus himantopus</i>	148 ± 33	0–817	97 ± 23	0–572	5.3
Bar-tailed godwit	<i>Limosa lapponica</i>	68 ± 21	0–754	16 ± 13	0–507	0.0
Sanderling	<i>Calidris alba</i>	63 ± 14	0–364	47 ± 11	0–332	0.2
Curlew	<i>Numenius arquata</i>	58 ± 22	0–830	0.07 ± 0.05	0–2	0.0
Spotted redshank	<i>Tringa erythropus</i>	43 ± 12	0–351	28 ± 10	0–306	5.0
Greenshank	<i>Tringa nebularia</i>	25 ± 6	0–202	15 ± 4	0–162	6.3
Turnstone	<i>Arenaria interpres</i>	17 ± 5	0–143	10 ± 3	0–101	4.6
Red knot	<i>Calidris canutus</i>	7.32 ± 4.43	0–166	2.97 ± 1.47	0–47	0.0
Whimbrel	<i>Numenius phaeopus</i>	5.5 ± 3.07	0–121	0.07 ± 0.05	0–2	0.0
Oystercatcher	<i>Haematopus ostralegus</i>	3.95 ± 0.79	0–17	0	0	...
Ruff	<i>Philomachus pugnax</i>	3.1 ± 1.79	0–71	2.2 ± 1.22	0–48	21.6
Little ringed plover	<i>Charadrius dubius</i>	2.07 ± 1.70	0–68	1.65 ± 1.57	0–63	0.0
Common sandpiper	<i>Actitis hypoleucos</i>	0.25 ± 0.08	0–2	0.2 ± 0.07	0–2	75.0
Marsh sandpiper	<i>Tringa stagnatilis</i>	0.15 ± 0.10	0–4	0.02 ± 0.02	0–1	0.0
Red-necked phalarope	<i>Phalaropus lobatus</i>	0.1 ± 0.06	0–2	0.1 ± 0.06	0–2	0.0
Total		6253 ± 758	53–20775	2466 ± 368	49–13,438	2.2

Note figures refer to counts made in the ponds selected for our study (i.e. only part of the salines).

*Highest counts exceeded the 1% threshold for the flyway population used to identify wetlands of international importance for a given species (Delany & Scott, 2002).

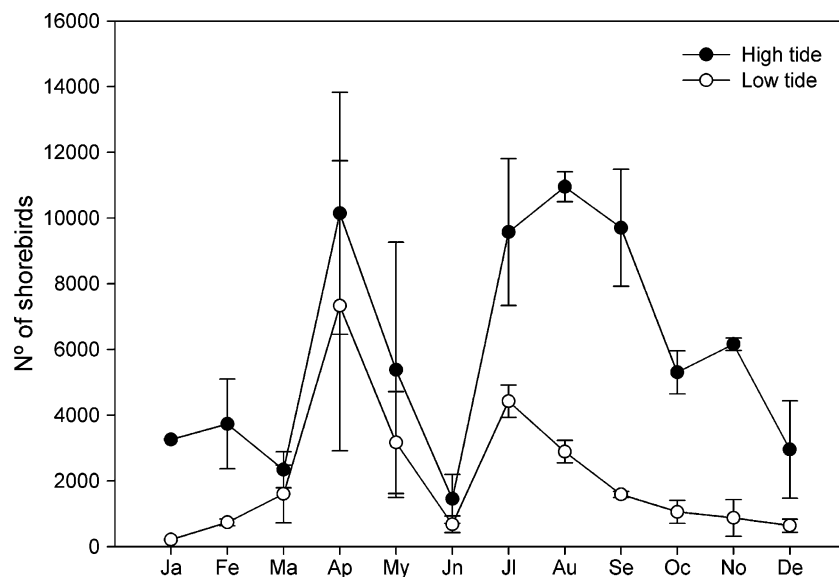


Figure 4. Total number of shorebirds counted (mean \pm SE, $n=4$ counts for each month) in our 12 study ponds in the Odiel salt pans at high and low tide, 2001.

interactions were also highly significant. Thus, we recorded strong spatial, temporal and tidal effects on the distribution of shorebirds that interacted in a complex way.

