

Contribution to the knowledge of the distribution of *Chaoborus* species (Diptera: Chaoboridae) in the NE Iberian Peninsula, with notes on the spatial and temporal segregation among them

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ABSTRACT

Contribution to the knowledge of the distribution of *Chaoborus* species (Diptera: Chaoboridae) in the NE Iberian Peninsula, with notes on the spatial and temporal segregation among them

Phantom midges are characteristic inhabitants of standing waters and are well known for their diel migrations. Despite the extensive body of literature covering their ecology, there are still knowledge gaps with regards to the factors that determine their distribution. Furthermore, although spatial and temporal segregation patterns among chaoborids have long been reported, the prevalence of such patterns in shallow waters remains unclear. We investigated the distribution of *Chaoborus* species, as well as their spatial and temporal segregation and diel mesohabitat migration, in the NE Iberian Peninsula. We detected three *Chaoborus* species (*C. crystallinus*, *C. pallidus* and *C. flavicans*), with the latter being the most dominant, and co-occurrences among these species being very low. *C. flavicans* did not perform diel horizontal migrations, although in one of the ponds it showed high affinities to vegetated areas during both day- and night-time, similar to its potential predators. Therefore, although we did not observe the role of diel horizontal migrations as an antipredator mechanism in shallow water bodies, aquatic vegetation could confer refuge to the chaoborid larvae.

Key words: *Chaoborus*, shallow waterbodies, diel mesohabitat migration, segregation, Iberian Peninsula.

RESUMEN

Contribución al conocimiento de la distribución de las especies de *Chaoborus* (Diptera: Chaoboridae) en el NE de la Península Ibérica, con notas sobre la segregación espacial y temporal entre ellas

Las larvas del género *Chaoborus* son unos habitantes típicos de aguas estancadas con unos patrones muy marcados de migración vertical diaria. Aunque existe una extensa bibliografía de su papel ecológico y biológico, existen aún algunos interrogantes en relación a su distribución. Además, aunque los patrones de segregación espacial y temporal en los caobóridos están bien documentados, en aguas someras siguen sin estar claros. Nuestro estudio se centra en la distribución de las especies del género *Chaoborus* en el NE de la Península Ibérica, su segregación espacial y temporal y las migraciones diarias entre mesohábitats. Se detectaron tres especies del género *Chaoborus* (*C. crystallinus*, *C. pallidus* y *C. flavicans*), siendo la última la más abundante, y unas coocurrencias entre estas especies muy bajas. *C. flavicans* no mostró ninguna migración diaria horizontal, aunque en una de las charcas presentó una afinidad mayor por las zonas vegetadas tanto de día como de noche, al igual que sus predadores potenciales. Por lo que, aunque no se observaron patrones de migración horizontal diaria como mecanismo antipredador en masas de agua someras, la vegetación acuática podría suponer un refugio para las larvas de *Chaoborus*.

Palabras clave: *Chaoborus*, aguas someras, migración diaria en el mesohabitat, segregación, Península Ibérica.

INTRODUCTION

The Chaoboridae family (commonly known as phantom midges) includes 50 extant species in 6 genera and 2 subfamilies (Wagner *et al.*, 2008). The genus *Chaoborus* is the most speciated, including 42 species with a worldwide distribution (except Antarctica) (Borkent, 1993; Wagner *et al.*, 2008). *Chaoborus* larvae are a typical element of standing waters, and in large water bodies, they display a well-known vertical migration to avoid visual predators (i.e., they reside in the bottom during the day as a refuge, and they migrate at night to feed; Sæther, 1972). Although there is a wide knowledge of the biological and ecological roles of the different *Chaoborus* species, the geographic distribution of some species still has large gaps (Borkent, 1979; Berendonk, 2002). In the case of the Iberian Peninsula the genus is widely distributed (e.g., Carles-Tolrá & Saloña, 2004; Gerales & Boavida, 2004; Abellán *et al.*, 2006; Trigal *et al.*, 2007; Florencio *et al.*, 2009; Alarcón-Elbal *et al.*, 2011; Martínez-Sanz *et al.*, 2012). However, the identity and the exact distribution of the different species, and the factors that determine this distribution, are still not completely known.

