

Spatio-temporal Distribution of Simuliids (Diptera) and Associated Environmental Factors in two Mediterranean Basins of Southern Spain

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ABSTRACT

The distribution of simuliid species in rivers Guadaira and Guadalete (south of the Iberian Peninsula) is examined in relation to some associated environmental factors. The most abundant and widespread species in the study area were *Simulium velutinum*, *Simulium intermedium* and *Simulium pseudoequinum*, whereas *Simulium lineatum*, *Simulium ruficorne* and *Metacnephia blanca* were very rare. Stepwise multiple regression revealed that *S. velutinum* was positively influenced by chemical oxygen demand, whereas *S. pseudoequinum* and *S. sergenti* depended on altitude (negatively) and current velocity (positively). The coefficient of correlation between distance between sites and Jaccard's index of similarity of the sites showed that the simuliid community at different sites changed as a direct function of distance. *Simulium xanthinum* was found only at higher altitude sites, where water quality was best. Most of the remaining species were opportunistic. The number of simuliid species in the basins of rivers Guadaira and Guadalete was lower than that reported for other, nearby basins. The similarity in species composition between these basins was low.

Key words: Simuliidae, environmental preferences, temporary streams, similarity

RESUMEN

Este estudio se centra en la distribución de Simúlidos en las cuencas de los ríos Guadaira y Guadalete (sur de la Península Ibérica) y algunos de los factores ambientales asociados. Los resultados mostraron que las especies más abundantes y más ampliamente distribuidas en el área de estudio fueron *Simulium velutinum*, *Simulium intermedium* y *Simulium pseudoequinum*, mientras que *Simulium lineatum*, *Simulium ruficorne* y *Metacnephia blanca* fueron muy raras. Los análisis estadísticos realizados revelaron que la distribución de *S. velutinum* dependía positivamente de la demanda química del oxígeno, mientras que *S. pseudoequinum* y *S. sergenti* dependían de la altitud (negativamente) y de la velocidad de la corriente (positivamente). Las correlaciones obtenidas entre la distancia existente entre los cauces y sus índices de similaridad de Jaccard mostraron que las diferencias en la composición de las comunidades aumentaban con la distancia. *Simulium xanthinum* solo se encontró en los sitios de mayor altitud, donde la calidad del agua era la mejor. Para el resto de las especies, la mayoría mostró un carácter oportunista. El número de especies en las cuencas estudiadas fue más bajo que los encontrados en otras cuencas próximas, y la similaridad entre ellas fue igualmente baja.

Palabras clave: Simuliidae, preferencias ambientales, cauces temporales, similitud

INTRODUCTION

Simuliids make up an important component of stream communities, acting as intermediate links between particle dynamics and predators (Malmqvist, 1994; Malmqvist *et al.*, 1999). Their

aquatic stages are mainly conditioned by water current and food (Morin & Peters, 1988). This dependence on the flow rate is related to the procurement of food (Palmer *et al.*, 1993), though it may also play an important part in avoiding predators (Malmqvist & Sackmann, 1996; Muotka, 1993).

Macroinvertebrate communities of two adjacent basins in the south of the Iberian Peninsula were studied to obtain information about their environmental preferences and importance as biological indicators of water quality (Gallardo-Mayenco & Prenda, 1994; Gallardo-Mayenco *et al.*, 1994; 1995; 1998; Prenda & Gallardo-Mayenco, 1992; 1996; 1999). The goal of this work is to describe the spatio-temporal distribution of simuliid species inhabiting the study area and to examine its relationships to environmental factors.

