

SEASONAL VARIATION IN SPECIES COMPOSITION AND LARVAL SIZE OF THE BENTHIC CHIRONOMID COMMUNITIES IN BRACKISH WETLANDS IN SOUTHERN ALICANTE, SPAIN

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Abstract: Benthic Chironomidae were studied in two shallow, brackish, eutrophic wetlands in Alicante province in eastern Spain (Levante lake in El Hondo Natural Park and Múrtulas ponds in Santa Pola Natural Park). Core samples were taken monthly from eight points in each site from March to August 1999. Levante was more eutrophic, less saline, and held more and larger chironomid larvae than Múrtulas. Larvae of six taxa were identified at Levante and five at Múrtulas. *Chironomus apralinus* and *C. salinarius* morphotypes dominated at Levante, whereas *Tanytarsus* spp. and *C. salinarius* dominated at Múrtulas. In generalized linear models, there were significant effects of site, month, and site X month interactions on larval size at both family and taxon levels. On average, *C. salinarius* larvae were larger at MUR, probably due to a lower proportion of smaller instars and lower growth rates. Although the overall trend was for a reduction in mean larval size over time in both wetlands, mean size peaked in March at Levante and in May at Múrtulas.

Key Words: chironomidae, size distribution, *Chironomus*, *Tanytarsus*, *Procladius*, benthic larvae, seasonal variation

INTRODUCTION

When compared to the situation in northern Europe, there is still much uncertainty about the taxonomy of Chironomidae in the Mediterranean region. The classification of *Chironomus* species in Spain is incomplete, pending detailed comparison of larval, exuvial, and adult material (J. Casas pers. comm.). To date, studies of benthic chironomids in lentic wetlands in Spain have concentrated on reservoirs, mountain lakes, and coastal lagoons (Drake and Arias 1995, Real et al. 2000). Here, we present a first examination of the benthic larval

community present in two shallow inland wetlands in southern Alicante that differ in size and trophic status. We quantify the changes in abundance of different larval morphotypes over the spring and summer period and use exuvial and adult material to aid species identification. We also quantify the changes in larval size for different taxa in order to shed light on their life cycles in these wetlands and to establish whether these cycles are themselves affected by wetland type. We also look for correlations between larval density and larval size to assess whether interspecific competition affects larval growth (Tokeshi 1995, Batzer et al. 1997).

Table 1. Details of the two wetlands and points sampled. Depth difference = difference between the shallowest and deepest sampling points in each site, Turbidity = range of Secchi disk depth (MUR was too shallow to measure but had a lower turbidity). For DP (depth at the sampling points), CON (conductivity), TMP (temperature at a depth of 5 cm), DEM (distance to emergent vegetation), SS (suspended solids), and Chlorophyll *a*, we present mean \pm s.d. and the range observed (in parentheses) over the study period. The Community of Irrigators of El Hondo provided data on suspended solids and chlorophyll *a*, and at LEV they recorded maxima of 435 $\mu\text{g l}^{-1}$ phosphates, 2.9 mg l^{-1} nitrates and 1 mg l^{-1} nitrites. Data for three ponds at MUR are combined (giving total surface area, maximum depth of the deepest pond, etc).

	LEV	MUR
Surface area (ha)	405	7
Maximum depth (cm)	150	50
Depth difference	27.9	23.5
Turbidity (cm)	19.8 \pm 6.7 (12-49)	—
DP (cm)	46.4 \pm 17.9 (2-69)	15.2 \pm 10.3 (0.01-32)
CON (mS cm^{-1})	8.8 \pm 3.9 (6.2-17.6)	16.8 \pm 3.2 (10.8-22.3)
TMP ($^{\circ}\text{C}$)	21.5 \pm 6.4 (9.6-29.3)	22.6 \pm 6.1 (11.5-30.7)
DEM (m)	7.2 \pm 12.6 (0.1-50)	4.3 \pm 2.8 (0.1-10)
SS (mg l^{-1})	38.8 \pm 8.2 (30-49)	—
Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)	56.5 \pm 38.6 (9.3-91.3)	—

Despite the enormous importance of the southern Alicante wetlands for waterbirds and their protection under the International Convention on Wetlands as Ramsar sites (Bernués 1998), there are no previous studies of the benthos in these wetlands (see Rodrigo et al. 2001 for a study of plankton).

STUDY SITES

El Hondo is a complex of 25 brackish wetlands (total 1,650 ha) in the south of Alicante province, Spain (38°11'N, 00°45'W) including two shallow lakes (total 1,100 ha) used as reservoirs to store irrigation water. El Hondo is protected as a Natural Park (Viñals et al. 2001). We chose one of the storage lakes, Levante (LEV), as one of two study sites (Table 1). Large *Phragmites australis* (Cav.) Trin. reedbeds form the dominant emergent vegetation at LEV, with smaller areas of *Scirpus litoralis* Schrader and other species (Cirujano et al. 1995). Submerged vegetation is dominated by *Potamogeton pectinatus* L., with smaller amounts of *Ruppia maritima* L., *Zannichellia* spp., charophytes, and other species. The inflow to LEV contains high concentrations of organic matter and contaminants from the polluted Segura river and run-off water from agricultural and urban areas (Viñals et al. 2001). During our study, nutrient status and chlorophyll indicated that LEV was highly eutrophic (Table 1). The fish community is dominated by *Mugil cephalus* L., *Cyprinus carpio* L., and *Anguilla anguilla* L.