Although the actual coexistence of two or more species of *Chaoborus* in the same water body is not rare (Stahl, 1966), spatial and temporal segregation patterns among chaoborid species have been largely reported (e.g., Von Ende, 1979; Kurek *et al.*, 2010). Different strategies devoted to avoid or reduce interspecific competition have been described, such as adaptation to different environmental characteristics (Lamontagne *et al.*, 1994; Kurek *et al.*, 2010) or to habitats with different predation pressure (Von Ende, 1979; Garcia & Mittelbach, 2008), intraguild predation (Von Ende, 1979; Persaud & Dillon, 2010), different capacities of dispersion (Berendonk & Bonsall, 2002), or different phenologies (Von Ende, 1982).

Diel migrations are behavioural strategies adopted by chaoborids and represent a trade-off between living in resource-rich surface waters with a high predation risk and living in resource-

poor deep waters with a low predation risk. These diel migrations have been generally considered a response to fish presence (e.g., Dawidowicz *et al.*, 1990; Tjossem, 1990) but they have also been observed in temporary pools (Bass & Sweet, 1984). Within this context, diel patterns of *Chaoborus* species have been studied extensively in lakes, but much less attention has been paid to these movements in shallow water bodies. The refuge effect of the deeper parts of shallow water bodies might not be as important as in lakes because benthic predators in wetlands are generally very well represented (Batzler & Ruhí, 2013). In these cases, the presence of different mesohabitats (i.e., vegetation structure) could serve as refuge for *Chaoborus* spp. larvae, and the existence of diel mesohabitat or horizontal migrations could be determined by the differential abundance of prey in open waters relative to vegetated areas. Overall, vertical diel migrations may be weaker than horizontal ones in shallow temporary ponds, but few studies have analysed the diel patterns of *Chaoborus* species in these environments (however, see Bass & Sweet, 1984).

The present study investigates the regional distribution of chaoborids in the shallow lentic waters of the NE Iberian Peninsula and studies coexistence patterns among the different species. Due to the different adaptive strategies of *Chaoborus* species (e.g., different predator avoidance behaviour or adaptation to different environmental characteristics; Berendonk & Bonsall, 2002; Kurek *et al.*, 2010), we first intended to investigate the contribution of two main environmental factors, namely water permanence and fish predation, to their regional distribution. Second, as it is known that several *Chaoborus* species may be able to avoid interspecific competition (both spatially and temporally; e.g., Von Ende, 1982), we wished to examine whether there was spatial and/or temporal segregation among coexisting chaoborids. Third and finally, as diel migrations of *C. flavicans* have often been described to be mechanisms to avoid planktivorous fish (e.g., Dawidowicz *et al.*, 1990), we intended to evaluate whether *C. flavi-*

cans larvae display diel mesohabitat/horizontal migrations in two shallow, fishless ponds. Within this context, we also evaluated diel mesohabitat migrations of zooplankton and potential predators of *Chaoborus* spp. larvae that occurred in these ponds to identify the ultimate causes of *C. flavicans* migrations.

MATERIALS AND METHODS

Sampling

A survey comprising a total of 124 freshwater wetlands was conducted in Catalonia (NE Iberian Peninsula) haphazardly from 1993 to 2013 (Table S1, Available at www.limnetica.net/internet). All water bodies except one were shallow (i.e., < 6 m deep). Wetlands were classified according to their hydrology (57 wetlands were permanent and 67 were temporary) and fish presence (36 were fish-bearing and 88 were fishless). Sampling was conducted by sweeping during the day with a dip-net 22-cm in diameter and of a 250- μ m mesh size (which was also used in all subsequent studies), covering all mesohabitats. Samples were preserved in situ with formaline 4% or ethanol at 70%. Larvae and pupae of Chaoboridae were identified to the species level using Sæther (1972) and Balvay (1977). Because the sampling effort employed to assess the regional distribution was not the same for all of the sampling points included in the database (some samples were quantitative and some were qualitative), a presence/absence matrix (3 species \times 124 sites) was built.