STUDY AREA AND METHODS

Rivers Guadaira and Guadalete are two adjacent river basins in the south of the Iberian Peninsula, influenced by Mediterranean climate. An environmental gradient exists based on the altitude above sea level and affecting the physico-chemistry of the stream water. Thus, water current is faster at the upper reaches, and suspended solids, salinity and organic matter are higher downstream (Table 1; Gallardo-

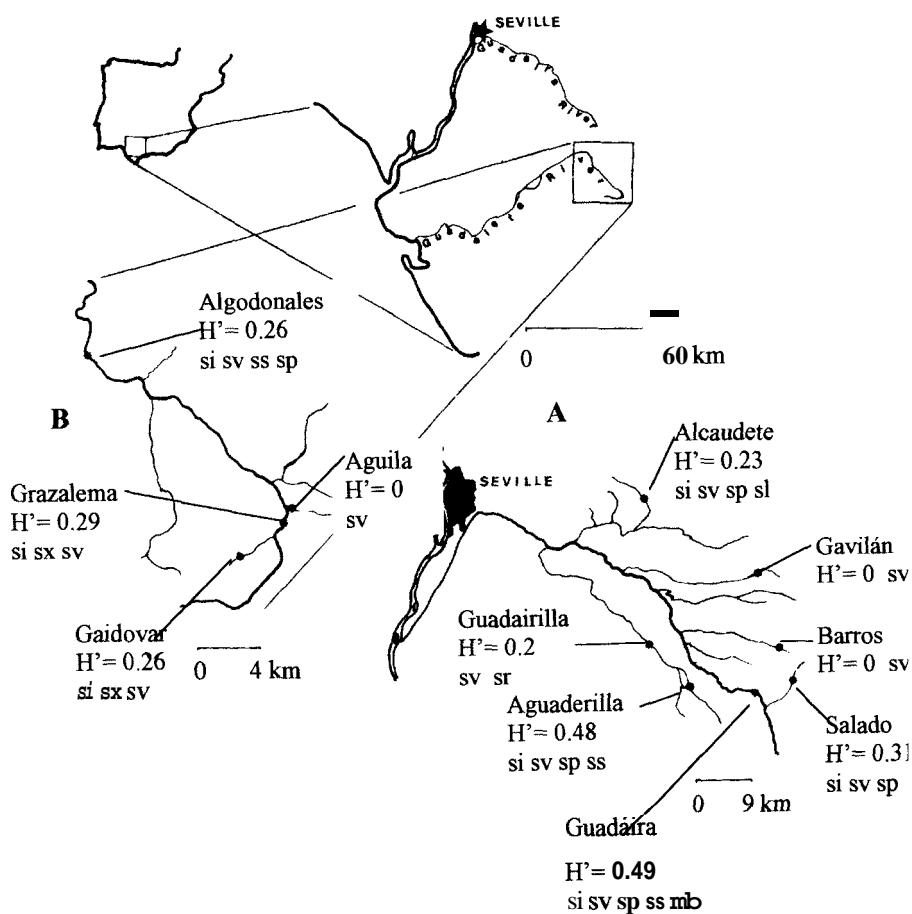


Figure 1. Situation of sites sampled: A) Guadaira river basin, B) Upper Guadalete river basin. H' = Shannon Diversity index; mb: *M. hlanici*, si: *S. intermedium*, sl: *S. lineatum*, sp: *S. pseudequinum*, sr: *S. ruficorne*, ss: *S. sergenti*, sv: *S. velutinum*, sx: *S. xanthinum*. Situación de los sitios muestreados: A) Cuenca del Río Guadaira, B) Tramo alto de la Cuenca del Río Guadalete. H' = diversidad de Shannon; mh: *M. blanca*, si: *S. intermedium*, sl: *S. lineatum*, sp: *S. pseudequinum*, sr: *S. ruficorne*, ss: *S. sergenti*, sv: *S. velutinum*, sx: *S. xanthinum*.

Table 1. Means and ranges of the physico-chemical variables measured in the basins of rivers Guadaira and Guadalete. Means are compared using *t* tests. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, N = number of samples. *Medias y rangos de las variables físico-químicas medidas en las cuencas de Guadaira y Guadalete. Se incluyen las comparaciones de los *t* test, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, N = número de muestras.*

