Chironomid (Insecta: Diptera) assemblages from a gradient of lotic and lentic waterbodies in river floodplains of France: a methodological tool for paleoecological applications

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Abstract

The chironomid species inhabiting a natural dead arm (the Pilet dead Arm), two artificial backwaters (the Saxy Dyke field and the Ranchier Dyke Field) and the main channel of the lower Rhône River (South of France) were studied. A between-class (between-station) Correspondence Analysis (CA) showed that, on the scale of the alluvial plain, habitat is a major factor influencing the species assemblages. The assemblage composition on the transversal floodplain gradient was compared with existing data on assemblages from the main channel of the Garonne River (South of France) and three of its floodplain waters (two side arms and one oxbow lake). In order to work at the level of taxonomic determination commonly used in paleoecological studies, the overall dataset (lower Rhône + Garonne) was analyzed to the genus level. The genus level analysis confirmed that chironomid assemblages can be used to characterize the connectivity of small waterbodies with the main river channel and 44 chironomid genera were classified according to their hydrological preferences (lentic habitat taxa, ubiquitous taxa and lotic habitat taxa). This classification was then applied to a paleoecological dataset from the Saint-Omer basin (North of France) in order to test the potential of chironomids for paleoecological studies on fluvial environments. The results presented here highlighted this potential and indicate that river chironomid assemblages can be used as descriptors for alluvial habitats, and allow researchers to evaluate the level of connectivity of these habitats with the main river channel during floods. River chironomid assemblages are a promising tool for reconstructing past hydrological changes and for obtaining information on paleoflood periodicity.

Introduction

All over the world, the history of human civilization is often related to rivers, since rivers are often the starting point of civilizations, as well as the places of economic and cultural exchanges (Bravard and Magny 2002). Fluvial systems, by their morphological changes and their dynamics, also track climatic changes that took place during the Quaternary (e.g., Lowe and Walker 1997; Knox 2000; Mol et al. 2000), with the most common example being the transition from

Late-Glacial braided to Holocene meandering morphologies in response to reduced sediment loads. Consequently, the study of modern and historical functioning processes of fluvial systems are of major interest for ecologists and paleoecologists. For this reason, the sedimentary deposits of fluvial terrasses and alluvial plains have traditionally been considered an important archive for paleolimnologists (Lowe and Walker 1997).

Many paleoecological studies are designed to reconstruct the climatic history of continental regions based on the composition of lake sediments, which are often sampled in mountain lakes with small drainage basins, where relatively few anthropogenic disturbances or other physical constraints (e.g., geomorphologic forcing, hydrological variability, tectonic movement) occur. However, many regions such as coastal areas around the North Sea are, for geomorphological or geological reasons, lacking long-term lacustrine records. In order to fill this gap, it is important to develop other paleoecological tools for reconstructing fluvial paleoenvironments.

Most studies designed to reconstruct fluvial paleoenvironments focus mainly on the chemical or physical composition and dynamics of river sediments (Berendsen and Stouthamer 2000; Makaske 2001). Few authors have used biopaleoecological approaches, except in a some multidisciplinary studies, most of which have dealt with pollen and geomorphological markers (Arnaud-Fassetta et al. 2000; Lewis et al. 2001), tree-rings (Brooks et al. 2002) and diatoms (Medioli and Brooks 2003). This could be explained by the fact that fluvial systems are more complex and dynamic systems than lakes. For example, river sediment analyses may be particularly affected by taphonomic problems, such as the poor subfossil preservation in sandy sediment or in relatively dry depositional environments (Waller 1993). In addition, many methodological problems occur. For example, lateral river shifts may lead to discontinuity in sedimentation (incisions or pauses in sedimentation). These potential hiatuses lead to a multiplication of coring sites and dating sequences in order to provide more accurate interpretations of the data. However, as in lacustrine studies, it seems likely that a paleolimnological approach could be useful in fluvial systems (Amoros et al. 1987; Amoros and Van Urk 1989).

Paleoenvironmental reconstructions of river systems can be carried out for at least two purposes: (i) to study the development of aquatic systems following human interventions and to assess possible means of restoration (Brown 2002); and (ii) to indirectly reconstruct past climates and precipitation levels from streamflow data (e.g., Kiely 1999; Rîmbu et al. 2002), and so, to provide long term historical data on paleoflood events (Knox 2000; Brooks et al. 2002). Therefore, it is important to develop functional biological descriptors (e.g., groups of taxa with known ecological profiles which can describe the hydrosystem functioning), which are well preserved in floodplain sediments, and which can be used to reconstruct a classification of floodplain environments. This classification is based on sampled habitats from the lotic to the more lentic areas such as the main channel, side arms, dead arms, isolated meanders, completely clogged meanders and peat bogs (i.e., from the eupotamal to the paleopotamal *sensu* Amoros et al. (1987) and Ward et al. (2002)). During the last 20 years, studies on large rivers have focused on floodplain waters, and the data obtained have made it possible to better describe these waters (Bravard et al. 1986; Junk et al. 1989; Amoros and Petts 1993; Ward and Stanford 1995). Among the various groups of macroinvertebrates colonizing the aquatic parts of alluvial plains, Cladocera (Jacquet et al. 1984; Jurasz and Amoros 1991) and Coleoptera (Castella et al. 1984; Smith and Howard 2004) have been proposed as potential indicators. Chironomids also play a key role in the alluvial systems (Franquet et al. 1995). They colonize all types of habitats from the main channels to the most isolated, temporary environments (Wilson 1980). Like Cladocera, chironomids are mainly primary consumers, detritivores or herbivores, and they constitute an important link in the trophic structure (Tokeshi 1995a). In addition, in searching for functional biological descriptors, we must also take into account that river systems are becoming increasingly affected by human activities. Chironomids are one of the few macroinvertebrate groups that may maintain relatively high faunistic richness and abundance under strong anthrogenic pressure (e.g., Ward and Stanford 1979; Brookes 1988; Franquet and Pont 1996).

On the lower Rhône River near Arles (south of France), many backwaters occur, varying from

natural oxbows to artificial environments. In this region, the floodplain is characterized by the presence of dyke fields (Brookes 1988) isolated from the main channel by the dykes constructed at the end of the 19th century, known as the 'Caissons Girardon' (Franquet and Pont 1996). These so-called 'Girardon's embankments' are linked, to various degrees, with the main channel of the river, and can be flooded, connected or completely isolated, depending on the discharge rate of the Rhône (Roditis and Pont 1993). These floodplain waters are characterized by their specific sedimentation dynamics, mainly related to the level of connectivity (itself dependent on the Rhône River water level) between alluvial water bodies and the main channel (Franquet et al. 1995). These connection-submersion dynamics have led to the development of a wide variety of bottom substrates (for example, sand in erosive zones and silty mud in deposition areas), which are fairly stable all year round. This substratum variability affects the species richness and diversity of the chironomid fauna (Franquet 1999).

The main aim of the present study is first to compare the chironomid assemblages observed in natural (dead arm) and artificial (Girardon's embankments) backwaters with those inhabiting the lower Rhône main channel. Secondly, we compare the chironomid classification based on our data with that published by Garcia and Laville (2001) for the main channel of the Garonne River and three of its floodplain waters (two side arms and one oxbow lake). This comparison will be done at the genus level in order to assess the effectiveness of this taxonomic identification level commonly used in paleoecological studies. The structure of chironomid faunistic assemblages will be used to establish a classification of chironomid taxa across the habitats of the alluvial plain and so to define more clearly the ecological preferences of chironomid taxa in the transversal floodplain gradient (i.e., in respect to the lateral connectivity gradient from the main channel to the floodplain margins). Finally, the chironomid classification described here will be applied to a paleoecological dataset from the Saint-Omer basin, Northern France (Gandouin 2003; Gandouin et al. 2005) so as to evaluate the potential for paleoclimatic reconstruction of fluvial chironomid assemblages. Gandouin et al. (2005) have reconstructed, with a coupled sediment-subfossil chironomid investigation, the past hydrological changes of the Saint-Omer basin for the mid-Holocene period. These authors concluded that it was necessary to refine the chironomid tools by carrying out further studies on the ecological status of modern chironomids along gradients across the floodplains of large rivers. The present paper addresses these issues.

