

Shorebird predation affects density, biomass, and size distribution of benthic chironomids in salt pans: an enclosure experiment

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Abstract. *Chironomus salinarius* larvae are the dominant benthic organisms in the salt pans of the Odiel marshes, southwest Spain, an area internationally important for migratory shorebirds. Predator enclosures were used to examine the effects of shorebirds on chironomid larvae for periods of 32 to 46 d during spring migration. During the 1st experimental period, shorebird numbers were relatively low, peaking at 4 feeding birds/ha. During the 2nd period, shorebird numbers were higher, peaking at 32 feeding birds/ha. The changes in larval density and biomass from the beginning to the end of each period were significantly greater in enclosures than in controls. Predation decreased larval density by 35% and 32% during periods 1 and 2, respectively. Predation decreased larval biomass by 37% and 49% during periods 1 and 2, respectively. Predation also changed prey size distributions, reducing the proportion of larger larvae. These effects did not vary significantly between periods, suggesting that increased predation in period 2 was compensated for by higher larval growth or recruitment in period 2. Variation in predation effects was not related to variation in the initial larval density or biomass in a given plot.

Key words: shorebirds, predation, enclosures, *Chironomus salinarius*, size distribution, salt pans, Odiel marshes.

Predation plays a fundamental role in structuring benthic invertebrate communities (Thrush 1999). Chironomid larvae are extremely abundant or dominant in the benthos in a variety of aquatic ecosystems, and their abundance and size distribution often are influenced by insect or fish predators (Armitage et al. 1995, Kornijów 1997, Batzer 1998). Chironomid larvae are also important prey for a variety of waterbirds (Krapu and Reinecke 1992, Rehfish 1994), yet very little is known about the influence of avian predators on chironomid communities (Armitage et al. 1995). Only one study (Székely and Bamberger 1992) has shown an influence of avian predation on larval abundance, and no study has shown an influence on larval size.

Hypersaline systems such as salt pans have relatively simple food webs (Britton and Johnson 1987), making them ideal for studies of predator–prey interactions. More than 20,000 shorebirds use salt pans

in the Odiel Marshes in southwest Spain during migration. Chironomid larvae are the dominant invertebrates in the benthos, and they are a major prey item of shorebirds (Sánchez et al. 2005, 2006). Shorebirds are episodic predators likely to have major effects on invertebrate prey because they have high foraging intake and energy demands, and they are present in large concentrations at stopover and wintering sites (Wilson 1991, Masero and Pérez-Hurtado 2001, Kvist and Lindström 2003). Shorebirds may double their body mass in 20 d during migration (Hicklin and Smith 1984). They can reduce benthic prey abundance (Weber and Haig 1997, Sutherland et al. 2000) and influence prey size (Botto et al. 1998) in intertidal ecosystems. However, to our knowledge, their effect on prey abundance or size in salt pans has not yet been studied.

We investigated the impact of predation by shorebirds on the population of benthic chironomids in the Odiel salt pans. Enclosure experiments were used to compare the effects of shorebirds on the density,

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biomass, and size of larvae at 2 different bird densities at the beginning and peak of spring migration. The hypotheses that predation effects would be more pronounced during the period with higher bird density and in plots with higher prey density or biomass were tested.

Study Site

Our study was carried out in spring 2002 within the 1185 ha of salt pans in the Odiel Marshes (lat 37°17'N, long 6°55'W) at the mouths of the Odiel and Tinto rivers. The Odiel Marshes are protected as a Natural Park by the regional government, as a UNESCO Biosphere Reserve wetland of international importance under the Ramsar Convention, and as a Specially Protected Area of the European Union (Bernués 1998). The salt pans support internationally important numbers of Black-winged Stilt, *Himantopus himantopus*, Kentish Plover, *Charadrius alexandrinus*, Avocet, *Recurvirostra avosetta*, Ringed Plover, *Charadrius hiaticula*, Black-tailed Godwit, *Limosa limosa*, and Dunlin, *Calidris alpina* (Sánchez et al. 2006).

Habitats in the salt pans exist along a gradient of salinity generated by salt production. Our study was conducted in secondary evaporation ponds that provide shorebirds with good access to abundant chironomids (Sánchez et al. 2006). *Chironomus salinarius* Kieffer, a widespread species complex requiring further taxonomic study (Armitage et al. 1995), was the only chironomid species recorded in the benthos of the secondary evaporation ponds. This species is multivoltine and has an average of ~5 generations/y in another coastal system in southwest Spain 100 km from the Odiel Marshes (Drake and Arias 1995). No fish, crabs, or shrimps were present in the ponds, and shorebirds were the only abundant predators in the area studied. Flamingos and other waterbirds did not use the study area during the experiment. No other invertebrates recorded in the wetlands are known to prey on *C. salinarius* larvae (MIS and AJG, unpublished data).