	River Guadaira basin			River Guadalete basin		
	N	range	mean	N	range	mean
altitude (metres asl)**	7	70-240	147	4	240-660	410
temperature (°C)	31	8-27	16.7	19	9-24	15.1
water current (cm s ⁻¹)**	30	0-60	20.8	19	5-130	39.7
suspended solids (mg l ⁻¹)***	28	0-320	125.4	18	0-23	10.5
conductivity (mS cm ⁻¹)***	31	0.2-14.6	4.5	17	0.2-1.3	0.7
chloride (meq l ⁻¹)***	28	0.8-205	47.7	19	0.6-7.9	2.0
sulphate (meq l ⁻¹)**	31	0-20.7	6.1	19	0.4-11.5	2.8
alkalinity (meq l ⁻¹)	31	2.3-6.3	4.5	19	3.3-6	4.7
permanganate value (mg l ⁻¹)*	31	0.2-12.8	5.5	19	0.9-9.6	3.1
phosphate (μM)*	31	0-3	0.6	19	0-19.1	2.7
nitrate (μM)*	31	0-1100	201.5	19	0-72.4	34.8
nitrite (μM)	31	0-15.9	2.2	19	0-3.9	0.8
ammonia (μM)	28	0-235	20.7	18	0-301	36.5
chlorophyll-a (pg l ⁻¹)	31	0-15.7	2.8	17	0-5.3	1.2

Mayenco *et al.*, 1994; 1998; Prenda & Gaillard-Mayenco, 1999).

From January 1988 to January 1989, 31 bimonthly samples were taken from 7 sites in the basin of river Guadaira and 19 from 4 sites in the

basin of river Guadalete. Two sampling methods were employed, i.e. kick samples using a triangular 35-cm long net, and directly stirring the substratum to a depth of 3 – 6 cm with a square 20-cm box. The results were expressed semi-quantit-

Table 2. Average number of individuals per unit effort (X) and standard deviation (SD) of simuliid species collected in the study area from January 1988 to January 1989. f: number of sites where each species was present; AAT: adjusted average temperature (°C); t range, range of temperatures at which each simuliid species was found; altitude range (metres above sea level); n: number of sites sampled; N: frequency (over 50). *Media (X) (en individuos por unidad de esfuerzo) y desviación estándar (SD) de las especies de simúlidos recogidas en el área de estudio; f: número de sitios donde cada especie estuvo presente; AAT: temperatura media ajustada (°C); t range, rango de temperaturas en que se ha recogido cada especie; rango de altitud (en metros sobre el nivel del mar); n: número de sitios muestreados; N: frecuencia (sobre 50).*

	River Guadaira			River Guadalete			N	AAT	Altitude t range	
	n = 7	X	SD	f	n = 4	X	SD	f		
<i>Metacnephia blanca</i>	1.4	3.7	1	0				1	14	180
<i>Sirnulium lineatum</i>	0.05	0.1	1	0				1	12	70
<i>Simulium ruficorne</i>	0.2	0.4	1	0				1	23	80
<i>Sirnulium velutinum</i>	73.0	84.5	7	3.7	3.9	4	32	17.7	8-27	660-70
<i>Sirnulium intermedium</i>	11.4	15.9	4	1.3	2.1	3	18	15.9	8-23	660-70
<i>Sirnulium pseudequinum</i>	10.3	21.2	4	5.6	11.1	1	10	15.9	10-27	240-70
<i>Simulium sergenti</i>	0.4	1.1	2	1.2	2.4	1	4	15.5	12-19	240-120
<i>Simulium xanthinum</i>	0			0.1	0.1	2	3	14	9-14	660-380

tatively, as units of effort (u.e.). One u.e. is the sum of one net plus one box sample.

In the basin of river Guadaira, three types of streams were sampled, classified according to the permanence of water, i.e. permanent streams (Guadaira), semipermanent streams (Salado, Barros and Guadairilla), and temporary streams (Aguaderilla, Gavilán and Alcaudete). Two types of stream were sampled in the basin of river Guadalete, i.e. permanent streams (Algodonales, Grazalema and Gaidoar), and temporary streams (Aguila) (Fig. 1). Temporary streams were those completely dry during the drought period; semipermanent streams were made up of isolated pools during the drought period while permanent streams were those with flow throughout the year. Streams in the basin of river Guadaira are generally subject to major perturbations such as flash floods and drought. The drought period is usually between May to October every year. By contrast, streams of river Guadalete have a more regular hydrology (Gallardo-Mayenco, 1993). The reader is referred to previously published work for more information on the hydrology of the two basins and methods of sampling and of physico-chemical analysis (Gallardo-Mayenco, 1993; Gallardo-Mayenco & Prenda, 1994).