In addition to the regional distribution study, three complementary field studies were carried out to describe (i) habitat and (ii) the temporal segregation among the different species, and (iii) the diel horizontal migration of *C. flavicans*.

Habitat segregation study

To describe the affinity of different species to different aquatic habitats, a study was conducted in the Can Jordà wetlands in Garrotxa Volcanic Zone Natural Park (42°08'41"N, 02°30'25"E,

527 m a.s.l.), where a group of several permanent and temporary wetlands are found in close association. In the same area (distance < 20 m), we delimited a permanent and a temporary wetland that are interconnected only after extreme flooding. On 23/03/2011, when the temporary habitat had been flooded for at least one month, four 3-meter transects were performed in each habitat.

Temporal segregation study

To study the seasonal dynamics in the same pond of two different species, a study was carried out seasonally in Gorga de les Acàcies pond, in the Deveses de Salt area (41°58'54"N, 02°46'41"E, 79 m a.s.l.) between November 2010 and July 2011. The pond has a single basin and a low diversity of mesohabitats, which prevented habitat segregation between the present *Chaoborus* species. At each sampling date, the capture methodology consisted in 20 sweeps in rapid sequence covering all mesohabitats present in the pond.

Diel horizontal migration study

To determine whether diel mesohabitat segregation occurs in very shallow ponds (< 60 cm depth), a field study was performed in two temporary ponds: Peça del Forn pond (41°49'19"N, 02°58'12"E, 53 m a.s.l.) and Can Capçana pond (41°52'11"N, 02°53'42"E, 133 m a.s.l.), both in the Gavarres Area of Natural Interest. To capture Chaoboridae larvae, five 1-meter transects were performed in vegetated areas of each pond (mean depth of the transects = 37 cm in the Peça del Forn pond and 52 cm in the Can Capçana pond) and another 5 transects were performed in non-vegetated areas of each pond (mean depth of the transects = 38 cm and 41 cm, respectively). Samplings were conducted in the morning (8:00 h) and evening (20:00 h). The sampling took place at least one month after the ponds had been filled by rain water, in October 14th 2010 (Can Capçana pond) and in October 16th 2010 (Peça del Forn pond). Diel vertical migration was not assessed in this study due to the shallowness of the ponds.

To analyse whether the diel patterns of *C. flavicans* were due to the movements of their potential resource (i.e., zooplankton) or due to the movement of potential predators, we also evaluated the diel patterns of these two faunal groups. The abundance of potential predators of *C. flavicans* (i.e., Odonata, predatory Coleoptera and predatory Heteroptera) was estimated with the same transects used for capturing Chaoboridae. Zooplankton (i.e., Cladocera and Copepoda) were captured using 20 minnow traps per pond. Each trap was a 500 mL transparent plastic container (30 cm in length, 8 cm in diameter) equipped with an inverse-funnel opening, similar to those used by Beladjal *et al.* (1992). Ten iron bars (5 in the vegetated areas and 5 in the non-vegetated areas) were fixed to the pond bottom, and a set of two traps was attached to each iron bar. One trap was fixed at 5 cm below the water surface, and the other was fixed at 5 cm above the bottom of the pond. Traps were active during two 10-hour periods. The first period (from 10 a.m. to 8 p.m.) was

used to detect the position of zooplankton during the day, and the second period (from 10 p.m. to 8 a.m.) was used to detect the position of zooplankton at night. After each 10-hour period (1 hour after dawn and dusk), the zooplankton captured in the traps were preserved in 96% ethanol and subsequently counted, measured and identified to the high-taxa level using a stereomicroscope. To study the diel patterns of zooplankton, the captures of the two traps of each iron bar were summed, thus taking into account the movement of zooplankton in all of the water column.