Methods

Exclosure experiments were conducted in 4 ponds during 2 different periods. Period 1 coincided with the beginning of spring migration. Exclosures were in place for 32 to 38 d between 12 February 2002 and 26 March 2002. Period 2 included the peak of migration. Exclosures were in place for 37 to 46 d between 19 March 2002 and 3 May 2002. These dates were chosen on the basis of regular censuses of shorebirds during the same months in 2001.

At the end of period 1, exclosures and controls were moved to new positions 2 m from their original

positions. Because of the time required to extract invertebrates from the samples in vivo in the laboratory (see below), all ponds could not be sampled on the same day. The slight overlap between the 2 periods was caused by the delay between sampling and moving the exclosures and controls in the first and last ponds. However, all exclosures and controls were established or sampled on the same day within a given pond.

Exclosures

In each period, 20 exclosures paired with 20 controls were installed in the salt pans. Five pairs of controls and exclosures were established in the 0- to 20-cm water-depth range used by feeding shorebirds in each of 4 ponds. Pairs were separated by 20 to 30 m. The control and exclosure in each pair were placed at the same water depth, separated by 5 m. The 2 structures varied slightly in their relative position to the pond edge, but the assignment of replicates to locations was random.

Invertebrate sampling

At the beginning and end of each period, 3 samples of benthos were taken from random locations within each exclosure and control. A 5-cm-diameter corer was used to sample the top 3 cm of soft sediments overlying an impenetrable clay bed. Different halves (chosen at random) of the 1 × 1 m plots were sampled at the beginning and end of each period to avoid resampling disturbed sediments. Each sample was washed through 0.5-mm and 0.1-mm sieves within 24 h of collection. Invertebrates were separated from remaining sediments by flotation in saturated brine collected from crystallization ponds. The invertebrates were counted and stored in 70% alcohol.

Chironomid larvae retained on the 0.5-mm sieve were measured to the nearest 10 µm using an image analyzer. Body-length data were transformed into estimated dry mass using the regression equation of Smock (1980). The actual (not estimated) dry mass of larvae retained on different sieves was measured for 24 samples taken at different times and in different periods. The dry mass of the smaller larvae retained on the 0.1-mm sieve was relatively unimportant (see results), so dry mass of larvae retained on the 0.1-mm sieve was not estimated for the remaining samples.

Censuses of shorebirds

Shorebirds in the 123-ha study area were censused monthly from January to May 2002. The total number of individuals present and the number of individuals that were feeding were recorded for each shorebird species. Censuses were carried out at high tide when

tidal flats were unavailable as alternative foraging habitat and shorebird densities in the salt pans were highest (Sánchez et al. 2006).

Statistical analyses

Data from the 3 benthic samples taken within each enclosure or control were pooled before analysis. Two of the enclosure/control pairs were removed from the analyses for period 2 because they dried after a drop in water level.

Generalized mixed Linear Models (GLMs, McCullagh and Nelder 1989) were used to analyze the effects of treatment (enclosure or control) and experimental period on density, estimated biomass, and size of chironomid larvae. Pond and enclosure/control pairs nested within ponds were included as random factors using the GLIMMIX macro in SAS (version 8.2, SAS Institute, Cary, North Carolina). Link functions were used to transform the dependent variables to meet assumptions of GLM. The link function in GLM specifies a nonlinear transformation of the predicted values so that the distribution of predicted values is one of several special members of the exponential family of distributions (e.g., Poisson, binomial). Various link functions (see McCullagh and Nelder 1989) are used commonly, depending on the assumed distribution of the dependent variable values. They include the identity link $f(z) = z$ and the logit link $f(z) = \log(z/[1 - z])$.

The density of larvae (number/3 samples) from the beginning to the end of a period was represented as $(\log_{10}[\text{final number} + 1] - \log_{10}[\text{initial number} + 1])$, and the estimated biomass (mg/3 samples) was represented in a similar way to overcome heteroscedasticity. An identity link function and normal error distribution were used to model density, biomass, and mean size of larvae retained on a 0.5-mm sieve at the end of each experimental period.