Our other study site was 9 km away in the neighboring Salinas de Santa Pola (38°11'N, 00°38'W), a brackish to saline complex of 550 ha (excluding a larger area of industrial salines), which is also protected as a Natural Park. We chose the three most accessible of 16

ponds in the Múrtulas estate (MUR) surrounded by *Juncus*, *Carex*, saltmarsh vegetation (especially *Salicornia ramosissima* J. Woods, *Sarcocornia fruticosa* (L.) A.J. Scott, *Arthrocnemum macrostachyum* (Moric.) Moris and *Suaeda*), *Scirpus litoralis*, and *Phragmites australis*. The dominant submerged macrophytes were *Ruppia cirrhosa* (Petagna) Grande and *P. pectinatus*. The inflow is run-off water from the surrounding agricultural areas. These ponds were smaller, shallower, and of a higher conductivity than LEV (Table 1). The sediments contain more sand and less silt. These ponds were formerly part of an industrial salt pan complex abandoned in 1979 (Marín and Giovanni 1997). The fish community includes *Gambusia affinis* Baird & Girard, *Aphanius iberus* Valenciennes, *Atherina boyeri* Risso, and *Pomatoschistus microps* Kroyer.

METHODS

Sampling Methods

LEV and MUR were sampled monthly from March to August 1999. Eight permanent sampling points were established at each site. These points differed in depth but were mainly within the shallow littoral zone facilitating access from the shore or by boat. Each month, two benthic samples were taken from each point with a corer of diameter 7.5 cm to a depth of 7.5 cm. Precise sampling sites were established randomly each month, ensuring that sediments were not disturbed in sites that were to be sampled later. Water levels fluctuated at each site, owing partly to management of LEV for irrigation. Thus, sites in the shallowest areas were sometimes dry and could not always be sampled, causing our sample size to vary from six to eight

Table 2. Total number of Chironomidae larvae from each taxon identified at each wetland between March and August 1999. n = number of samples taken that month (twice the number of points sampled).

		<i>P. choreus</i>	<i>C. type aprilinus</i>	<i>C. type halophilus</i>	<i>C. type plumosus</i>	<i>C. type salinarius</i>	<i>Tanytarsus spp.</i>	Total	n
LEV	March	1	109	0	16	11	20	157	12
	April	4	194	14	12	31	1	256	16
	May	30	638	8	14	112	9	811	16
	June	1	409	13	9	145	3	580	14
	July	3	288	24	2	110	0	427	16
	August	4	226	3	0	138	15	386	16
	TOTAL	43	1864	62	53	547	48	2617	90
MUR	March	9	3	0	1	42	54	109	16
	April	16	3	0	3	24	9	55	16
	May	4	8	0	0	70	18	100	12
	June	3	5	0	0	91	241	340	16
	July	17	9	0	1	70	203	300	14
	August	40	8	0	0	16	20	84	14
	TOTAL	89	36	0	5	313	545	988	88

points at each site (Table 2). Depth, conductivity, and the distance to the nearest emergent vegetation were measured at each sampling spot, and the water level at each wetland site was monitored continuously using a fixed pole with depth marks (Table 1). Sampling spots were not selected in relation to the presence or absence of submerged vegetation. Most samples in LEV (83%) and MUR (72%) were taken outside beds of submerged vegetation.

Within a day of collection, each sample was washed in the laboratory using sieves of 4-mm, 1-mm and 0.3-mm mesh. Chironomidae larvae collected from the 1-mm and 0.3-mm sieves were stored separately in 70% ethanol for later counting, identification, and measurement. No larvae were retained on the 4-mm sieve. Chironomid larvae were identified using Wiederholm (1983), Nocentini (1985), Webb and Scholl (1985), and Tachet *et al.* (1987). They were then measured to the nearest 0.05 mm using a microscope at 40 × magnification and digital callipers. For samples with more than 50 larvae of a given taxon from a given sieve, 50 were selected at random for measurement. Otherwise, all the larvae were measured. Some shrinkage of preserved larvae is likely to have occurred prior to measuring (Stanford 1973). Adult and exuvial chironomids were collected from the water surface or with emergent traps to aid identification of the species present in the benthic chironomid community.

Statistical Analyses

We analysed the variation among samples in the average size of larvae (as the dependent variable) using generalized linear models (GLMs; McCullagh and Nelder 1989). The effects of month, site, and density

(the number of larvae per benthic sample) were tested using the GLIMMIX macro for SAS program (SAS Institute 1996) with a normal error distribution and identity link. Each permanent sampling point was included as a random factor, and MONTH and SITE as fixed factors of six (March–August) and two (LEV and MUR) levels, respectively. This same model design was used for each chironomid taxa. The deviance of each fitted 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 points, via an *F* statistic (Crawley 1993).