Data analyses

To determine whether the presence of chaoborids was independent of the regional factors analysed (water permanence and fish presence), we performed a chi-square test of independence using Chaoboridae presence/absence (all species lumped together) across the set of 124 wetlands. Because all temporary wetlands were fishless,

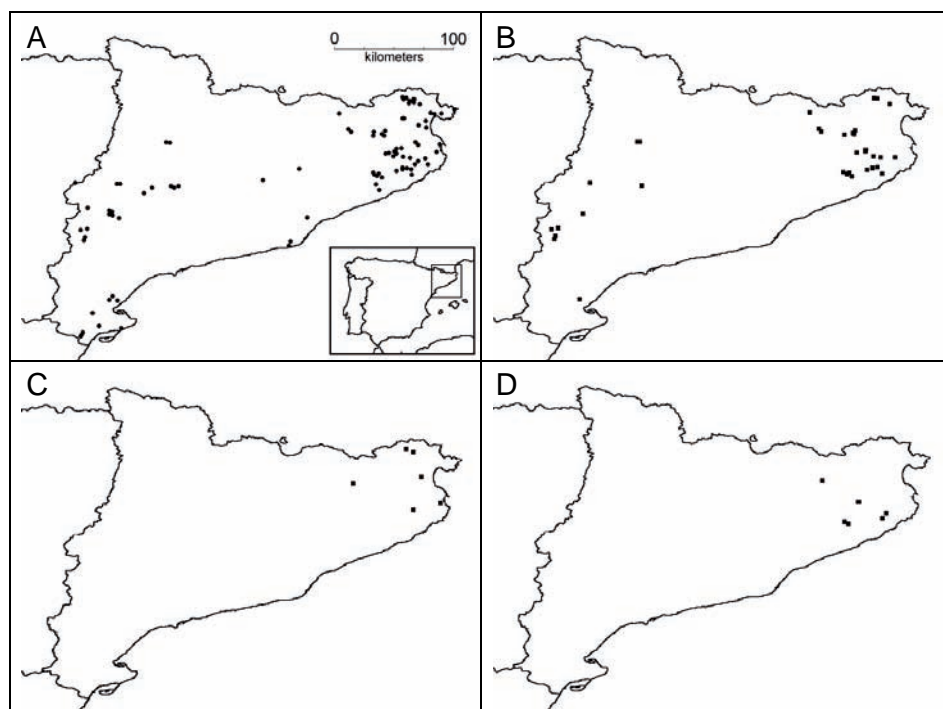


Figure 1. Map of the NE Iberian Peninsula showing the A) total sites sampled, B) sites with *Chaoborus flavicans*, C) sites with *Chaoborus crystallinus*, and D) sites with *Chaoborus pallidus*. Mapa del NE de la Península Ibérica mostrando la distribución de: A) localidades muestreadas; B) *Chaoborus flavicans*; C) *Chaoborus crystallinus*; D) *Chaoborus pallidus*.

we performed an additional chi-square test of independence for the fish presence factor but considering only the subset of permanent wetlands. To explore the affinity to water permanence or to fish presence of each species, two additional chi-square tests of independence (one for each factor) were performed for the subset of 50 sites where the genus *Chaoborus* was detected. We also analysed whether *Chaoborus* species tended to co-occur more or less than would be expected by chance (according to the particular relative occurrences) by means of a co-occurrence null model (C-score as co-occurrence index, sequential swap algorithm, 5000 permutations).

For the first case study (habitat segregation), we tested for differences in the abundances of *Chaoborus* species between the two habitats (i.e., temporary and permanent) with another chi-square test of independence. For the second case study (temporal segregation), a chi-square test of independence was conducted to determine whether proportions of *Chaoborus* species' abundances changed across seasons. For the third case study (diel mesohabitat pattern), 3 two-way ANOVAs were conducted separately for each pond (Peça del Forn and Can Capçana ponds). The two factors were vegetation (i.e., vegetated vs. non-vegetated) and time (i.e., day- vs. night-time), and the abundance of *C. flavicans*, predators and zooplankton were the dependent variables, respectively. All analyses were performed using the statistical program R (R Core Team, 2012) except for the co-occurrence null model, which was simulated in EcoSim (Entsminger, 2012).