Tests of the effects of each predictor on change in density, change in biomass, and mean larval size were done using F -statistics. The deviance of each fitted GLM 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 explanatory power of the model (Crawley 1993). The water depth at each enclosure/control pair was considered initially as an additional predictor (results not shown). However, no evidence was found for a depth \times treatment interaction as would have been expected had predation effects varied with depth. Period \times treatment interactions were not significant ($p > 0.37$) and were excluded from final models.

A logistic regression was used to analyze size

distributions of larvae in the samples from the end of each experimental period. A logit link and binomial error distribution were used to model the dependent variable, which was the ratio of the number of larvae retained on the 0.5-mm sieve (numerator) to the total number retained on the 0.5-mm and 0.1-mm sieves (denominator) (Crawley 1993).

GLMs were used to test whether the enclosure effect in a given 1×1 m plot depended on the density or biomass of larvae in that plot at the beginning of an experiment. The difference between the density in an enclosure and its paired control at the end of a period was used as the dependent variable (transformed as $\log_{10}([\text{final enclosure} + 1]/[\text{final control} + 1])$, and the average density for each pair at the beginning of a period as a predictor. Period was a fixed factor and pond was a random factor. The dependent variable was modeled using an identity link and a normal error distribution. This analysis was repeated using biomass instead of density. The interactions between initial density or biomass and period were not significant.

Matched-paired t -tests were used to analyze the change in the density and biomass of larvae in controls between the beginning and end of each period.

Results

Chironomus salinarius was the dominant invertebrate in the sediments throughout the study (Table 1). In period 1, *C. salinarius* larvae and small numbers of *C. salinarius* pupae were the only invertebrates recorded, whereas in period 2, small numbers of *Ochthebius* beetles also were recorded.

Larval density

Density of larvae did not differ between controls and enclosures at the beginning of each experimental period (Fig. 1A). At the end of period 1, 35.0% more chironomid larvae were found in enclosures than in controls. At the end of period 2, 32.2% more larvae were found in enclosures than in controls. In spite of these enclosure effects, the density of larvae in controls did not decrease during the study (Fig. 1A). Density in controls did not change between the beginning and end of period 1 ($t = -0.95$, $p = 0.35$), but density in controls increased significantly between the beginning and end of period 2 ($t = -3.69$, $p = 0.002$).

Density increased significantly more in enclosures than in controls (GLM testing partial effects of treatment and period, $F_{1,49} = 5.83$, $p = 0.019$; Fig. 1A), and density increased more in period 2 than in period 1 ($F_{1,49} = 4.7$, $p = 0.035$). The period \times treatment interaction was not significant ($F_{1,48} = 0.78$, $p = 0.38$). Initial larval density did not affect the difference in

TABLE 1. Proportion of samples in which benthic invertebrates were recorded (PO) and the % of total individuals collected in the sampling period (PI) that they represented.

	Period 1 (n = 240)		Period 2 (n = 216)	
	PO (%)	PI (%)	PO (%)	PI (%)
<i>Chironomus salinarius</i> larvae	100	98.3	100	99
<i>C. salinarius</i> pupae	19.2	1.7	21.3	0.92
<i>Ochthebius</i> spp.	0	0	0.9	0.026