RESULTS

Excluding numerous small Ostracoda (not counted), Chironomidae represented 86% of individual benthic invertebrates recorded at MUR and 93% at LEV. The next most abundant taxon was the isopod *Lekanesphaera hookeri* Leach representing 5% of invertebrates at MUR and 2% at LEV.

Among benthic larvae, we identified six Chironomidae taxa, including *Procladius* sp. (Tanypodinae, exuvial material was identified as *P. choreus* Meigen) and *Tanytarsus* spp. (*Tanytarsini*, exuvial material from LEV was identified as *T. horni* Goetghebuer and *T. tika* Tourenq). Four *Chironomus* morphotypes were identified as *Chironomus* type *aprilinus* Meigen, *C. type plumosus* Linnaeus, *C. type salinarius* Kieffer, and *C. type halophilus* Kieffer. The latter applies to larvae that were similar to typical *C. halophilus* type larvae but had only one pair of ventral tubuli instead of two. These four morphotypes are likely to correspond to distinct species (J. Casas pers. comm.).

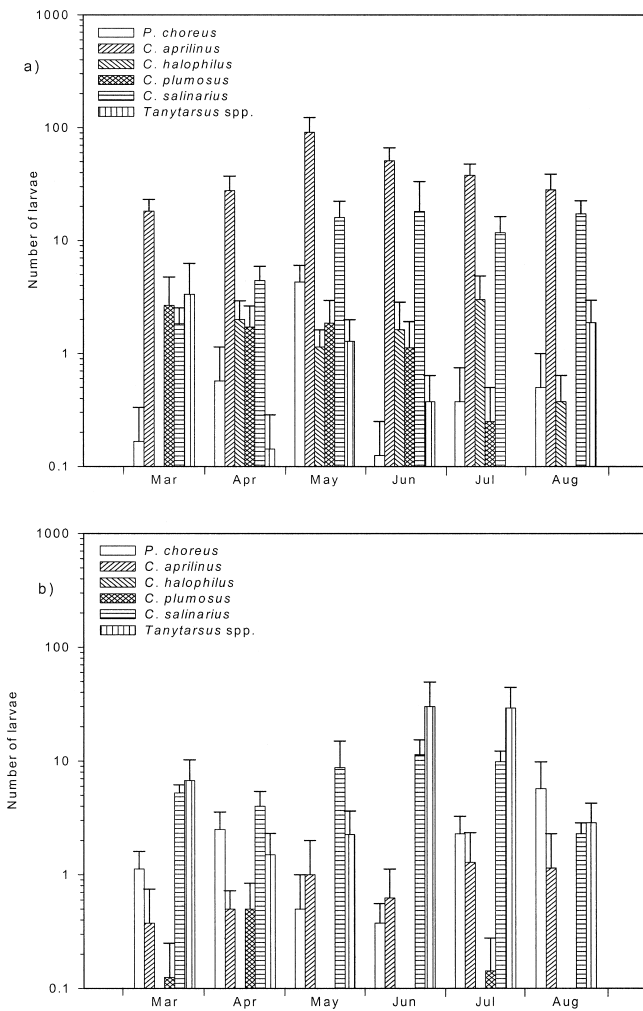


Figure 1. Changes in the abundance (mean \pm s.e. of the number of larvae per sample) of different Chironomidae larvae over time in a) Levante and b) Murtulas. Note the logarithmic scale.

The following taxa were identified at LEV using adult or exuvial material but were not observed as larvae: *Glyptotendipes* type *barbipes* Kieffer, *Microchironomus deribae* Freeman (both Chironomini), and *Cricotopus ornatus* Meigen (Orthoclaadiinae). The following additional taxa were identified at other El Hondo wetlands using adult or exuvial material: *Cricotopus caducus* Hirvenoja, *Halocladius* sp. (both Orthoclaadiinae), and *Dicrotendipes barbipes* Goetghebuer (Chironomini).

Throughout the study, chironomid larvae were consistently more abundant at LEV than MUR (Table 2, Figure 1). There were major differences between LEV and MUR in the relative abundance of different Chironomidae taxa (Table 2, Figure 1). In LEV, *C. aprilinus* type and *C. salinarius* type were the most abundant taxa, and both were most abundant from May through August (Figure 1a). In MUR, *Tanytarsus* spp.

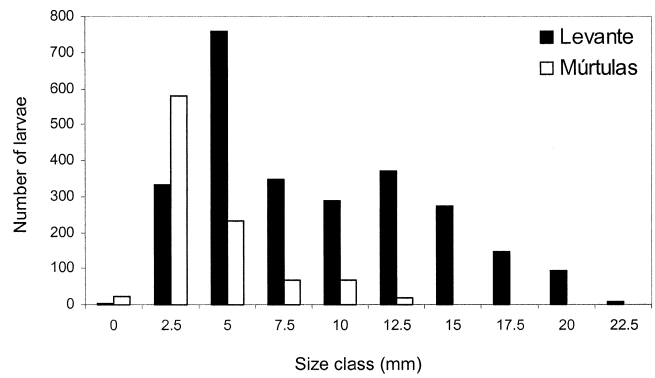


Figure 2. Overall size distribution of Chironomidae larvae from the two wetlands pooling all larvae for the whole study period. “0” refers to the size class 0–2.45 mm, “2.5” to 2.5–4.95 mm, etc.

and *C. salinarius* type were the most abundant taxa, with *Tanytarsus* spp. peaking in abundance in June and July, and *C. salinarius* type peaking in abundance from May to July (Figure 1b). *Chironomus plumosus* type and *P. choreus* were present at low densities in both wetlands throughout the study, while *C. halophilus* type was only recorded at LEV and at low densities (Table 2, Figure 1).