The seasonal patterns in abundance varied greatly between shorebird species. Amongst the more abundant species (Table 3), dunlins (*Calidris alpina*) and little stints (*Calidris minuta* (Leisler)) showed only a strong spring migration. In contrast, black-tailed godwits (*Limosa limosa*), curlew sandpipers (*Calidris ferruginea*), redshanks (*Tringa tetanus* (L.)), avocets (*Recurvirostra avosetta* (L.)), kentish plovers (*Charadrius alexandrinus* (L.)) and black-winged stilts (*Himantopus himantopus* (L.)) showed only a strong autumn migration. Ringed plovers (*Charadrius hiaticula* (L.)) and grey plovers (*Pluvialis squatarola* (L.)) showed both a strong spring and a strong autumn migration.

Relationship between the abundance of chironomids and of shorebirds

When we analyze the use of the salines by shorebirds throughout the year, we find that the proportion of birds observed feeding was strongly correlated with the availability of chironomid larvae ($r_s=0.88$, $p=0.033$, $n=6$). The proportion of birds feeding was highest in May when the

abundance of chironomid larvae was greatest (Fig. 5). There was also a strong positive correlation between the number of larvae available in each pond and the number of feeding shorebirds (using annual means, $r_s=0.66$, $p=0.019$, $n=12$).

In the traditional salines, a higher proportion of the surface area of ponds is available for foraging (25% on average, compared with 10% for industrial salines, Table 1). Nevertheless, the highest densities of shorebirds were recorded in the industrial salines, where the peaks corresponding to the spring and autumn migrations were very pronounced (Fig. 6). In the traditional salines the highest density was recorded during the winter period in February (Fig. 6). On average, 8.5% of available foraging habitat was found in the traditional salines (Table 1). Thus, 15 of 16 shorebird species with average counts of more than 10 individuals made more use of the industrial salines for foraging than would be expected at random (Table 3).

Discussion

Chironomus salinarius is a chironomid species (complex) that is particularly tolerant of high salinities (Armitage et al., 1995) and is often recorded as the only benthic invertebrate species. In

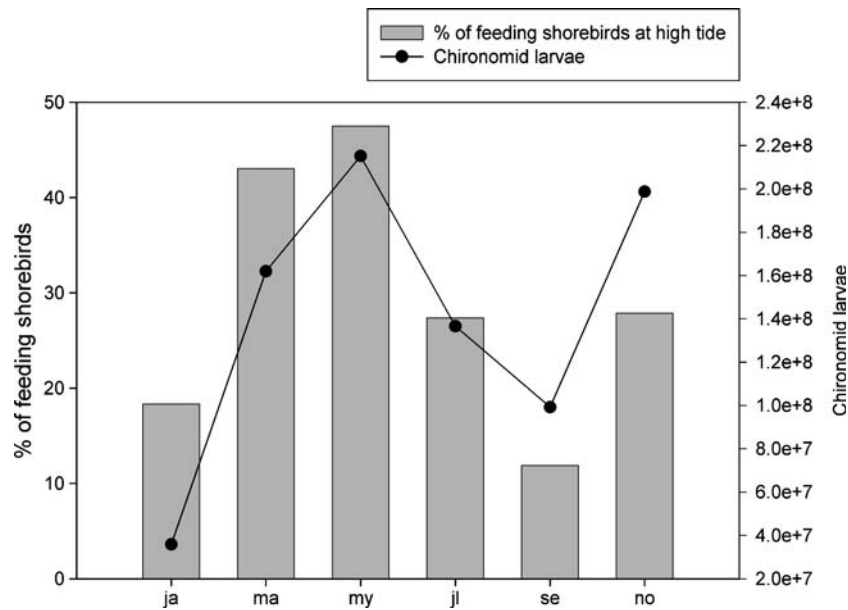


Figure 5. Fluctuations in the percentage of shorebirds that are feeding, compared with changes in the number of chironomid larvae available. Using the bird census conducted at that date closest to the date of benthic sampling, we calculated the proportion of birds present at high tide that were feeding. Using densities of larvae and the surface area of ponds that were available to shorebirds (i.e. ≤ 20 cm), we estimated the number of larvae available.