To determine which of the measured physico-chemical variables (i.e. altitude, current velocity, temperature, suspended solids concentration, alkalinity, conductivity, chloride, sulphate, chemical oxygen demand (COD), nitrate, nitrite, ammonia, phosphate, and chlorophyll *a* concentration) explained the variations in abundance of simuliid species, a stepwise multiple regression analysis was performed of simuliid species abundance (dependent variables) on all physico-chemical parameters (independent variables). This analysis was used to study simuliids present in both river basins. All variables were log ($x + 1$) transformed.

For each simuliid species an adjusted average temperature (AAT) was calculated, multiplying the frequency of individuals of each species caught on each date and at each site by the temperature measured and then summing up all of these values (Gallardo-Mayenco *et al.*, 1998).

RESULTS AND DISCUSSION

Simuliid distribution and abundance

The simuliid species found in the study area can be classified into three groups according to the different altitude ranges where they are predominantly found (Table 2):

1. Species found only in streams of the river Guadaira basin: *Metacnephia blinci* (Grenier & Theodorides), *Simulium (Wilhelmia) lineatum* (Meigen), and *Simulium (Nevermannia) ruficorne* Macquart.
2. *Simulium (Simulium) xanthinum* Edwards, found only in streams of the river Guadalete basin.
3. Species found in streams of both basins: *Simulium (Eusimulium) velutinum* (Santos Abreu), *Simulium (Simulium) intermedium* Roubaud, *Simulium (Wilhelmia) pseudequinum* Séguy, and *Simulium (Wilhelmia) sergenti* Edwards. No significant differences were found between the abundance of these species (*t* test, $p > 0.1$).

Species which were only occasionally found were *M. blinci* (Guadaira basin in March), *S. ruficorne* (Guadairilla stream in August), and *S. lineatum* (Alcaudete stream in January). The most abundant and widespread species were *S. velutinum*, *S. pseudequinum* and *S. intermedium* (Table 2). *S. velutinum* was the only species found at Barros, Gavilán and Aguila (Fig. 1).

The species found mainly at low temperatures were *S. lineatum*, *S. xanthinum* and *M. blinci* (AAT= 12, 14, and 14 °C, respectively) while *S. ruficorne* was found at higher temperatures (AAT= 23 °C) (Table 2). The thermophilic behaviour of *S. ruficorne* has been described by Giudicelli *et al.* (1985). *S. intermedium* and *S. velutinum* were widespread species across the altitude range (Table 2).

The River Guadaira basin was more species rich (7) than the Guadalete basin (5). Highest richness (R) and Shannon's diversity index (H') were found at the Guadaira stream (i.e. R= 5 and H'= 0.49) and at the Aguaderilla stream (R= 4 and H'= 0.48) (Figure 1). No significant correla-

Table 3. Stepwise multiple regression results for species present in the two basins. CVE: cumulative variation explained (* p<0.05; ** p<0.01; *** p<0.001). *Resultados del análisis de regresión múltiple para las especies presentes en las dos cuencas. CVE: variación acumulativa (*p<0.05; **p<0.01; ***p<0.001)*

Species	Factor	CVE (%)	Relationship	F
<i>Simulium velutinum</i>	COD (permanganate value)	46.7	positive	7.9*
<i>Simulium pseudequinum</i>	water current velocity altitude	40.2 64.4	positive negative	12.6**
<i>Simulium sergenti</i>	water current velocity altitude	67.3 73.4	positive negative	18.6***

tions between altitude and richness or diversity of the simuliid communities were found (i.e. $r = -0.06$ and $r = -0.051$ for altitude vs. richness and altitude vs. diversity, respectively).

McCreadie *et al.* (1997) found no significant correlation between Jaccard's coefficient of similarity of simuliid communities at different sites and distance between the sampling sites. They concluded that simuliid species were able to inhabit all sites considered and that recolonization increased the similarity between the streams

they had sampled. We have analysed our samples in the same way and did not find any significant correlation ($r = -0.062$) when the whole dataset (11 sites) was included in analyses. However, when the sites with only one or two species (i.e. Barros, Gavilán, Aguilá and Guadairilla streams; Figure 1) were excluded, a significant negative correlation (i.e. $r = -0.478$, $p < 0.05$) was found; i.e. similarity between simuliid communities diminished with distance between sites.