Study area

The study was conducted in backwaters and the main channel of the lower Rhône River at a point located 6 km upstream of Arles (France), just before the Camargue Rhône delta (Figure 1). In this area, the main channel is $\sim$ 400 m wide and $\sim$ 4 m deep (at low flow rates). The discharge rate of the lower Rhône River (Figure 2) is very variable and characteristic of rivers subjected to multiple meteorological factors (Béthemont 1972; Fruget 1992). At the study site, the mean discharge rate is 1700 $m^3 s^{-1}$. The mean daily discharge rate ranges from 500 $m^3 s^{-1}$ at low water level to 4300 $m^3 s^{-1}$ during the annual floods. In November 2003, exceptionally severe flooding led to an all-time maximum flow rate of up to 13,000 $m^3 s^{-1}$.

The chironomids inhabiting the lower Rhône were sampled at four stations (Figure 1). Three of these stations were located in backwaters, the Pilet dead arm (43°45′30″ N and 4°37′ E), the Ranchier Dyke field (43°44′45″ N and 4°37′30″ E) and the Saxy Dyke field (43°44′ N and 4°41′55″ E), and one in the main channel (43 ° 44′ N and 4° 42′E). The last station is characterized by a coarse substrate; a paving of loose pebbles accounts for 96% of the substrates present in the study area (Nicolas and Pont 1996). The Saxy Dyke field is connected to the main channel when the discharge rate of the river is over 1600 $m^3 s^{-1}$, and is submerged when the discharge rates are more than 2200 $m^3 s^{-1}$ (Figure 2). For the last 30 years, these thresholds were crossed at 20 and 25% of the mean daily discharge rates, respectively. The other two stations in this study are more frequently isolated from the main channel (around 90% of the time): the Ranchier Dyke field is connected when the rate of discharge is greater than 2300 $m^3 s^{-1}$ and submerged when it is greater than 3000 $m^3 s^{-1}$; the Pilet dead arm is connected at rates of flow of more than 2500 $m^3 s^{-1}$ and submerged when they

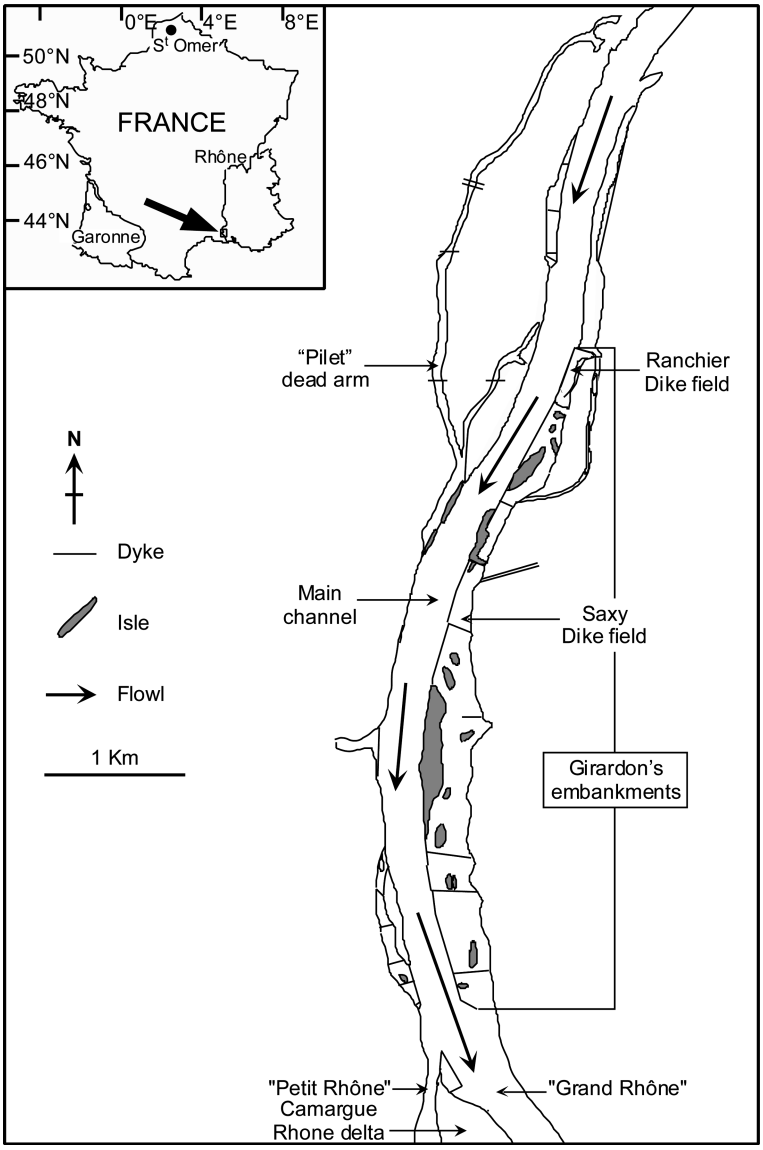


Figure 1. The study area on the Lower Rhône River (southern France).

are greater than 7000 m^3 s^{-1}. The substratum of the Saxy Dyke field is the most highly diversified: it contains blocks (10%), coarse substrates (pebbles and gravel) (32%) and fine sediment (sand and silty mud) (58%) (Franquet 1999), whereas substrates at the two most isolated stations mainly consist of fine sediments (96–99%). Other environmental variables, such as water temperature (°C), specific conductivity (μS), oxygen concentration (mg l^{-1}), oxygen percent saturation (%) and pH, were measured in the study area and discussed in several studies (Franquet et al. 1995; Franquet 1996, 1999; Franquet and Pont 1996). For this present paper, the study sites have been selected according to the degree in which they are linked with the main channel.

Material and methods

The chironomid sampling consisted of collecting drifting pupal exuviae just after the emergence of imagoes (Coffman 1973; Wilson 1980; Laville and Viaud-Chaumet 1985). Exuviae were collected

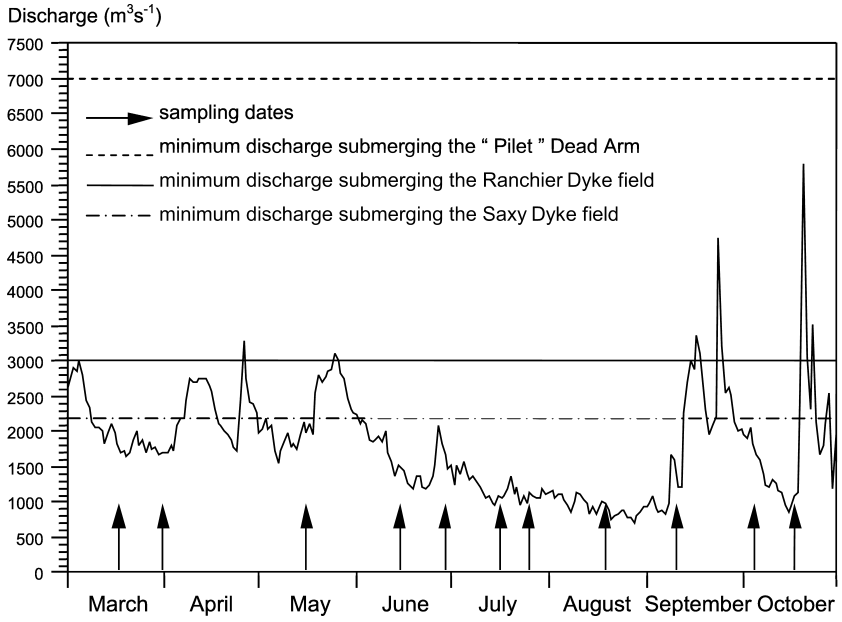


Figure 2. Discharge rate in $m^3\ s^{-1}$ in the main channel between March and October 1994, and level of submersion of the study areas (horizontal lines). Arrows show sampling dates.

with a one-meter long plankton net with a 250 μm mesh size. A flow-meter fixed below the net was used to measure the volume of the filtered water and hence allowed the calculation of the number of exuviae collected per m^3 (Wilson and Bright 1973). In the main channel, the net was attached to the left bank. At the other three stations, which were variably lentic, the net was placed in front of a boat moving slowly along a clearly defined route (net line) in order to collect floating exuviae. In these lentic stations, where the accumulation zones could be large, the net lines take into account the percents of open water and accumulation zones respectively (Franquet 1996).