Chironomidae larvae were generally much larger at LEV than at MUR (Figure 2), owing to the greater abundance of large *Chironomus* taxa. Of the four *Chironomus* taxa at LEV, *C. salinarius* type was the smallest, the other three regularly exceeding 15 mm in length (Figure 3a). The most abundant taxon at MUR, *Tanytarsus* spp., was the smallest taxon observed at either site (Figure 3b).

The large difference in average size of Chironomidae larvae between wetlands was maintained throughout the study period (Figure 4). At LEV, average larval size dropped sharply between March and April but then remained fairly constant (Figure 4). A different pattern was observed at MUR, where average size peaked in April and May and dropped to a minimum in June (Figure 4). Both the abundant taxa at LEV (*C. aprilinus* type and *C. salinarius* type) showed the drop in mean size between March and April (Figure 5a), whereas there were no consistent seasonal trends for the abundant taxa at MUR (Figure 5b).

Closer inspection of the size distributions for a given month for the most abundant taxon observed at either site (*C. aprilinus* type at LEV) showed a bimodal distribution corresponding to third and fourth instars (Figure 6). Both these instars were recorded throughout the study period, but the larger fourth instar was the most abundant in March and July, and the third instar from April to June (Figure 6).

GLMs showed that there were significant effects of MONTH and SITE on the mean length of Chiron-

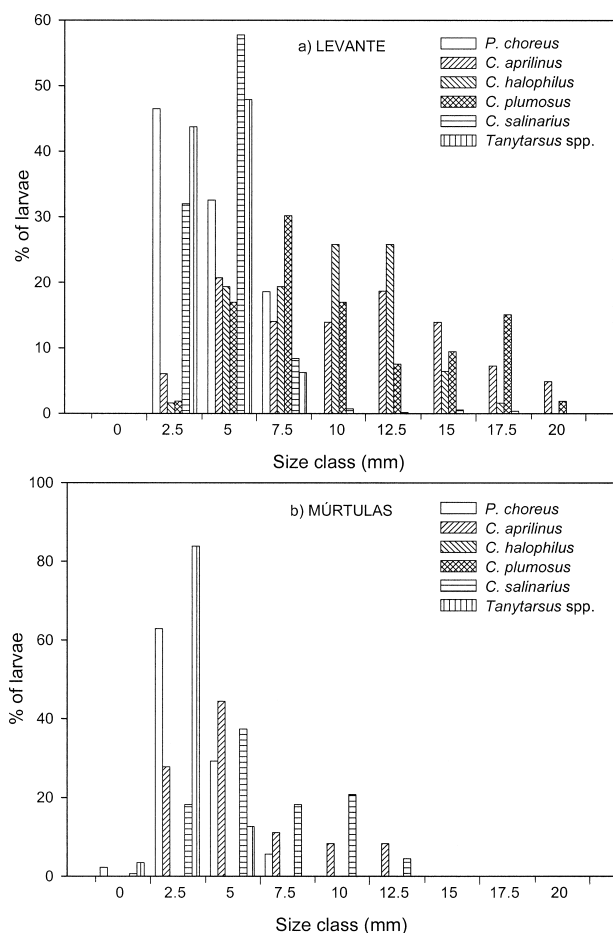


Figure 3. Size distribution of different Chironomidae taxa pooled over the whole study period for a) Levante and b) Murtulas. "0" refers to the size class 0–2.45 mm, "2.5" to 2.5–4.95 mm, etc. Note the change in scale on the y axis.

omidae larvae, with LEV having the larger larvae (Table 3). Only two taxa were sufficiently abundant in both sites to allow us to model the effects of MONTH and SITE on their mean size: *P. choreus* and *C. salinarius* type. There was a significant effect of MONTH on *P. choreus* but no effect of SITE (Table 3). In contrast, *C. salinarius* type were significantly larger at MUR than at LEV without an overall effect of MONTH (Table 3). There were also significant interactions between MONTH and SITE on overall larval size and on *C. salinarius* size (Table 3); thus, the seasonal trends in size were significantly different at the two wetlands (Figure 5).

Separate GLMs were used to analyze seasonal changes in size for taxa that were only numerous at one wetland. These models showed that there were significant effects of MONTH for *C. aprilinus* type at LEV and for *Tanytarsus* spp. at MUR (Table 4).