Table 1. Occurrence and co-occurrence (%) of the three *Chaoborus* species across the 50 water bodies where Chaoboridae were recorded. *Ocurrencia y co-ocurrencia (%) de las tres especies de Chaoboridae de las 50 masas de agua con presencia de Chaoboridae.*

Occurrence alone	<i>C. crystallinus</i>	8%
	<i>C. flavicans</i>	74%
	<i>C. pallidus</i>	8%
Co-occurrence	<i>C. crystallinus</i> - <i>C. flavicans</i>	2%
	<i>C. crystallinus</i> - <i>C. pallidus</i>	0%
	<i>C. flavicans</i> - <i>C. pallidus</i>	6%
	<i>C. flavicans</i> - <i>C. pallidus</i> - <i>C. crystallinus</i>	2%

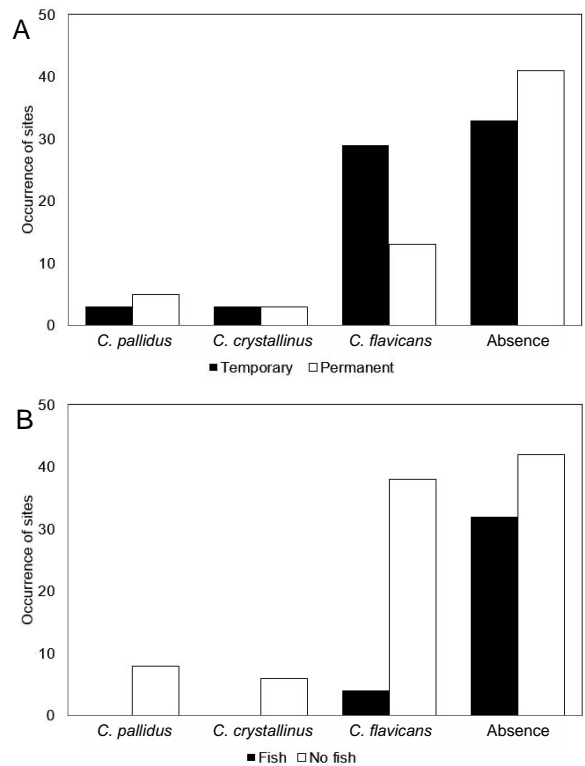


Figure 2. Bar plot showing the regional occurrences of each *Chaoborus* species across the two environmental factors studied: A) water permanence, and B) fish presence. *Gráfico de barras mostrando las ocurrencias a nivel regional para cada especie de Chaoborus, según los dos factores ambientales estudiados: A) permanencia del agua, y B) presencia de peces.*

RESULTS

Distribution, co-occurrences among *Chaoborus* species and habitat use

Chaoborus larvae or pupae were detected in 50 out of the 124 surveyed water bodies (see Table S1). Three species of *Chaoborus* were found: *C. flavicans* (Meigen, 1830), *C. crystallinus* (De Geer, 1776) and *C. pallidus* (Fabricius, 1781). *C. flavicans* was the most widespread species, being present in 84% of the water bodies where chaoborids were recorded (Fig. 1). *C. pallidus* and *C. crystallinus* were rare, being present in 16% and 12% of the wetlands, respectively (Fig. 1, Table 1). Co-occurrences among species were generally low (Table 1) but not significantly different from what would be

expected by chance (observed C-index = 0.283; simulated C-index by the null model = 0.290; $P_{(\text{obs} \leq \text{expected})} = 0.62$; $P_{(\text{obs} \geq \text{expected})} = 1$). The species pair that co-occurred most often was *C. flavicans*-*C. pallidus* (6%). *C. crystallinus*-*C. flavicans* showed low values of co-occurrence (2%) and we did not observe any co-occurrence between *C. crystallinus* and *C. pallidus*. The three species (i.e., *C. flavicans*-*C. pallidus*-*C. crystallinus*) co-occurred in only a single water body (2%).

