

Seasonal and diel periodicity of the drift of pupal exuviae of chironomid (Diptera) in the Mundo River (S.E. Spain)

Nicolás Ubero-Pascal, Mar Torralva, Francisco Oliva-Paterna¹
and Jorge Malo

Universidad de Murcia

With 2 figures and 2 tables

Abstract: The diel and seasonal drift of Chironomidae exuviae was assessed for one year in a non-regulated stretch of a Mediterranean river in south-east Spain. Pupal exuviae of chironomids were collected by drift netting, and 43 species were identified. Maximum densities were captured in summer and minimum densities in winter. Orthocladiinae were the most widely represented group with 19 species being identified in high densities. Overall, the time preferred by the chironomid community for emergence changed with the seasons, although the principal species maintained their daily cycles of emergence.

Introduction

SCHREIBER (1985) considered that invertebrate drift is a common phenomenon in streams and described the importance of this phenomenon in the biotic process of these ecosystems. The diel periodicity of invertebrate drift was first studied by WATERS (1962), MÜLLER (1966) and ELLIOT (1967) and such studies continue to hold interest for many authors (FLECKER 1992, BREWIN & ORMEROD 1994, SMOCK 1994).

In this paper, we shall confine ourselves to a study of the Chironomidae family, one of the main groups that make up most benthic river communities of invertebrates. Chironomids are important in these communities for their abundance and diversity, two of the main parameters which are used for measuring the condition of benthic invertebrate communities (RUSE 1995).

¹ **Authors' address:** Departamento de Biología Animal (Zoología), Universidad de Murcia, Campus de Espinardo, 30100 Murcia, España.

Diel and seasonal changes in the structure of the chironomid assemblages were monitored in the River Mundo (SE Spain) by collecting the floating pupal exuviae (skins) discarded by emerging adults. This is a simple way of collecting data on species composition and relative abundance of such assemblages (COFFMAN 1973, WILSON & BRIGHT 1973, FEND & CARTER 1995, RUSE 1995), although "to this advantage may be added the ethical and non-destructive nature of sampling inanimate cast cuticles" (HARDWICK et al. 1995).

Although several authors (RIERADEVALL & PRAT 1986, VILCHEZ-QUERO & LAVANDIER 1986, HAYES & MURRAY 1988, EVRARD 1994, RUSE 1995) have studied the diel periodicity of chironomid emergence in a given season of the year, this paper describes and compares the diel periodicity of chironomid community drift in the four seasons.

Material and methods

The study area was a stretch of the River Mundo, a tributary stream of the River Segura ($38^{\circ} 35'$, $2^{\circ} 0' W$), about 82 km long and flowing directly into a reservoir. Its hydrological regime is typically Mediterranean, with a minimum flow in summer and a maximum flow in spring and autumn. This study was made 62 km downstream of the headwaters, near the town of Lietor. The river at this point is not regulated, is 2–3 m wide and has a depth of 20–30 cm. The substratum is composed of stones, gravel, sand and mud.

The study area was sampled four times during one year: in spring (25–26 April, 1996), summer (13–14 July), autumn (2–3 November) and winter (14–15 February, 1997).

In a 200 m stretch of river, drift samples were taken every 3 h during one complete 24 h period (eight drift samples per season sampling). The first drift sample was taken at the downstream end of the chosen stretch, and each subsequent drift sample was taken 2 m upstream of the previous sample. This procedure was used in an attempt to minimize substratum disturbance. Before taking the drift samples, a 250 μ m mesh net was placed upstream of the chosen stretch in order to avoid interference from exuviae drifting from the upstream zones. The drift net, measuring $33 \times 33 \times 100$ cm and with a mesh of 250 μ m, was placed for 60 min in the middle of the stream, where the water flow was fastest. The samples taken were fixed in formaldehyde (7–10%), and different physical and chemical parameters were measured "in situ" with portable field instruments.

The number of chironomid exuviae collected was related to the volume of water passing through the net in order to compare abundance between samples. For this purpose the drift net area and the current velocity were multiplied. The current velocity values used were the mean values of the data measured upstream and downstream of the drift net.

The chironomid exuviae were identified using the keys of LANGTON (1991).

Results

The variations in water temperature during each sampling period showed a certain similarity in all the seasons (Fig. 1).

