Spatio-temporal Distribution and Ecological Preferences of Coexisting Hydropsychid Species (Trichoptera) in Two Mediterranean River Basins (S Spain).

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Summary

The hydropsychids of two Mediterranean river basins in southern Spain (Guadaira and Guadalete) were investigated from January 1988 to January 1989. The distribution of hydropsychids along an environmental gradient related to altitude varied depending on species. Two distinct species assemblages were observed, one located in the lower altitude sites (the "downstream assemblage" comprising *Hydropsyche pictetorum*, *Hydropsyche exocellata* and *Cheumatopsyche lepida*) and the other in the upper-most areas (the "upstream assemblage" comprising *Hydropsyche punica*, *Hydropsyche infernalis*, *Hydropsyche instabilis*), which displayed a statistically significant preference for this type of habitat. Finally, *H. pictetorum*, selected the lowest sites. From a temporal point of view most species displayed a high variability in density dynamics between sites, suggesting a strong plasticity in life-cycle phenology.

INTRODUCTION

Hydropsychid larvae are rheophilic net-spinning inhabitants of stream riffles where they filter suspended particulate matter (McElhone *et al*., 1987; Czachorowski, 1989). Due to their feeding habits, hydropsychid larvae play an important role in processing organic matter in river systems, and dominate many streams in terms of biomass and secondary production (Mackay and Wiggins, 1979; Georgian and Thorp, 1992).

In Mediterranean streams Hydropsychidae, in addition to the Hydroptilidae, were considered the most important caddisfly families, both in terms of abundance and species richness (Giudicelli *et al*., 1985). In the Iberian Penninsula hydropsychids rank 5th in caddisfly richness with 22 species (González *et al*., 1987, 1992) and represents a significant fraction of the total macroinvertebrate biomass in Mediterranean streams (Prenda, 1993).

Generally, larvae of hydropsychid species have similar ecological requirements, and therefore the interspecific competition within coexisting members of this family may be very significant. The coexistence of several species of this caddisfly family in the same river basin is facilitated by longitudinal replacement of species (Camargo, 1992; Voelz and Ward, 1992), by temporal segregation in their life cycle (Recasens and Puig, 1987) and/or by microhabitat partitioning (Czachorowski, 1989). Also, in streams found in a Mediterranean climate frequent hydrologic disturbances may facilitate the coexistence of closely related hydropsychid species (Bournaud *et al*., 1986; Resh *et al*., 1990).

In previous studies, we have observed a strong environmental gradient between headwaters and lower altitude areas in two Mediterranean streams. This gradient affected invertebrate distribution, especially that of Mollusca (Gallardo *et al*., 1994), Plecoptera and Ephemeroptera (Prenda and Gallardo, unpublished data). The objectives of this study were: 1) to determine the distribution of the hydropsychid species along the altitudinal profile of two Mediterranean river basins (altitudinal replacement); 2) to examine the relationship between the observed species distribution and the environmental gradient; and 3) to explore the temporal hydropsychid species succession.

METHODS AND MATERIALS

This study was carried out in two Mediterranean river basins: the Guadaira and Guadalete rivers (South Spain) (Fig. 1). The Guadaira river, as most streams in the basin, has a high natural salinity that diminishes downstream (Table 1). The basin relief is gentle and land use is almost totally agricultural (intensive unirrigated herbaceous crops and olive trees). The headwater of the Guadalete basin is a mountainous area, with natural forests and pastures, and some agriculture. Here in most streams, the water flows all year round and the salinity is much lower than that in the Guadaira basin (Table 1).

Seven sites in the Guadaira basin (in this paper we will only refer to two sites at which any hydropsychids were collected) and four sites in the Guadalete were sampled, approximately six times each (January, March, May, August and October 1988, and January 1989). On each sampling trip, several physico-chemical parameters of the water were measured (see Table 1). A sample of macroinvertebrates was taken using a combination of a triangular net (kick method) and a 0.25 m^2 square box (mesh size 0.5 mm, in both cases). Hydropsychid abundance is expressed as individuals per unit effort (i.p.u.e), with one unit effort equaling the sum of a net sample during 30 s plus 1 box sample. A complete description of the study area, sampling procedure and analytical techniques can be found in Prenda and Gallardo (1992), Gallardo (1993), and Gallardo and Prenda (1994).