The analysis of habitat use at the regional scale (Fig. 2) showed that the presence of Chaoboridae (regardless of the species identity) was dependent on both water permanence ($\chi_1^2 = 5.67$; $p = 0.017$) and fish presence, if we considered either only permanent wetlands ($\chi_1^2 = 11.73$; $p < 0.001$) or all wetlands together ($\chi_1^2 = 16.32$; $p < 0.001$). The proportions of the different species (considering only sites where *Chaoborus* spp. was present) were independent of water permanence ($\chi_2^2 = 3.30$; $p = 0.192$) and fish presence ($\chi_2^2 = 1.43$; $p = 0.488$), implying that the pattern was species-consistent (i.e., all species occurred mainly in temporary or permanent but fishless wetlands).

Habitat segregation

Estany Vell de Can Jordà was the only site that recorded all 3 *Chaoborus* species co-occurring. The abundances among *Chaoborus* species were significantly different between habitat type ($\chi_2^2 = 100.46$; $p < 0.0001$) (Fig. 3). *Chaoborus flavicans* was dominant in the temporary wetland (89.7%), whereas *C. pallidus* was the most abundant species in the permanent wetland (73.8%). *C. crystallinus* was rare (< 3%) in both habitats.

Temporal segregation

Two species were present in the Gorga de les Acàcies pond: *C. flavicans* and *C. pallidus*. The temporal analysis (Fig. 4) showed a different proportion of the species abundances seasonally ($\chi_3^2 = 113.73$; $p < 0.001$), with *C. pallidus* being more abundant in winter and *C. flavicans* dominating in autumn and spring.

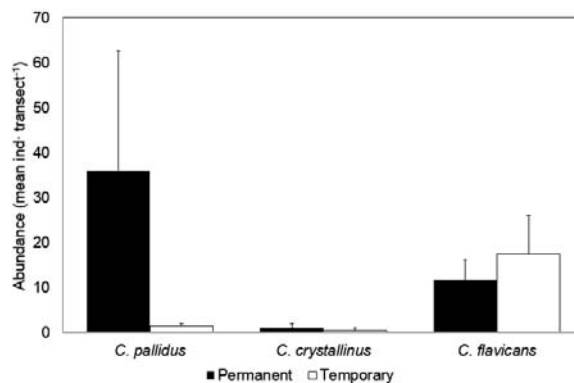


Figure 3. Bar plot of the habitat segregation study in Can Jordà wetlands, showing mean abundances and standard deviation of the three recorded species of *Chaoborus* in the two habitats studied. Gráfico de barras de la segregación de hábitat en los humedales de Can Jordà, mostrando las abundancias y las desviaciones estándar de las tres especies de *Chaoborus* en los dos hábitats analizados.

Diel horizontal migration

The diel mesohabitat analysis was performed to compare the abundances of *C. flavicans*, their potential predators and their potential resource (i.e., zooplankton) in vegetated vs. non-vegetated zones and during day- vs. night-time. For the Peça del Forn pond, the abundances of *C. flavicans* and those of predators were significantly higher in the vegetated area than the non-vegetated area ($F_{1,16} = 5.36$, $p = 0.034$;

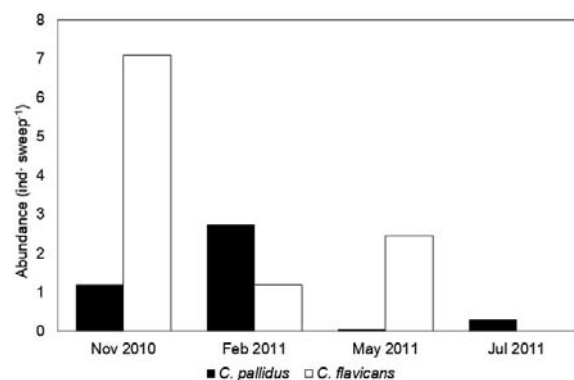


Figure 4. Bar plot of the temporal segregation study in the Gorga de les Acàcies pond, showing the abundances of the two recorded species of *Chaoborus* from November 2010 to July 2011. Gráfico de barras de la segregación temporal en la charca de la Gorga de les Acàcies, mostrando las abundancias de dos especies de *Chaoborus* desde Noviembre de 2010 a Julio de 2011.