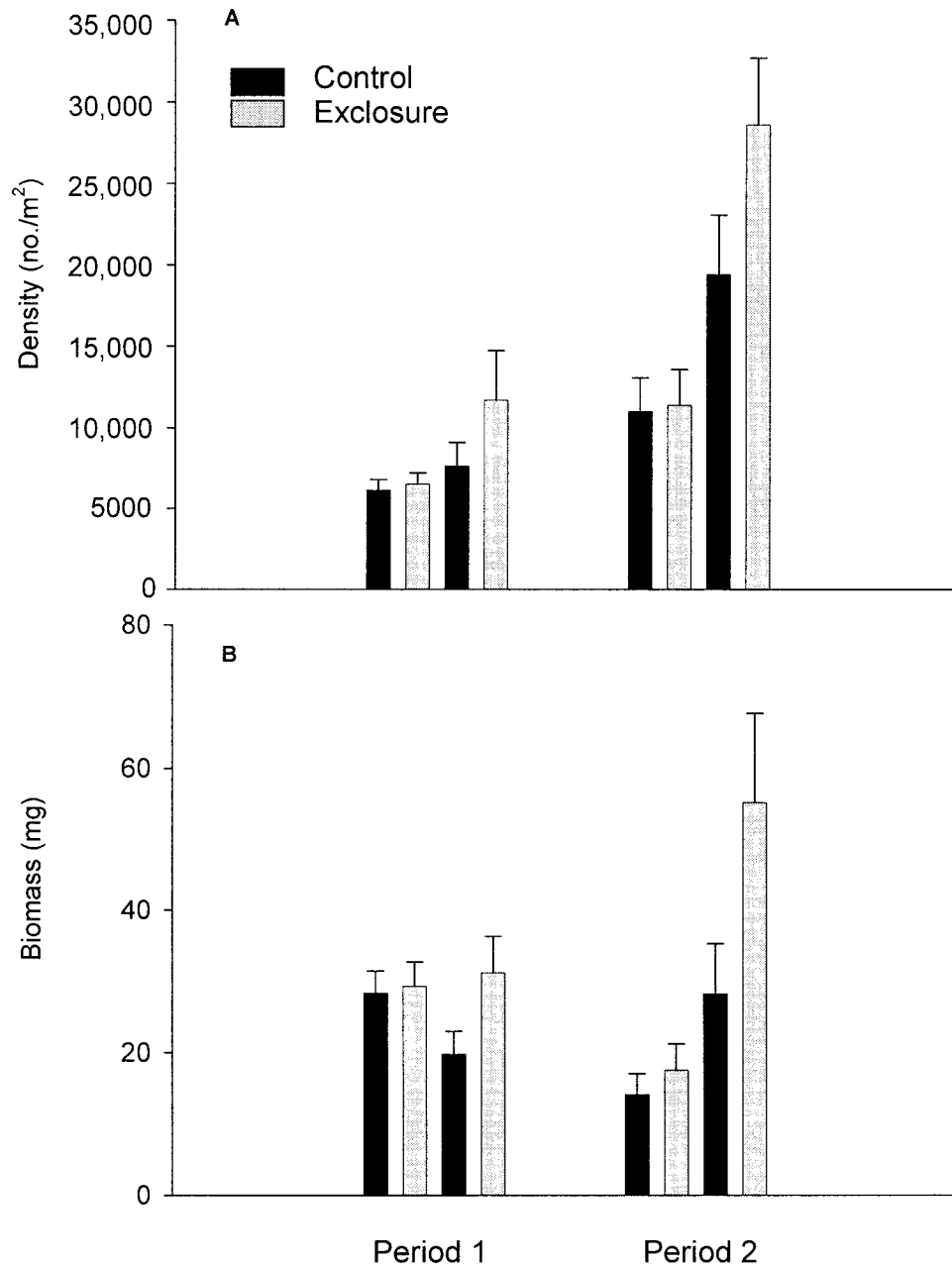


FIG. 1. Mean (+1 SE) density (A) and estimated biomass (B) of *Chironomus salinarius* larvae at the beginning (first 2 bars in the set) and end (last 2 bars in the set) of exclosure experiments.

density between exclosures and controls at the end of experimental periods ($r = -0.02$, $F_{1,31} = 0.03$, $p = 0.85$).

Larval biomass

The dry mass of small larvae retained on the 0.1-mm sieve made up only $3.8 \pm 1.8\%$ (mean ± 1 SE, $n = 24$) of total biomass of larvae from the 0.1-mm and 0.5-sieves combined. The estimated biomass of larvae retained on the 0.5-mm sieve did not differ between controls and exclosures at the beginning of each experimental period (Fig. 1B). At the end of period 1, biomass was 36.7% higher in exclosures than in controls. At the end of period 2, biomass was 48.9% higher in exclosures than in controls. Biomass decreased significantly in controls during period 1 ($t = 2.37$, $p = 0.028$) but did not change significantly during period 2 ($t = -2.00$, $p = 0.062$).

Biomass increased significantly more in exclosures than in controls (GLM testing partial effects of treatment and period, $F_{1,49} = 17.86$, $p = 0.0001$; Fig. 1B), and biomass increased more in period 2 than in period 1 ($F_{1,49} = 41.42$, $p < 0.0001$). The period \times treatment interaction was not significant ($F_{1,48} = 0.03$, $p = 0.86$). Initial larval biomass did not affect the difference in biomass between exclosures and controls at the end of experimental periods ($r = -0.19$, $F_{1,31} = 1.30$, $p = 0.26$).