To examine the relationship between the physico-chemical conditions of the water and hydropsychid species, a Principal Component Analysis (PCA) of the matrix sites x variables was performed. Each variable represented the mean value of the 6 sampling dates of log-transformed physico-chemical data. To test the environmental preferences of each species the frequency distribution of the first principal component (PC1) scores (expected frequencies) and the distribution of the sites in which each species was found (observed frequencies), were compared. A Chi-squared goodness of fit test was used to determine whether or not significant differences existed between the environmental conditions available and those selected by the hydropsychids. When the species are randomly distributed according to the physico-chemical conditions, the observed and expected frequency distributions should not be significantly different (for more details see Grossman and Freeman, 1987; Gallardo *et al*., 1994; Prenda *et al*., 1997).

For each hydropsychid species an adjusted average temperature (AAT) was calculated. This was done by multiplying the frequency of individuals of each species caught in each date/site (f_i) by the temperature measured in this date/site (t_i), and then summing up all of these values:

$$AAT = \Sigma f_i * t_i$$

This adjustment prevents the risk of bias towards the mean temperature of the sites in which one species was captured against those temperatures measured in sites with extreme temperatures but where a small fraction of individuals was caught.

RESULTS

Distribution patterns

A total of six hydropsychid species were collected in the Guadaira and Guadalete river basins (Table 2). Although seven sites were sampled in the Guadaira basin, hydropsychids were found in only two. Only those sites in which any component of this caddisfly family was captured, will be discussed.

The hydropsychid species in the Guadaira and Guadalete river basins can be grouped into two assemblages (Table 2): the "downstream assemblage" composed of *Hydropsyche pictetorum* Botosaneanu & Schmid, *Hydropsyche exocellata* Dufour, and *Cheumatopsyche lepida* (Pictet) and the "upstream assemblage", composed of *Hydropsyche punica* Malicky, *Hydropsyche infernalis* Schmid and *Hydropsyche instabilis* (Curtis). The three components of each assemblage coexisted only in three of the six sites sampled, the lowest (site 1), the upper (site 6) and in site 2 (at very low densities) (Table 2). In site 2 the highest salinity values were recorded, with a significant chloride and sulphate concentration (Table 1) and with a semipermanent flow regime (the water did not flow during the summer, when it was confined to small unconnected pools). The other three intermediate sites (3, 4 and 5) contained only one or two species. *H. pictetorum* was not found in Guadalete basin whereas the upstream assemblage was only in this basin. *H. punica* was the only hydropsychid species collected in site 4 (temporal flow regime, i. e. this stream had water only during the wet season and during the summer was completely dry) and site 5, which had the greatest density of any hydropsychid in the study area. Also, this species was the least abundant in site 6 (Table 2).

All these facts point to the opportunistic behaviour of *H. punica*, specially due to its capacity to colonize and thrive in temporal habitats.

A negative correlation between species inhabiting sites 1 and 6 was not observed indicating no competitive exclusion (Kendall rank correlation test, P> 0.14 in all cases; n = 6 for site 1 and n = 5 for site 6).

The AAT indicates the average temperature corrected by the frequency of individuals of one species collected in each site, and it can be indicative of its thermal preferences. *C. lepida* and *H. exocellata* showed preference for warmer conditions (24.3 and 23.3 ºC of AAT, respectively). *H. infernalis* and *H. instabilis* were mostly found in cooler sampling sites (10.0 and 11.5 ºC of AAT, respectively) (Table 2).

Water physico-chemical preferences

The sites sampled in Guadaira and Guadalete river basins could be ranked according to a gradient in water physico-chemical conditions based on altitude. The water velocity in the higher altitude sites was greater whereas the organic matter content, suspended solids, salinity, temperature and chlorophyll "a" concentration were lower than those in the sites sampled at lower altitudes (Fig. 2a). The distribution of hydropsychids along this environmental gradient varied depending on species (Fig. 2b). *H. infernalis*, *H. instabilis* and *H. punica* preferred the higher altitude habitat conditions (chi-squared= 49.5, 49.5 and 21.5 respectively, 2 d.f., P<0.0001 in all cases). The distribution of *H. exocellata* and *C. lepida* missmatch with the expected distribution of sites (chi-squared=4, 2 d.f., P= 0.14, in both cases). Thus, these species did not seem to prefer any specific environmental condition, from those available at the study area. Finally, *H. pictetorum*, selected the lower altitude sites (chi-squared= 6.3, 2 d.f., P= 0.043) (Fig. 2b).