Since the mean duration of emergence periods is about two weeks (Tokeshi 1995b), field sampling campaigns were carried out twice per month (Figure 2). However, no sampling could be carried out when the rate of flow of the river was higher than 2200 $m^3\ s^{-1}$ (submersion of the Saxy Dyke field in April, May and September), or when the wind was too strong (only one sampling in August). In these cases, it was too difficult to estimate the origin of the material collected. In addition, in order to determine the diurnal patterns of emergence and to ensure that the samples were representative for emergence during the entire diurnal cycle, each station was sampled twice per day (morning and evening).

In the field, the content of each net was transferred to a vial and preserved in 5% formaldehyde. At the laboratory, samples were rinsed and pupal exuviae were sorted and identified under a binocular microscope. When the number of exuviae was excessively high, sub-sampling was performed using a Motoda subsampler (Motoda 1959). In most cases, identification was carried out to the species level using Langton (1991), but some of the more problematic specimens were grouped together (*Cricotopus annulator* G. + *curtus* Hirv. + *triannulatus* (Macq.), *Nanocladius bicolor* (Zett.) + *rectinervis* (K.) + *distinctus* (Malloch), *Procladius sagittalis* (K.) + *choreus* (Mg.), *Polypedilum quadriguttatum* K. + *aegyptium* K., *Tanytarsus mendax* K. + *brundini* Lind., *Tanytarsus eminulus* (Walk.) + *heusdensis* G.).

A between-class (between-station) Correspondence Analysis (CA) (Dolédec and Chessel 1989; Chessel and Dolédec 1993) was carried out on a matrix coupling 44 samples (11 dates $\times$4 stations) and 89 taxa. Taxa present at only one station were eliminated. The absolute abundances were log-transformed ($x = \log(n + 1)$) to normalize the data. This analysis highlights any spatial effects by

maximizing the between-station differences (Dolédec and Chessel 1987, 1989; Beffy and Doledec 1991). Samples collected in the main channel were not taken into account for the definition of the F1– F2 factorial plane; they were only projected as passive samples. The main channel was therefore used as reference point; this approach reduced the impact of the different sampling methods between the main channel and the backwaters on the analysis.

In order to compare our data with the data published on the Garonne River (Garcia and Laville 2001), a CA was also performed on a combined dataset (lower Rhône + Garonne). This dataset was a matrix coupling 44 genera (shared by the two rivers) and eight stations (four in the Rhône River and four in the Garonne River). The Garonne's stations were located in the main channel (MCGa), two side arms (SA1 and SA2), and one oxbow lake (Ox) (Garcia and Laville 2001). For each of the eight stations, the abundance of each of the 44 taxa (genera) was expressed in % of the total abundance of each taxon per river. Taxa present at only one station were eliminated. Including all axes of the CA, a cluster analysis was then carried out on the factorial coordinates, using the Euclidean distance and Wards criteria (Lebart et al. 1997). This analysis made it possible to identify some groups of genera as descriptors of environmental conditions. The between-class CA focused on the break-down of the variability of the results depending on the habitat factor (Dolédec and Chessel 1987, 1989; Beffy and Doledec 1991; Franquet 1996). Three classes were chosen for this purpose: (1) lotic stations (Main Channel-Rhône, Main Channel-Garonne), (2) semilotic stations (Saxy Dyke field, Side Arm 1) and (3) lentic stations (Pilet dead arm, Ranchier Dyke field, Oxbow and Side Arm 2). Multivariate analyses were carried out using the ADE software program (Thioulouse et al. 1997).

The taxonomic identification level chosen resulted in two advantages. (i) It minimizes potential biogeographical effects (several species could be related to one biogeographical region contrary to the genus which is more cosmopolitan). Hence, only the station effect is taken into account (i.e., the place of the station in the transversal floodplain gradient). (ii) Because chitinous head capsules of chironomids are usually well preserved in sediments (Hofmann 1986), paleolimnologists use larval remains instead of pupal exuviae (like in modern limnology). However, although identification of larval stages beyond the genus level is sometimes possible (e.g., Eggermont and Verschuren 2003a, b), the identification at the species level from larval remains (head capsules) is difficult. Hence, expressing data at the genus level fits with the identification level usually used in paleoecological studies.

The chironomid classification resulting from the Lower Rhône River-Garonne River comparison has been applied to a paleoecological dataset from a sediment core of the Saint-Omer basin (50°47′ N and 2°13′ E). The techniques of chironomid subfossil extractions and diagram zonation (CA and cluster analysis) are detailed in Gandouin et al. (2005). The software program GpalWin (Goeury 1997) was used to store the data and produce the present summary diagram of the subfossil chironomid communities. The chironomid taxa identified at Saint-Omer were subdivided into the following four ecological categories:

- Taxa associated only with lentic habitats;
- Taxa associated only with lotic habitats;
- Taxa identified as ubiquitous;
- The 'other chironomids' category includes taxa which cannot be exactly identified and taxa which are not documented by the present chironomid classification. This fourth category did not provide any valuable ecological information, but it was used to compute percentages and to assess the relative weights of the three other categories.

Results

Transversal gradient of the Lower Rhône floodplain

A total of 89 species were identified from the samples collected between March and October 1994. Seventy eight of these species were recorded in the Saxy Dyke field, 69 in the Pilet dead arm, 66 in the main channel and 50 in the Ranchier Dyke field. Thirty four species were common in all four sampled stations and 25 in three of them (Appendix 1).

Twelve dominant species or groups of species were found in the lower Rhône. Each of these had

a relative abundance of ≥5% in at least one station. *Cricotopus annulator* G. + *curtus* Hirv + *triannulatus* (Macq.), *Nanocladius rectinervis* (K.) + *bicolor* (Zett.) + *distinctus* (Malloch) and *Rheotanytarsus rhenanus* Lehm. predominate in the main channel and the Saxy Dyke field, whereas *Cladotanytarsus mancus* (Walk.) is present only in the main channel, and *Cricotopus bicinctus* (Mg.), *Polypedilum quadriguttatum* K. + *aegyptium* K and *Thienemanniella* spp. only in the Saxy Dyke field. *Cladopelma virescens* (Mg.), *Microchironomus tener* (K.) and *Procladius choreus* (Mg.) + *sagitalis* (K.) predominate in the Ranchier Dyke field and the Pilet dead arm, whereas *Dicrotendipes nervosus* (Staeg.) and *Polypedilum nubeculosum* (Mg.) predominate only in the Pilet dead arm.

The break-down of the total variance of the data on all 89 species, at the four stations and on the 11 dates, indicates that the hierarchical model takes into account 64% of the total variability (inertia). The station effect explained 28% of this variability, and the date/station effect explained 36%. The first axis (F1) resulting from the CA, summarizing 88% of the total between-station inertia, very clearly highlights a faunal gradient running from the Saxy Dyke field (with negative factorial coordinates) to the most isolated stations, the Ranchier Dyke field and the Pilet dead arm (with positive factorial coordinates, Figure 3a). The second axis (F2), explaining 10% of the between-station variability, will not be discussed here.