The pupal exuviae collected represent 43 different species of chironomid (Table 2), classified as follows: Tanypodinae (2 species), Diamesinae (2 species), Orthocladiinae (19 species), Chironomini (11 species) and Tanytarsini (9 species).

The seasonal variations in both abundance and species number can be observed in Fig. 2. The highest density occurred in summer (650 exuviae/1,000 m³) and the lowest densities in autumn (230 exuviae/1,000 m³) and winter (280 exuviae/1,000 m³). However, species number was higher in autumn (28 species) than in the other three seasons (23 species in winter, 24 species in summer and 25 species in spring).

The density variations during one-day (diel density cycle) differed from season to season (Fig. 2). In spring, maximum abundance was observed at night (22–23 h) with a minimum just before dawn (4–5 h) and during the afternoon (16–17 h). In autumn, maximum abundance was observed in the eve-

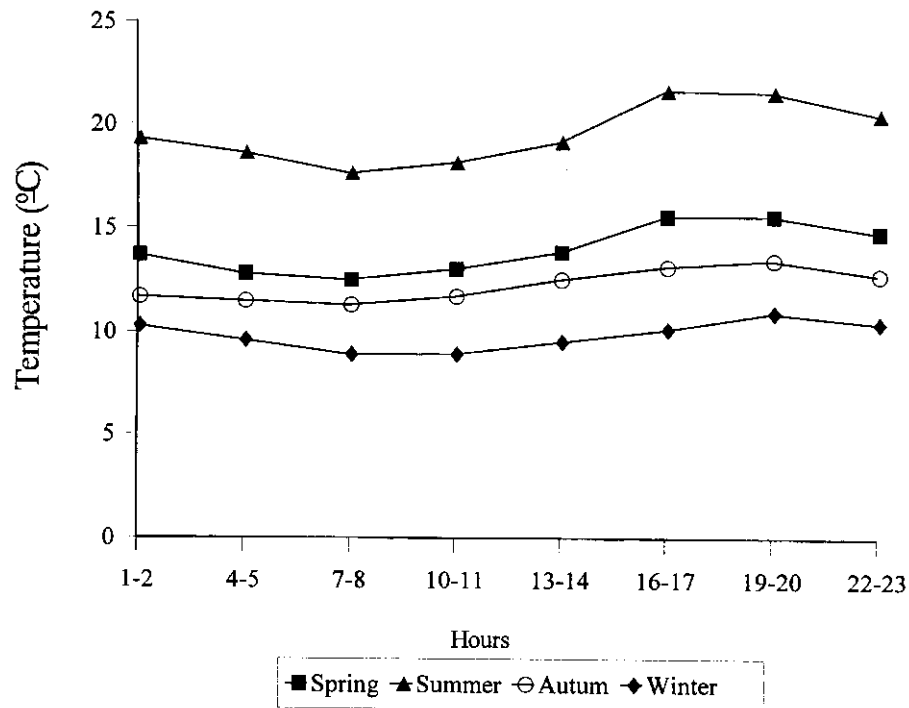


Fig. 1. Diel variations of temperature in Mundo River.