Temporal succession

Comparing the temporal succession of species at sites 1 and 6 (in which the two hydropsychid assemblages defined in the study area were complete), two very different patterns emerged (Fig. 3). In the lower site (site 1) the maximum hydropsychid abundance was recorded during August. On the other hand, in the upper-most site (site 6), August was the month with the fewest hydropsychids.

Comparison of the frequency distribution of species abundance between sites led us to examine the potential phenotypic plasticity in the life cycle phenology at a regional scale. Thus, *C. lepida* reached its maximum density in August at sites 1 and 2, and in March at site 3 (Fig. 4). *H. exocellata* displayed three different maxima, in March, in May and in August, for sites 3, 2, and 1, respectively. *H. punica* presented three different patterns of frequency distribution (Fig. 4). At the temporal site (site 4) the species reached its maximum density in May, before the stream dried up. In site 5, where it was the only hydropsychid species collected, it reached two maxima, one in August and other one in winter (January). At site 6, where *H. punica* coexisted with two other species (Fig. 3), the species reached its maximum density in October, when the other two sympatric species were at lower densities.

DISCUSSION

The longitudinal succession of hydropsychid species may be a consequence of different feeding habits (Voelz and Ward, 1992), metabolic needs (Roux *et al*., 1992), or differential competitive abilities of the various species along the watercourse (Mackay and Wiggins, 1979; Tachet *et al*., 1992). In the study area, factors such as specific environmental tolerances to certain physico-chemical variables cannot be discarded as a limiting factor to the distribution of hydropsychids (Camargo, 1992). For instance, the strong changes in salinity or suspended matter between the headwaters and the lower altitude areas may affect the species distribution. Also, the different thermal regime of each sampling site (at least between the higher and lower sites) (Prenda, 1993) may favor some hydropsychid species instead of others.

According to De Moor (1993) caddisfly richness and species diversity are negatively correlated with chloride concentration and suspended solids. In the study area salinity did not affect species richness but it may have influenced species composition. In the Guadaira and

Guadalete basins the "upstream assemblage" was composed of three selective species that preferred headwater conditions and probably their tolerance to the physico-chemical conditions were not as broad as the rest of the species collected in the study area. On the other hand, two of the three hydropsychid species that made up the "downstream assemblage" (*H. exocellata* and *C. lepida*) did not show any preference with respect to the physico-chemical variables studied. They could be considered generalists (Prenda and Gallardo, 1996). These species are considered by several authors as salinity tolerant (Millet and Prat, 1984; González del Tánago and García de Jalón, 1987; Gallardo, 1994). Lenat (1984) observed that an increase in suspended solids due to agriculture practices favored the dominance of *Cheumatopsyche* sp. The preference of *H. pictetorum* for the most downstream habitat conditions is remarkable. This species was considered halophilic by Gallardo (1994).

In relation to the wide physico-chemical tolerances of the "downstream assemblage", these species, despite their rheophilic character, were able to colonize (and two of them to reach their maximum densities) sites almost without flow (0.06 m s^{-1}, maximum water flow measured in August in the Guadaira basin). Also, the thermal tolerance of some of the members of this assemblage has been stressed in previous papers, especially that of *H. exocellata* (Bournaud *et al.*, 1987; Dolédec and Tachet, 1989; De Soto *et al.*, 1994). However, *C. lepida* was considered by Bournaud *et al*. (1987) as a coldwater species. Generally, these thermal preferences were in close agreement with those found by Perrin and Roux (1978), who observed a blooming of hydropsychids in summer.

There are several examples of hydropsychid altitudinal succession in the Iberian penninsula, similar to that found in the study area (Table 3).

Coexisting hydropsychid species in the Guadaira and Guadalete river basins did not display any negative correlation in their densities. Apparently, from a numerical point of view, the potential competitive interaction between these species did not affect their relative abundances. This result is similar to that obtained by Czachorowski (1989) who did not find any significant negative correlation between the densities of *Hydropsyche siltalai*, *H. angustipennis* and *H. pellucidula*.