Table 4. Average number of individuals per unit effort (X) and standard deviation (SD) of simuliid species collected in temporary, semipermanent and permanent water flows. No significant differences were found between abundances of species at any of the three types of environment (Kruskal-Wallis test for three-way comparisons and U Mann-Whitney test for two-way comparisons); n: number of sampling sites; f: number of sites at which each species was present. Water current velocity (in cm s^{-1}). *Abundancia relativa (X) y desviación estandar (SD) de las especies de simúlidos según la permanencia del agua. No hubo diferencias estadísticas en las abundancias de cada especie entre las diferentes clases de ambientes en que éstas fueron encontradas (tests de Kruskal-Wallis y de U Mann-Whitney para tres y dos comparaciones respectivamente); n: número de sitios muestreados; f: número de sitios en los que cada especie estuvo presente. Rango de la corriente del agua en cm s^{-1} .*

	temporary (n = 4)			semipermanent (n = 3)			permanent (n = 4)			water current range
	f	X	SD	f	X	SD	f	X	SD	
<i>S. intermedium</i>	2	6.9	10.6	1	3.2	5.6	4	11.9	20.5	10-60
<i>S. velutinum</i>	4	91.5	108.9	3	47.6	46.1	4	4.2	3.8	0-100
<i>S. pseudequinum</i>	2	1.9	2.2	1	2.1	3.6	2	20.1	27.4	6-100
<i>S. sergenti</i>	1	0.02	0.04	0			2	1.9	2.3	25-33
<i>M. blanci</i>	0			0			1	2.5	5.0	50
<i>S. xanthinum</i>	0			0			2	0.1	0.1	25-33
<i>S. ruficorne</i>	0			1	0.4	0.7	0			0
<i>S. lineatum</i>	1	0.1	0.2	0			0			15

Physico-chemical preferences and water temporality

Stepwise multiple regression for species present in both basins (i.e. *S. velutinum*, *S. intermedium*, *S. pseudequinum* and *S. sergenti*) explained a large part of the variance in their abundance (Table 3). The regression for *S. velutinum* included chemical oxygen demand (permanganate value), explaining 46.7 % of the variance in the abundance of this species ($F=7.9$, $p<0.05$; direct relationship). Regressions for *S. pseudequinum* and *S. sergenti* the pattern included altitude and water current velocity, which together explained 64.4 % and 73.4% of the variance in abundance, respectively (Table 3). For both *S. pseudequinum* and *S. sergenti*, the water current velocity had a positive effect on abundance. Abundance of the two species, on the other hand, decreased with altitude. An environmental gradient exists from highlands to lowlands in the study area. The current velocity varies notably downstream (Table 1), suggesting that species may spread out at random in the study area. The positive relationship of *S. velutinum* to COD (permanganate value) could be explained by the ability of this species to occupy various types of environment, including water with high content in organic matter. The regression model for *S. intermedium* could not explain any variance in abundance.

S. intermedium, *S. velutinum* and *S. pseudequinum* were found in all temporary, semipermanent, and permanent habitats (Table 4). *S. velutinum* and *S. pseudequinum* were found across the widest range of current velocities. *S. ruficorne* was only found when there was no flow, in August, at the Guadairilla stream, which is a semi-permanent stream. Crosskey (1967) described this species as the only simuliid able to inhabit still waters.

Temporal distribution patterns

Figures 2A and 2B show the relative abundance (in individuals per unit effort) of *S. velutinum*, *S. intermedium* and *S. pseudequinum*. These three

species were the most abundant and frequent simuliids in the study area throughout the survey. The three species were found across a diversity of current velocities at different dates and sites. We did not find any significant correlation between the relative abundances of the three species and the current velocity ($p>0.1$ in all cases), except for *S. velutinum* at Gavilán stream ($p<0.001$), and Algodonales stream (marginally significant, $p=0.052$). Individuals in the pupal stage were often found (Figs. 2A and 2B). Breeding and emergence of adult simuliids is common in warm streams throughout the year (De Moor, 1992).