Larval size distributions

The larvae retained on the 0.5-mm sieve had a bimodal size distribution indicating the presence of 3rd and 4th (final) instars (Fig. 2). Mean size at the ends of the experimental periods did not differ between exclosures and controls (GLM, period 1: $F_{1,18} = 1.07$, $p > 0.32$, period 2: $F_{1,17} = 1.59$, $p > 0.22$). Mean size was significantly larger at the end of period 1 than period 2 (controls: $F_{1,11} = 26.31$, $p = 0.0003$, exclosures: $F_{1,12} = 31.34$, $p > 0.0001$).

At the end of period 1, the proportion of larvae retained on the 0.5-mm sieve was $43.9 \pm 5.5\%$ (mean ± 1 SE) for controls and $52.1 \pm 5.6\%$ for exclosures. At the end of period 2, the proportion was $47.8 \pm 6.1\%$ for controls and $50.8 \pm 5.8\%$ for exclosures. The proportion of larvae retained on the 0.5-mm sieve was significantly higher in exclosures than in controls (GLM testing partial effects of treatment and period, $F_{1,49} = 5.02$, $p = 0.03$), but did not differ significantly between periods ($F_{1,49} = 2.64$, $p = 0.11$). The period \times treatment interaction was not significant ($F_{1,48} = 0.82$, $p = 0.37$).

Shorebird censuses

In total, 18 species of shorebirds were recorded. All 18 species were observed feeding in the salt pans, and

12 species were observed feeding inside our control plots (Table 2). During period 1, numbers of migrating shorebirds in the study area were relatively low (Fig. 3) with a maximum count of 3118, of which 13.9% were feeding (Table 2). Numbers increased during period 2 (Fig. 3) to a maximum of 4835, of which 80.7% were feeding (Table 2). The taxonomic composition of the shorebird community shifted between periods 1 and 2. Redshanks, *Tringa totanus*, Avocets, and Black-tailed Godwits were relatively abundant during period 1, whereas Curlew Sandpipers, *Calidris ferruginea*, and Dunlins were dominant during period 2 (Table 2). Fifty-three percent of the 3904 birds observed feeding at the end of period 2 (30 April) were Curlew Sandpipers and 43% were Dunlins.

Discussion

Shorebird effects on chironomid larvae

We recorded strong effects of exclosures on the density, size distribution, and especially, biomass of chironomid larvae. We observed no effects of exclosures on the environment. In the absence of other predators, our exclosure effects can be explained only by predation by shorebirds. Moreover, our experiments may have underestimated the effects of shorebirds on chironomid larvae because the net movement of mobile benthic chironomid larvae may have been out of our small exclosures where densities were elevated (Wilson 1989).

Other authors have shown that shorebirds have high intake rates and have suggested that they are likely to consume a significant fraction of the production of benthic chironomid larvae (Rehfish 1994, Masero and Pérez-Hurtado 2001). However, exclosure experiments such as ours are needed to demonstrate that shorebird predation leads to a reduction in the density or standing crop of larvae because loss of larvae via predation potentially may be compensated by other effects. In particular, reduced interspecific competition may lead to lower mortality rates or higher growth rates in chironomid larvae (Armitage et al. 1995). Indeed, experiments excluding shorebirds or other avian predators have not always produced detectable effects on chironomids (Smith et al. 1986, Ashley et al. 2000) or other benthic invertebrates (Raffaelli and Milne 1987, Wilson 1991, Lopes et al. 2000). To our knowledge, the only other study in which avian predation has been shown to reduce the density of chironomid larvae is one conducted in an inland oxbow lake (Székely and Bamberger 1992).

We did not measure chironomid production or density-dependent feedback processes, so our results cannot be translated into a precise estimate of the