The number of larvae in the sample did not enter as a significant predictor in any of the models of larval

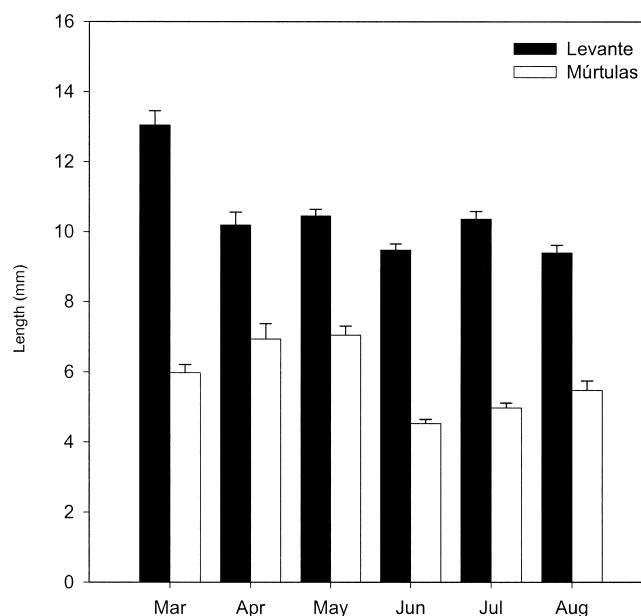


Figure 4. Seasonal changes in size (mean \pm s.e.) of Chironomidae larvae at the two wetlands.

size (whether for individual taxa or for all Chironomidae combined) that included the effects of MONTH and SITE. In other words, there was no evidence that larval density helped explain the variation in mean size between samples in a given wetland at a given date.

DISCUSSION

The abundance of benthic chironomid larvae at LEV was consistent with their importance in the diet of stiff-tail ducks *Oxyura* spp. collected from this site (Sánchez et al. 2000). The dominance of *Chironomus* spp. over other groups of chironomids at LEV is a strong indication of eutrophication (Lindgaard 1995, Brodersen and Lindgaard 1999, Brooks et al. 2001). The difference in community structure indicate that MUR is less eutrophic, as supported by water chemistry (Table 1). We do not believe that the differences in sampling depth between MUR and LEV (Table 1) had a major influence on community structure. Sampling depth was generally shallower at MUR, but there was much overlap with LEV. In a larger dataset for these sites with more core samples but a less detailed identification, we found no influence of depth on the abundance of all larvae combined, of *P. choreus* larvae or of *Chironomus* spp. larvae (authors unpublished data).

The most abundant larvae at LEV were morphotypes resembling *C. salinarius* and *C. halophilus* (two species groups associated with brackish wetlands), *C. aprilinus*, and *C. plumosus* (a species group especially tolerant of eutrophication, Armitage et al. 1995, Brodersen and

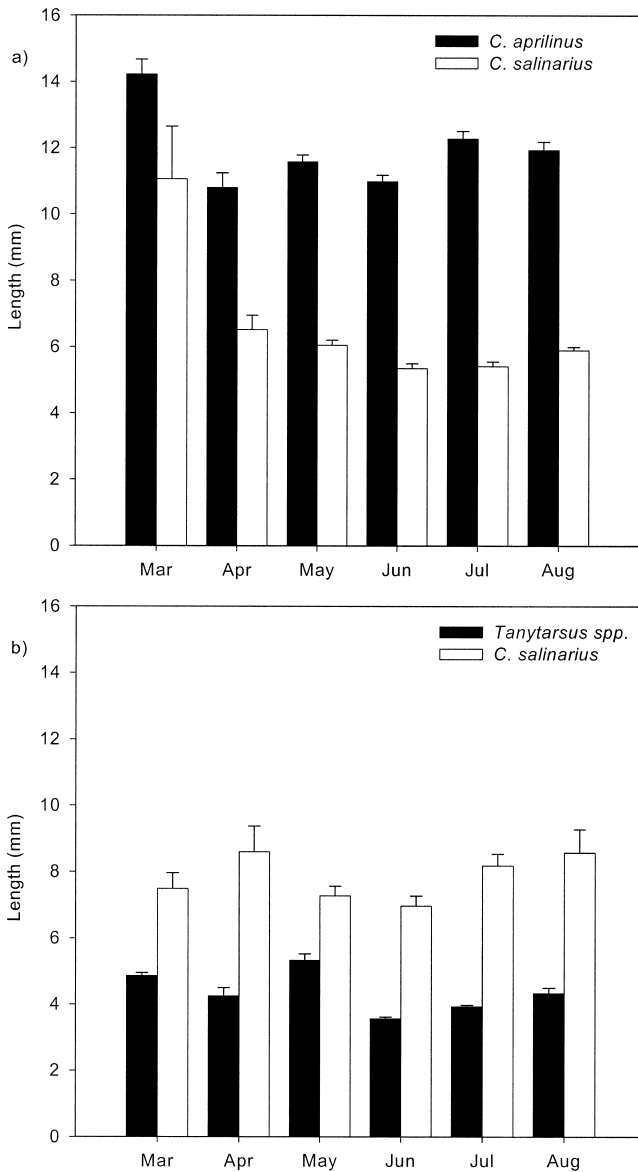


Figure 5. Seasonal changes in size (mean \pm s.e.) for different Chironomidae taxa at a) Levante and b) Múrtulas. Data are only shown for those taxa for which 10 or more larvae were observed in any given month at a given wetland.