CONCLUSIONS

The most abundant and frequent species (i.e. *S. velutinum*, *S. intermedium*, *S. pseudequinum* and *S. sergenti*) did not follow any pattern in their spatial distribution in the study area. *S. velutinum*, *S. intermedium* and *S. pseudequinum* were found in all temporary, semi-permanent and permanent habitats.

Stepwise multiple regression analyses showed that only COD (permanganate value), altitude and current velocity had any influence on the distribution of simuliid species. The more abundant simuliid species took advantage of water flow at sites where the supply of nutrients was high. Availability of large amounts of organic matter in lowland sites could thus explain the development of large populations in downstream sites (Lenat, 1984; Paimer & O'Keeffe, 1995). A versatile feeding strategy is favoured under these conditions (Currie & Craig, 1987).

The high percentage of individuals in pupal stages may be due to the existence of overlapping generations. This is often related to the pioneer character of simuliid species (Malmqvist *et al.*, 1991), which would have been favoured by the warm temperatures of the study area. This type of breeding would assure a fast recolonization by imagoes at sites where floods can remove most insects (Resh *et al.*, 1988).

The correlation between Jaccard's similarity and distance at sites with three or more species

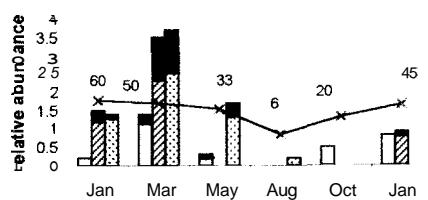
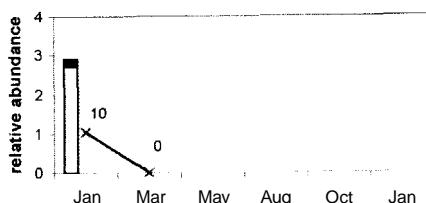
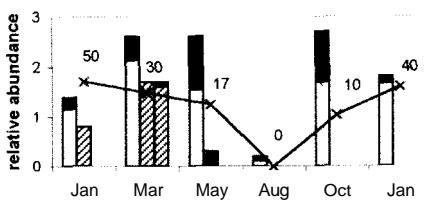
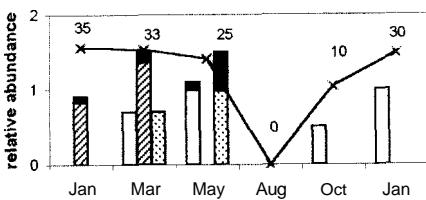
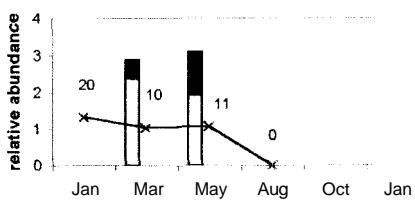
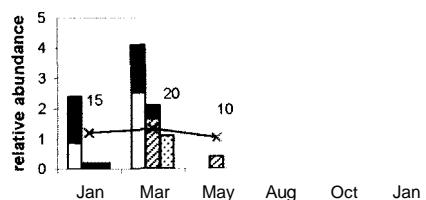
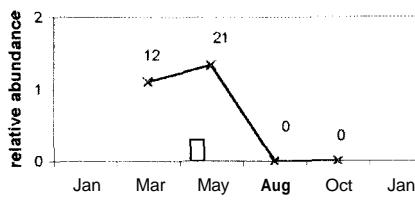
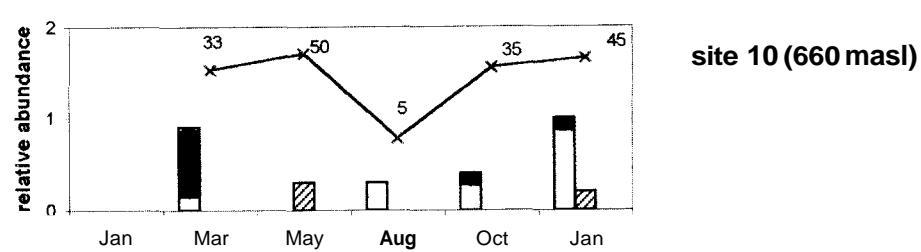
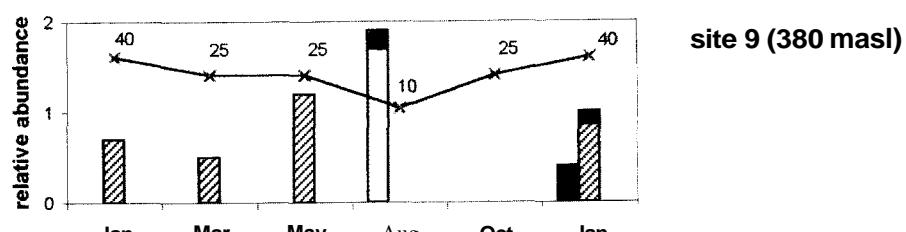
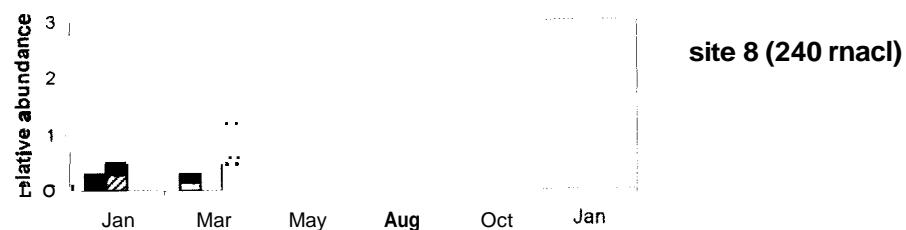
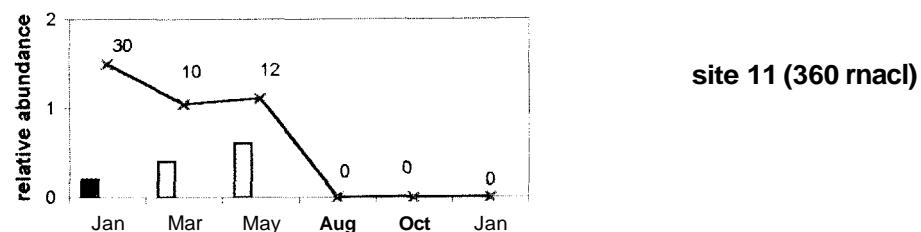
A GUADAIRA RIVER BASIN**PERMANENT STREAM****site 1 (180 masl)****TEMPORARY STREAMS****site 6 (140 masl)****SEMIPERMANENT STREAMS****site 2 (240 masl)****site 5 (120 masl)****site 3 (200 masl)****site 7 (70 masl)****site 4 (80 masl)**