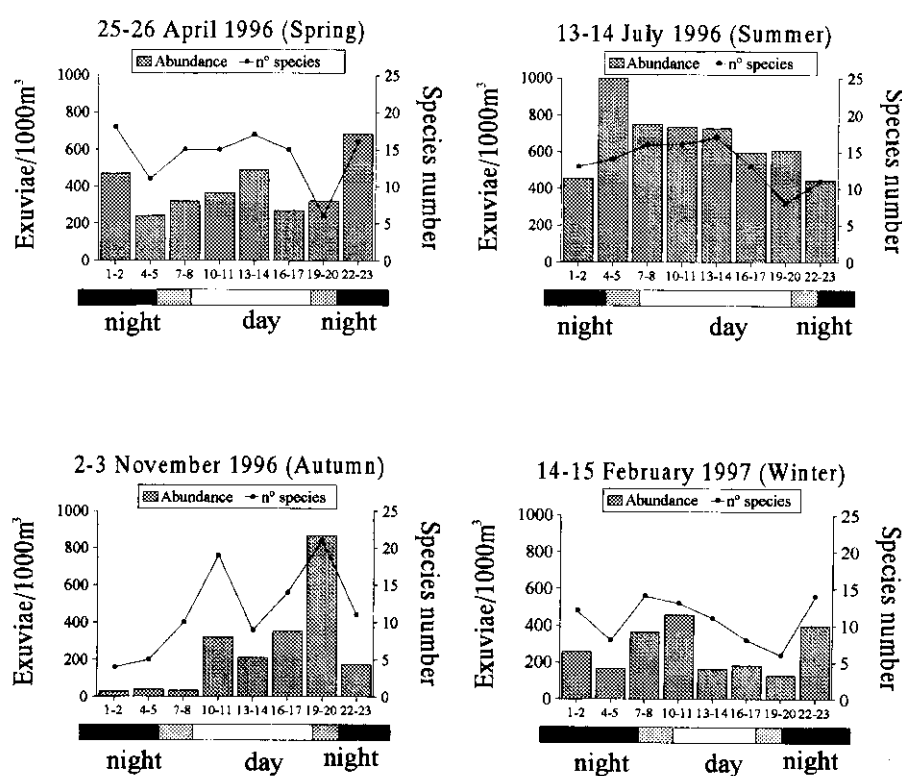


Fig. 2. Diel variations of abundance and species number of chironomid pupal exuviae in Mundo River.

ning (19–20 h) and the minimum during the night. In winter, the maximum was in the morning (10–11 h) and the minimum in the evening (19–20 h). The diel abundance cycle in summer differed from those of the other seasons, with a maximum at dawn (4–5 h) and a minimum near midnight (22–23 h and 1–2 h).

Fig. 2 reveals how the diel species number cycle was correlated with the diel abundance cycle, the maximum and minimum data of these two cycles tending to coincide, except in summer when the maximum number of species was observed in the morning (8–9 h) and the afternoon (19–20 h) and the minimum at night (1–2 and 4–5 h). In summer, then, the diel species number cycle shifted from the diel abundance cycle, while in spring and winter, it varied very little from the diel abundance cycle.

In each season, therefore, the greatest drift of chironomid exuviae occurred at different hours of the day. In summer, the maximum drift coincided with the lowest water temperature of the day, whereas in winter it coincided with the highest water temperature. In spring and autumn, the maximum drift coincided

Table 1. Regressions between temperature and chironomids densities and species number.

| r^2 | Spring | Summer | Autumn | Winter |
|----------------|--------|---------|--------|--------|
| Density | 0.024 | 0.275 | 0.617* | 0.238 |
| Species number | 0.092 | -0.602* | 0.304 | 0.264 |

* $p \leq 0.05$

with intermediate water temperatures. When water temperature was related to abundance and species number by regression analysis (Table 1), significant correlations were observed in autumn and summer. The correlation was positive in the case of chironomid exuviae abundance in autumn ($r^2 = 0.617$, $p \leq 0.05$) and negative in the case of species number in summer ($r^2 = -0.602$, $p \leq 0.05$).

Species distribution of the different chironomid subfamilies and tribes differed during the year. Tanypodinae and Diamesinae were caught in winter and summer only. Orthocladiinae, with 19 species represented, were the dominant group, all of them being caught in autumn, but only eleven in summer. In each season five species of Chironomini were caught, except in winter when only one was caught. The maximum number of species of Tanytarsini was caught in summer (6 species) and the minimum number in winter (3 species).

Table 2 shows the density of drifting exuviae of each species in the different seasons. Although some species occurred in all the samples, those which were dominant showed a preference to emerge in one season only: *Orthocladius rubicundus* in spring; *Parametriocnemus stylatus*, *Cricotopus annulator*, *Cricotopus vierriensis* and *Rheocricotopus atripes* in summer; *Cladotanytarsus vanderwulpi* and *Corynoneura lobata* in autumn, and *Rheotanytarsus pentapoda* in winter. *Orthocladius rivicola* and *Orthocladius pedestris* emerged mainly in both winter and spring.

The diel drift cycles of some species differed substantially from the overall seasonal pattern described previously. In spring, most of the high density species, such as *Cricotopus annulator*, *Cricotopus sylvestris*, *Orthocladius pedestris* and *Rheocricotopus atripes*, drifted during the night, although some species drifted mainly at dawn (e.g. *Micropsectra atrofasciata*), at dusk (e.g. *Cricotopus curtus* and *Rheotanytarsus pentapoda*), or during the hours of daylight (e.g. *Orthocladius rubicundus*).