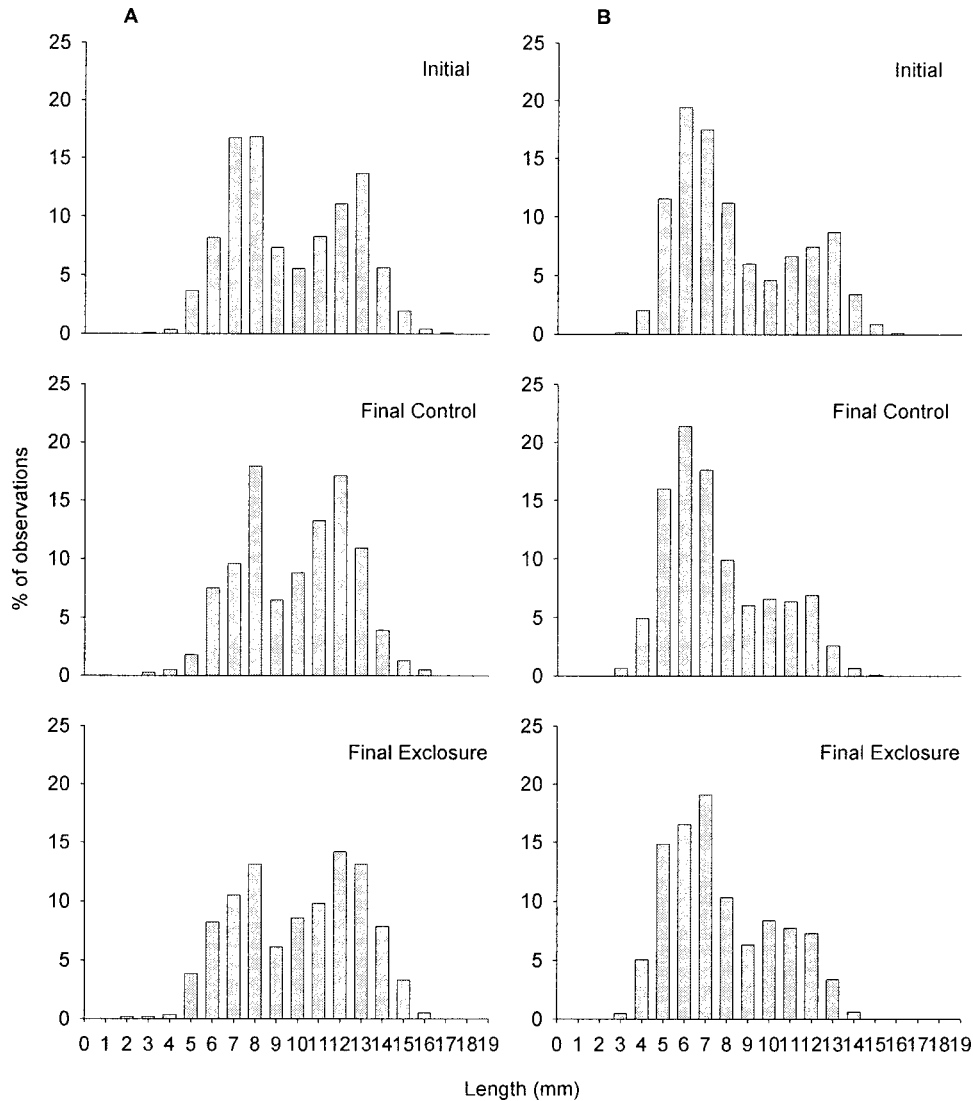


FIG. 2. Size-frequency distribution of *Chironomus salinarius* larvae at the beginning and end of exclusion experiments for period 1 (A) and period 2 (B). Only larvae retained on a 0.5-mm sieve are included. Initial data were pooled for controls and exclusions.

proportion of larval production or standing crop consumed by shorebirds (Mitchell and Wass 1996). Nevertheless, our results suggest top-down control of chironomids by shorebirds and indicate that shorebirds have an important influence on chironomid dynamics in this system, at least during spring migration.

Size-selective predation

The highly significant effect of shorebird predation on larval biomass was a result of significant decreases in both larval density and the proportion of large larvae. Shorebirds appear to have selected larvae large enough to be retained on a 0.5-mm sieve (mean length ± 1 SE = 8.09 \pm 0.04 mm, range = 1.55–16.78 mm) over larvae that were retained only on a 0.1-mm

sieve (mainly 1st and 2nd instars). To our knowledge, our study provides the first evidence of size-selective predation on chironomid larvae by shorebirds, and the first direct evidence that avian predation can change the size distribution of chironomid prey. Size-selective predation on invertebrates by shorebirds is well documented (Goss-Custard 1977, Worrall 1984, Dierschke et al. 1999), but size-selective predation has led to a measurable change in the size distribution of prey in only a few studies. Botto et al. (1998) recorded an increase in the mean size of polychaetes following shorebird predation. Thrush et al. (1994) recorded changes in bivalve size in shorebird exclusions, but they attributed the changes to interactions between adult and juvenile bivalves. We found significant evidence that shorebird predation decreases the

TABLE 2. Total numbers of shorebirds counted from January to May 2002 in the 123-ha study area. Numbers in parentheses are the number of birds that were feeding. * indicates species seen feeding in control plots.