The dominant species, except for *Cladopelma virescens*, were found at all four stations. They were relatively ubiquitous, as they occupy a fairly broad ecological niche (Figure 3b). However, there are some moderately abundant and more specialized species (occupying a narrow niche, Figure 3b). The latter mainly colonize the main channel and the Saxy Dyke field: *Paratrichocladius rufiventris* (Mg.), *Potthastia longimanus* K., *Eukiefferiella clypeata* (K.), *Kloosia pusilla* (L.), *Cardiocladius fuscus* K., *Eukiefferiella claripennis* (Lundb.), E. *lobifera* G., *Tvetenia calvescens* (Edw.), *Eukiefferiella ilkleyensis* (Edw.), *Rheocricotopus atripes* (K.), *Orthocladius ashei* Soponis, *O. oblidens* (Walk.), *O. rubicundus* (Mg.), *Rheotanytarsus photophilus* (G.), *Rheocricotopus fuscipes* (K.), and *Prodiamesa olivacea* (Mg.). Several taxa were found to mainly colonize the lentic stations: *Tanypus punctipenis* Mg., *Cladopelma virescens*, *Chironomus nuditarsis* Keyl, *C. plumosus* (L.), *Endochironomus albipennis* (Mg.), *Glyptotendipes pallens* (Mg.), *Chironomus* Pe4 (Langton 1991), *Cryptotendipes usmaensis* (Pag.), *Parachironomus arcuatus* (G.), *Microchironomus tener* (K.) and *Lipiniella arenicola* Shil.

Lower Rhône River–Garonne River comparison

Among the 64 genera listed, 52 inhabit the Lower Rhône River and 56 the Garonne River. Forty-four genera were found in both rivers. The between-station CA Figure 4) shows the existence of a clear gradient running from the most lotic stations (in particular, the main channel of the Garonne) to the most isolated ones (both on the Rhône (PDA and RDF) and on the Garonne (OX)). This analysis showed that the habitat factor explains 45% of the variability expressed in the overall data set. On the first axis F1 (summarizing 46% of the total between-station inertia), the most lotic stations on the lower Rhône, SDF and MCRh, seem to be more lentic in nature than the Garonne stations, SA1 and MCGa.

Not surprisingly, the ecological valences of individual taxa at the generic levels appear to be much broader than at the species levels. However, the cluster analysis (Figure 5) shows that the 44 genera are distributed in three groups. A first group can be defined as lotic, because it contains some genera that colonize main channels and side arms (cf. MCGa, SA1, MCRh and SDF), such as *Brillia*, *Cardiocladius*, *Cricotopus*, *Eukiefferiella*, *Micropsectra*, *Nanocladius*, *Orthocladius*, *Tvetenia*, *Paracladopelma*, *Paratrichocladius*, *Potthastia*, *Rheocricotopus*, *Rheotanytarsus*, *Synorthocladius* and *Thienemaniella*. A second group is identified as ubiquitous and includes *Chironomus*, *Cladotanytarsus*, *Cryptochironomus*, *Demicryptochironomus*, *Harnischia*, *Lipiniella*, *Microchironomus*, *Paratendipes*, *Paralauterborniella*, *Polypedilum*, *Procladius*, *Prodiamesa olivacea*, *Stictochironomus*, *Tanypus* and *Virgatanytarsus*. The third group is lentic and includes some genera, such as *Ablabesmyia*, *Cladopelma*, *Dicrotendipes*, *Endochironomus*, *Glyptotendipes*, *Kiefferullus*, *Limnophyes*, *Microtendipes*, *Tanytarsus*, *Parachironomus*, *Parakiefferiella*, *Paratanytarsus*, *Phaenopsectra* and *Psectrocladius*, which only colonize the very rarely connected stations (cf. OX, PDA and RDF).

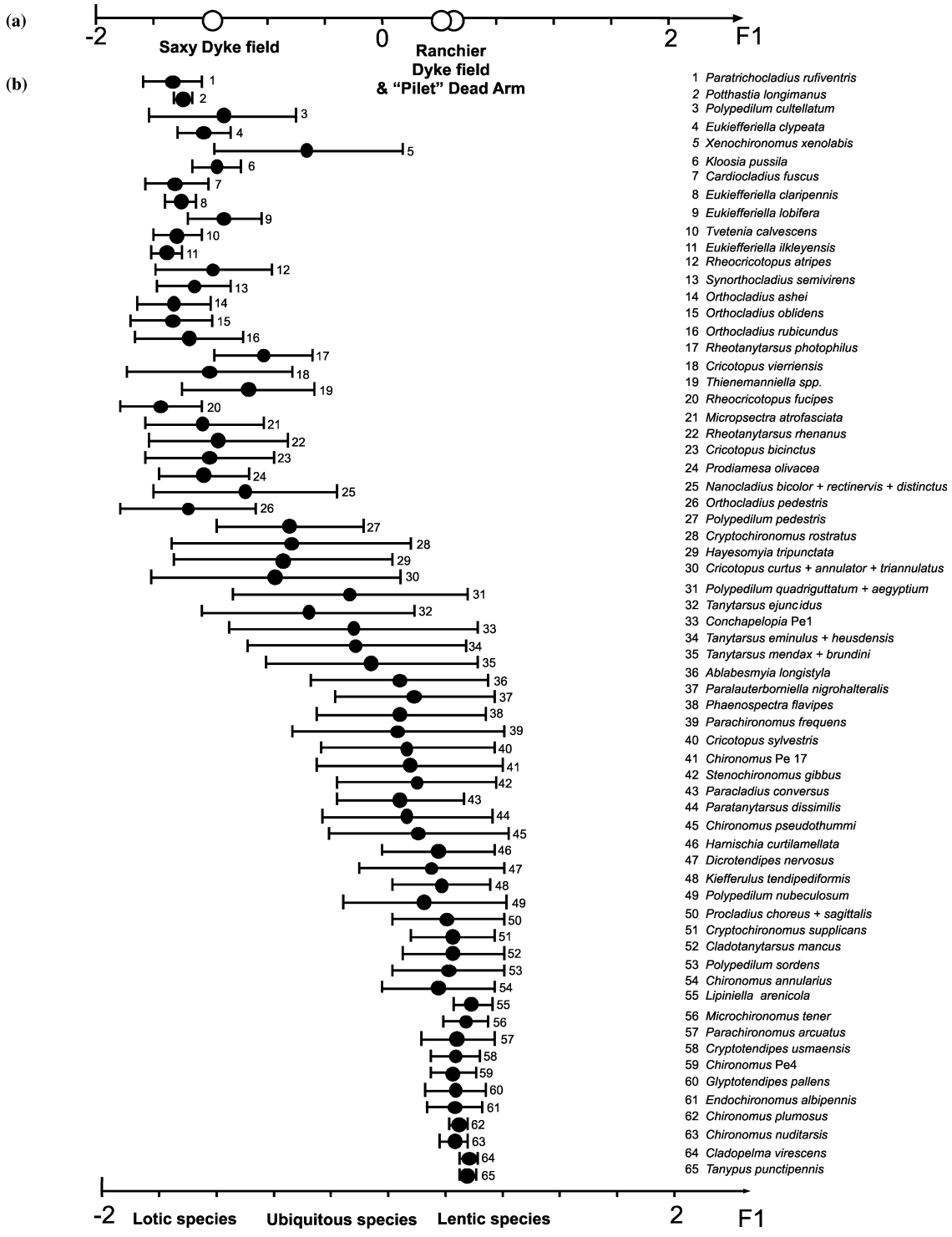


Figure 3. Results of the between-class (between-station) Correspondence Analysis (CA) at the species-level. (a) Center of gravity of the sample coordinates of each station. (b) Mean coordinates of all samples where each species is present. Dots represent means and lines represent variances on the first axis. All 65 species, present in > 1 sample, are listed and ranked according to their order on the first CA axis (summarizing 88% of the total between-station inertia).