In summer too, the general pattern of species emergence tended to be nocturnal, (*Cricotopus curtus*, *Dicrotendipes notatus*, *Cladotanytarsus vanderwulpi* and *Rheotanytarsus pentapoda*), although some species drifted at other hours of the day (*Cricotopus sylvestris* at dawn, *Orthocladius oblidens* at dusk, or *Orthocladius rubicundus* during daylight hours).

Table 2. Seasonal mean abundance of chironomid exuviae in Mundo River.

| Species (exuviae/1000 m ³) | Spring | Summer | Autumn | Winter |
|---|--------|--------|--------|--------|
| Tanypodinae | | | | |
| <i>Ablabesmyia longistila</i> FITTKAU | – | 1.1 | – | 2.9 |
| <i>Rheopelopia ornata</i> (MEIGEN) | – | 2 | – | 0.5 |
| Diamesinae | | | | |
| <i>Pothastia gaedii</i> (MEIGEN) | – | 0.6 | – | 0.5 |
| <i>Sympothastia zavreli</i> PAGAST | – | – | – | 0.6 |
| Orthoclaadiinae | | | | |
| <i>Cardiocladius fuscus</i> KIEFFER | – | 4.9 | 3.6 | 1.5 |
| <i>Corynoneura lobata</i> EDWARDS | 4.6 | – | 41.3 | 0.5 |
| <i>Cricotopus annulator</i> GOETGHEBUER | 37.8 | 168.3 | 17.6 | 2.6 |
| <i>Cricotopus curtus</i> HIERVENOJA | 13.1 | 4.4 | 3.8 | 1.6 |
| <i>Cricotopus sylvestris</i> (FABRICIUS) | 19.5 | 11.1 | 6.4 | 3 |
| <i>Cricotopus vierriensis</i> GOETGHEBUER | 20.9 | 73.1 | 6 | 0.5 |
| <i>Eukiefferiella coeruleascens</i> (KIEFFER) | 8.1 | – | 13.5 | – |
| <i>Eukiefferiella ilkleyensis</i> (EDWARDS) | 12.5 | 4.6 | 19.9 | 3.5 |
| <i>Eukiefferiella similis</i> GOETGHEBUER | – | – | 0.8 | – |
| <i>Limnophies minimus</i> (MEIGEN) | 1.6 | – | 0.8 | – |
| <i>Orthocladus oblidens</i> (WALKER) | 7.4 | 8.6 | 6.4 | 11.8 |
| <i>Orthocladus pedestris</i> KIEFFER | 21.8 | – | 3.8 | 18.8 |
| <i>Orthocladus rivicola</i> KIEFFER | 83.5 | – | 11.5 | 99.3 |
| <i>Orthocladus rubicundis</i> (MEIGEN) | 70.6 | 37.3 | 14.8 | 7.1 |
| <i>Parametriocnemus stylatus</i> (KIEFFER) | 31.3 | 203.3 | 0.8 | 13.1 |
| <i>Rheocricotopus atripes</i> (KIEFFER) | 15.8 | 36.5 | 15.8 | 4.8 |
| <i>Synorthocladus semivirens</i> (KIEFFER) | – | – | 0.8 | – |
| <i>Thienemanniella clavicornis</i> (KIEFFER) | – | – | 1.5 | 1.6 |
| <i>Tvetenia calvescens</i> (EDWARDS) | 0.9 | 4.9 | 0.6 | 4 |
| Chironomini | | | | |
| Chironomini Pe.4 LANGTON | 1.1 | 2.9 | – | – |
| <i>Cladopelma virescens</i> (MEIGEN) | 0.4 | – | – | – |
| <i>Cryptochironomus rostratus</i> KIEFFER | – | – | 1.1 | – |
| <i>Dicrotendipes nervosus</i> (STAEGNER) | – | – | 0.8 | – |
| <i>Dicrotendipes notatus</i> (MEIGEN) | – | 6.1 | – | – |
| <i>Endochironomus</i> Pe.1 LANGTON | 1 | – | 5.1 | – |
| <i>Microtendipes diffinis</i> (EDWARDS) | – | 2.3 | 0.8 | 1 |
| <i>Phaenopsectra flavipes</i> (MEIGEN) | – | – | 2 | – |
| <i>Polypedilum convictum</i> (WALKER) | 1.8 | – | – | – |
| <i>Polypedilum sordens</i> (VAN DER WULP) | 2.9 | 0.6 | – | – |
| <i>Polypedilum quadriguttatum</i> KIEFFER | – | 0.6 | – | – |
| Tanytarsini | | | | |
| <i>Cladotanytarsus vanderwulpi</i> (EDWARDS) | – | 14.4 | 70.3 | – |
| <i>Micropsectra apposita</i> (WALKER) | 8.6 | – | – | – |
| <i>Micropsectra atrofasciata</i> KIEFFER | 6.8 | – | – | – |
| <i>Rheotanytarsus curtistylus</i> (GOETGHEBUER) | – | – | 2 | – |
| <i>Rheotanytarsus distinctissimus</i> BRUNDIN | – | 1.8 | 2.6 | 1.1 |
| <i>Rheotanytarsus pentapoda</i> KIEFFER | 17.8 | 60.1 | – | 85.6 |
| <i>Tanytarsus brundini</i> LINDBERG | 1.8 | 10.3 | 0.8 | – |
| <i>Tanytarsus heusdensis</i> GOETGHEBUER | – | 2.8 | – | 0.6 |
| <i>Virgatanytarsus albisutus</i> (SANTOS ABREU) | 3.8 | 2.4 | – | – |