Coexisting species could further reduce competition by several alternative mechanisms, such as: 1) the use of different microhabitats or specific positions within the substrate (Czachorowski, 1989; Englund, 1991); 2) body size differences [Sweeney and Vannote (1981) observed that closely related mayfly species were ecologically segregated, and therefore reduced potential competition]; or 3) different feeding habits based in different net mesh sizes

(Voelz and Ward, 1992). Mechanisms 2) and 3) can be related due to the different mesh size made by larvae in a different developmental stage. Hildrew and Edington (1979) found that *H. pellucidula* and *H. siltalai* coexisted in the same microhabitat, but in a different larval stage due to the differences in the net size made by each species.

Czachorowski (1989) observed that *C. lepida* and *H. siltalai* overlapped in their life cycles, but they coexisted via colonization of different microhabitats. McElhone *et al*. (1987) support the microhabitat partitioning between *H. exocellata* and *C. lepida*. These authors found that *Cheumatopsyche* sp. was tolerant of lower water velocities, whereas *Hydropsyche* spp. were strongly dependent on high water velocities in a Canadian stream. On the contrary, Dolédec and Tachet (1989) considered *H. exocellata* as less rheophilic than *C. lepida*. Thus, a probable explanation for hydropsychid coexistence at sites 1 and 3 was a microhabitat segregation between *H. exocellata* and *C. lepida* and a probable temporal (size) segregation between these species and *H. pictetorum* (see Fig. 3). In a study by Dolédec and Tachet (1989), the lag in development of *H. exocellata* and *C. lepida* populations, besides distinct microhabitat preferences, was hypothesized as a mechanism contributing to their temporal coexistence.

At site 2, hydropsychid density was very low. This could prevent any competitive interaction between the three sympatric species inhabiting this site. However, *C. lepida* and *H. exocellata* displayed a clear temporal segregation (see Fig. 4). Sites 4 and 5 were inhabited by one species only. Finally, in order to explain the sympatry of the three coexisting species at site 6, a probable life cycle asynchrony, along with a different life cycle length could be speculated based on their different temporal dynamics. The lack of knowledge on microhabitat preferences of any of site 6 species does not exclude the possibility that microhabitat partitioning could be a significant mechanism facilitating the coexistence of these species.

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Table 1. Mean values (± 1 S.E.) of selected physico-chemical variables at the six localities of the Guadaira and Guadalete river basins from January 1988 to January 1989. The stream type (P: permanent, S: semipermanent and T: temporal) of each site are also indicated. N: number of times each site was sampled.

	GUADAIRA		**GUADALETE**			
sampling site	**1**	**2**	**3**	**4**	**5**	**6**
altitude	180	240	240	360	380	660
temporality	P	S	P	T	P	P
temperature (°C)	15.5 ± 2.8	17.5 ± 3.20	18.0 ± 2.30	15.3 ± 2.90	14.0 ± 2.3	13.2 ± 1.40
water current (m s^{-1})	0.36 ± 0.08	0.25 ± 0.08	0.74 ± 0.20	0.17 ± 0.06	0.28 ± 0.05	0.34 ± 0.08
suspended solids (mg l^{-1})	163.3 ± 32.3	111.7 ± 28.2	16.7 ± 2.20	16.7 ± 3.30	2.5 ± 0.8	10.0 ± 3.20
permanganate value (mg O$_2$ l^{-1})	3.52 ± 0.70	5.87 ± 1.18	3.66 ± 0.55	5.00 ± 2.30	2.68 ± 0.23	2.16 ± 0.56
conductivity (mS cm^{-1})	3.40 ± 0.28	6.77 ± 0.94	1.12 ± 0.09	0.37 ± 0.09	0.67 ± 0.07	0.46 ± 0.10
chloride (meq l^{-1})	18.85 ± 0.72	70.06 ± 14.6	5.06 ± 0.74	1.03 ± 0.17	0.88 ± 0.09	1.02 ± 0.27
sulphate (meq l^{-1})	6.20 ± 1.38	9.42 ± 1.99	4.54 ± 1.87	0.73 ± 0.12	3.97 ± 1.04	0.98 ± 0.30
alkalinity (meq l^{-1})	5.12 ± 0.15	4.87 ± 0.31	4.36 ± 0.33	5.17 ± 0.03	4.30 ± 0.07	5.36 ± 0.24
silicate (µM l^{-1})	191.5 ± 35.7	181.7 ± 38.7	137.6 ± 14.3	133.9 ± 39.3	95.6 ± 11.2	80.6 ± 14.4
phosphate (µM l^{-1})	0.77 ± 0.48	0.40 ± 0.27	3.30 ± 0.94	0.00 ± 0.00	5.88 ± 2.70	0.16 ± 0.16
nitrate (µM l^{-1})	102.86 ± 28.3	13.08 ± 3.22	50.84 ± 5.35	22.27 ± 19.0	32.75 ± 1.20	28.84 ± 12.5
nitrite (µM l^{-1})	1.57 ± 0.46	0.60 ± 0.29	2.14 ± 0.63	0.17 ± 0.03	0.35 ± 0.13	0.36 ± 0.31
ammonium (µM l^{-1})	10.76 ± 7.51	24.62 ± 16.8	23.94 ± 12.9	3.40 ± 1.80	29.92 ± 17.44	12.13 ± 8.00
chlorophyll "a" (µg l^{-1})	2.30 ± 0.79	2.65 ± 0.51	1.28 ± 0.43	1.77 ± 1.77	1.50 ± 0.36	0.48 ± 0.13
N	6	6	5	3	6	5