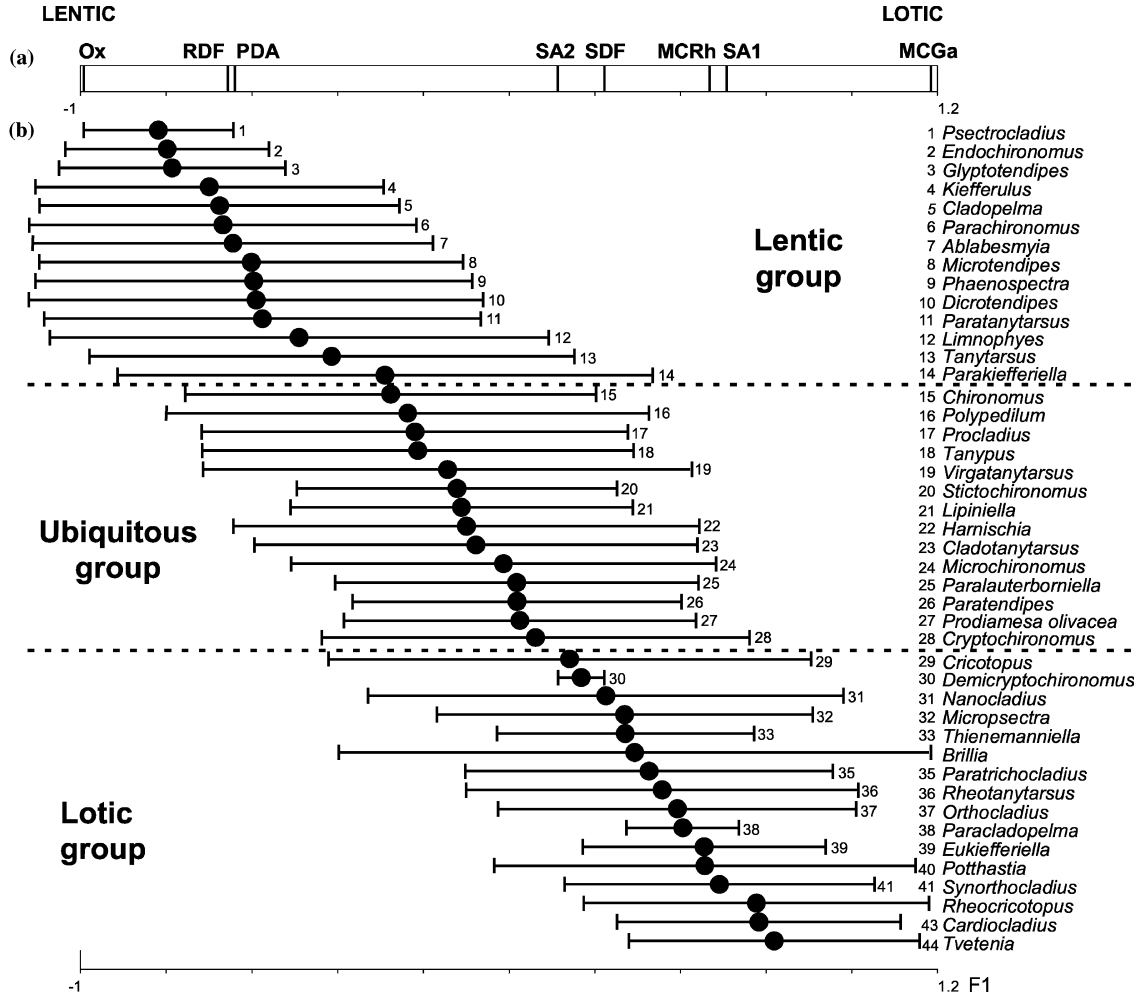


Figure 4. Comparison between lower Rhône River and Garonne River chironomid assemblages: results of the between-class (between-station) genus-level Correspondence Analysis (CA). (a) Center of gravity of the sample coordinates of each station. (b) Means and variances of the species coordinates on the first axis. All 44 genera, presented in more than one sample, are listed and ranked according to their order on the first CA axis (summarizing 46% of the total between-station inertia). Ox: Oxbow; RDF: Ranchier Dyke Field; PDA: Pilet Dead Arm; SA2: Side Arm 2; SDF: Saxy Dyke Field; MCRh: Main Channel-Rhône; SA1: Side Arm 1; MCGa: Main Channel-Garonne.

Application to the Saint-Omer data

The chironomid classification described here was applied to the Saint-Omer subfossil chironomid data. Thirteen of the 85 taxa identified at Saint-Omer were assigned to the category of chironomids associated with lentic habitats, twelve with lotic habitats, and eight taxa assigned as ubiquitous (Table 1). The lithological and faunal results have been described by Gandouin et al. (2005). According to these authors, faunal zones SMch-1, SMch-3 and SMch-5 were defined as lentic, whereas zones SMch-2 and SMch-4 were defined as lotic zones (each zone represents a temporal period). Using the present statistical classification, dynamics of the relative abundances of the three ecological categories of taxa are shown in Figure 6. These dynamics are very well correlated with the previous results (Gandouin et al. 2005), except for the zone SMch-1 (from 964 to 805 cm). In this zone, previously defined as lentic, two samples (865 and 805 cm) are characterized by more lotic taxa. In zones SMch-2 (from 795 to 735 cm) and SMch-4 (from 685 to 625 cm), previously characterized as