In autumn, the majority of species drifted at dusk (e.g. *Corynoneura lobata*, *Cricotopus annulator*, *Cricotopus vieriensis*, *Endochironomus* Pe. 1 and *Cladotanytarsus vanderwulpi*), although, as in other seasons, some species drifted during daylight hours (e.g. *Eukiefferiella coerulescens*, *Orthocladius rubicundus* and *Rheocricotopus atripes*) or at night (e.g. *Phaenopsectra fluviipes*).

Finally, the general pattern of species emergence tended to be nocturnal during winter (e.g. *Cricotopus sylvestris*, *Orthocladius oblidens* and *Parametriocnemus stylatus*). As in the other seasons, there were exceptions with, for example, some species drifting just before dawn (e.g. *Orthocladius pedestris*, *Orthocladius rivicola* and *Rheotanytarsus pentapoda*), during daylight hours (e.g. *Eukiefferiella ilkleyensis* and *Orthocladius rubicundus*), or at dusk (e.g. *Rheotanytarsus distinctissimus*).

Looking at the year as a whole, the following assertion can be made: *Cricotopus rubicundus* drifted preferably during daylight hours, *Cricotopus sylvestris* before dawn, and *Cricotopus curtus* and *Cladotanytarsus vanderwulpi* after dusk. *Rheotanytarsus pentapoda* completely changed its hours of drifting according to the season.

Discussion

If we compare the number of chironomid species recorded in the River Mundo with the data recorded from other Mediterranean rivers, there are clear differences in species richness. The River Mundo, with 43 species identified, has a greater species richness than the Matarraña River, with 35 species only (MALO 1993), although poorer than the River Llobregat, with 62 species (RIERADEVALL & PRAT 1986), and River Guadalquivir, with 64 species (VILCHEZ-QUERO & LAVANDIER 1986). These differences might be even greater in the case of the last two rivers if their Chironomidae fauna were studied throughout the year.

The Orthoclaudiinae contributed the highest densities and greatest species numbers, followed by the Chironominae (Chironomini and Tanytarsini), which reflects the finding of other studies (RIERADEVALL & PRAT 1986, VILCHEZ-QUERO & LAVANDIER 1986, RUSE 1995). The low densities of groups like the Tanypodinae can be explained by the fact that the larvae migrate to the shore before they reach the pupa stage (VILCHEZ-QUERO & LAVANDIER 1986).

There is a clear seasonal variation in chironomid drift densities (GRAESSER 1988). We observed the greatest densities in summer, which agrees with the finding of other authors (ARMITAGE 1977, SCHREIBER 1995), while the lowest densities were observed in winter. Other authors observed the highest densities

to occur in spring (BENSON & PEARSON 1987, KOETSIER & BRYAN 1989, SAGAR & GLOVA 1992).

Few chironomids were observed to emerge regularly throughout the day, most emerging at particular times. Furthermore, ARMITAGE (1995) observed a considerable temporal and seasonal intraspecific variation in diel emergence.