the nearby Cádiz Bay, this species is thought to have about five generations a year (Arias & Drake, 1994). Such multivoltinism is characteristic of latitudes such as those of southern Spain, where

high temperatures allow high growth rates (Huryn, 1990). The presence of pupae throughout the annual cycle in our samples confirms that this species must have many generations a year, since the

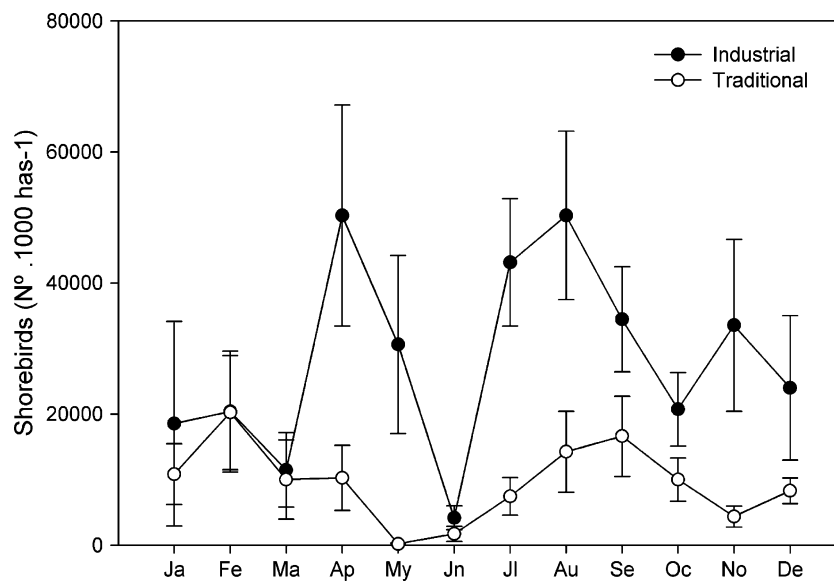


Figure 6. Average monthly density of shorebirds recorded at high tide in industrial and traditional salines. Densities were recorded based on the total surface area of salines.

benthic pupal stage lasts a few days at most (Armitage et al., 1995).

For the salines as a whole, we observed a marked seasonality in the abundance of larvae of this species, with peaks in May and November. This pattern contrasts with those observed in marine soft-bottom habitats in temperate regions, where abundance of invertebrates peaks in winter and spring (Service & Feller, 1992). Our results are also different to those found in a tidal lagoon in Cádiz bay, where the abundance of larvae peaked from late summer until winter (Drake & Arias 1995). This difference is probably related to the differences in habitat and management of water levels at each site (see Drake & Arias 1995). Differences in management of water levels between individual ponds are also likely to explain the strong POND*MONTH interaction we observed at our site.

In our study site, the main salinity gradient is spatial between ponds rather than temporal between months of different temperatures (as observed in other Mediterranean aquatic systems), and we recorded a negative correlation between the salinity of each pond and the larval density. Thus, high salinities allow *C. salinarius* to monopolise benthic resources, but further increases appear to reduce growth and/or survival rates. Similar effects of extreme salinities on the density of chironomid larvae have been recorded in other wetland types (Galat et al., 1988; Hammer et al., 1990). A negative correlation between larval abundance and salinity was also recorded in Cádiz Bay (Arias & Drake, 1994), but it confounds spatial and temporal variation and is hard to interpret.

Chironomid larvae are one of the principal food items of shorebirds in the coastal wetlands of southern Europe (Pérez-Hurtado et al., 1997), unlike northern Europe where polychaetes, gastropods and bivalves tend to be dominant prey (Goss-Custard et al., 1977a; Worrall, 1984; Dit Durell & Kelly, 1990; but see Rehfisch, 1994). The high density and availability of *C. salinarius* (together with that of *Artemia*) makes the Odiel salines an important foraging habitat for shorebirds, especially during the migration periods. During autumn passage, most birds used the salines only at high tide when the tidal marshes were unavailable, leaving to feed in the tidal marshes at low tide. Similar results have been reported in salines

elsewhere (Masero et al., 2000). However, during spring passage we found most shorebirds to remain in the salines at low tide, suggesting that the salines provided a relatively better foraging habitat in spring than in autumn. The strong relationship detected between changes in the density of chironomid larvae and in the numbers of feeding shorebirds suggests that the birds make decisions about feeding in salines and which pond to feed in based largely on the availability of chironomids. Previous studies in other regions have shown that shorebirds respond to variation in prey density, with a positive correlation between prey density and bird density (Goss-Custard, 1970; Goss-Custard et al., 1977a, 1991; Velasquez, 1992). The same pattern appears to occur in the Odiel salines.