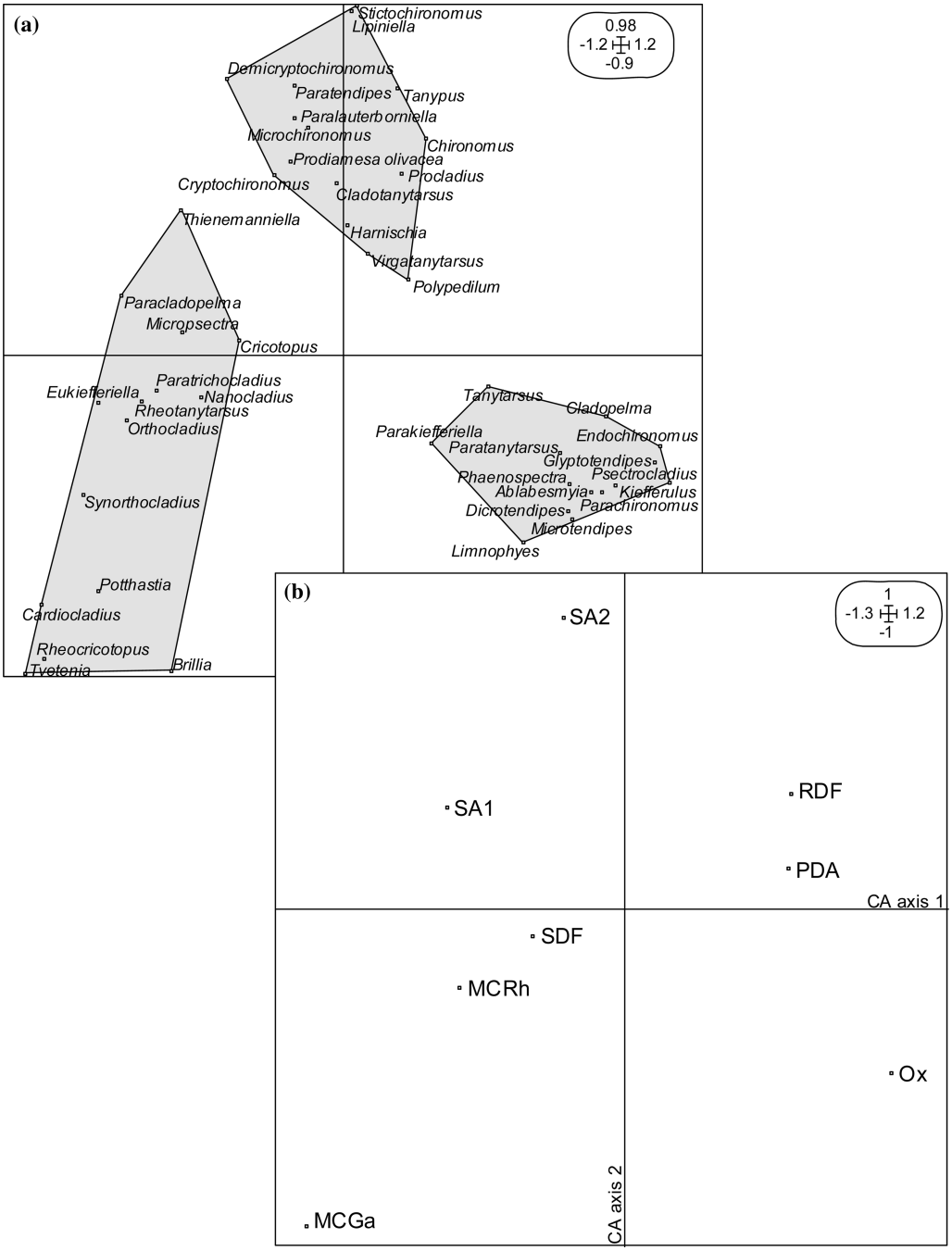


Figure 5. Comparison between the lower Rhône River and the Garonne River: projection onto the factorial planes of axes F1 × F2 of a between-class (between-station) genus-level Correspondence Analysis (CA). The first axis summarizes 46% of the total between-station inertia, the second axis summarizes 25%. (a) Plot along axes F1 and F2 of the 44 genera identified in the lower Rhône River and Garonne River. Cluster analysis led to the identification of three faunal groups (pale grey areas). (b) Plot along axes F1 and F2 of the eight stations analyzed (lower Rhône and Garonne). Ox: Oxbow; RDF: Ranchier Dyke Field; PDA: Pilet Dead Arm; SA2: Side Arm 2; SDF: Saxy Dyke Field; MCRh: Main Channel-Rhône; SA1: Side Arm 1; MCGa: Main Channel-Garonne.

Table 1. Ecological classification of the chironomid taxa identified at Saint-Omer (Gandouin et al. 2005) according to the classification described in the present paper.

Lentic taxa	Ubiquitous taxa	Lotic taxa
Ablabesmyia Johannsen	*Chironomus* Zett.	*Brillia* K.
Cladopelma K.	*Cladotanytarsus* K.	*Cricotopus* v.d.W.
Dicrotendipes K.	*Cryptochironomus* K.	*Demicryptochironomus* Lenz
Endochironomus K	*Paralauterborniella* Lenz	*Eukiefferiella* Th.
Glyptotendipes K.	*Paratendipes* K.	*Micropsectra* K.
Kiefferullus G.	*Polypedilum* K.	*Nanocladius* K.
Limnophyes Eaton	*Procladius* Skuse	*Orthocladius* v.d.W.
Microtendipes K.	*Prodiamesa* K.	*Paracladopelma* Harnisch
Parachironomus Walk.		*Paratrichocladius*Sant. A.
Paratanytarsus Thien. and Bause		*Rheocricotopus* Thien. and Harnisch
Phaenopsectra K.		*Synorthocladius* K.
Psectrocladius K.		*Tvetenia* K.
Tanytarsus K.		

Thirteen taxa were assigned to the category of chironomids associated only with lentic habitats, 12 taxa are associated only with lotic habitats and eight taxa are identified as ubiquitous.

lotic, the relative abundances of lotic taxa are always higher than those of lentic taxa. In the lentic zones SMch-3 (from 725 to 705 cm) and SMch-5 (from 615 to 605), the relative abundances of lentic taxa are always higher than those of lotic taxa.

Discussion

Species ecology

The autoecology of the species studied at the lower Rhône sampling sites appear to be largely in agreement with other available data (e.g., Laville 1979, 1981; Rossaro 1984). *Cricotopus curtus + annulator + triannulatus*, which predominates in the main channel and the Saxy Dyke field, have been characterized as lotic species, which require relatively high oxygen levels (Laville 1979). Likewise, *Cricotopus bicinctus*, which predominate in the Saxy Dyke field, is a common species in lotic conditions ranging from spring habitats to large lowland rivers (Laville 1981; Rossaro 1984) and has also been reported from the littoral zones of reservoir lakes (Laville 1981). In these environments, the larvae colonize a range of microhabitats, but mainly prefer substrates of the roller-gravel type (Pinder and Clare 1980; Berg and Hellenthal 1991) and macrophytes (Rossaro 1984). The genus *Nanocladius* appears to be mainly rheophilous, although *N. bicolor* can be found in more stagnant environments (Cranston 1982; Langton 1991). *Rheotanytarsus* was also reported by Thienemann (1954) as a genus characteristic of habitats subject to strong currents, colonizing coarse substrates. The genus *Cladotanytarsus* may colonize all kinds of freshwater and brackish environments, but shows a preference for those with rather coarse sediments and low organic matter contents (McGarrigle 1980; Bass 1986). This is in agreement with the findings at the lower Rhône River where *Cladotanytarsus* predominated in the channel, the Saxy Dyke field and the Pilet dead arm.

Among the species which were well represented in the Pilet dead arm and the Ranchier Dyke field, *Procladius choreus + P. sagittalis* are species characteristic of muddy substrates in both lotic and lentic environments (Franquet 1999). The genus *Microchironomus* is also relatively ubiquitous. It leads a benthic or phytophilic life in running or standing waters. Likewise, *Dicrotendipes nervosus* seems to be characteristic of the stagnant parts of large rivers, and is found mainly in large lowland rivers and reservoir lakes (Laville 1979).

Chironomid classification at the genus level: limits and relevance of the method

On the scale of the alluvial plain, this study confirms that the habitat factor is important in structuring chironomid species assemblages (Franquet 1996, 1999; Garcia and Laville 2001) as