Figure 2. Relative abundances (i.p.u.e.) of *Simulium velutinum* (empty bars), *S. intermedium* (line crossed bars) and *S. pseudequinum* (stippled bars), and water current velocities (in cm s^{-1}) (line outside the bars) $\log(x + 1)$ transformed. At each site sampled throughout the sampling period: A) sites belonging to the Guadaira river basin and B) sites belonging to the Guadalete river basin. The solid area of bars shows the percentage of total number of individuals which is in the pupal stage. Abundancia relativa de *Simulium velutinum* (barras vacías), *S. intermedium* (barras de líneas cruzadas) y *S. pseudequinum* (barras punteadas), y valores de velocidad de la corriente (en cm s^{-1}) (líneas fuera de las burras). Valores transformados según la ecuación $\log(x + 1)$. A) sitios pertenecientes a la cuenca del río Guadaira; B) sitios pertenecientes a la cuenca del río Guadalete. La zona rellena de las barras representa el porcentaje de individuos encontrados en estadio de pupa.

B GUADALETE RIVER BASIN**PERMANENT STREAMS****TEMPORARY STREAM****Fig 2. (Cont.)**

was contrary to that of McCreadie *et al.* (1997), who detected an increase in similarity with time after recolonization. We think that the simuliid species in the study area exploited the environment more successfully at lower-lying sites than at upstream sites. An increase in similarity of communities at distant sites with the passage of time, as McCreadie *et al.* (1997) have suggested, might only apply to sites with similar characteristics. In contrast, in streams like those studied here, differences between communities increased with time.