Lindgaard 1999, Brooks et al. 2001). Unlike the other three species, *C. plumosus* is widespread in Spanish reservoirs (Real et al. 2000). It is noteworthy that, according to our provisional identifications, the benthic community contained five of the seven chironomid species that were abundant in the study of Rehfish (1994) in brackish artificial lagoons 15° further north in England.

All Chironomidae taxa are probably multivoltine at our study sites, in contrast to the spring and autumn emergence typical of temperate wetlands (Armitage et al. 1995). Adult chironomids emerge all year round at our sites (authors unpublished data). Velasco et al. (in press) reported 4–7 generations a year for *Baeotendipes*

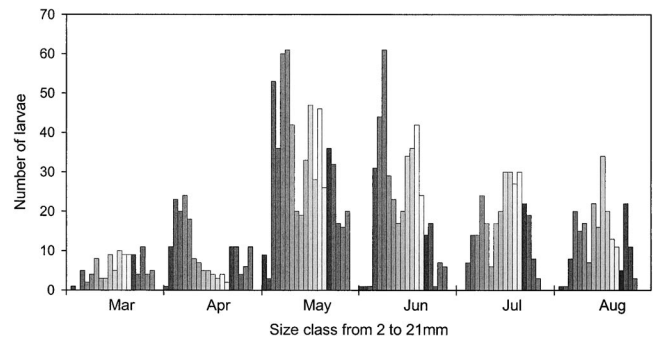


Figure 6. Frequency distribution of size classes of *C. aprilinus* type larvae for each month at Levante. Size classes run from 2–2.95 mm on the left to 21–21.95mm on the right.

noctivaga Kieffer (Chironomini) in a saline lagoon 40 km away from our study site. In Cádiz bay, southern Spain, Drake and Arias (1995) estimated five generations per year for *C. salinarius*, with overlapping cohorts. In another Spanish wetland, *P. choreus* was found to have four generations a year (Prat and Rieradevall 1995).

Our smallest mesh size (0.3 mm) led to the loss of most first and second instar larvae and a major underestimation of the overall densities (Drake and Arias 1995). Our sampling intervals of a calendar month were too long to enable precise determination of the life cycles of the Chironomidae taxa during the study period. These problems are common to studies of chironomid population dynamics (Tokeshi 1995). However, the greater size of *C. salinarius* and *C. aprilinus* larvae and predominance of fourth instars at LEV in March (Figure 6) suggest that there may be some tendency for Chironomidae larvae to overwinter as fourth instars and for emergence to peak after temperatures rise in spring, as observed at more northerly latitudes (Tokeshi 1995). Larval growth rates and emergence rates are likely to be reduced in winter when water temperatures often drop below 12°C (Drake and Arias 1995). Larvae of *C. salinarius* and other species are reported to grow faster and pupate at shorter lengths in warmer months (Drake and Arias 1995).

We found that seasonal change in overall size distribution of chironomid larvae occurred in both our study sites and cannot be attributed simply to changes in the relative abundance of different taxa, as there are major changes in larval size over time within a given taxon. We also found that, in the case of *C. salinarius* type larvae, seasonal changes in larval size for a given taxon can be very different in two nearby wetlands. This suggests that life cycles of *C. salinarius* may vary between LEV and MUR, perhaps in relation to their differences in depth or salinity.

MUR had a lower overall density of Chironomidae larvae, a lower average size, and, thus, a lower larval

Table 3. Summary of generalized linear models testing the effects of SITE (factor of two levels, MUR and RES) and MONTH (factor of six levels from March to August 1999) on the mean size of all Chironomidae larvae and of individual taxa. Results of each main effect are given in the absence of their interactions, with the degrees of freedom for the numerator (df_N) and denominator (df_D) and the F statistic. When SITE has a significant effect, its direction is specified. DE = percentage of additional deviance explained in comparison to null models that include sampling point as a random factor. For model estimates, see Appendix I. Significant SITE X MONTH interactions were observed for Chironomidae larvae ($F_{5,130} = 3.11$, $p < 0.05$, DE = 27.6%) and *C. salinarius* larvae ($F_{5,97} = 7.32$; $p < 0.0001$, DE = 33.6%).

	DE	Effect	df_N	df_D	F	P	Direction
Chironomidae larvae	19.1	MONTH	5	135	7.09	<.0001	
		SITE	1	135	55.41	<.0001	LEV>MUR
<i>P. choreus</i> larvae	67.0	MONTH	5	28	12.27	<.0001	
		SITE	1	28	1.14	0.2958	
<i>C. salinarius</i> type	7.8	MONTH	5	102	2.24	0.0562	
		SITE	1	102	7.18	0.0086	MUR>LEV

biomass than LEV. This is consistent with the lower trophic status and reduced availability of soft sediments in this wetland and with its greater salinity (Table 1). Several field studies have found that the biomass of benthic Chironomidae in the littoral decreases as salinity increases (Timms 1981, Hammer *et al.* 1990, Reh-fisch 1994), and experimental work suggests that this is a causal relationship (Galat *et al.* 1988). In mixohaline wetlands like the ones we have studied, many species are likely at the limit of their salt tolerance and cannot survive in the most saline microhabitats.