Most authors describe maximum emergence as occurring at night (VILCHEZ-QUERO & LAVANDIER 1986, BREWIN & ORMEROD 1994, EVRARD 1994, SCHREIBER 1995) or at dusk (RIERADEVALL & PRAT 1986, HARDWICK et al. 1995) with a minimum at dawn. In our study of the River Mundo, the period at which the highest densities were recorded changed with the season.

Seasonal differences in the time of emergence peaks have also been observed in other running waters (COFFMAN 1974, SAGAR & GLOVA 1992). In spring and mid-autumn maximum diel emergence occurred during the mid-late afternoon, while in the summer and early-autumn two maxima were observed. In another study, GENDRON & LAVILLE (1993) observed that in spring the majority of species had a bimodal emergence pattern with peaks just after dawn (7–9 h) and around sunset (18 h). In the autumn, the species tended to have a unimodal pattern of emergence, some at noon only and others at night. Such behaviour was not observed in our study, where two diel peaks occurred in spring and winter, one during the brightest time of day (10–11 or 13–14 h) and the other one at night (22–23 h). Only one diel peak occurred in summer (at night) and in autumn (at dusk). We believe that this difference results from the fact that we consider all the species as a whole, whereas in fact each species will have its own behaviour.

Environmental cues for the timing of emergence have been attributed to changes in light intensity and/or water temperatures (ARMITAGE 1995). Some authors, such as WILLIAMS (1982), SAGAR & GLOVA (1992), BREWIN & ORMEROD (1994) and FEND & CARTER (1995), have observed a correlation between water temperature and drift. However, we found significant correlations in autumn and summer only. In accordance with EVRARD (1994), we suggest that the photoperiod may be the most important parameter in the emergence of many species such as *Cricotopus rubicundus*, *C. sylvestris*, *C. curtus* and *Cladotanytarsus vanderwulpi*.

As regards the principal species caught, the preference of some species to emerge in a particular season agrees with the observations of RUSE (1995). For example, *Cricotopus* genus *C. annulator* emerges in summer and *Orthocladius rubicundus* in spring, while *Tanytarsus brundini* emerges in both spring and summer. However, while RUSE (1995) observed that *Corynoneura lobata* emerges throughout the year, we observed it to emerge mainly in autumn.

Some of the main species we caught preserved their preference for emerging at a given time throughout the year. In some cases, this preference coincided with those reported elsewhere, *Parametriocnemus stylatus*, for example,

emerging at night and *Corynoneura lobata* at dusk (EVRARD 1994). Some species changed their time of emergence according to the season, showing a nocturnal emergence pattern in summer but with peaks at dusk in winter (COFFMAN 1974, COBO & GONZÁLEZ 1991). In our case, such a variation was observed in *Rheotanytarsus pentapoda*, *Orthocladius oblidens*, *Cricotopus annulator* and, particularly, *Cladotanytarsus vanderwulpi*, this last species emerging at night in summer and at dusk in autumn.

We believe that this study adds to our knowledge of Chironomidae and confirms that the drift patterns of some chironomid taxa may vary seasonally in Mediterranean rivers.

References

- ARMITAGE, P. D. (1977): Invertebrate drift in the regulated River Tess, and an unregulated tributary Maize Beck, below Cow Green dam. – *Freshwat. Biol.* **7**: 167–183.
- (1995): Behaviour and ecology of adults. – In: ARMITAGE, P. D., CRANSTON, P. S. & PINDER, L. C. V. (eds.): *Chironomidae: Biology and ecology of non-biting midges*. – Chapman & Hall Publisher, London, pp. 195–224.
- BENSON, L. J. & PEARSON, R. G. (1987): The role drift and effect of season on macroinvertebrate colonization of implanted substrata in a tropical Australian stream. – *Freshwat. Biol.* **18**: 109–116.
- BREWIN, P. A. & ORMEROD, S. J. (1994): Macroinvertebrate drift in streams of the Nepalese Himalaya. – *Freshwat. Biol.* **32**: 573–583.
- COBO, F. & GONZAÉLEZ, M. A. (1991): Étude de la dérive des exuvies nymphales de Chironomidés dans la rivière Sar (NO. Espagne) (Insecta, Diptera). – *Spixania* **14**: 193–203.
- COFFMAN, W. P. (1973): Energy flow in a woodland stream ecosystem: II. The taxonomic composition and phenology of the Chironomidae as determined by the collection of pupal exuviae. – *Arch. Hydrobiol.* **71**: 281–322.
- (1974): Seasonal differences in the diel emergence of a lotic Chironomidae community. – *Entomol. Tidskrift/Suppl.* **95**: 42–48.
- ELLIOT, J. M. (1967): Invertebrate drift in a Dartmoor stream. – *Arch. Hydrobiol.* **63**: 202–237.
- EVRARD, M. (1994): Évolution journalière de la dérive des exuvies nymphales de Chironomidae (Diptera) dans une rivière salmonicole (Le Samson, Belgique). – *Belg. J. Zool.* **124**(2): 115–126.
- FEND, S. V. & CARTER, J. L. (1995): The relationship of habitat characteristics to the distribution of Chironomidae (Diptera) as measured by pupal exuviae collections in a large river system. – *J. Freshwat. Ecol.* **10**(4): 343–359.
- FLECKER, A. S. (1992): Fish predation and the evolution of invertebrate drift periodicity: evidence from Neotropical streams. – *Ecology* **73**: 438–448.
- GENDRON, J. M. & LAVILLE, H. (1993): Diel emergence patterns of drifting chironomid (Diptera) pupal exuviae in the River Aude (Eastern Pyrenees, France). – *Neth. J. Aquat. Ecol.* **26**: 273–279.
- GRAESSER, A. K. (1988): Invertebrate drift in three flood-prone streams in the South Westland, New Zealand. – *Verh. Int. Verein. Limnol.* **23**: 1422–1426.