Table 2. Mean relative densities (i.p.u.e ± 1 S.E.) and percentage of total abundance (below in parenthesis) of the six hydropsychid species collected at the six localities of the Guadaira and Guadalete river basins from January 1988 to January 1989. AAT: adjusted average temperature (see Methods); N: total number of individuals collected.

	GUADAIRA		**GUADALETE**					
sampling site	**1**	**2**	**3**	**4**	**5**	**6**	**AAT**	**N**
Hydropsyche pictetorum	0.96 ± 0.40 (94.5)	0.06 ± 0.06 (5.5)	0 (0)	0 (0)	0 (0)	0 (0)	18.9	17
Cheumatopsyche lepida	5.58 ± 5.24 (74.4)	0.17 ± 0.17 (2.2)	2.10 ± 2.10 (23.3)	0 (0)	0 (0)	0 (0)	24.3	101
Hydropsyche exocellata	6.75 ± 6.08 (56.9)	0.83 ± 0.65 (7.0)	5.13 ± 3.83 (36.1)	0 (0)	0 (0)	0 (0)	23.3	171
Hydropsyche punica	0 (0)	0 (0)	0 (0)	1.50 ± 1.04 (4.8)	12.36 ± 4.64 (78.9)	3.06 ± 1.43 (16.3)	15.1	237
Hydropsyche infernalis	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	5.66 ± 3.60 (100)	10.0	119
Hydropsyche instabilis	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	7.02 ± 3.04 (100)	11.5	129

Table 3. Altitudinal distribution of hydropsychid species in the Iberian penninsula, according to different authors.

species	**altitudinal distribution**	**geographical location**	**reference**
H. instabilis	upstream	Central Spain	(1)
"	"	Northeastern Spain	(2) (3)
"	"	Northwestern Spain	(4)
H. punica	upstream	South Spain	(5)
H. pictetorum	downstream	Central Spain	(1)
"	"	Northwestern Spain	(4)
H. exocellata	downstream	Northeastern Spain	(3)
"	"	Northwestern Spain	(4)
"	"	Portugal	(6)
C. lepida	downstream	Portugal	(6)

(1) HERRANZ and GARCIA DE JALON (1984), (2) MILLET and PRAT (1984), (3) GONZALEZ *et al*. (1985), (4) DE SOTO *et al.* (1994), (5) GARCIA DE JALON and GONZALEZ DEL TANAGO (1986), (6) TERRA and MOLLES (1987)