Although larvae were smaller at MUR, this is a reflection of the different community composition and the dominance of smaller taxa such as *Tanytarsus* spp. in this wetland. The only taxon that was reasonably abundant in both wetlands (*C. salinarius* type) had a larger mean size at MUR. The reason for this is unclear, but it is most likely that larger mean size reflects slower growth rates (e.g., due to a poor food supply or higher salinity). The maximum size of *C. salinarius* larvae was actually greater at LEV (Figure 3), and the lower mean size at this wetland probably reflects a large proportion of smaller instars and greater growth rates (as argued by Drake and Arias 1995). However, in the absence of cytological or genetic studies, we cannot rule out the possibility that our larvae identified as *C. salinarius*

type include more than one species and that larvae at MUR and LEV were from different species.

Previous studies have often found evidence for a negative correlation between larval density and size over space while controlling for temporal variation, suggesting that competition often inhibits larval growth (Tokeshi 1995, Batzer *et al.* 1997). We have not found such negative correlations for any of the taxa studied. At both LEV and MUR, *C. aprilinus* type and *C. salinarius* type larvae were largest in the months when they were at their lowest densities (compare Figures 1 and 5), as would be expected under intraspecific competition. However, it is more likely that these are the months when different cohorts are reaching maturity.

In the absence of comparable studies, it is unclear to what extent the seasonal patterns we have observed in larval size distribution are consistent with similar patterns at other wetlands of the Mediterranean region. In the only other study we are aware of, the size of *C. salinarius* larvae reduced gradually from January to June in Cádiz Bay, possibly owing to the influence of water temperature on growth rates (Drake and Arias 1995). These seasonal patterns in size distribution may have broader implications for the ecology of wetland ecosystems (e.g. owing to their implications for water-birds, fish, or other predators that select chironomid larvae on the basis of size) (Batzer *et al.* 1993, Kornijów 1997).

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Table 4. Summary of generalized linear models testing the effects of MONTH (factor of six levels) on the mean size of taxa that are only abundant at LEV (*C. aprilinus* type) or MUR (*Tanytarsus* spp.), with the degrees of freedom for the numerator (df_N) and denominator (df_D) and the F statistic. DE = percentage of additional deviance explained in comparison to null models that include sampling point as a random factor. See Appendix I for details of the model estimates.

	DE	df_N	df_D	F	P
<i>C. aprilinus</i> at LEV	19.37	5	70	3.46	0.0074
<i>Tanytarsus</i> at MUR	40.53	5	31	4.34	0.0041