- HARDWICK, R. A., COOPER, P. D., CRANSTON, P. S., HUMPHREY, C. L. & DOSTINE, P. L. (1995): Spatial and temporal distribution patterns of drifting pupal exuviae of Chironomidae (Diptera) in streams of tropical northern Australia. – *Freshwat. Biol.* **34**: 569–578.
- HAYES, B. P. & MURRAY, D. A. (1988): IX. Running waters (continued). Diel variation in chironomid emergence and implications for the use of the pupal exuviae in river classification. – *Verh. Int. Verein. Limnol.* **23**: 1261–1266.
- KOETSIER, P. & BRYAN, C. F. (1989): Winter and spring macroinvertebrate drift in an outpocketing of the lower Mississippi river, Louisiana (USA). – *Hydrobiologia* **185**: 205–209.
- LANGTON, P. H. (1991): A key to pupal exuviae of West Palearctic Chironomidae. – Privately published: Huntington, England, 386 pp.
- MALO, J. (1993): Comunidades bentónicas de ríos mediterráneos. – Ph. D. Murcia University, 176 pp.
- MÜLLER, K. (1966): Die Tagesperiodik von Fließwasserorganismen. – *Z. Morph. Ökol. Tiere* **56**: 91–142.
- RIERADEVALL, M. & PRAT, N. (1986): Diel pattern of chironomid drift in the Llobregat River (NE Spain). – *Oecologia aquatica* **8**: 61–70.
- RUSE, L. (1995): Chironomid emergence from an English chalk stream during a three year study. – *Arch. Hydrobiol.* **133**: 223–244.
- SAGAR, P. M. & GLOVA, G. J. (1992): Invertebrate drift in a large braided New Zealand river. – *Freshwat. Biol.* **27**: 405–416.
- SCHREIBER, E. S. G. (1995): Long-term patterns of invertebrate stream drift in an Australian temperate stream. – *Freshwat. Biol.* **33**: 13–25.
- SMOCK, L. A. (1994): Movements of invertebrates between stream channels and forested floodplains. – *J. N. Amer. Benthol. Soc.* **13**(4): 524–531.
- VILCHEZ-QUERO, A. & LAVANDIER, P. (1986): Composition et rythme journalier de la dérive des exuvies nymphales de Chironomidés dans le Guadalquivir (Sierra de Cazorla – Espagne). – *Annls. Limnol.* **22**(3): 253–260.
- WATERS, T. F. (1962): Diurnal periodicity in the drift of stream invertebrates. – *Ecology* **43**: 316–320.
- WILLIAMS, D. D. (1982): Emergence pathways of adult insects in the upper reaches of a stream. – *Int. Rev. ges. Hydrobiol.* **67**: 223–224.
- WILSON, R. S. & BRIGHT, P. L. (1973): The use of chironomid pupal exuviae for characterizing streams. – *Freshwat. Biol.* **3**: 283–302.

Submitted: 5 August 1998; accepted: 7 March 1999.