The number of simuliid species in Guadaira and Guadalete river basins was smaller to that reported for other nearby basins (Table 5). The similarity in species composition between these basins was low. *S. pseudequinum* was the only species common to all of them. Ross & Merritt (1978) observed that temperature influenced the geographical and local distribution of simuliid

species, but we did not find significant differences between the water temperatures of the two basins in our study (*t* test = 1.377, *p*=0.202). *Wilhelmia* and *Eusimulium* species in the four areas are compared in Table 5. Percentages are those typically found across the Mediterranean region (Crosskey, 1967).

Our results are in agreement with those in Malmqvist *et al.* (1999), who contended that richness of species and abundance of simuliids might be favoured by perturbations so that high richness and abundance will be found at sites frequently affected by severe floods and/or droughts. Thus, high diversity and abundance of simuliids in streams of the River Guadaira basin could be partly explained by the variable flow. Also, the diversity and density of both competitors and predators of simuliids are reduced in perturbed conditions (Malmqvist *et al.*, 1999).

Table 5. Taxonomic composition of simuliid fauna present in areas of Andalusian streams (Spain), i.e. Guadaira and Guadalete basins (this study), the Málaga basins (González *et al.*, 1987) and Yeguas stream (González *et al.*, 1986). *N*: number of species; *S* guadaira, *S* guadalete, and *S* Málaga: similarity between the three areas, i.e. (number of shared species / (species only at site A + species only at site B – shared species))^{*} 100; *W + E* percentage of *Wilhelmia* and *Eusimulium* species. *Composición taxonómica de la fauna de simúlidos de algunas áreas de Andalucía: Guadaira y Guadalete (este trabajo), Málaga (González *et al.*, 1987) y Yeguas (González *et al.*, 1986)*. *N*: número de especies; *S* guadaira, *S* guadalete, y *S* málaga: similaridad entre estas áreas: (especies comunes/(especies en el sitio A + especies en el sitio B – especies comunes))^{*} 100; *W + E* porcentaje de especies pertenecientes a los géneros *Wilhelmia* y *Eusimulium*.

Guadaira	Guadalete	Málaga	Yeguas
<i>Metacnephilius blanchi</i>	<i>Simulium velutinum</i>	<i>Simulium cryophilum</i>	<i>Prosimulium gr. hirtipes</i>
<i>Simulium ruficorne</i>	<i>Simulium intermediate</i>	<i>Simulium ruficorne</i>	<i>Prosimulium (Urosimulium) sp.*</i>
<i>Simulium velutinum</i>	<i>Simulium pseudequinum</i>	<i>Simulium latinum</i>	<i>Metacnephilia nuragica</i>
<i>Simulium lineatum</i>	<i>Simulium sergenti</i>	<i>Simulium lineatum</i>	<i>Metacnephilia blanchi</i>
<i>Simulium pseudequinum</i>	<i>Simulium xanthinum</i>	<i>Simulium pseudequinum</i>	<i>Simulium angustitarse</i>
<i>Simulium sergenti</i>		<i>Simulium sergenti</i>	<i>Simulium armoricanum</i>
<i>Simulium intermediate</i>		<i>Simulium nitidifrons</i>	<i>Simulium cryophilum</i>
		<i>Simulium variegatum</i>	<i>Simulium vernum</i>
			<i>Simulium aureum</i>
			<i>Simulium pseudequinum</i>
			<i>Simulium bezzii</i>
			<i>Simulium gr. ornatum</i>
			<i>Simulium variegatum</i>
<i>N</i>	7	5	8
<i>S</i> guadaira		50	36
<i>S</i> guadalete			18
<i>S</i> málaga			6
<i>W + E</i>	57	60	50
			17
			15

later identified as *Prosimulium juncii* (González 1997)

Simulium xanthinum was only found in streams with good water quality (Grazalema and Gaidoar) in January and March. This species could be used as an indicator of good water quality in streams. However, our results suggest that the simuliid community as a whole is not a suitable indicator of the water quality of streams (Palmer & O'Keeffe, 1995).

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