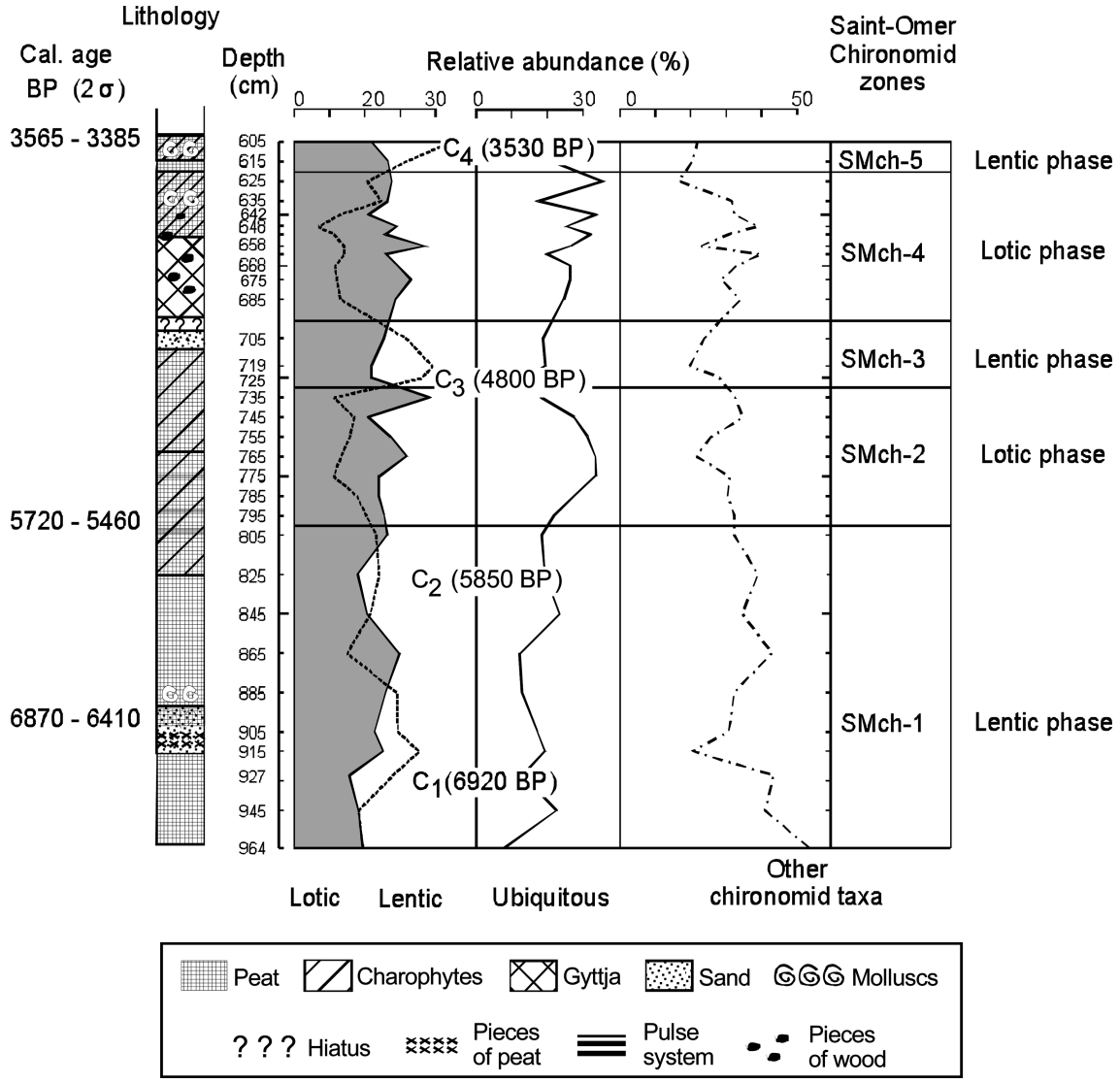


Figure 6. Relative abundances (%) of groups of lotic (12 taxa), lentic (13 taxa), ubiquitous (eight) and other (52 taxa) chironomid taxa vs. depth (cm) (lotic taxa are shown in grey and lentic taxa in dotted line). Calibrated age B.P. (2σ) and core stratigraphy are shown on the left; the chironomid zones (SMch-1 to 5) described in Gandouin et al. (2005) are shown on the right.

well as in chironomid assemblages identified to the genus level. Consequently, it is possible to assign genera to one of the ecological categories: lotic, ubiquitous (semi-lotic to lentic) and lentic. However, before using river chironomid subfossils for paleoenvironmental reconstruction purposes, two main limits must be taken into account. The first is the broad ecological valence of the genus identification level. This limit is related to the ecological valences of the species themselves and by the amalgamation of several species into a single taxon (genus). For example, in the genus *Tanytarsus*, five species, *T. mendax* K., *T. brundini*, *T. ejuncidus* (Walk.), *T. eminulus* and *T. heusdensis*, are present in the Garonne River mainly in the more lentic environments (OX and SA2), whereas all five species are ubiquitous in the lower Rhône River. It is also the case with the genus *Limnophyes*, where one species (*Limnophyes* sp.) was rather ubiquitous in the lower Rhône River and two species

(*L. paludis* Armitage and *L. punctipennis* (G.)) were only present in the Garonne oxbow (OX). Consequently, the first question that arises concerns the use of the genus level as the taxonomic level of determination. This limit is a recurrent problem in paleoecology when different species within a genus may have contrasting ecological affinities (cf. Lowe and Walker 1997). In order to minimize any risk of such a bias, we always took care to base conclusions on assemblages of taxa (genera) rather than on one particular taxon (genus). In addition, working on assemblages of taxa yields a second advantage. If the ecology of one taxon may have evolved through time, the odds of an entire suite of taxa evolving new ecological requirements in a uniform manner are too small to be taken into consideration (cf. Elias (1994) about species constancy in the Quaternary).

A second problem, related to the potential of sedimentary heterogeneity, might limit the relevance of the present chironomid classification for paleoecological purposes. Microhabitats within each sampled macrohabitat (e.g., main channel, oxbow lake) on the transversal gradient are rather homogeneous (lentic zones have finer and more muddy substrates, whereas lotic zones have coarser substrates). However, if the coring site overlaps an accumulated zone of fine sediment within the main channel (Gaschignard et al. 1983), the interpretation of the data could be biased. The resulting chironomid assemblage could then be interpreted as being more lentic and characteristic of isolated zones than this assemblage actually is (in the main channel). This variability of chironomid assemblages related to substrate composition is also described in lacustrine paleoecological studies, as reported by Brooks (2000) or Heiri (2004). This potential heterogeneity raises questions about the representativeness of a single coring site in these complex environments, but should be partially corrected for by the use of multi-proxy investigations (Lowe and Walker 1997). Hence, the integration of different data sources (e.g., pollen, diatoms, plant macrofossils, insects and sediment, etc.) is recommended in order to reduce the risk of a bias resulting from local factors. For example, pollen (easily transported over long distances) may provide a more regional environmental assessment than lithological analyses or plant macrofossils, which are better descriptors of local environmental conditions.

As demonstrated above, the chironomid classification proposed here is affected by the same limitations as paleoecological studies which justifies its application to a paleoecological dataset.

Paleoecological application

According to Gandouin et al. (2005), some species and genera of chironomids can be qualitatively assigned to different ecological categories related to current speed (lentic versus lotic conditions). Gandouin et al. (2005) based their inferences on the published scientific knowledge (e.g., Wielderholm 1983; Franquet 1996; Garcia and Laville 2001). This method, coupled with lithological analysis and carried out on a sediment core in the floodplain of the Aa river (Saint-Omer basin, Northern France), allowed them to reconstruct the mid-Holocene hydrodynamic conditions in the basin. These authors also discussed the correlations of the Saint-Omer lotic phases with several climatic events known to have occurred during this period in Europe. The classification presented in this study applied to the Saint-Omer chironomid dataset is consistent with the previous interpretations (Gandouin et al. 2005). We consider the only two ambiguous samples (865 and 805 cm), characterized by more lotic taxa in the SMch-1 lentic zone, insufficient to question the previous zonation. In addition, Gandouin et al. (2005) have already shown that the hydrodynamic profile of SMch-1 may be more influenced by the proximity of the sea than climatic signal. This proximity induced high groundwater level which allowed peat or gyttja deposition in tidal-paleochannels. During this period, the Saint-Omer basin did not function like a typical river system. Hence, the chironomid classification presented here may be biased and inferred hypotheses should be carefully interpreted.

Given the present results, the use of chironomids to provide a descriptive index for alluvial habitats, may has considerable potential for paleoecological studies of fluvial environments. In view of the positive correlations observed between precipitation and the flow rates of waterways (e.g., Kiely 1999; Rîmbu et al. 2002), chironomids may be used to reconstruct past hydrodynamic conditions in a fluvial system, and to draw some indirect conclusions about past climatic conditions.