FIGURE CAPTIONS

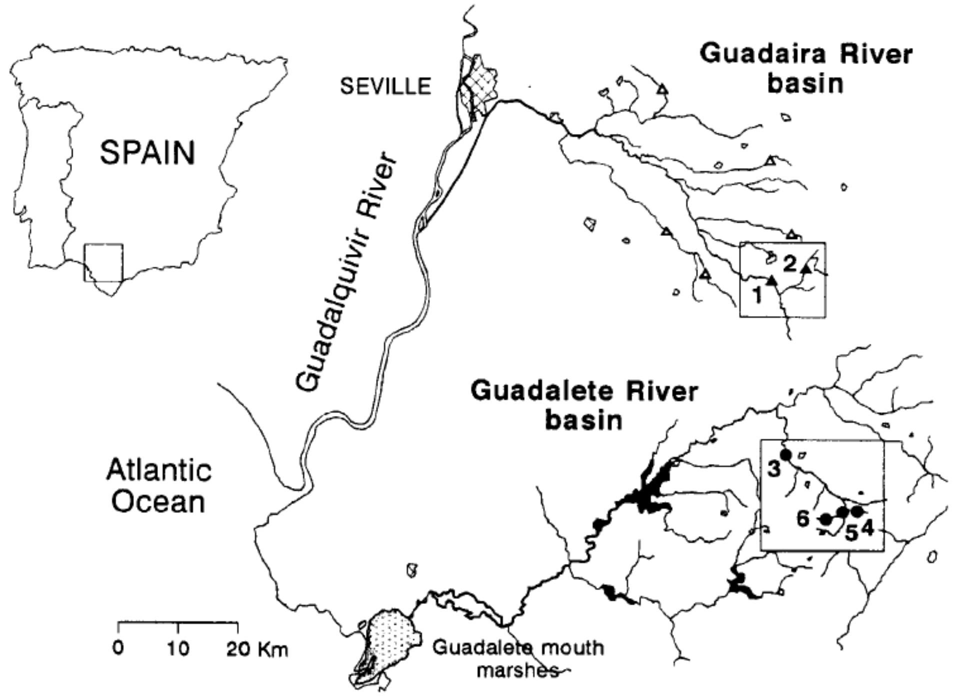

Fig. 1. Map of the study area showing the sites sampled (filled circles and triangles). Non-filled triangles are sampled sites without caddisflies. Towns are represented by hatched polygons.