$F_{1,16} = 25.92$, $p < 0.001$, respectively), but no significant differences were found between day- and night-time ($F_{1,16} = 0.07$, $p = 0.799$; $F_{1,16} = 1.10$, $p = 0.309$, respectively). Additionally, the interaction between both factors was not significant either ($F_{1,16} = 1.21$, $p = 0.286$; $F_{1,16} = 1.96$, $p = 0.181$, respectively). In contrast, the relative abundance of zooplankton was significantly higher during day-time than night-time ($F_{1,16} = 16.30$, $p < 0.001$), but no significant differences were found between vegetated and non-vegetated zones or in the interaction between both factors ($F_{1,16} = 3.40$, $p = 0.084$; $F_{1,16} = 0.07$, $p = 0.801$, respectively). In the Can Capçana pond, there was a significant distribution of predators according to both factors ($F_{1,16} = 49.61$, $p < 0.001$ for time, and $F_{1,16} = 6.98$, $p = 0.018$ for vegetation), indicating that more predators occurred during night-time and in vegetated areas than during day-time and in non-vegetated areas. Zooplankton abundances were not influenced by vegetation ($F_{1,16} = 2.12$, $p = 0.165$) but were higher during day-time than night-time ($F_{1,16} = 19.31$, $p < 0.001$). Moreover, the interaction between both factors was not significant ($F_{1,16} = 2.08$, $p = 0.168$). Finally, there were no significant differences in the abundances of *C. flavicans* between vegetated and non-vegetated zones ($F_{1,16} = 2.51$, $p = 0.133$) or between day- and night-time ($F_{1,16} = 0.26$, $p = 0.615$), with the factor interaction not being significant either ($F_{1,16} = 1.15$, $p = 0.300$).

DISCUSSION

This study detected all 3 Chaoboridae species that had been previously recorded in the Iberian Peninsula (Carles-Tolrà, 2002; Boix *et al.*, 2005): *C. flavicans*, *C. crystallinus* and *C. pallidus*. Furthermore, knowledge on the distribution of *C. pallidus*, only known from the Gavarres mountain range so far (Boix *et al.*, 2005), was extended to eight distinct populations.

All species were detected in both permanent and temporary wetlands. *C. flavicans* clearly dominated at the regional scale independent of

wetland type, whereas the other two species were rarer. *C. flavicans* is a wide-spread species inhabiting all types of lentic environments, from shallow temporary ponds to lakes or dams (e.g., Miracle, 1976; Prat, 1980; Boix & Sala, 2002). However, in our study (focused on shallow wetlands), we found that *C. flavicans* was associated with temporary wetlands and fishless permanent ponds. It is known that *C. flavicans* is able to live in both fish-bearing and fishless water bodies (Berendonk, 1999; Garcia & Mittelbach, 2008), but the predation pressure of some fish species on *C. flavicans* can be important (Margaritora *et al.*, 2001; Regmi *et al.*, 2013). On the contrary, *C. crystallinus* and *C. pallidus* appeared in temporary or fishless permanent ponds. Both species had already been recorded in small ponds (Seminara & Bazzanti, 1984; Berendonk & Bonsall, 2002), and at least in the case of *C. crystallinus*, they are known to avoid oviposition in fish-bearing waters (Berendonk, 1999). However, the regional dominance of *C. flavicans* could not only be explained by the presence of fish as all species occurred mainly in fishless wetlands. Berendonk and Bonsall (2002) also found a clear local dominance of *C. flavicans* over *C. crystallinus*, due to the distinct lifestyle strategies found among *Chaoborus* spp. larvae. These authors found that *C. flavicans* lives in lakes (where it can develop large populations) and ponds, creating a population structure that consists of a series of small habitat patches within the range of a large habitat patch (i.e., a mainland-island metapopulation structure; Berendonk & Bonsall, 2002). In contrast, despite their relatively higher dispersal capacity, *C. crystallinus* presents higher risks of local extinction due to its different metapopulation structure, namely a large network of similar small patches (usually small fishless ponds; Berendonk & Bonsall, 2002). Another factor that could contribute to its relatively higher risk of local extinction is the decreasing number of fishless waters, due to increasing exotic fish introductions (e.g., Leyse *et al.*, 2004; Catalan *et al.*, 2006). Furthermore, the low concentration (or absence) of UV-absorbing compounds in *C. crystallinus* and *C. pallidus* (Nagiller & Sommaruga, 2009)