Shorebird species	30 January	28 February	30 March	30 April	29 May
<i>Tringa nebularia</i> *	12 (4)	17 (1)	19 (5)	14 (11)	0 (0)
<i>Limosa limosa</i> *	164 (146)	36 (3)	0 (0)	0 (0)	0 (0)
<i>Limosa lapponica</i>	0 (0)	214 (1)	80 (0)	61 (14)	59 (2)
<i>Tringa totanus</i> *	106 (65)	214 (73)	325 (155)	200 (106)	77 (26)
<i>Tringa erythropus</i> *	0 (0)	1 (1)	53 (22)	4 (4)	0 (0)
<i>Actitis hypoleucos</i>	0 (0)	0 (0)	8 (0)	1 (1)	0 (0)
<i>Recurvirostra avosetta</i> *	101 (10)	145 (126)	8 (7)	2 (2)	2 (2)
<i>Calidris alpina</i> *	9 (9)	16 (13)	5 (5)	2149 (1684)	321 (265)
<i>Calidris canutus</i>	0 (0)	0 (0)	0 (0)	13 (0)	44 (38)
<i>Calidris minuta</i> *	3 (3)	3 (3)	3 (1)	1 (1)	0 (0)
<i>Calidris alba</i> *	12 (12)	14 (9)	0 (0)	17 (14)	141 (131)
<i>Calidris ferruginea</i> *	0 (0)	1951 (165)	6 (6)	2306 (2052)	9 (9)
<i>Charadrius hiaticula</i> *	0 (0)	0 (0)	0 (0)	12 (8)	25 (17)
<i>Charadrius alexandrinus</i>	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Pluvialis squatarola</i> *	0 (0)	364 (0)	131 (0)	48 (5)	29 (8)
<i>Himantopus himantopus</i> *	31 (15)	139 (35)	250 (118)	0 (0)	3 (3)
<i>Arenaria interpres</i>	1 (0)	2 (2)	0 (0)	7 (2)	1 (1)
<i>Philomachus pugnax</i>	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)
Total	440 (265)	3118 (434)	880 (319)	4835 (3904)	711 (502)

proportion of chironomid larvae that are large enough to be retained on a 0.5-mm sieve, but no evidence that it influences the size distribution of these larger larvae (Fig. 2). In other studies, size-selective predation by shorebirds did not influence

the size distribution of their prey (e.g., Weber and Haig 1997). Hence, we cannot rule out the possibility that shorebirds also showed prey-size selection within the range of larvae large enough to be retained on the 0.5-mm sieve.

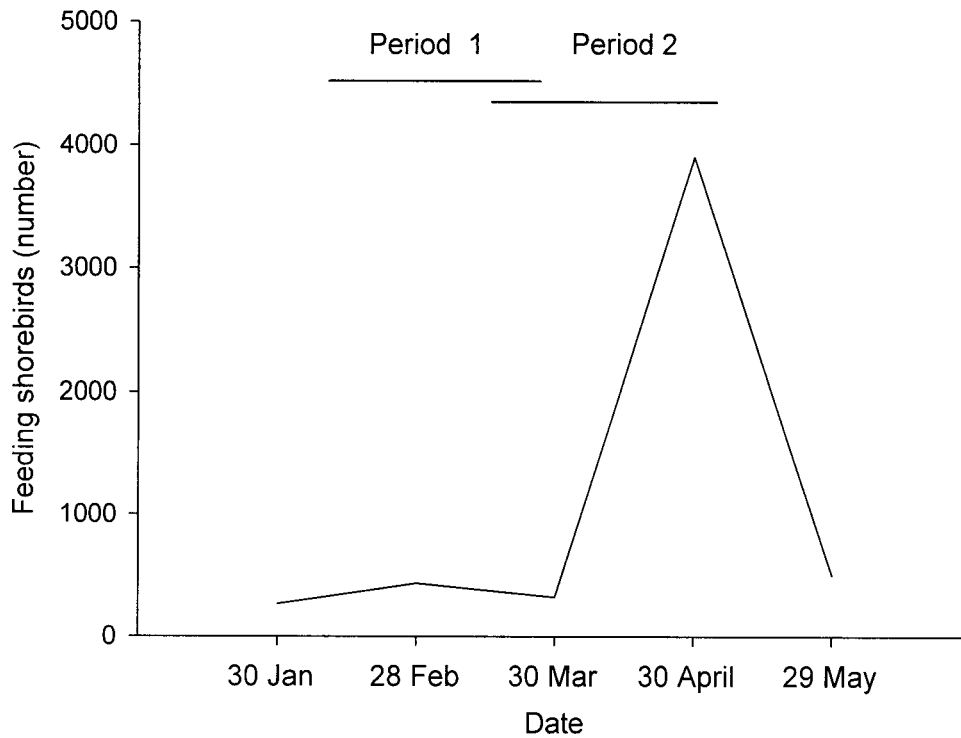


FIG. 3. Numbers of shorebirds feeding in the study area in relation to the timing of the enclosure experiments in the Odier salt pans.