Further evidence that changes in the density of chironomid prey determine these changes in the use of salines by foraging shorebirds comes from a diet study of the redshank (Sánchez et al., 2005). Pellets collected in spring 2001 were dominated by invertebrate prey from the salines (chironomid larvae and pupae, and Coleoptera), while those collected in autumn were dominated by prey from the tidal marshes (isopods, bivalves and polychaetes). Of 39 pellets collected in spring, 59% contained chironomid larvae, compared to only 6.6% of 121 pellets from the autumn (Sánchez et al., 2005). Nevertheless, the abundance of chironomid pupae in these pellets (found in 74.4% of pellets in spring and 9.9% in autumn), despite the relative rarity of pupae in the benthos suggests that, as well as feeding on chironomids in the sediments, shorebirds also take pupae as they come to the surface and before the adults have had time to emerge (Sánchez et al., 2005).

Changes in use of the salines by shorebirds will also depend on fluctuations in the availability of prey in tidal marshes between seasons. We have no data to assess how prey abundance in tidal marshes differed between spring and autumn. Between the spring and autumn migrations, we also observed an important shift in the composition of the shorebird community, e.g. with relatively more dunlins and little stints in spring and more black-tailed godwits, avocets and black-winged stilts in autumn. Given the differences in diet and habitat use by these species, these changes may also have influenced the relative increase in the use of salines for foraging during the spring migration.

We found that the more traditional manner of salt production did not produce a higher availability of chironomid prey, and did not provide a preferred habitat for waders. Waders were found at a higher density in the industrial salines, perhaps because these ponds were larger than traditional ones (Fig. 1) and thus permit more effective vigilance against predators (Cayford, 1993), and because the traditional salines suffered more disturbance from a road.

The extent to which a high production of chironomid larvae is translated into a good foraging habitat for shorebirds depends largely on appropriate management of water levels (Velasquez, 1992; Rehfisch, 1994). Smaller shorebird species are those that are most limited in the depth range where they can feed, and also those most dependent on alternative, artificial habitats such as salines since their low body mass and high metabolic rate requires them to feed practically all day round (Goss-Custard et al., 1977b; Fasola & Canova, 1993). Some species such as avocets are less limited by water depth, as they also feed on *Artemia* in deeper parts of our study site (by swimming and taking brine shrimps close to the surface).

The high ecological and conservation value of the Odiel salines is obvious given the numbers and diversity of birds that it supports. For six different species, our partial counts sometimes exceeded the 1% threshold for the flyway population used to identify wetlands of international importance for a given species (Table 3). The salines offer both a good food supply and disturbance-free areas for resting, two key factors that determine the habitat use by shorebirds (Goss-Custard, 1969). Nevertheless, the quality of the habitat as a foraging area could be increased by changing management practices to increase the accessibility of chironomids to shorebirds, and particularly by using drawdowns to increase access to deeper areas during the migration periods. At the moment, the proportion of chironomid production that is consumed by birds is relatively low compared to lagoons managed specifically for birds (Rehfisch, 1994). In most of the ponds, the majority of the benthos is inaccessible to shorebirds throughout the year (Table 1). On the other hand, in those areas of our study ponds where shorebirds are able to feed, enclosure experiments show that shorebird predation has a “top-down” effect in regulating

the density of chironomid larvae (Sánchez et al., 2006). This suggests that the foraging intake of a shorebird feeding at a given moment is likely to be limited by shorebird use of the site in the previous weeks, and underlines the potential benefits of drawdowns so that the Odiel salines can provide a more efficient refuelling site for a larger number of migratory shorebirds.

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