could also contribute to explaining the observed preference of these species for ponds that are shaded by canopy and/or macrophytes.

From our regional survey we concluded that the observed co-occurrences (10%) were neither more nor less frequent than should be expected by random draws from the Chaoboridae regional pool. Nevertheless, in the field studies we detected spatial and temporal segregation patterns among *Chaoborus* species that showed a partial overlap. For instance, in the habitat segregation study, we found that the temporary wetland was dominated by *C. flavicans* and that the permanent wetland was dominated by *C. pallidus*. Similarly, in the temporal field study, we observed that the relative abundances of both *C. flavicans* and *C. pallidus* changed over time. In North America, it has been observed that the segregation of *Chaoborus* species may be caused by competitive exclusion or by intraguild predation. In that case, *C. punctipennis* (Say, 1823) is known to be eliminated by *C. americanus* (Johannsen, 1903) in fishless bog lakes due to the early phenology and large size of *C. americanus* (Von Ende, 1979). *C. punctipennis* may also co-occur with *C. flavicans*, but their different phenologies allow for different larval size, hence reducing interspecific competition for prey (Von Ende, 1982).

It is widely known that *Chaoborus* larvae perform diel vertical migrations in several aquatic environments, including temporary ponds (e.g., Bass & Sweet, 1984; Meerhoff *et al.*, 2007; Lagergren *et al.*, 2008). The existence of diel horizontal migrations has also been reported in *Chaoborus* spp. larvae, but these have usually been associated with incomplete vertical migrations (Voss & Mumm, 1999) or during food shortages (at a seasonal scale; Liljendahl-Nurminen *et al.*, 2002). In our study, *C. flavicans* did not display, overall, a diel horizontal migration. However, in one of the ponds (Peça del Forn pond), *C. flavicans* was more abundant in vegetated than in non-vegetated areas during both day- and night-time. Its horizontal distribution was not explained by any mesohabitat migration of zooplankton but coincided with the distribution of its potential predators (anisopteran odonates were the most abundant predator in

this pond). Although *Chaoborus* spp. larvae typically inhabit open waters (Sæther, 1972) they are sometimes associated with other mesohabitats, such as emergent or floating-leaved plants (Smiley & Tessier, 1998; Iglesias *et al.*, 2007), where they can avoid visual predators (Folsom & Collins, 1984; Burks *et al.*, 2001). It is well known that aquatic vegetation influences the structure of macroinvertebrate communities, not only by providing food resources (e.g., Burdett & Watts, 2009) but also by offering physical refuge from predation (e.g., Hampton & Duggan, 2003; Paukert & Willis, 2003; Gascón *et al.*, 2013). Although we cannot rule out the possibility that chaoborids were performing diel vertical migration using sediment as a refuge, as has been documented (Bass & Sweet, 1984; Gosselin & Hare, 2003), our study suggests that in shallow water bodies, vegetation structure may play an important role as a refuge for chaoborid larvae.

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