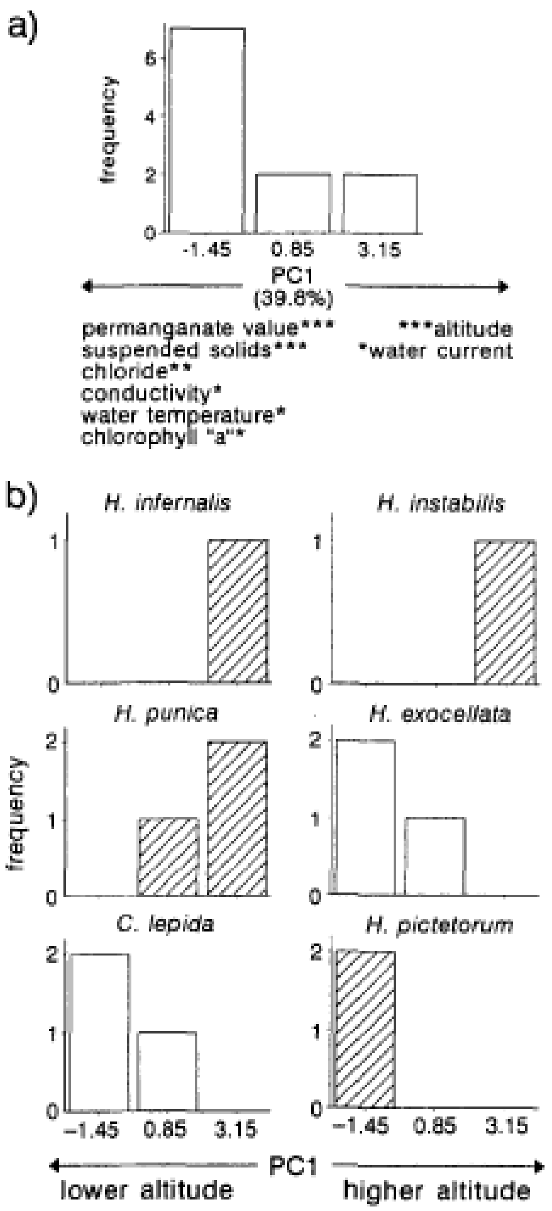

Fig. 2. a) Frequency distribution of first principal component (PC1) scores for water physico-chemical conditions availability in Guadaira and Guadalete river basins. The variables significantly correlated with the component are listed below the histogram (positively correlated variables in the right side and negatively correlated in the left side). * $P<0.05$, ** $P<0.01$, *** $P<0.001$. In parenthesis is the percentage of variance accounted for PC1. b) Frequency distribution of species use data. Hatched bars represent use data significantly different (chi-squared goodness of fit test) from physico-chemical conditions (for details see Methods).

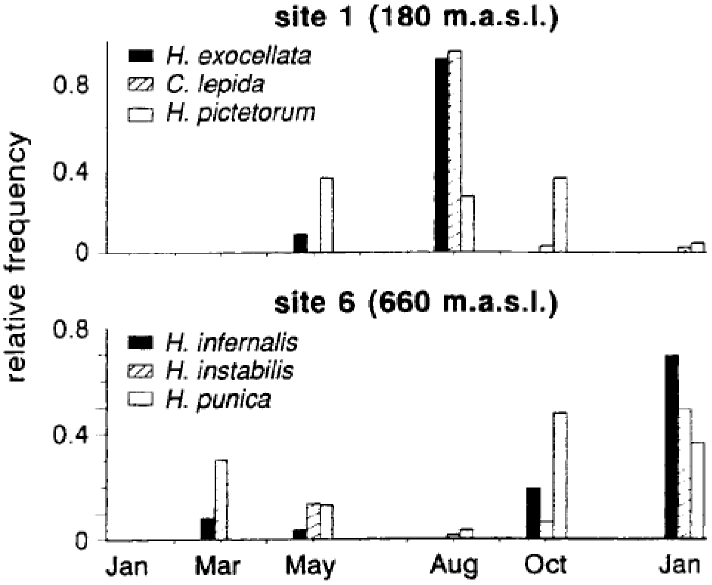

Fig. 3. Temporal changes in the relative frequency of hydropsychid species abundance at sites 1 and 6 in Guadaira and Guadalete basins.

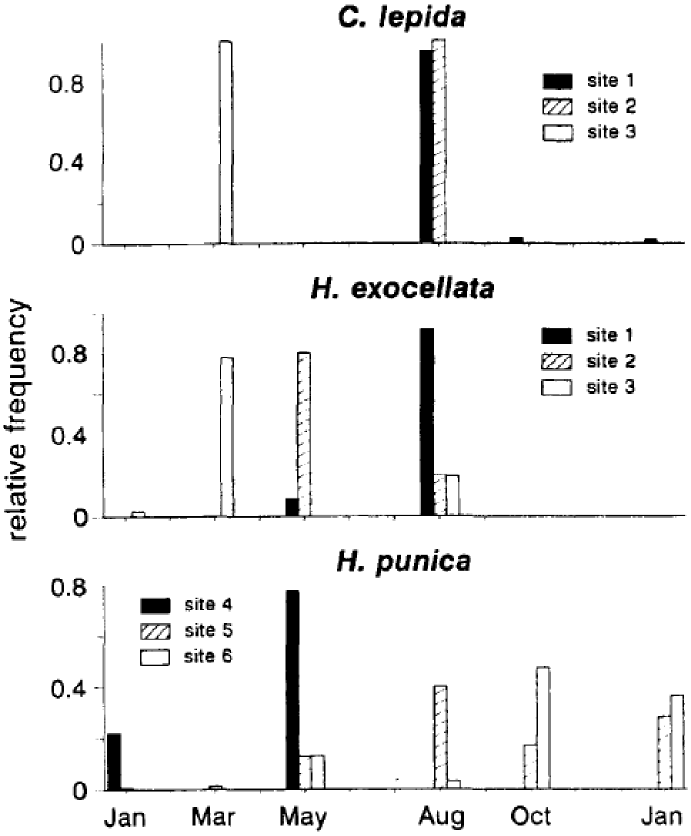

Fig. 4. Temporal changes in the relative frequency of some hydropsychid species abundance at three sites in Guadaira and Guadalete basins.