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LITERATURE CITED

- Armitage, P., P. S. Cranston, and L. C. V. Pinder. 1995. The Chironomidae: the Biology and Ecology of non-Biting Midges. Chapman and Hall, London, United Kingdom.
- Batzer, D. P., F. de Szalay, and V. H. Resh. 1997. Opportunistic response of a benthic midge (Diptera: Chironomidae) to management of California seasonal wetlands. *Environmental Entomology* 26:215–222.
- Batzer, D. P., M. McGee, and V. H. Resh. 1993. Characteristics of invertebrates consumed by mallards and prey response to wetland flooding schedules. *Wetlands* 13:41–49.
- Bernués, M. (ed.). 1998. Humedales Españoles inscritos en la Lista del Convenio de Ramsar. Ministerio de Medio Ambiente, Organismo Autónomo de Parques Nacionales, Madrid, Spain.
- Brodersen, K. P. and C. Lindegaard. 1999. Classification, assessment and trophic reconstruction of Danish lakes using chironomids. *Freshwater Biology* 42:143–157.
- Brooks, S. J., H. Bennion, and H. J. B. Birks. 2001. Tracing lake trophic history with a chironomid-total phosphorus inference model. *Freshwater Biology* 46:513–533.
- Cirujano, S., L. Medina, J. B. Peris, and G. Stübing. 1995. Estudio de la flora y vegetación de los Parajes Naturales de las Salinas de Santa Pola, El Hondo y las Lagunas de la Mata y Torrevieja. Real Jardín Botánico, Madrid, Spain.
- Crawley, M. J. 1993. GLIM for Ecologist, Blackwell Scientific Publications, Cambridge, United Kingdom.
- Drake, P. and A. M. Arias. 1995. Distribution and production of *Chironomus salinarius* (Diptera: Chironomidae) in a shallow coastal lagoon in the Bay of Cádiz. *Hydrobiologia* 299:195–206.
- Galat, D. L., M. Coleman, and R. Robinson. 1988. Experimental effects of elevated salinity on three benthic invertebrates in Pyramid Lake, Nevada. *Hydrobiologia* 158:133–144.
- Hammer, U. T., J. S. Sheard, and J. Kranabetter. 1990. Distribution and abundance of littoral benthic fauna in Canadian prairie saline lakes. *Hydrobiologia* 197:173–192.
- Kornijów, R. 1997. The impact of predation by perch on the size-structure of *Chironomus* larvae—the role of vertical distribution of the prey in the bottom sediments, and habitat complexity. *Hydrobiologia* 341/343:207–213.
- Lindegaard, C. 1995. Classification of water-bodies and pollution. p. 385–404. In P. D. Armitage, P. S. Cranston, and L. C. V. Pinder (eds.) *The Chironomidae: the Biology and Ecology of non-Biting Midges*. Chapman and Hall, London, United Kingdom.
- Marín, C. and P. Giovanni. 1997. Nature and Workmanship. Artificial Wetlands in the Mediterranean Coast. International Scientific Council for Island Development, Paris, France.
- McCullagh, P. and J. A. Nelder. 1989. *Generalized Linear Models*, 2nd ed. Chapman & Hall, London, United Kingdom.
- Nocentini, A. 1985. Chironomidi, 4 (Diptera: Chironomidae: Chironominae, larve). Guide per il riconoscimento delle specie animali delle acque interne italiane. Vol. 29. Consiglio Nazionale delle Ricerche, Verona, Italy.
- Prat, N. and M. Rieradevall. 1995. Life cycle and production of Chironomidae (Diptera) from Lake Banyoles (NE Spain). *Freshwater Biology* 53:511–524.
- Real M., M. Rieradevall, and N. Prat. 2000. *Chironomus* species (Diptera, Chironomidae) in the profundal benthos of Spanish reservoirs and lakes, factors affecting distribution patterns. *Freshwater Biology* 43:1–18.
- Rehfishch, M. M. 1994. Man-made lagoons and how their attractiveness to waders might be increased by manipulating the biomass of an insect benthos. *Journal of Applied Ecology* 31:383–401.
- Rodrigo, M. A., X. Aremengol-Díaz, R. Oltra, M. J. Dasi, and W. Colom. 2001. Environmental variables and planktonic communities in two ponds of El Hondo wetland (SE Spain). *Internationale Revue der gesamten Hydrobiologie* 86:299–315.
- Sánchez, M. I., A. J. Green, and J. C. Dolz. 2000. The diets of the White-headed Duck *Oxyura leucocephala*, Ruddy Duck *O. ja-maicensis* and their hybrids from Spain. *Bird Study* 47:275–284.
- SAS Institute Inc. 1996. SAS System for Mixed Models. Cary, NC, USA.
- Stanford, J. A. 1973. A centrifuge method for determining live weights of aquatic insect larvae, with a note on weight loss in preservative. *Ecology* 54:449–451.
- Tachet, H., M. Bournaud, and P. Richoux. 1987. Introduction à l'étude des macroinvertébrés des eaux douces. Association Française de Limnologie, Paris, France.
- Timms, B. V. 1981. Animal communities in three Victorian lakes of differing salinity. *Hydrobiologia* 81:181–193.
- Tokeshi, M. 1995. Life cycles and population dynamics. p. 224–268. In P. D. Armitage, P. S. Cranston, and L. C. V. Pinder (eds.) *The Chironomidae: the Biology and Ecology of non-Biting Midges*. Chapman and Hall, London, United Kingdom.
- Velasco, J., A. Millán, A. Perán, and B. Martínez. In press. Estudio de la producción secundaria de quironómidos en una laguna experimental del Parque Regional de las salinas y arenas de San Pedro del Pinatar, un caso aplicado a la gestión. *Actas del XI Aula de Ecología "Investigación y Gestión en Espacios Naturales."* Consejería de Medio Ambiente, Junta de Andalucía, Sevilla, Spain.
- Vinais, M. J., W. Colom, T. Rodrigo, M. J. Dasi, J. Armengol, R. Oltra, and R. Miracle. 2001. Rasgos característicos de un humedal mediterráneo artificializado y su problemática ambiental, El Hondo de Elche (Alicante, España). *Humedales Mediterráneos* 1:147–154.
- Webb, C. J. and A. Scholl. 1985. Identification of larvae of European species of *Chironomus* Meigen (Diptera, Chironomidae) by morphological characters. *Systematic Entomology* 10:353–372.
- Wiederholm, T. 1983. Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. *Entomologica Scandinavica*, 19.

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Appendix I. Details of generalized linear models of the fixed effects MONTH (factor of 6 levels from March to August 1999) and SITE (factor of two levels, LEV and MUR), listing the model estimate and their standard errors. August and MUR are aliased.

Effect	Chironomidae larvae		<i>P. choreus</i> larvae		<i>C. salinarius</i> larvae		<i>C. aprilius</i> larvae, LEV		<i>Tanytarsus</i> spp. larvae, MUR	
	Est.	S. E.	Est.	S. E.	Est.	S. E.	Est.	S. E.	Est.	S. E.
Intercept	4.707	0.532	4.084	0.386	7.425	0.610	11.35	0.819	4.300	0.235
March	2.917	0.539	2.825	0.556	1.854	0.809	3.132	0.959	0.448	0.334
April	1.864	0.538	2.098	0.484	1.237	0.799	0.658	0.934	-0.149	0.414
May	1.941	0.544	1.361	0.524	-0.231	0.811	0.624	0.878	1.026	0.389
June	0.867	0.531	-0.067	0.610	-0.031	0.791	-0.464	0.915	-0.570	0.333
July	1.026	0.518	-0.552	0.496	-0.085	0.747	0.097	0.913	-0.306	0.315
LEV	4.276	0.574	0.431	0.405	-1.252	0.467				