Our results may not have been a simple consequence of size selection by shorebirds. Some authors have attributed size-selective predation on benthic invertebrates by vertebrate predators to the vertical stratification of invertebrates by size within the sediments, and they have suggested that smaller polychaetes or chironomids were selected because they were closer to the sediment surface (Hershey 1985, Botto et al. 1998). We doubt that larger larvae in our study were selected because they were more accessible than small larvae. The smallest 1st instars were likely to have been particularly close to the sediment surface because 1st instars are the principal stage for dispersal through the water column (Armitage et al. 1995). Moreover, only 3 cm of sediments, all of which were accessible to most of the shorebird species, were sampled in our study.

In soft-bottom habitats, the effects of exclusion experiments on invertebrate size distributions can be complicated by interactions between different size classes of the dominant prey (Thrush et al. 1994) because presence of predators can suppress prey growth rates (Nakaoka 2000). The effects of exclusion experiments on invertebrate size distributions also can be complicated by the impact of foraging activities on the sediments (bioturbation, Hines et al. 1990).

Factors influencing predation

Predation effects were not related to initial larval biomass or density, suggesting that shorebirds did not feed preferentially in plots where prey abundance was highest. Cummings et al. (1997) found that shorebirds did not increase their foraging intake in small plots where prey abundance was increased, and they suggested that shorebirds show aggregative responses only at spatial scales larger than small plots. In the Odiel Marshes, shorebirds select those salt pans with higher densities of larvae (Sánchez et al. 2006).

Predation effects were not related to the depth of the water column (at least over the 0–20-cm range studied). Different shorebird species may respond differently to variation in depth or larval size when foraging optimally. Perhaps no overall optimal foraging response was detectable at a community level in our study because of the range of shorebird species present and the way in which they partitioned the habitat among different water depths (Ntiamoa-Baidu et al. 1998).

The number of foraging shorebirds was much greater in period 2 than in period 1, but this difference was not reflected in significant differences in observed predation effects. Detectable predation effects did not increase as predator abundance increased (contrary to

Botto et al. 1998), and even relatively low numbers of shorebirds produced detectable predation effects. Indeed, larval biomass in controls decreased significantly during period 1 but not during period 2.

Higher predation rates in period 2 than in period 1 may have been compensated for by higher larval recruitment or growth rates in period 2 than in period 1. Both recruitment and growth rates may have increased between early February and late April in association with increased water temperature (Drake and Arias 1995). We consider it unlikely that our results could be explained by a higher rate of larval emigration from the exclosures in period 2 than period 1 because larval density was higher outside exclosures in period 2 than in period 1 (Fig. 1).

Our results suggest that the effects of predation on benthic prey populations may depend on the timing of the predation in relation to larval life cycles, as well as on the intensity of predation. A relatively small amount of consumption during a period of low recruitment or growth may have greater consequences for prey populations than a much greater amount of consumption at a time of peak productivity (Mitchell and Wass 1996).

Consequences for migratory shorebirds

Our results indicate that the availability of chironomid prey to a migratory shorebird depends on the timing of the arrival of the bird at the marsh because larval abundance varies significantly with date. Moreover, larval availability also should depend on the number of birds on the marsh before an individual bird arrives because predation by earlier arrivals will reduce the availability of prey at a given moment. The foraging intake rates of shorebirds decrease as the density of benthic midge larvae decreases (Székely and Bamberger 1992). Thus, decisions on the timing of migration may be influenced by prey depletion at stopover sites (Schneider and Harrington 1981) such as the Odiel Marshes. These changes in prey abundance and intake rates also may influence the time birds need to spend at stopover sites to reach the body condition required to continue on to breeding sites. Any delay in arrival at breeding sites is likely to reduce breeding success (Sandercock et al. 1999).

Our results cannot be attributed to a single predator species. All shorebird species in our study site feed on chironomid larvae (MIS, personal observation), and most species were seen feeding inside our experimental controls (Table 2). Taken together, our results suggest that interspecific competition between shorebird species may be an important process in this system.

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