However, based on our study of the level of connectivity between the main channel and the different floodplain locations of the Rhône and Garonne rivers, it seems difficult to really quantify past hydrological changes. In contrast to temperature inference models (e.g., Lotter et al. 1997; Laroque et al. 2001; Heiri et al. 2003) where July temperature can be directly estimated from chironomid assemblages, the present study and the proposed chironomid classification, although focusing on habitat factors, are only able to provide indirect qualitative information on landscape and climate dynamics. At the landscape scale, it is probable that many other factors, such as erosion sediment, transport and deposition (cf. Ward et al. 2002) occur, and pose serious problems for quantification. As chironomids are not directly influenced by the rate of precipitation and river-discharge, a future model of quantification should take into consideration several other parameters, such as evaporation, percolation into ground water, substratum of the river catchment, riparian vegetation, etc. These parameters are difficult to quantify because of their interdependency (e.g., evaporation is dependent on vegetation, which itself dependents on the nature of the substratum, which itself influences the percolation process). Based on river chironomid assemblages, it seems more prudent to work at a more qualitative and general scale, instead of quantifying paleoprecipitation levels, as has already been reported by Vandenberghe et al. (1998) for changes in channel pattern. We maintain that river chironomids are useful tools for paleoclimatic and paleoenvironmental purposes, e.g., to obtain qualitative information about paleoflood periodicity.

In conclusion, the present classification at genus level, based on modern chironomid assemblages, offers a tool that could be potentially applied to other river systems of mid-European latitudes. Since the geographical limits of utilization of this classification have only been tested on a single paleoecological dataset, it is however necessary to determine the potential application of this approach to other regions. This classification could be used along with other proxies (e.g., sediments, pollen, molluscs, coleopterans, etc.), in order to minimize possible biases and to confirm the hypotheses inferred from subfossil chironomid assemblages.

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Appendix

Appendix 1. Absolute abundances of the 89 taxa sampled in the lower Rhône River. RDF: Ranchier Dyke Field; PDA: Pilet Dead Arm; SDF: Saxy Dyke Field; MCRh: Main Channel-Rhône.

Chironomid taxa	MCRh	SDF	RDF	PDA
Potthastia longimanus K.	3	3	0	0
Prodiamesa olivacea (Mg.)	3	7	1	1
Brillia flavifrons Joh.	0	2	0	0
Brillia modesta (Mg.)	1	1	0	1

Appendix 1. Continued.

Chironomid taxa	MCRh	SDF	RDF	PDA
Cardiocladius fuscus K.	7	5	0	0
Cricotopus bicinctus (Mg.)	20	13	2	3
Cricotopus annulator G. + *curtus* Hirv. + *triannulatus* (Macq.)	21	16	4	15
Cricotopus sylvestris (Fabr.)	9	11	15	11
Cricotopus trifascia Edw.	2	1	0	0
Cricotopus vierriensis G.	3	5	0	1
Eukiefferiella claripennis (Lundb.)	4	4	0	0
Eukiefferiella clypeata (K.)	3	3	0	0
Eukiefferiella ilkleyensis (Edw.)	3	4	0	0
Eukiefferiella lobifera G.	6	4	0	0
Heleniella serratosioi Ringe	1	0	0	0
Limnophyes sp.	1	4	0	2
Nanocladius rectinervis (K.) + *bicolor* (Zett.) + *distinctus* (Malloch)	21	19	5	8
Orthocladius ashei Soponis	10	8	1	1
Orthocladius oblidens (Walk.)	5	7	0	1
Orthocladius pedestris K.	3	6	0	3
Orthocladius rivulorum K.	1	2	0	0
Orthocladius rubicundus (Mg.)	7	9	0	2
Paracladius conversus (Walk.)	1	1	0	2
Parakiefferiella wulkeri Moub.	1	1	0	2
Parakiefferiella smolandica(Br.)	3	2	0	0
Paratrichocladius rufiventris (Mg.)	4	6	0	0
Psectrocladius brehmi (K.)	0	0	0	2
Rheocricotopus atripes (K.)	12	14	0	1
Rheocricotopus fucipes (K.)	4	4	0	1
Rheorthocladius ruffoi (Rossaro and Prato)	0	1	1	2
Synorthocladius semivirens (K.)	16	11	0	1
Thienemanniella spp.	11	18	2	2
Tvetenia calvescens (Edw.)	8	9	0	0
Tvetenia verralli (Edw.)	0	1	0	0
Ablabesmyia longistyla Fitt.	1	6	5	6
Hayesomyia tripunctata (G.)	4	5	1	4
Conchapelopia Pe 1	0	1	1	1
Procladius choreus (Mg.) + *sagitalis* (K.)	11	14	12	21
Tanypus punctipennis Mg.	0	0	4	5
Cladotanytarsus mancus (Walk.)	14	7	8	12
Micropsectra atrofasciata (K.)	7	11	0	2
Paratanytarsus dissimilis Johannsen	4	12	11	13
Rheotanytarsus photophilus(G.)	5	6	1	0
Rheotanytarsus rhenanus Lehm.	17	13	3	6
Tanytarsus eminulus (Walk.) + *heusdensis* G.	5	10	4	12
Tanytarsus mendax K. + *brundini* Lind.	8	13	10	16
Tanytarsus ejuncidus (Walk.)	10	8	2	11
Tanytarsus pallidicornis(Walk.)	0	0	0	2
Virgatanytarsus arduennensis (G.)	0	1	0	2
Cryptochironomus rostratus K.	6	5	2	2
Cryptochironomus supplicans (Mg.)	4	5	8	16
Chironomus nuditarsis Keyl	1	0	3	8
Chironomus Pe17 (Langton 1991)	5	5	4	15
Chironomus Pe4 (Langton 1991)	2	1	5	14
Chironomus riparius Mg.	0	1	1	2
Chironomus pseudothummi Str.	1	2	3	2
Chironomus annularius auct. Nec de Geer	0	2	1	6
Chironomus bernensis Klötzli	0	0	0	1
Chironomus luridus Str.	0	1	0	2

Appendix 1. Continued.

Chironomid taxa	MCRh	SDF	RDF	PDA
Chironomus plumosus (L.)	0	0	2	8
Cladopelma virescens (Mg.)	2	0	8	13
Cryptotendipes usmaensis (Pag.)	0	3	2	18
Demicryptochironomus (irmakia) sp. 3 Reiss	0	2	0	0
Dicrotendipes notatus (Mg.)	0	0	1	1
Dicrotendipes nervosus (Staeg.)	10	14	10	15
Endochironomus albipennis (Mg.)	0	1	10	8
Glyptotendipes pallens (Mg.)	0	3	12	20
Glyptotendipes signatus (K.)	0	0	1	3
Harnischia curtilamellata (Mall.)	13	12	6	20
Kiefferulus tendipediformis (G.)	1	9	9	18
Kloosia pussila (L.)	6	2	0	0
Lipiniella araenicola Shil.	3	3	7	6
Microtendipes chloris (Mg.)	0	1	0	1
Microchironomus tener (K.)	5	5	10	15
Parachironomus arcuatus (G.)	2	5	9	16
Parachironomus frequens (Joh.)	3	6	2	8
Paracladopelma mikiana (G.)	1	2	0	0
Paralauterborniella nigrohalteralis (Mall.)	2	4	0	6
Paratendipes albimanus (Mg.)	6	10	4	5
Phaenospectra flavipes (Mg.)	4	13	9	18
Polypedilum quadriguttatum K. + *aegyptium* K.	16	14	2	14
Polypedilum cultellatum G.	0	6	0	0
Polypedilum nubifer (Skuse)	0	0	1	2
Polypedilum nubeculosum (Mg.)	8	12	13	19
Polypedilum pedestre (Mg.)	1	5	2	1
Polypedilum sordens (v. d. W.)	1	4	4	13
Stenochironomus gibbus (Fabr.)	2	2	0	3
Stictochironomus maculipennis (Mg.)	0	1	1	1
Xenochironomus xenolabis (K.)	2	2	0	0

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